Albano Augusto Figueiredo Rodrigues

ASSESSING IMPACTS FROM FUTURE CLIMATIC SCENARIOS ON THE DISTRIBUTION OF FLORA AND VEGETATION AT MADEIRA ISLAND

Dissertação de Doutoramento na Área de Geografia, especialidade em Geografia, orientada pelo Senhor Professor Doutor António Campar de Almeida e co-orientada pelo Senhor Professor Doutor Miguel Pinto da Silva Menezes de Sequeira, apresentada ao Departamento de Geografia da Faculdade de Letras da Universidade de Coimbra.

Março de 2013

• U C •

UNIVERSIDADE DE COIMBRA

Albano Augusto Figueiredo Rodrigues

Assessing impacts from future climatic scenarios on the distribution of flora and vegetation at Madeira Island

Departamento de Geografia | Department of Geography
Faculdade de Letras | Faculty of Humanities
Universidade de Coimbra | University of Coimbra

Coimbra, 2013

Dissertação apresentada à Faculdade de Letras da Universidade de Coimbra para obtenção do grau de Doutor em Geografia.

Dissertation submitted in partial fulfilment of the requirements for the degree of Doctor in Geography at the Faculty of Humanities, University of Coimbra, Portugal.

Orientador / Thesis Supervisor

Professor Doutor António Campar de Almeida. Departamento de Geografia da Universidade de Coimbra.

Co-orientador / Thesis co-Supervisor

Professor Doutor Miguel Pinto da Silva Menezes de Sequeira. Centro de Competências Ciências da Vida, Universidade da Madeira.

Este trabalho foi realizado com o apoio da Fundação para a Ciência e a Tecnologia, através da Bolsa de Doutoramento com a referência SFRH/BD/27810/2006 (FSE e MCTES).

This dissertation was supported by Fundação para a Ciência e a Tecnologia (Portuguese Science Foundation) through the grant SFRH/BD/27810/2006 (FSE / MCTES).

… às minhas piquenas …

Agradecimentos │Acknowledgements

Devo começar por expressar os meus sinceros agradecimentos aos meus orientadores, que acompanharam de forma dedicada o desenvolvimento deste trabalho, ao longo de um trajeto sinuoso. Ao Professor Doutor António Campar Almeida, do Departamento de Geografia da Universidade de Coimbra, agradeço as orientações, a disponibilidade e as proveitosas discussões, o espírito crítico mas sereno. Ao Senhor Professor Miguel Pinto da Silva Menezes de Sequeira, do Centro de Ciências da Vida da Universidade da Madeira, no papel de co-orientador, pela preciosa ajuda no conhecimento da flora e vegetação da Ilha da Madeira, pela pronta e proveitosa colaboração, pelo entusiasmo, pela discussão de ideias e pelo apoio logístico.

Quero ainda expressar a minha gratidão ao Centro de Competências de Ciências da Vida da Universidade da Madeira, por ter acolhido este trabalho e me ter facilitado a utilização das instalações.

Ao Professor Pedro Miranda e Doutora Maria João Cruz, enquanto colaboradores do Projeto SIAM, pela cedência da informação relativa aos cenários climáticos, informação fundamental para poder concretizar os objectivos propostos .

À Direção Regional de Florestas da Região Autónoma da Madeira, na pessoa do seu Diretor, o Sr. Eng.º Paulo Rocha da Silva, e aos colaboradores, pelo apoio prestado nas saídas de campo.

À Direção Regional de Cartografia e Cadastro da Região Autónoma da Madeira, nas pessoas da Sr.ª Diretora Maria João Cancela Seiça Neves, e do Chefe do Núcleo de Gestão de Informação Geográfica, o Geógrafo Duarte Costa, pela cedência de fotografia aérea, que facilitou a recolha de informação em campo.

À Aida, pelo apoio na realização de trabalho campo, pela pronta ajuda, e pelas dicas culinárias.

À Joana Vicente, pela pronta e genuína ajuda neste início de caminhada pela modelação.

O meu agradecimento a todos aqueles que, de forma direta ou indireta, contribuíram para que este trabalho se concretizasse.

RESUMO

As alterações climáticas estão identificadas como uma das ameaças mais importantes à biodiversidade à escala global. Neste sentido, é pertinente a avaliação de impactes potenciais, como forma de orientar a definição de medidas que permitam mitigar possíveis efeitos ou definir estratégias de adaptação.

Área em estudo │ A Ilha da Madeira, um pequeno território localizado na margem subtropical do sector oriental do Atlântico Norte, é considerado um *hotspot* de diversidade, sendo de destacar o elevado número de endemismos exclusivos e a presença de tipos de vegetação de elevado interesse do ponto de vista da conservação.

Objectivos │ O principal objetivo deste trabalho é avaliar os impactes potenciais das mudanças climáticas na distribuição potencial de espécies e comunidades clímax com maior representatividade na ilha da Madeira, tendo por referência dois cenários futuros (HadCM3 – A2 e B2) para o horizonte temporal 2070/99, baseados no modelo CIELO como técnica de regionalização de cenários para ilhas.

Metodologia │ A avaliação de impactes baseia-se na comparação de resultados relativos à área prevista como adequada à ocorrência das espécies nas condições atuais e em cenários climáticos futuros. Para a identificação de áreas com condições adequadas à ocorrência das espécies são utilizadas diferentes técnicas de modelação (envelopes bioclimáticos, métodos de base regressiva, métodos de classificação e métodos do tipo *machine learning)*. O processo de calibração dos modelos baseia-se na utilização de um conjunto selecionado de variáveis ambientais e informação relativa à distribuição atual das espécies. Para cada contexto (condições atuais, cenários A2 e B2) e para cada espécie obtém-se um modelo de consenso, que resulta da combinação dos modelos produzidos pelas diferentes técnicas de modelação, sendo que apenas os modelos com bom desempenho (AUC > 0.7) são utilizados neste processo. Os procedimentos de calibração, projeção e produção de modelos de consenso são levados a cabo na plataforma BIOMOD. A produção de modelos para as comunidades resulta da combinação ponderada de modelos de consenso obtidos para um conjunto de espécies entendidas como características ou com importância estrutural.

Estrutura │ O primeiro capítulo apresenta um enquadramento relativo aos efeitos das mudanças climáticas no passado geológico, no passado recente e impactes previstos em função das mudanças climáticas projetadas para o futuro; procurando-se centrar esta análise na Macaronésia. O segundo capítulo está dedicado à caracterização da área em estudo, a Ilha da Madeira. Além da informação relativa à ilha são ainda apresentados dados para outras ilhas e arquipélagos da Macaronésia, uma decisão que se prende com a reduzida dimensão territorial, com a influência de processos mais vastos ou similares a outras ilhas, ou ainda com a necessidade de estabelecer uma comparação para melhor definir as condições da área em estudo. No terceiro capítulo é feita a apresentação da metodologia utilizada, tendo havido a preocupação de discutir as vantagens e constrangimentos que lhe estão associados. Neste capítulo é ainda feita uma abordagem ao esquema conceptual associado à modelação preditiva de base estatística, bem como às fontes de incerteza associadas a esta aproximação metodológica. No quarto capítulo são apresentados os resultados da modelação para as espécies e para as comunidades, os quais são discutidos no quinto capítulo. Neste último capítulo, o quinto, além de uma análise dos grandes padrões de comportamento, são ainda discutidas algumas questões relacionadas com a contribuição de alguns factores para o enviesamento dos resultados dos modelos.

Resultados │ É significativa a variabilidade de resultados em termos de alterações na área prevista como adequada à ocorrência dos diferentes *taxa* e tipos de vegetação em função dos cenários climáticos considerados, sendo possível diferenciar três grandes tipos de comportamento:

i) espécies que registam ganhos importantes e perdas de área pouco significativas, sendo este um comportamento comum entre as espécies tolerantes à secura que ocupam principalmente altitudes inferiores a 200m na face sul da ilha. Esta tendência, definida como hipótese inicial, é comum em espécies associadas ao zambujal, como é o caso do zambujeiro (*Olea maderensis*), do massaroco (*Echium nervosum*), da figueira-do-inferno (*Euphorbia piscatoria*) e do buxo da rocha (*Maytenus umbellata*). Destaca-se ainda um pequeno grupo de espécies endémicas associadas às arribas litorais da ilha, as quais, apesar de apresentarem atualmente uma área de distribuição restrita, têm previsto um aumento muito significativo da área em cenários climáticos futuros.

ii) Espécies que apresentam previsões opostas em termos de alteração da área adequada à sua ocorrência nos cenários considerados (A2:perda; B2:ganho). As espécies incluídas neste grupo estão associadas a condições ecológicas e áreas de distribuição diversas, sendo possível encontrar tanto espécies endémicas protegidas de distribuição restrita (ex.: *Melanoselium* decipiens), como espécies mais comuns com importante papel na estrutura de comunidades, como é o caso do til *(Ocotea foetens*) ou da urze molar (*Erica arbórea*), elementos estruturantes da laurissilva temperada e do urzal arbóreo. respetivamente.

iii) espécies que apresentam um clara perda de área em ambos os cenários considerados, podendo atingir os 100% no caso de espécies endémicas exclusivas de distribuição atual restrita aos cumes da ilha, como é o caso da arméria (*Armeria maderensis*), da ameixieira de espinho (*Berberis maderensis*) ou da sorbeira (*Sorbus maderensis*). A previsão de ausência de condições climáticas adequadas no futuro cria condições favoráveis à extinção, um cenário que adquire ainda mais importância se considerarmos a influência sinergética de outros fatores, como a perturbação pelo fogo ou a perda de habitat devido a processos de invasão por espécies exóticas.

Vários são os factores, no entanto, cuja influência poderá favorecer desvios em relação à previsões apresentadas pelos modelos. Entre estes factores pode destacar-se a disponibilidade de habitat, cujas propriedades podem não ter sido captadas integralmente pelos modelos, o que pode ter suportado a previsão de áreas de ocorrência sobredimensionadas, um resultado que pode estar associado à resolução espacial utilizada (200m x 200m). A disponibilidade poderá ainda estar condicionada devido a ocupação que impede a instalação das espécies, como nas situações em que essas áreas mantenham um uso agrícola. Também a invasão por espécies exóticas pode desempenhar um papel importante ao nível da redução da área disponível para instalação das espécies nativas. No caso de áreas perturbadas pelas atividades humanas, e considerando o cenário de recente abandono das atividades primárias, algumas espécies exóticas invasoras poderão suplantar as nativas na ocupação de áreas previstas como adequadas para ambas, uma tendência detectada para algumas espécies arbóreas invasoras (*Acacia melanoxylon*, *A. Mearnsii*, *Pittosporum undulatum*). Este cenário pode adquirir especial relevo no futuro, dado o aumento significativo de áreas previstas como adequadas à ocorrência de espécies exóticas invasoras e espécies nativas em cenários climáticos futuros.

ABSTRACT

Climate change is identified as a major threat to biodiversity at global scale. Under such context, it is considered prudent to assess potential impacts, as a strategy to support the definition of mitigation and adaptation measures.

Study area │ Madeira Island is a small territory located at the subtropical margin of the eastern North Atlantic, and assigned to the Macaronesia biogeographic region. Such territory is considered an hotspot of biodiversity, a status supported on the significant number of exclusive endemics and presence of vegetation types with high interest in terms of conservation, considering the high plant diversity and services provided (habitat, tourism, water balance, erosion control).

Objectives │ The main purpose of this work is to assess climate change impacts on the potential distribution of species and vegetation types at Madeira Island (Portugal). The analysis is based on two future climatic scenarios for the period 2070/99 (A2 and B2), which are obtained through regionalization, based on the CIELO model, from large scale scenarios produced by the HadCM3 model (Hadley Centre Coupled Model, version 3).

Methodology │The assessment of changes on species distribution is supported on niche-based modelling techniques of correlative nature, which are used to estimate species' niche. The estimation, based on detected relationships between environmental variables and species' occurrences, is used to predict species' suitable area for current and future climatic conditions. The modelling procedure is supported on the BIOMOD platform, which permit to run different modelling techniques (bioclimatic envelopes, regression, classification methods, and machine learning methods). The weighted combination of results from different modelling techniques supports the creation of one consensus model for each species and each context (current conditions, scenarios A2 and B2), using only models with good performance (AUC > 0.7). The assessment of changes for the community level is based on a weighted combination of results for selected species, interpreted as characteristic or with structural importance to the community.

Structure │The first chapter introduces climate change issue in different time scales, and aims to gather information about the impacts on ecosystems inferred or described for geological and historical periods. The chapter also includes a brief

description about recorded impacts related to recent climate change, and predicted impacts for future climatic projections as well, focusing description in the Macaronesia region as much as possible. The second chapter is dedicated to a characterization of the study area on the domains that are more important to the issue under discussion, namely climatic, flora and vegetation features. The characterization presented for the island is complemented with information for other Macaronesian archipelagos, a decision based on the small size of the island, and the influence of large-scale processes, which also affect other islands. The third chapter aims to provide support to the methodological options of this work, and discuss the advantages and drawbacks of using a species distribution modelling approach of correlative nature when assessing potential impacts from future climatic scenarios. The chapter also aims to provide a brief discussion on concepts that are critical to the interpretation of models results. The fourth chapter is dedicated to modelling results for species and communities, including results for the identification of areas of potential conflict with selected alien invasive trees. All the results are analysed and discussed in the fifth chapter, based on the identification of groups of species that present similar trends in terms of predicted changes on suitable area. The discussion includes reference to the potential role of some factors that might alter predictions projected by climatic models, such as the invasion by non-native invasive trees, or land-use. It is also presented an analysis about the influence of biasing factors on models results.

Results │There is a significant variability in the sense and magnitude of predicted changes for suitable area among species and types of vegetation considered. Considering the results, species might be classified in one of three groups:

i) Species that register a significant increase on suitable area and irrelevant loss on both future climatic scenarios. This group includes mainly species that are drought-tolerant, which are mostly associated to altitudes below 200m on the southern face of the island. The predicted increase on suitable area is higher under the scenario A2, and is significant for species associated to the wild olive mircoforest (*Mayteno umbellatae-Oleetum maderensis*), such as the wild olive (*Olea maderensis*), the pride of Madeira (*Echium nervosum*), the fish-stunning spurge (*Euphorbia piscatoria*), and for the Madeira shrubby bittersweet (*Maytenus umbellata*), which all maintain a significant part of their current suitable area under future climatic scenarios. With such response, there is a small group for which models predict a very significant increase on suitable area, despite their restricted current distribution to coastal cliffs.

ii) Predicted changes on suitable area are highly dependent on the climatic scenario considered, generally forecasting a decrease for the scenario A2 and an opposite trend for the scenario B2. This group includes species with high interest for conservation (e.g. *Melanoselinum decipiens*), or with importance for the structure of communities, such as the stinkwood tree (*Ocotea foetens*) or the heath tree (*Erica arborea*), elements of the temperate laurel forest and heath tree microforest respectively.

iii) Species that register significant loss in terms of suitable area under future climatic scenarios, which might reach total loss (100%) in the case of endemic species that are currently restricted to small populations on the summits of the island. This is the case for the exclusive endemics *Berberis maderensis*, *Armeria maderensis* and *Sorbus maderensis*. The predicted absence of suitable conditions under future climatic scenarios supports the definition of a scenario prone to extirpation. Such hypothesis might be reinforced by the synergic contribution from other factors, which are already in place, such as the disturbance by fire, or the habitat loss by invasion from exotic species.

In fact, there are different factors in place that might swift predicted changes based only on scenarios of climate change. Among them, the availability of habitat might be a significant factor in the case of species that are habitats specialists. By one side, suitable area might be more overestimated, a fact that is often associated to the resolution in use (200x200m). On the other side, the available habitat could be also limited by the fact that it has a type of land-use that impedes species installation, such as agriculture. Or, it is also possible that it is already occupied by tree alien invasive species. In fact, the invasion by non-native species might play an important role on reducing the area available for native species under future scenarios. Native species are currently absent on significant areas predicted as suitable because of human intervention. And those areas are also suitable for alien invasive tree species. Under such context, and based on the unequal capacity of the species to compete, it is expected that significant areas become invaded by alien invasive trees, namely *Acacia melanoxylon*, *A. mearnsii*, and *Pittosporum undulatum.*

CAP I - CLIMATE CHANGE: PAST, PRESENT AND FUTURE

Summary

1 INTRODUCTION

> "*Overall, it can be said that climate variability results from complex interactions of forced and free variations because the climate system is a highly non-linear, dissipative system with many sources of instabilities*."
>
> (Peixoto & Oort, 1992:37)

Climate change and invasion by non-native species are listed, among other factors (habitat change, pollution, overexploitation of natural resources) as a major cause for biodiversity loss and species extinction (UNEP, 2010), considered important threats for Macaronesian extant native forests (Guimarães & Olmeda, 2008).

Such impacts might be particularly serious on hotpspots of biodiversity, and mainly noted in the case of endemic species restricted to fragmented and scarcely represented habitats. Despite differences in terms of magnitude and sense in the projected changes, it is expectable that the effect might be inflated on small-inhabited islands by synergic processes, namely as consequence of disturbance from human activities (Mimura *et al.*, 2007). Under such context, it is considered prudent to assess potential impacts on such territories, as a strategy to define mitigation and adaptation measures.

This work is focused on assessing changes on distribution patterns for plant species and communities under projected climatic scenarios on Madeira Island, a small territory considered an hotspot in terms of plant diversity (Jardim & Sequeira, 2008). The assessment is based on the use of the *species distribution modelling* approach, a tool very often applied on studies with similar purposes. Despite the focus on native plants, especially endemics, results for three alien invasive trees are presented, a decision based on the secondary aim of identifying areas of potential conflict between the two groups.

At the start of this work, and based on the predicted increase on temperature and decrease on precipitation forecasted by the two climatic scenarios in use, four main hypotheses are considered:

i) native species tolerant to dryness will register an increase on suitable area under future climatic scenarios;
ii) temperate laurel forest and the heath tree microforest may suffer a significant contraction on suitable area under future climatic scenarios;
iii) exclusive endemics currently restricted to the highest summits of the island might face the extirpation of suitable climatic conditions in the future;
iv) areas of potential conflict between native and alien invasive species will increase under future climatic scenarios.

In terms of results, it is expected that this work will contribute to:

i) progress on current knowledge about species distribution on Madeira Island,
ii) identify species and climax communities that are more vulnerable to changes on climatic conditions,
iii) assess the areas that present higher susceptibility to invasion by widespread alien invasive trees.

At the end, the production of specific outputs will provide tools that can be used to support decisions on territory management and conservation, tools that are identified as crucial for such purposes (Sala *et al.*, 2000; Borges *et al.*, 2008).

2 CLIMATE CHANGE

> "*Natural climate variability was the rule rather than an exception and the evolution of life on Earth was closely linked to climate and its change*."
>
> (Quante, 2010:9)

The subject *climate change* is one of the topics that gained especial attention in the last two decades in different domains. Such interest on the subject is mainly based on the assumption that climate is changing on modern days, changes that are likely causing disruption on ecosystems and put in danger the survival of societies on certain regions of the world. The concern about such issue has increased after the production of climatic projections for the future, which are expected to cause significant impacts.

Despite all the data compiled and produced, there are important uncertainties surrounding the subject, namely the rate and magnitude of the climatic changes.

At the scientific level, several contributions on a wide variety of fields emerged, aiming to improve our knowledge about causing factors, impacts, vulnerability and ability to mitigate and adapt to the resulting changes. Some scientific outputs have contributed to improve the discussion. The *Assessment Reports on Climate Change* published by the Intergovernmental Panel on Climate Change (1990, 1996, 2001, 2007) played an important role on making new scientific results available to different types of audience (scientific community, policymakers and general public). The *Fourth Assessment Report* in particular (IPCC, 2007b) represents a significant advance on the comprehension of past and recent climate changes, improving our ability to understand patterns and scales of climatic projections for future climatic scenarios.

Although the increasing confidence patent in the reports, the complexity and resilience of natural systems involves uncertainty and pose limitations to our ability to fully understand the magnitude and direction of climate change. And different aspects are still identified as sources of uncertainty:

- difficulty on identifying climate change as the main cause of environmental change, among others (e.g. land-use change, invasion by alien species), namely on territories where changes are the synergetic product of complex contributions from different factors, hampering the isolation and evaluation of the contribution of such threats on a global scale (Valladares, 2006),
- uncertainty associated to the occurrence, magnitude and direction of the future climatic scenarios (Walther, 2004),
- uncertainty on predictions at regional and local scales because of the interference of local geographical factors, which are not considered in the models used to project climatic conditions (Santos & Miranda, 2006),
- incomplete knowledge on the behavior and interactions for the components of the climatic system and their own role on future climates, such as clouds, land use change and the coupling between climate and the biogeochemical cycles (IPCC, 2007b),
- the complex nature of the climatic variability, due to external forcing or internal instabilities and feedbacks to non-linear interactions among the compounds, introduces uncertainty on the identification and quatification on human influence on climate (Quante, 2010).

The level of uncertainty increases when assessing impacts from climate change on specific domains and at high spatial resolutions. In the case of assessing impacts on ecosystems, the above uncertainties sum to those associated to the lack of knowledge about the organisms, namely about their resilience to environmental changes, capacity to adapt or to dispersal (Midgley *et al.*, 2007). Reporting to the case of Madeira Islands, some of the most concerning species for conservation are exclusive endemics, which resilience to changes on environmental conditions is unknown. It is only expected that current habitats fragmentation by human influence might reinforce their susceptibility to impacts from climate change (Travis, 2003).

2.1 CLIMATE CHANGE AND ASSOCIATED IMPACTS

The assessment of climate change impacts on ecosystems received special attention in ecological studies during the last two decades. Such growth is evident for studies focused on current climatic conditions or based on projections for past and future environmental scenarios. The increasing availability of ecological data for different spatial and time resolutions, and a considerable evolution on software have been supported such growth.

The significant worldwide effort to improve knowledge on impacts from climate change on vegetation can be assigned to three main time perspectives:

- **past changes** – studies exploring relationships between vegetation features and past ecological conditions, based on fossil and pollen records, carbon dating, ice and sediment cores, and interpretation of historical data;
- **current assessment** – long-term monitoring studies on areas identified as highly vulnerable to climatic change (high mountain ecosystems and Artic regions), in order to detect shifts on phenology, growth and distribution patterns related to recent changes on climate. Such studies improve our knowledge about the vulnerability of species and habitats;
- **future predictions** - studies focused on developing methodological approaches to improve our ability to understand current relationships between flora/vegetation and environmental conditions, and project such relationships under new ecological scenarios. A significant number of studies are based on the species distribution modeling approach.

Such structure guides the following review for reported impacts, assessed or predicted, from climate change on different time scales.

2.1.1 LEARNING FROM THE PAST

The assessment of climate change impacts on vegetation must be based on the assumption that the magnitude of the impact is deeply influenced by the time scale. The massive changes on landscape occurred at the geological scale (million years) should only be used as reference when assessing current impacts or predicting for the future, once current and future climatic trends and changes are analysed at the scale of decadee or centuries.

In order to build a framework about climate change and vegetation response over geological and historical times within Macaronesia, a revision of available data for different time frames is presented in the following text:

- climate change at geological scale (million years - Ma): Late Miocene to Pleistocene,
- climate change during the Holocene (thousand years - Ka),
- climate change during the historical period (X-XIX) (hundred years),
- current climate change (after the 50ties of the last century (decade scale).

2.1.1.1 CLIMATE CHANGE DURING THE NEOGENE (23 – 2.6 MA)[1]

The Miocene is the period of appearance for most of the extant islands of the Madeiran, Selvagens and Canarian archipelagos (for a revision see Fernández-Palacios *et al.*, 2011). Together with other former-islands, currently seamounts, they have very likely created a chain of islands, an important complex of structures available to be colonized at first, and be a source for dispersal events in a stepping-stone mode latter on, namely for younger islands. Such perception is coherent with the assumption that some of the taxa present today on Macaronesian archipelagos are relicts from the Palaeotropical flora that were able to colonize the Palaeomacaronesia. Such colonization occurred before the extinction of such taxa on continental Africa and Europe, an event determined by the

---

[1] - Timescale according the International Chronostratigraphic Chart, version 2013/01, published by the International Commission on Stratigraphy (http://www.stratigraphy.org/index.php/ics-chart-timescale).

climatic deterioration associated to the desertification cycles established in the Sahara region (latest Miocene – Early Pliocene, 6-5 Ma) and the increasing dryness and cooling associated to the Pliocene-Pleistocene transition (3-2 Ma) (Barrón & Peyrot, 2006).

2.1.1.1.1 CLIMATIC CHANGES IN THE SOUTHEASTERN NORTH ATLANTIC AND MEDITERRANEAN AREAS

The climatic deterioration occurred during the late Miocene-Pliocene on current territories of Europe and North Africa is associated to an increase on dryness, supporting the transition from an equatorial-like climate, without seasonality, to a seasonal semi-arid one (Barrón & Peyrot, 2006). Such aridification supported the expansion of savannah and steppe-like biomes, and the contraction of the forest, a fact confirmed by fossil records for related fauna (Aguirre, 2003).

Global and regional changes contributed to reinforce dryness and cooling along the Pliocene. At a global scale, changes on atmospheric circulation are very likely the result of a new pattern in the oceanic circulation in the North Atlantic, set after the closure of the Panama Isthmus (2.5 Ma) (Tenorio *et al.*, 1990; Jiménez-Moreno *et al.*, 2010). Subsequently, the definition of an oscillation between the influence of high and low-pressure cells along the year sets a seasonal thermal regime, resulting on intermittent, but progressive, “mediterranization” of southern Europe and North African climate. Initiated during the Miocene, and increasingly defined by a climatic rhythm structured around summer drought, it is supported by a reduction on rain and the transference of the rainy period from summer to winter (Fauquette *et al.*, 1999; Carrión *et al.*, 2010).

At a regional scale, the global cooling trend is reinforced by orogenic events in the current Mediterranean area, becoming a supplementary source of disturbance for vegetation (Jimenez-Moreno *et al.*, 2007), and establishing new migratory routes, namely for taxa coming from the center of the Euro-Asian continent (neo-mediterranean flora) (Capelo *et al.*, 2007). The progressive cooling and dryness supported the expansion of mesothermic elements (Arctotertiary geoflora), at the expense of a severe contraction of the so-called Palaeotropical geoflora, dominant at both margins of the Tethys Sea until the Middle Miocene (Tenorio *et al.*, 1990; Barrón & Peyrot, 2006; Jiménez-Moreno & Suc, 2007; Carrión *et al.*, 2010). According to Mai (1989) the Palaeotropical geoflora was a complex of forest types (paratropical rain forest, subtropical rain and laurel forests, temperate laurel forest and a edaphic controlled laurel-conifer forest) that integrates a great diversity of conifers, palms, lauroid-leaved elements and ferns. Named as "Madrean-Tethyan" flora by Axelrod (1975), such flora is the potential source for the paleo-endemic element of the flora currently present in the Macaronesia (Mai, 1989; Rodríguez-Sánchez *et al.*, 2009), which is clearly identified in Southern Europe during the Middle Miocene (Jiménez-Moreno & Suc, 2007).

Changes on vegetation occur in parallel with a progressive decrease on plant diversity, an impoverishment resulting from the disappearance of termophilous (megathermic) and high water-demanding plants, despite the increase of warm-temperate (mesothermic) and seasonal-adapted taxa (Catalán, 1996; Barrón & Peyrot, 2006; Jimenez-Moreno *et al.*, 2007; Jiménez-Moreno *et al.*, 2010). In the Mediterranean area the reduction on summer rainfall already supports the definition of a dry and warm season similar to current summer, a process associated to the establishment of a climatic Mediterranean rhythm (Carrión *et al.*, 2010). Such increase on aridity prompts the reinforcement of paleomediterranean-type xerophytic elements on the southern territories of current Europe (e.g. *Olea, Pistacia, Phyllirea* and sclerophyllous *Quercus* sp.) (Tenorio *et al.*, 1990; Fauquette *et al.*, 1999; Postigo-Mijarra *et al.*, 2009). While the detected cooling contributes to the expansion of the Arctotertiary flora in the northern Mediterranean domains, which determines the definition of mixed forests, progressively enriched by warm-temperate (mesothermic) deciduous elements coming from higher altitudes (see Jimenez-Moreno *et al.*, 2007).

In terms of spatial patterns, the vegetation of the Middle Miocene (13.8 – 11.6 Ma) seems to respond to a stronger lattitudinal gradient on precipitation (Jiménez-Moreno & Suc, 2007). The North/Northwest Mediterranean domain, where climate was warmer and more humid, it is accepted that vegetation was associated to a broad-leaved evergreen and warm-temperate mixed forests, with a temperate deciduous forest on middle elevations (Fauquette *et al.*, 1999). The western Iberia, climatically influenced by the Atlantic Ocean, was very likely associated to a complex mosaic of vegetation types (Castro *et al.*, 2005; Pais, 2010). Such complex could combine subtropical taxa, some of them occupying potentially swampy/riparian habitats (Jimenez-Moreno *et al.*, 2007), *Ericaceae* on the non-arboreal taxa, arboreal elements of evergreen *Quercus* (Carrión *et al.*, 2010) and an increase of Mediterranean elements (Pais, 2010), namely Mediterranean xerophytes (*Olea, Phillyrea, Cistus*) on calcareous areas (Diniz, 1984 - cit. by Fauquette *et al.*, 1999). On the southwestern Mediterranean domain is clear a progressive reduction of subtropical elements and an increase on Mediterranean xerophytes. On a belt along the Mediterranean coast of Iberia (Andalucia – Cataluña), dry conditions are reflected on the significant presence of termophilous taxa, namely subdesertic elements associated to semi-desert conditions (Jiménez-Moreno & Suc, 2007; López-Merino *et al.*, 2009; Carrión *et al.*, 2010). Such conditions would have more similarity to those found on the North African coastal territories. On such areas, dominated by an open subdesertic landscape, there is an higher presence of Cupressaceae, subdesertic and steppic elements, probably associated to lower values of precipitation than those predicted for the northern Mediterranean margin (Quézel, 1978; Fauquette *et al.*, 1999).

Such vegetation patterns testify the progressive decline of the Palaeotropical broad-leaved evergreen forests, a trend droven by a displacement and reduction on importance of the Palaeotropical lauroid taxa (laurophyll vegetation) (Benito-Garzón, 2002). Pollen analysis and fossil records for the Early Pliocene (Zanclean – 5.3 – 3.6 Ma) in Southern Europe identify an especially impoverished laurel forest, where some Palaeotropical related taxa were identified (*Cinnamomum, Persea, Ficus* (non-carica group), *Myrica*, *Laurus, Ocotea*), possibly with similar conditions to those extant on current Macaronesia (Catalán, 1996). In fact, megathermic and mega-mesothermic elements associated to the Palaeotropical broad-leaved evergreen forest became progressively rare during the early Pliocene on southern Europe (Catalán, 1996; Kovar-Eder *et al.*, 2006; Jimenez-Moreno *et al.*, 2007). In the Iberian Peninsula, a territory that plays an important role as refugium for the Palaeotropical elements, such flora persists until the late Pliocene, becoming generally extinct at the Piacenzian (2.7 – 3.3 Ma) (Postigo-Mijarra *et al.*, 2009). The longer permanence of Paleotropical flora at the Iberian Peninsula is supported by pollen records from the Atlantic face of the Iberian Peninsula (Rio Maior - Portugal), dated from the Piacenzian (3.6 – 2.6 Ma); very likely benefiting from the average lower altitude and the buffering effect of the Atlantic Ocean (see Pais, 2010). That condition would expand the time span for the colonization of the Palaeomacaronesia from the Iberian Peninsula. Dispersal of Palaeotropical taxa to the Palaeomacaronesia, from continental areas, could have started in the Oligocene-early Miocene, associated to the emergence of the first islands (60-20 Ma), seamounts on modern days (see Fernández-Palacios *et al.*, 2011); before the extinction of taxa registered on continental territories because of the Pliocene-Pleistocene climatic deterioration. Studies on the origin and timing of radiation for endemic flora associated to long distance dispersal events indirectly support such assumption. Based on five plant groups Kim *et al.* (2008) identify three *windows* of colonization (colonization events), from the Middle Miocene (15.2 Ma - *Aeonium*), Late Miocene (*Sonchus* – 8.47 Ma; *Crambe* - 8.15 Ma), and early Pliocene (*Echium* - 3.73 Ma; *Sideritis* – 3.3 Ma). The colonization events along the Miocene and early Pliocene were certainly favored by the existence of an important number of emerged islands, forming a chain of islands from the coasts of the Iberian Peninsula to the coasts of North Africa (Keller *et al.*, 2000). Such chain would support the events of colonization from the Mediterranean area (Kim *et al.*, 2008), followed by subsequent dispersal among islands.

The permanence of Palaeotropical relicts at the Macaronesia until modern days is interpreted as a consequence of the buffering effect of the Atlantic Ocean during periods of intense climatic deterioration over continental areas. Even though, the **Pliocene** and **Pleistocene** climatic deterioration possibly led to a gradual impoverishment and restriction of the laurel forest, accepting a previous wide covering scenario in the islands during the Miocene (Fernández-Palacios *et al.*, 2011). Such trend is supported by modelling results based on fossil records for *Laurus* L. (Rodríguez-Sánchez & Arroyo, 2008), despite its higher resistance to climatic stress comparing to other trees of the laurel forest (González-Rodríguez *et al.*, 2005). Such range restriction would favor the definition of low-saturated taxa habitats, creating the chance for the establishment of new founders. In fact, colonization events are very likely restricted to colonization windows (Carine, 2005), characterized by contexts when dispersal events are coincident to suitable conditions to the founders (Whittaker *et al.*, 2008). According to Kim *et al.* (2008), in the Macaronesia those contexts would very likely occur after islands emersion, after environmental crisis linked to climatic deterioration and catastrophic volcanic episodes (episodes of active volcanism), or in association to profound climatic and geologic changes on the Mediterranean and North Africa. Such circumstances are responsible for the creation of new habitats and even new ecological niches because of increasing altitudinal gradients along with island construction, fundamental to the establishment of new founders. The occurrence of such natural disturbances could possibly promoted rapid speciation, inter-island and inter-archipelago colonization for some plant groups (Kim *et al.*, 2008).

2.1.1.1.2 CLIMATIC CHANGES OVER THE MACARONESIA

The geographic conditions of the Palaeomacaronesia in the upper Miocene were different than today, not only in terms of climatic conditions, but also in number and configuration of the islands (Meco *et al.*, 2007; Meco, 2008). A warm, wet and non-seasonal tropical climate (equatorial-type), the same type that supported the presence of the Palaeotropical flora in Europe and North Africa until the Miocene, persisted until the middle Pliocene (4.1 Ma), an assumption based on the identification of marine fossil faunal records related to organisms of shallow waters of modern-days warm seas, which are identified on Miocene-Pliocene coastal marine deposits in eastern Canaries (Meco *et al.*, 2003; Meco *et al.*, 2007; Meco, 2008), and on Miocene deposits on Madeira island (Mayer 1864, cited by Meco, 2008). Usually named as "Senegalese fauna"[2], its presence sustains the existence of an equatorial-type climate over the Macaronesia, an interpretation that is reinforced by the presence of corals on the eastern Canaries (Lanzarote and Fuerteventura) (Meco, 2008), and excludes the operation of a cold current similar to the extant Canary current (Meco *et al.*, 2003). These warm and wet climatic conditions would very likely support a wider distribution of the laurel forest on islands until the middle Pliocene (Fernández-Palacios *et al.*, 2011).

The first climatic change recorded in Palaeomacaronesia occurs on the late Pliocene (3.2 - 2.7 Ma), determined by a process of climatic cooling and increasing

---

[2] - *Warm guests*, *Strombus fauna* and *Senegalese fauna* are concepts used in the literature to designate an assemblage of marine organisms (gastropods, bivalves) identified for the Pleistocene Mediterranean and Macaronesian coasts and currently restricted to warm seas associated to equatorial climates, such as the Guinean Gulf, Caribbean, and Indian Ocean.

dryness (Meco, 2008), following a pattern described for the continental areas. It is accepted as a consequence of the formation of ice-sheets at the higher latitudes of the Northern Hemisphere, prompted by the new organization on oceanic circulation patterns established after the definitive closure of the Panama Isthmus. The new pattern supports the onset of a cool marine current on the southeastern sector of the North Atlantic, in association to a theoretically progressive influence from a subtropical high-pressure cell (Azores High) that persists during longer periods of the year. Such redefinition of the oceanic and atmospheric circulation patterns are responsible for increasing aridity in European and African continents (onset of arid and desertic climates on Africa) (Meco *et al.*, 2003; Barrón & Peyrot, 2006), and support the gradual shift from tropical to Mediterranean-type climate (cool and humid winters / warm and dry summers) on the Palaeomacaronesian islands, the first evidence of climatic change (Meco, 2008).

The definition of a dry season was very likely responsible for an impoverishment and range contraction of the laurel forest, effects probably smoothed, at least partially, by the humidity carried by the trade winds, accepting that the onset of a cool marine current (canarian current) is associated with a trade winds impulse (Rognon & Coudé-Gaussen, 1996). Favorable conditions could have remained on significant areas, at least on mid-elevations of windward slopes on the higher islands, directly influenced by the cloudbanks of the trade-wind inversion, an ongoing process on current days. Even on a context where the inversion was set at higher altitudes, because of higher average temperatures, islands' windward faces were very likely largely buffered, once islands would be theoretically larger and higher than today (Fernández-Palacios *et al.*, 2011).

The installation of a seasonal and drier climate over the islands might have occurred in parallel to a fall in the water temperature, as a consequence of the general cooling occurred in the North Atlantic, contemporary to the formation of ice-sheets on Northern Hemisphere (Artic region), and the onset of the cool marine current (Barrón & Peyrot, 2006). Such conditions are incompatible to the presence of warm-seas fauna (e.g. *Strombus*, *Saccostrea*, *Nerita*), which disappear from the Canarian coasts during the middle Pliocene (Meco, 2008).

The definition of a dryer climate on coastal areas, interrupted by humid episodes, is consistent with the climatic interpretation provided by Meco (2008) for sedimentary sequences of the eastern Canaries (Gran Canaria, Fuerteventura, Lanzarote). According the author, the intercalation of heavy and low calibrated alluvial deposits between eolian bioclastic sand dunes of marine origin, associated to North Atlantic prevalent winds and lower sea levels, suggests the existence of torrential episodes on a context of climatic deterioration. Such sequence is interpreted as an indicator for a prevaling arid climate (2.7 Ma) with important humid pauses, and is one of the proxies accepted for the occurrence of a climatic changes during the middle-late Pliocene (Meco, 2008).

Some of the Pliocene biogenic dunes end on a clayish palaeosol, which represents a wet and warm pause under a general arid climate. The inference of less severe climatic conditions for the palaeosol evolution is supported by the presence of rhizolits, calcareous concretions around vegetation roots and other parts of the plants, testifying the colonization of the dunes by psamophyl vegetation. Another argument is the presence of *Antophora* nests (2.9 Ma: Fuerteventura, Gran Canaria), indicating humid pauses that are coincident to the onset of a glacial stage on the Northern Hemisphere (Meco, 2008). The existence of palaeosols enriched on *Antophora* nests, performing conditions of invasion similar than those occurring today, can be associated to the predominance of easterly atmospheric circulations, possibly prompting more frequently rain episodes over the islands and supporting the arrival of Saharan dust to the Canaries, a possible explanation for the increase on the clay fraction on such deposits (Meco, 2008).

The sequence ends with a thick, extensive calcrete on the eastern Canaries, related to a deep arid phase (arid to hyper-arid climate) set after a humid one (palaeosol). Its higher thickness on coastal sectors of valleys open to the north is interpreted as a consequence of prevalent northerly winds (trade winds) (Meco, 2008). Such peak of dryness, associated to the arid climate of the Piacenzian (3 Ma), marks the transition to the Pleistocene glacial-interglacial oscillation (Meco, 2003; Meco, 2008).

The depositional sequence (dominant sand dune deposits - intercalated alluvial deposits with torrencial facies – palaeosol – calcrete) testifies a profound climatic deterioration along the middle and late Pliocene, testifying the change from humid to dry climatic conditions (Meco, 2008).

In Europe, the transition between the Pliocene and Pleistocene is marked by an intensification of cooling events, at a point that glacial-interglacial cycles get defined in the Northern Hemisphere (Lisiecki & Raymo, 2005). Such cooling, registered by a significant increase on *Artemisia*, is associated to an expansion of the East Antarctic Ice Sheet and the onset of the Arctic Ice Sheet (Barrón & Peyrot, 2006). In Europe, such process could have been amplified by an ongoing uplift of regional mountains associated to Alpine orogenesis, which affects south and southeastern Europe domain (Jimenez-Moreno *et al.*, 2007). This is the milestone associated to the process of massive extinction of Palaeotropical flora on Iberian Peninsula, driven by an increasing aridity on summer and a marked cooling on the Mediterranean basin (Postigo-Mijarra *et al.*, 2010), even before the intense cooling associated to Pleistocene glaciations (Mai, 1989). There is a significant reduction or even disappearance of Lauraceae, Taxodiaceae, Magnoliaceae, and Cyatheaceae taxa (Mai, 1989; Postigo-Mijarra *et al.*, 2010), and vegetation types currently associated to specific tropical environments, such as mangroves (Hooghiemstra *et al.*, 2006; Jimenez-Moreno *et al.*, 2007).

2.1.1.2 CLIMATE CHANGE DURING THE QUATERNARY (2.6 MA – PRESENT)

Changes on climate during the Quaternary explain structure, floristic composition and dynamics of current Iberian Peninsula woods (Tenorio *et al.*, 1990; Castro *et al.*, 2005). The distribution of modern-day relicts can be related to environmental changes in the past, namely the oscillation between glacial and warm interglacial periods on the Quaternary period, which promoted processes of range contraction/expansion (Habel & Assmann, 2010). On a context of a more cold and arid environment occurs the expansion of desert-like communities, associated to grasslands and steppes (see Carrión *et al.*, 2010), in counterbalance to a deep range contraction of communities dominated by broad-leaved trees and termophytes, widely distributed during the Pliocene. In Europe, the derived shifts occurred during such cold periods to southern territories and lower altitudes (Tenorio *et al.*, 1990), namely for termophilous species, were barred by physical constraints. The existence of physical barriers, namely transversal mountains and the Mediterranean Sea, had a deep contribution to extinction, which explains the lower diversity of Europe comparing with similar latitudes in the American or Asian continents (Tenorio et al., 1990).

2.1.1.2.1 THE COLD PERIODS OF THE PLEISTOCENE (2.6 MA – 11.7 KA)

The climate of the early Quaternary is marked by an oscillation between glacial and interglacial periods (Quante, 2010). Such climatic pulsation promoted deep changes on vegetation, adjustments based on the definition of migratory and extinction events (Carrión *et al.*, 2010). Extinction over large areas of species' range occurred during glacial periods, especially under episodes of marked dryness and rapid temperature change (Hewitt, 2000; Twitchett, 2006; Tzedakis *et al.*, 2006). The ongoing climatic changes occurred during early and middle Pleistocene transitions had especially deep effects on Arctotertiary taxa distribution ranges in Europe (Postigo-Mijarra *et al.*, 2010), even promoting a significant extinction (Postigo-Mijarra *et al.*, 2009). Such loss on biodiversity occurs on a context of increasing severity of glaciations (Bradley, 1999), associated to a shrink on interglacial length periods, wider temperature fluctuations, and a fall in temperature along with marked dryness (Lisiecki & Raymo, 2005). The new climatic conditions support an increase on cold-tolerant species, such as *Artemisia* and chenopods (Tzedakis *et al.*, 2006). At the Iberian Peninsula the landscape registered an increase on stepic/herbaceous communities, with a small presence of trees (*Betula, Juniperus, Pinus*). Warm temperate deciduous vegetation and mediterranean evergreen termophilous taxa, responsible by the precedent displacement of the Palaeotropical taxa, were displaced to the lower altitudes on costal areas, where climate present less adverse conditions (Tenorio *et al.*, 1990; Castro *et al.*, 2005; Postigo-Mijarra *et al.*, 2010). Specific climatic, geomorphological and phytochorological attributes have very likely contributed for the persistence or later disappearance of Arctoterciary (Postigo-Mijarra *et al.*, 2010) and few Paleotropical taxa during Pleistocene glacial periods (Postigo-Mijarra *et al.*, 2008), comparing to central Europe, playing an important role as refugium (Postigo-Mijarra *et al.*, 2009). The restriction of extensive glaciations to mountain ranges and the existence of great diversity of habitats that worked as refugia, such as deep valleys and territories with milder climatic conditions on coastal regions, were determining factors (Castro *et al.*, 2005; Postigo-Mijarra *et al.*, 2010). In fact, some of the taxa that are restricted to such areas are considered to be Palaeotropical relicts, restricted to such refugia (Myrica faya)3,

---

[3] - Dubious interpretation according to BENITO-GARZÓN (2002).

Rhododendron ponticum subsp. *baeticum*, *Prunus lusitanica*) (Mai, 1989; Silva, 1991; Costa *et al.*, 1998; Benito-Garzón, 2002). With the exception of the Laurus nobilis, such Palaeotropical taxa remained restricted to such areas, while the temperate deciduous vegetation and Mediterranean evergreen termophilous taxa (*Quercus ilex, Phillyrea latifolia, Arbutus unedo*) expanded during interglacial periods (Fauquette *et al.*, 1999; Tzedakis *et al.*, 2006; Carrión *et al.*, 2010; Jiménez-Moreno *et al.*, 2010).

But the refugium condition is far more undeniable for the Macaronesian archipelagos. Besides the affinities with the Iberian Peninsula in terms of shared (*Asplenium hemionitis* L., *Culcita macrocarpa* C. Presl., *Davallia canariensis* (L.) Sm, *Diplazium caudatum* (Cav.) Jermy, *Dryopteris gaunchica* Gibby and Jermy, *Stenogramma pozoi* (Lag.) Iwatsuki, *Pteris imcompleta* Cav., *Woodwardia radicans* (L.) Sm) or related relicts (potential source-area for dispersal events for Macaronesian endemic taxa: *Laurus novocanariensis*, *Laurus azorica*, *Prunus lusitanica* subsp. *hixa*) (Castroviejo *et al.*, 1986-2012; Castro *et al.*, 2005), the islands also provide shelter to species that get extinct in Europe (Capelo *et al.*, 2007), once again because of significantly weaker climatic changes on the Macaronesia.

The Pleistocene climatic oscillation is registered in the Macaronesia by sedimentary sequences where marine terraces occur in alternation with continental sedimentation. The sequences of deposits have been clearly attributed to Pleistocene marine transgression-regression cycles of glacioeustatic origin, despite the interference of uplifting and isostatic processes that hinder the rigorous inference of glacio-eustatic sea-level fluctuations and correlative climatic conditions (Meco *et al.*, 2007; Zazo *et al.*, 2007; Madeira *et al.*, 2010; Ramalho *et al.*, 2010).

A comparison of the sedimentary sequences points out the existence of a latitudinal climatic gradient during the Pleistocene in the Macaronesia. Such gradient, with a similar pattern than the current one, might have supported a higher influence from polar conditions on the northern archipelagos, namely on the Azores, with cooler temperatures during the cold periods, in opposition to reinforced tropical influence on the southern archipelagos. The Pleistocene dominance of marine deposits with warm-seas fauna in the sedimentary sequence described for the Cape Verde (Zazo *et al.*, 2007; Zazo *et al.*, 2010) contrasts to the identification of such conditions solely during the last interglacial (MIS 5.5.) in the Azores (Ávila *et al.*, 2009), the warmest stage of the Pleistocene (Meco, 2008).

Sea level oscillations (transgression-regression), registered on sedimentary sequences, support the inference of climatic cycles (warm/wet - cool/arid). The main transgression phases (sea level rise) are associated to warmer and wetter periods set at the beginning of the main interglacials, and are registered by marine deposits on some islands (Cape Verde, Canaries, Azores). The regression phases are connected to arid and cooler periods, allowing the deposition of eolian sands, a feature identified on all Macaronesian archipelagos (Cape Verde - (Zazo *et al.*, 2007); Canaries - (Meco, 2008); Madeira - (Goodfriend *et al.*, 1996); Azores - (Ávila *et al.*, 2009).

The oscillation between marine deposits and aeolian sand dunes is reported for the early Pleistocene on Cape Verde (Sal Island) (Zazo *et al.*, 2007; Zazo *et al.*, 2010), registering the oscillation between transgression and regression phases. Such oscillation is recorded on a sedimentary sequence installed over a wave-cut erosion platform originated during a transgressive stage, where marine deposits are intercalated by eolian sand dunes. Such conditions are very likely correlated to an oscillation between warm-wet and cooler-arid phases. The absence of the so-called “Senegalese fauna” on the marine deposits (transgressive stage) could be an indication of lower sea water temperatures comparing to the subsequent period. Such scenario is consistent with the glaciation cycle of the low Pleistocene, registered in the Canaries by a re-incision of the drainage net under a scenario of lower sea level (Meco, 2008), which performs a weakening of the tropical influence over the Palaeomacaronesia. Such conditions change in the late Early Pleistocene, when climate registered a reinforcement of the tropical conditions (climatic warming), associated to the Termination V (MIS 11.3 – 424 Ma). In fact, based on Antarctic ice cores analysis for precedent periods, it is accepted that the MIS 16.2 (659 Ka) corresponds to particularly low sea level and very cold conditions; and the precedent interglacial of the Termination V (MIS 13: 528 Ka – 474 Ka) is considerably colder than the subsequent interglacials (EPICA, 2004). The warming is registered by the arrival of “Senegalese marine fauna” to the southern Macaronesian archipelagos - Cape Verde and Canaries (Zazo *et al.*, 2007; Meco, 2008). On Cape Verde, the marine deposits that integrate such fossil records are on top of eolian sand dunes, a type of deposit (eolian sands) that is not described in the Pleistocene fraction of the sedimentary sequence at Sal Island (Zazo *et al.*, 2007; Zazo *et al.*, 2010). And the presence of "Senegalese marine fauna" associated to high stands sea level is described for subsequent marine deposits crossing the Last Interglacial (MIS 5.5: 130-115 Ka). Such order can be interpreted as indicative of a general climatic warming trend, only interrupted by the climatic cooling associated to the last glaciation set at the Upper Pleistocene. Because of the similitude between current faunas and fossil records for the middle and late Pleistocene interglacials, it is expected that sea water temperature on Cape Verde coasts during such period was at least as warm as is today (Zazo *et al.*, 2007; Zazo *et al.*, 2010). The absence of sand dunes on Cape Verde dated to that period (middle and early late Pleistocene) suggests a weak climatic oscillation for that period, which would increase on northernmost islands of the Macaronesia. The sequences described for the Pleistocene in the Canaries suggest a deeper climatic oscillation (Meco *et al.*, 2003; Meco *et al.*, 2007), especially after the Termination V (MIS 11.3 – 424 Ma). The main interglacials of this period, corresponding to uneven isotopic marine stages (MIS 11.3, 9.3, 7.1, 5.5), are associated to warm and wet climatic conditions, identified on sedimentary sequences by marine deposits of transgressive facies. Once again, the presence of warm-seas fauna fossil records ("Senegalese marine fauna") in the deposits indicates warmer climatic conditions. After the interglacials, the progressive lowering on temperature and increasing aridity resulted in a cooler and arid climate. This long, arid, and cool phase supports the disappearance of the warm-sea fauna and the set of a cycle of heavy eolian deposition and dunes building in the Canaries, intercalated by palaeosols representing humid pauses under a general arid climate (Meco *et al.*, 2003; Meco, 2008).

On Madeira Island the record of such climatic oscillation is restricted to the peninsula of São Lourenço. Despite similarities in terms of deposition patterns to other Macaronesian islands, the sedimentary sequence, attributed to the middle and late Pleistocene, is dominated by eolian sand dunes and marked by the absence of marine deposits with warm-seas fauna, attributed to highstands sea level of the interglacials. According to Goodfriend *et al.* (1996) the sequence is associated to eolian accumulation under scenarios of falling sea levels from middle Pleistocene (MIS 9.3 – Termination IV: 334 Ka) to Holocene. Sea level changes are registered by an alternation between units of i) black and white sands, corresponding to medium and high sea stands, ii) black sand units corresponding to changes between medium to lower sea levels, and iii) fine sediments (clay and silt) associated to the lowest sea stands of the cold stages. The warmer and more humid periods are identified in the eolianite sequente by marks of pedogenic processes (moderately developed soil profiles) and higher content on vestiges for plant colonisation on black and white sand units (e.g. large root concretions or rhizoliths), possibly by shrubs or small trees. Those vestiges suggest amelioration on climatic conditions during warm and wet interglacial stages, which are consistent with the conditions described for the Canarian palaeosols. In the Canaries, the high presence of oothecae locust insect fossils in the palaeosols, identified as calcareous concretions by Rognon & Coudé-Gaussen (1987), represent a survival strategy under a general arid climate with humid pauses, and mark the main warmer interglacials of the upper Pleistocene and Holocene, where temperature, humidity and soil conditions where, at least seasonally, favorable, contrasting to dominant arid conditions responsible for heavy aeolian dunes deposits (Meco, 2008).

The time span between the interglacials, marked by the definition of arid climatic conditions, was apparently less dry in Madeira Island, comparing to the eastern Canaries. Such assumption is based on the existence of moderate to well-developed cambic horizons in the sequence, chronologically associated to the periods where the sequence is dominated in the Canaries by eolian sand dunes without vestiges of pedogenic processes or colonization by vegetation. Such conditions are described for black sand units, associated to regressive trends on sea level (Goodfriend *et al.*, 1996).

A specific attribute described for the Madeiran sedimentary sequence are the thick clay levels, attributed to the lower sea levels of the coldest stages of the middle and Upper Pleistocene. The fine fractions that dominate such units (silt and clay) are considered to have origin on fine marine sediments. Such material, originated from weathering of rocks on the adjacent land areas and accumulated at depths above the wave action, became exposed during the lowest sea-level stands (Goodfriend *et al.*, 1996). Such scenario is acceptable taking by reference the adjacent bathymetry and a scenario of low sea level, such as that one of the Last Glacial Maximum, when the Desert Islands could have been connected to Madeira Island (Fernández-Palacios *et al.*, 2011).

The absence of terrestrial gastropods on such layers move away the possibility of any connection to the clay levels described in the sedimentary sequences of Porto Santo, where clay levels, classified as palaeosols, are characterized by a large profusion of terrestrial gastropods, and are related to warm climatic periods (Soares, 1973). Such description defines a closer proximity to the paleosols of the eastern Canaries described for the period after the MIS 11.3, where the oothecae locust insect are in place with fossil structures associated to vegetation and terrestrial gastropods (Meco, 2008).

On Madeira island some of the black and white sand units are calcreted by large root concretions extending horizontally, proofing the existence of vegetation prior to a warm and very dry climate that support the calcrete formation. Moreover, the identification of a carbonate tree trunk is indicative for the presence of vegetation that could integrate shrubs or small tress (Goodfriend *et al.*, 1996). The definition of a calcrete layer over such unit reinforces the contemporary relationship to the eastern Canarian paleosols, and marks the onset of a climatic deterioration after a main interglacial, giving place to a new, long, cooler, and arid period interrupted by humid pauses. The paleosols associated to such humid pauses are usually calcreted at the top, representing a warm and arid phase that ends the climatic cycle based on an alternation between eolian sand dunes (arid) and paleosols (humid pauses) (Meco *et al.*, 2003; Meco, 2008). The formation of a calcrete over the sand dunes indicates the marine origin of such sand, certified by the high presence of bioclasts (Soares, 1973; Goodfriend *et al.*, 1996; Zazo *et al.*, 2007; Meco, 2008; Ávila *et al.*, 2009), confirming the relationship between the sediments sequence, climatic oscillation, and sea level changes. Despite expected spatial adjustments on the vegetation of the island in association to such climatic oscillation, the floristic composition should share similar attributes with current vegetation types. According to Marques (2013), based on the analysis of fossil records dated for the middle Pleistocene (2Ma), the vegetation had, at least on some areas of the island, a very significant presence of lauraceae species, namely *Ocotea foetens*, and pterifophytes, a combination that has great affinities with the extant temperate laurel forest (*Clethro arboreae-Ocoteetum foetentis*). The author also identifies other taxa that are interpreted as characteristic of the margins of such type of forest, such as high shrubs (*Erica arborea*, *Vaccinium* sp.). Such similarities in terms of floristic composition indicate that such taxa were able to cope with the climatic oscillation that characterizes the Pleistocene, which includes warmer and wetter periods than today. The area occupied by such forest should have expanded during the warm stages, and undergone a retraction during the cold periods.

Despite the absence of marine deposits of transgressive facies in the sedimentary sequence for the interglacials at Madeira and Porto Santo (Goodfriend *et al.*, 1996), it is expected that at least the Last Interglacial was warmer than today. Such absence could be the result of particular topographic conditions on the coast, or determined by significant coastal erosion. In that case, current sedimentary sequence might be a fraction of a larger depositional body in the past. Such absence is really unexpected for the Last Interglacial, once such deposits, integrating fossil records of warm sea water species of the "Senegalese marine fauna" and corals (*Siderastrea radians*), are described to all the Macaronesia range (Azores (Callapez & Soares, 2000; Ávila *et al.*, 2009)); Canaries (Meco *et al.*, 2003; Meco *et al.*, 2007; Meco, 2008); Cape Verde (Zazo *et al.*, 2007; Zazo *et al.*, 2010) and for the Mediterranean coasts (Zazo *et al.*, 2003). Such fossil records, integrated on shallow-marine (shoreface) deposits of transgressive facies associated to the interglacial highstand sea level, are direct indicators for the existence of warmer oceanic temperatures than modern ones (Zazo *et al.*, 2010), and allow to infer wet and warm climatic conditions, wetter than the Holocene interglacial (Goodfriend *et al.*, 1996) and the warmest of the Pleistocene (Meco, 2008). In fact, the identification of such deposits in the island of Santa Maria, the oldest island of the Azorean archipelago (5.2 – 8.12 Ma) and the only one with marine fossiliferous sediments (Ávila *et al.*, 2009), support a scenario of a wetter and warmer interglacial on the North Atlantic. Taking by reference the geological age of the island (5.2 – 8.12 Ma), the presence of such deposits supports the idea that the Last Interglacial is the warmest of the Pleistocene, once the deposits are installed over a wave-cut platform built on volcanic substrate during the marine transgression (Ávila *et al.*, 2009). So, the absence on Madeira and Porto Santo islands can only be interpreted under a scenario of deep changes on islands' configuration due to coastal erosion dynamics. The warm and wetter conditions associated to the last interglacial (MIS 5.5.) are represented in the sedimentary of Madeira Island by several units dominated by black and white sands calcreted by large root concretions and hizoliths, in some layers allowing the definition of a cambic horizon (Goodfriend *et al.*, 1996).

Despite similarities and consistency between the described sequences, it is possible to identify a climatic range within the Macaronesia.

It is inferable that middle and late Pleistocene climatic variability presents an increasing magnitude with latitude. The dominance of marine deposits on Sal Island's (Cape Verde) sedimentary sequence (Zazo, 2007), and the identification of such deposits only for the Last Interglacial in the Santa Maria (Azores) can give support to such idea. And despite the presence of warm-water gastropods associated to the "Senegalese marine fauna" in the deposits of Santa Maria, there is a significant similitude between current and fossil fauna. The similarities are associated to the presence of warm-temperate species, most of them persisting after the last glaciations to the present day (Ávila *et al.*, 2009). Thus, it is acceptable the prevalence of a warm-climate (Callapez & Soares, 2000), but contaminated by an increased polar influence if compared to the southern archipelagos. For the Canaries, and based on the type of fossil records identified in the sedimentary sequences described for the eastern islands for the Eemian stage (125 – 115 Ka) of the Last Interglacial, Meco (2008) suggests a tropical-type climate, having by reference the clear relationship to today Cape Verde or Guinean Gulf, conditions that could last in Gran Canaria until 83 Ka (Meco, 2008).

It is accepted that the presence of the *warm-guests* gastropods with West African or Caribbean affinities in the deposits malacofauna's performs the last event of migration northwards for species today found in lower latitudes, in the Guinea Gulf or restricted to Cape Verde Islands (Zazo *et al.*, 2010). Its local extirpation on Mediterranean coastas, Azores and Canaries is a consequence of drop on the sea temperature during the following glaciations (Zazo *et al.*, 2007; Ávila *et al.*, 2008) Besides, the presence of such fauna is incompatible with the existence of the Canarian marine current (Meco, 2008), suggesting the existence of distinct atmospheric and marine circulation patterns comparing to modern days. In fact, changes on the atmospheric circulation are proposed by Rognon & Coudé-Gaussen (1996) during glaciations, indicating the southward shift of the trade winds during the Last Glacial Maximum. The idea of changes on the winds regime during the Quaternary cold periods is also proposed by Lancaster *et al.* (2002), based on the analysis of different generations of Quaternary sand dunes over the western Sahara desert in Mauritania. Predicted changes on prevalent wind direction and higher wind strength, under a more arid climate, is inferred from significant increase on dust fallout in the Antartic Vostok ice core during the Last Glacial Maximum (EPICA, 2004).

The cooling set after the Last interglacial was registered in the sedimentary sequences for all the Macaronesia by the deposition of heavy sand dune deposits, and occurs in parallel to the installation of an arid regime and a sea level regression (Meco, 2008). Like before, the arid regime is broken up by humid pauses of narrow definition, which are followed by deep arid phases. Such humid breaks are registered by palaeosols, intercalated between sand dunes, covered by a calcrete layer associated to increasing aridity under a strongly seasonal contrasted climate. That sequence, common to all the Macaronesia during the Upper Pleistocene (126 – 11.7 Ka), replicates conditions set after the MIS 11.3 (420 Ka), with some differences between cycles and islands ((Goodfriend *et al.*, 1996; Ávila *et al.*, 2008; Meco, 2008).

The described alternation in the sedimentary sequences is clearly present in the Madeira's eolianite deposit, supporting a consistent correlation between changes on sea level and climatic oscillations. According to Goodfriend *et al.* (1996) climate became progressively drier after 88 000 yr BP. Moderately moist conditions were progressively replaced by a drier and cooler climate, a consequence related to the progressive installation of the last glacial stage. The coldest periods of the Upper Pleistocene are identified in the sequence by two clay units, the last one (closer to the top of the sequence) coincident to the Last Glacial Maximum (around 18000 Ka).

The dry and cool climate of the last glacial period might have imposed deep adjustments on vegetation. The vegetation of higher altitudes, integrating cold-tolerant species, would expand to lower altitudes, at the expenses of a range contraction of the laurel forest, after a predictable expansion during the Last Interglatial. The contraction to smaller areas, compared to a situation where the laurel forest could occupy all the islands (Fernández-Palacios *et al.*, 2011), opens a window to the installation of other vegetation types on the islands, namely a coniferous forest above and the termophilous woodlands below the laurel forest, as identified for the Canaries (De Nascimento *et al.*, 2009). Such response, stated by the low cold-tolerance of trees of the laurel forest (González-Rodríguez *et al.*, 2005), might have been especially severe at the young Azorean archipelago, both by intense disturbance by Pleistocene volcanic eruptions and the expansion of peatlands (mires) and *Juniperus-Erica* forests, currently restricted to higher altitudes on some islands (Dias *et al.*, 2007). In fact, during the Middle and Late Pleistocene, the higher altitudes might have been associated to forests dominated by coniferous (*Pinus*, *Juniperus*) and Ericaceae taxa (De Nascimento *et al.*, 2009; Dupont, 2011). Such vegetation conditions during the cold periods, namely for the Last Glacial Maximum, are consistent with the prevalence of a cooler and dryer climate at the core of the Macaronesia, associated to specific oceanic and atmospheric circulation patterns. Such assumption is supported by pollen spectra analysis from deep sea cores (Hooghiemstra *et al.*, 2006; Dupont, 2011) and sedimentary studies (Rognon & Coudé-Gaussen, 1996). At first, an increase in the percentage of Ericaceae pollen in marine sediments along the northern Sahara margin during the Last Glacial Maximum is confirmed, indicating an increase on mountainous ericaceous scrublands, and a reinforcement of Canarian pine during interglacials (Dupont, 2011). On Madeira island only the Ericaceae taxa (*Erica arborea* L. and *Erica platycodon* (Webb & Berthel.) Rivas Mart., Wildpret, del Arco, O. Rodr., P. Pérez, García Gallo, Acebes, T.E. Díaz & Fern. Gonz. subsp. *maderincola* (D.C. McClint.) Rivas Mart., Capelo, J.C. Costa, Lousã, Fontinha, R. Jardim & M. Seq.) show current significant abundance, once *Juniperus cedrus* has a very restricted distribution (non-climate determinants), and there are no records for the presence of native *Pinus*. The contraction of the laurel forests during that period is partially supported by modelling results based on fossil records for *Laurus* L. (Rodríguez-Sánchez & Arroyo, 2008).

Such adjustments on vegetation should follow changes on atmospheric circulation, driven by the southward shift of the polar front in association to the expansion of the European ice sheet and the advance of the winter sea ice limit to the northern Spain (Rognon & Coudé-Gaussen, 1996). Today the polar front closely follows the Greenland and eastern Canadian continental margins (Eynaud, 2010). Such reallocation would be very likely followed by a southward shift of the subtropical high-pressure cell (current Azorean High) and a subsequent displacement of the trade winds to latitudes of Cape Verde (Rougnon & Coudé-Gaussen, 1996). Accepting a southward shift of the North Atlantic polar front to Azores – Portugal latitudes (Iberian Peninsula margin) (Lehman & Keigwin, 1992; Rognon & Coudé-Gaussen, 1996; Eynaud *et al.*, 2009), Madeiran and Canarian archipelagos should be associated to prevalent westerlies during cold periods. Such conditions are registered by eolian sands of litoral origin on the sedimentary sequences in all the Macaronesia (Soares, 1973; Goodfriend *et al.*, 1996; Meco, 2008) and NW Africa (Rognon & Coudé-Gaussen, 1996), provenient from the emerged continental shelves during associated marine regression stages. The existence of a dry climate is also suggested by studies based on pollen spectra analysis for deep-sea cores (Wyputta & Grieger, 1999; Hooghiemstra *et al.*, 2006; Dupont, 2011).

Despite likely geographically restricted to the Moroccan coasts and offshore islands during the Upper Pleistocene, such aridity is reinforced by a cold marine current associated to a discharge current of meltwater from continental glaciars, sea ice and icebergs discharge in the Atlantic Ocean (Bond & Lotti, 1995), which induce adverse conditions to the occurrence of rain (Rognon & Coudé-Gaussen, 1996).

Such assumptions are also consistent to the identification of important changes on the vegetation on adjacent continental areas. Based on the pollen influx for different taxa (*Pinus*, *Artemisia* and "trade wind indicators" (*Alnus*, *Betula*, *Pinus*)), calculated from marine sediment along the African coast (Serrado, 1960; Oreskes, 2004), it is assumed that changes were associated to an expansion-contraction response of the Sahara desert to the Middle and Late Pleistocene climatic oscillation. Such behavior determines correlative adjustments on vegetation at both margins of the Sahara, by northward and southward migration of vegetation belts. According to Dupont (2011), the northward expansion of the desert during glacial episodes of the Middle and Late Pleistocene can be supported by an increase on pollen from taxa associated to the Saharan desert. The deep retraction, almost disappearance, of the Mediterranean vegetation is in opposition to the expansion of a steppe belt dominated by *Artemisia*, an increase on *Ephedra* and the significant presence of Caryophyllaceae, Chenopodiaceae, and Amaranthaceae on the pollen spectra, pointing to abundant desert vegetation in a large part of NW Africa. The maximum extension of the Mediterranean forest reached during the Marine Isotope Stage 5 (84 – 71Ka) suffers a severe geographical contraction, to an almost disappearance during the Last Glacial Maximum, despite the existence of expansion episodes during interglacial stages (Tzedakis *et al.*, 2004).

In the Macaronesia, the sea level minima of the glacial episodes supported the emersion of seamounts, and enhanced the possibility of dispersal among islands of the same archipelago, colonization of emerged islands from older islands, or between archipelagos, by stepping-stone processes (Fernández-Palacios *et al.*, 2011). Over the islands, such conditions were very likely responsible for the expansion of cold-tolerant taxa (*Juniperus*, *Erica, Ilex*) and contraction of the laurel forest, setting an elevational range that suffers small adjustements after the last Pleistocene glaciation (Fernández-Palacios *et al.*, 2011).

The general climatic amelioration set after the Last Glacial Maximum, based on temperature rise along with an increasing humidity, generally favored the installation of woods on inner areas in the Iberian Peninsula (van der Knaap & van Leeuwen, 1997), especially during the short-warming periods (Bölling, Allerod). But such trend is interrupted by the definition of short and severily cold periods, such as the Younger Dryas, supporting the expansion of stepic taxa (e.g. *Artemisia,* Chenopodiaceae, *Ephedra*) (Castro *et al.*, 2005). Such oscillation also affects the core of the Macaronesia (Madeiran and Canarian archipelagos), a fact that is registered by the alternation between wet (paleosols colonized by vegetation) and arid (aeolian deposits) conditions. On Eastern Canaries, the higher environmental moisture of the warmer phases interrupted the eolian deposition, allowing plant colonization and soil formation. Towards the end of the last glacial, wet conditions returned and produced the best-developed soil preserved in the sedimentary sequence (Meco, 2008). On Madeira Island such period was marked by a significant increase on moisture conditions, and is described as the maximum moisture period of the sequence, with a significant increase on precipitation (Goodfriend *et al.*, 1996).

2.1.1.2.2 CLIMATIC VARIABILITY ALONG THE HOLOCENE (11.7 KA – 2.5 KA[4])

The early and middle Holocene climatic conditions should have supported an expansion of the Laurel forest, giving continuity to a process of expansion initiated after the minimum reached during the Last Glacial Maximum. On Madeira Island, the presence of rhizolits and fossil records for snail fauna supports the inference of an open woodland or shrubby formation on the currently dryest section of the island, suggesting an amelioration of climatic conditions (Goodfriend *et al.*, 1996).

---

[4] - Period considered in the discussion, not accepted limits for the geological period.

On North Africa, the early Holocene (9 ka) is also associated to a wet climate, when steppe vegetation diminished rapidly, as registered by the decrease on Artemisia. This is the period of the "Green Sahara", when monsoon winds penetrated Africa very far northwards, because of the northward migration of the Inter-Tropical Convergence Zone (ITCZ). Such scenario is supported by an increase on pollen associated to grassy vegetation at Cape Verde latitudes in a scenario of a narrower desert belt (Hooghiemstra *et al.*, 2006; Dupont, 2011).

In the Iberian Peninsula woods achieve great expansion during the mesophytic optimum of the Atlantic period (7.5 – 5 ka). The northern sector of the Iberian Peninsula registers a significant increase on broad-leaved deciduous taxa (*Quercus*, *Fraxinus*, *Acer,* and *Fagus*), while the Mediterranean Iberia is associated to a reinforcement of the evergreen taxa (*Quercus* and *Olea*) (Castro *et al.*, 2005; Carrión *et al.*, 2010). Such pattern suffers small changes because of the climatic degradation associated to the subboreal period (5 – 2.5 Ka), which favors an increase on cold tolerant taxa on forests. In the Macaronesia climate became also slightly drier after 4 500 yr BP. A decrease in the rainfall and an increasing seasonality is registered by the implantation of vegetation with depper root system (Goodfriend *et al.*, 1996).

For the Holocene, another element comes into the equation used to explain changes on vegetation. At the Iberian Peninsula, the disappearance (e.g. *Cedrus, Picea* (Postigo-Mijarra *et al.*, 2009)), contraction (e.g. *Carpinus* (Postigo-Mijarra *et al.*, 2008)), or expansion (*e.g. Ceratonia*, *Castanea* and *Junglans*) of some taxa results from the synergic contribution of climate change and anthropogenic disturbance (Carrión *et al.*, 2010; Postigo-Mijarra *et al.*, 2010). It is widely accepted that current vegetation features at the Iberian Peninsula have a strong fingerprint from human activities, which became significant after the Atlantic period (Castro *et al.*, 2005). Although much more recent in the Macaronesia, human interference is also essential to understand current species geographical range (Goodfriend *et al.*, 1996; De Nascimento *et al.*, 2009; Connor *et al.*, 2012).

2.1.1.3 CLIMATE CHANGE DURING THE HISTORICAL PERIOD (18TH – 19TH CENTURIES)

Uncertainties associated to climatic reconstructions are considerably reduced for the last two millennia (Mann *et al.*, 2008; Wanner *et al.*, 2008). Despite some uncertainty and small differences among climatic reconstruction attempts, derived from different methodological options and selected proxies, it is evident the identification of similar climatic trends (see Quante, 2010). The agreement is based on a wide variety of high resolution proxies, such as ice cores, corals, tree rings, lake sediments, glacier length records and historical documents (Bradley, 1999; NRC, 2006; IPCC, 2007b). Such large-scale reconstructions for the last millennium, focused on surface temperature oscillation, provide a generally consistent identification of variations in the scale of few centuries, such as the oscillation between warm and cold periods. For historical times, such reconstructions clearly identify a small cooling period on Northern Atlantic Ocean, known as Little Ice Age, preceded and followed by relatively warming periods (Mann *et al.*, 2008). The Little Ice Age, centered on the 18th century, is characterized by a climatic degradation that last from the second half of the 13th century to the first half oh the 19th century, boundaries varying according to different authors (see Arques, 2005). Such period is characterized by long and severe winters, registered by the Flemish Renaissance painter Peter Brueghel, and cool and wet summers, a result from an increase in southern flow and blocking of the atmosphere circulation (Woodward, 1987).

The described changes in terms of climatic conditions for Europe, very often based on records related to phenology (Schleip *et al.*, 2008), are also identified for Madeira Island. Based on historical records for phenology, Silva (1993) identifies a warmer period during the 15th and 16th centuries, inferred from a significant advance in terms of cereals and grapes harvesting, and a cold and wetter period in the 17th and 18th centuries.

The period after the Little Ice Age registered a remarkable rise on temperature, a moderate warming that starts in the middle of the 19th century (Oerlemans, 2005; Quante, 2010). Such trend became more pronounced on the last fifty years, performing an unprecedented warmth in the preceding centuries (NRC, 2006; IPCC, 2007b) or even in the context of the last millennia (Mann, 2007).

The possible impacts on vegetation derived from that climatic oscillation should have had lower importance comparing to the deep disturbance associated to human activities, which contributed decisively to reduce significantly the areas occupied by native vegetation (see Cap. II: 1.3).

2.2 RECENT CLIMATE CHANGE – THE 20TH CENTURY

The identification of changes on ecossystems related to climate change is a difficult task for short-time periods and local scales, but can be revealed by systematic analysis across geographic regions, and using data for different types of organisms (Parmesan & Yohe, 2003).

Worlwide observations on different domains are consistent with the fact that trends for mean surface temperature show an increase in the rate of warming in the last decades, comparing to the trend per decade of the last century (IPCC, 2007b). The Fourth Assessment Report of IPCC (2007), presents a significant number of examples, all indicating a similar trend: worldwide glacier reduction, changes on precipitation regimes, snow cover decrease, decrease on the extent and thickness on sea ice, increase on the severity of droughts, even changes on the atmospheric circulation (IPCC, 2007b). According to paleoclimate data, such rise on average surface temperature along the 20th century has no similar in the precedent millennia, being the last decade the warmest of the century (IPCC, *Op. cit.*). In fact, the end of the 20th century presents a significant increase on temperature on all seasons, comparing to the last 120 years (Beniston *et al.*, 2003).

Although the world trend, usually named as *global warming*, such phenomenon is not homogeneous over space and time (Santos & Miranda, 2006; IPCC, 2007b; Engler *et al.*, 2011). In the period 1910-1945 it is mostly detected at the North Atlantic and bordering regions, while between 1976 and 2000 has great incidence on high latitudes at continental areas of the North Hemisphere on winter and spring, with the exception of the western subpolar North Atlantic (Rutishauser *et al.*, 2008). Such warming, specifically on the North Hemisphere, is greatly influenced by the minimum temperature regime over night, which increase is higher than the rate observed for average minimum temperature over day (Beniston *et al.*, 1994; Benito-Garzón, 2002; IPCC, 2007b).

The described trends are also detected within the Macaronesia. Analyses of climatic series identify a warming trend after the seventies, both for Madeira archipelago and Tenerife Island (Canary Islands). For Tenerife Sperling *et al.* (2004) report a decrease in the diurnal temperature range at altitudes below the trade wind inversion for the dry season during the last 30 years, more pronounced on the windward side of the island. According the authors such trend results from an increase on moisture and cloud cover below tradewind inversion. Such decrease in the diurnal temperature supports the warming trend detected on recorded mean temperature, which is more pronounced after the seventies of the last century. Such trends are not verified above the trade wind inversion (high altitudes), where the range in diurnal temperature increased during the last twenty years of the last century, and no significant trend on relative humidity has been identified. The authors oly point out the existence of partial evidence for a drying trend accross the trade wind inversion, linked to a potential increase on subsidence.

In the case of Madeira Island, and based on data for Funchal, Miranda *et al.* (2006) recognize a clear warming trend after 1975. Such trend is supported on the decrease of daily temperature range, associated to an higher rise of the minimum temperature, and an increase on the number of summer days (max. temperature > 25ºC) and tropical nights during summer (min. temperature > 20ºC). In terms of precipition, the authors only highlight the significant increase in the number of summers without precipitation, and they don't recognize a clear trend.

2.2.1 IMPACTS FROM RECENT CLIMATE CHANGE

Several studies have been conducted to assess the impacts of recent climate changes on terrestrial ecosystems. Among those studies, namely those focused on the response of vegetation, it is accepted a relationship between global warming and changes on natural biological systems (Parmesan & Yohe, 2003; Parmesan, 2006; Harper *et al.*, 2011). Such changes, accepted as derived impacts, are affecting physiology, phenology and the distribution of species (Hughes, 2000; Quante, 2010), and can be detected on different types of environments (Walther *et al.*, 2002; IPCC, 2007b) and organisms (Parmesan *et al.*, 1999; Root *et al.*, 2003; Maggini *et al.*, 2011).

Mountain areas and Arctic regions, classified as highly sensitive to environmental changes (Beniston & Haeberli, 2001; ACIA, 2004; Rammig *et al.*, 2010), have been receiving great attention on this subject. On that areas, changes on climate have been widely reported, and are mostly related to a recent decrease on mean snow depth and length of continuous snow cover, favored by early snow melting, and a decrease in the number of snowfall days associated to shorter winter periods (Laternser & Schneebeli, 2003; ACIA, 2004; Richter-Menge *et al.*, 2007). More significative on high latitudes (>50ºN), such changes are interpreted as the cause for detected shifts on species distribution, changes on phenology, growth and plant height (Keller *et al.*, 2000; Tape *et al.*, 2006). On Artic areas, such changes are identified as responsible for a green-up process that can be detected from satellite data (Myneni *et al.*, 1997), a trend that is associated to i) a lengthening of the active growing season (EEA, 2008), ii) an increase on size, abundance or even on the area occupied by shrubs (Stow *et al.*, 2004; Tape *et al.*, 2006), iii) and an expansion of the tree line (Kullman, 2001; Lloyd & Fastie, 2003; Lloyd, 2005), interpreted as a consequence of changes on vegetation and plant life-forms boundaries related to northward shifts (see Richter-Menge *et al.*, 2007). Such association is also described for high mountains, where shifts are detected (Keller *et al.*, 2000; Felde *et al.*, 2012), namely upward (Grabherr *et al.*, 1994; Pauli *et al.*, 1996; Gottfried *et al.*, 2012). Such shifts are gradually changing the floristic composition of mountain plant communities, mainly because of a decline of cold-adapted species, and an increase on species adapted to more warm climatic conditions (Walther *et al.*, 2005). Such process, called thermophilization of plant communities, is detected at regional (e.g. Peñuelas & Boada, 2003) and continental scales (Gottfried *et al.*, 2012). In fact, upward and northward range shifts are common on different regions of the world, and with rates higher than previously expected (Chen *et al.*, 2011).

At middle latitudes and low altitudes, studies identify significant and consistent long-term phenological changes associated to temperature rise (Menzel *et al.*, 2006), namely early onset of spring events and advance on harvest dates (EEA, 2008; Schleip *et al.*, 2008).

However, the idea that climate change is the cause for described changes it is not accepted by all the sicentific community, and a deep discussion remains active. One of the main reasons is related to the fact that climate change impacts on ecosystems on current days is less pronounced than those imprinted by human activities, such as those associated to habitat fragmentation (Walther, 2004). Moreover, past and present land-use is very likely introducing noise on the search for significant association between climate changes and changes on some ecosystems (Gehrig-Fasel *et al.*, 2007). Especially on temperate climates, modern landscapes must be understood as the result of influence by natural and human pressure driving forces, an important key to interpret current vegetation features (Kullman, 2001).

2.3 CLIMATIC PROJECTIONS FOR THE 21ST CENTURY

The comparison between future climate change projections and current observations after 1990 (IPCC, 2007b) makes clear that results from climate change impacts assessment based on projections must be interpreted with caution. Despite the fact that paleoecological reconstructions for the Mio-Pliocene period had identified similar patterns in terms of climatic gradients for some European territories (Kullman, 2001; Jimenez-Moreno *et al.*, 2007; Jiménez-Moreno & Suc, 2007), that doesn’t guarantee that climatic patterns won’t change in the future.

Climatic projections, driven by socio-economic scenarios, are associated to great uncertainty. Not only because of the wide range of projected changes on climatic elements by models and scenarios (IPCC, 2007), but also because of the fact that some climatic elements are sensitive to abrupt changes when a set of thresholds are crossed over, and relationships with other elements are unpredictable (Quante, 2010). Nevertheless, such projections perform an excellent opportunity to improve our knowledge about the determinants for species distributions, and can contribute to guide decisions for conservation and planning, or support the definition of mitigation and adaptation measures (Pereira *et al.*, 2010).

Projected climatic scenarios prepared by IPCC for the period 2090-2099, and comparing to the period 1980-1999, predict a warming trend that is estimated to range between 1.8ºC (admitted uncertainty - 1.1ºC to 2.9ºC) in the scenario B1, to +4.0°C in the scenario A1FI (admitted uncertainty - 2.4°C to 6.4°C) (IPCC, 2007b)[5]. Based on such values, the climatic scenarios A2 and B2, those used for reference in this work, can be considered as intermediate, once they project more moderate changes (A2: 3.4ºC; B2: 2.4ºC). According the Fourth Assessment Report of IPCC (IPCC, *op. cit.*), the warming trend is based on different factors. Aside from an expected increase in the frequency, intensity and length of heat waves, in opposition to a decrease in the cold episodes, it is also predicted a decrease in diurnal temperature range. That will very likely produce a decrease in the number of frosty days, what might produce a significant increase in growing season length in middle and high latitudes. This is one of the reasons that explain why it is expected that warming will be more pronounced at higher latitudes/altitudes, which is consistent to observed trends (IPCC, *op. cit.*). For precipitation predictions are more uncertain (McCarty, 2001), but point to significant decrease for mean annual values in the subtropics and lower middle latitudes, and an increase at high latitudes. The areas with a predicted decrease on annual precipitation might also experience an increase on the intensity and number of extreme events (IPCC, *op. cit.*). In fact, it is expected that shifts in the intensity and frequency of extreme weather events might produce very significant impacts, which could get more expression than those associated to changes on the climate long-term mean state (Beniston & Stephenson, 2004).

2.3.1 PREDICTED IMPACTS FOR FUTURE CLIMATIC PROJECTIONS

Predicted rise in temperature will very likely produce significant impacts, especially at high latitudes and high mountains' habitats (Engler *et al.*, 2011), namely because of a progressive decline of cold mountain habitats associated to a predicted decrease in the depth and duration of snow cover (Beniston *et al.*, 2003; Keller *et al.*, 2005; Anisimov *et al.*, 2007). As temperature-limited environments, it is expected that

---

[5] Values for all the scenarios: B1: +1.8°C (1.1°C to 2.9°C); B2: +2.4°C (1.4°C to 3.8°C); A1B: +2.8°C (1.7°C to 4.4°C); A1T: 2.4°C (1.4°C to 3.8°C); A2: +3.4°C (2.0°C to 5.4°C); A1FI: +4.0°C (2.4°C to 6.4°C) (IPCC, 2007).

small changes on temperature will produce significant changes on the habitats (ACIA, 2004).

In response to such predictions, it is expected that plants might adapt, adjusting their life cycles, or shifting their geographical ranges in order to find suitable places (Parmesan & Yohe, 2003; Walther, 2004). But species may not be able to adapt (Keller *et al.*, 2005), namely in case of fast changes. In fact, known episodes of extinction were frequently associated to climate change, under scenarios of warming or cooling, especially when such events were rapid, causing deeper impacts on ecosystems (van der Knaap & van Leeuwen, 1995; Valladares, 2006). Therefore, because of the different capacity to adapt or change their range, it is expected that changes on communities' composition will occur (Thuiller *et al.*, 2006; Pucko *et al.*, 2011).

In terms of changes on distribution, results obtained for Europe by Thuiller *et al.* (2006), based on a species distribution modelling approach, predict a northward shift for deciduous communities, and a large range reduction for broadleaved deciduous and coniferous species, in opposition to a predicted range expansion in Mediterranean trees, which will replace temperate deciduous broadleaved species in the southern part of temperate Europe. In fact, the greatest changes are expected in the transition between the Mediterranean and Euro-Siberian regions (Thuiller *et al.*, 2005) in the southwest Europe (Bakkenes *et al.*, 2002). Such results are also supported by the study carried out by Cheaib *et al.* (2012), based on significant diversity of modelling methods. However, such predictions are not in line with results obtained by González (2005), based on climatic projections calibrated from recent trends, and not based on IPCC emission scenarios. Results predict an expansion of broaleaved deciduous trees to areas currently associated to Mediterranean forests in Castilla-León, a projection based on the predicted increase on summer precipitation. However, observed changes doesn´t support the last projections (Peñuelas & Boada, 2003), but give consistency to the predicted increase on climatic aridity (Castro *et al.*, 2004), and support the results obtained by Cheaib *et al.* (2012) and Thuiller *et al.* (2006). On Mediterranean territories, predictons must also have in consideration land-use changes, which might become more determining than climate change (Sala *et al.*, 2000).

On the high mountains, predicted changes on distribution reveal an upward trend in the tree line (Leonelli *et al.*, 2011), a prediction that could be partially supported on the noisy interference of land use on current vegetation features (Gehrig-Fasel et al., 2007), or favored by simplistic approaches associated to models that aim to predict the impact of climate change on tree line, which should incorporate other types of data, namely information about physiology and reproductive biology (Grace *et al.*, 2002).

But other changes associated to climate change impacts might occur, and very likely more easy to detect, such as an increase on vulnerability to pathogens (Desprez-Loustau *et al.*, 2007), changes on forest productivity (Loustau *et al.*, 2005), changes on plant growth (Rammig *et al.*, 2010), or increased rates of mortality, causing important changes on communities' structure and composition (Ruiz-Benito *et al.*, 2013). In the limit, species might get extinct, and predictions support that such threat may be significant for European plants even in moderate scenarios of climate change (Thuiller *et al.*, 2005).

2.3.1.1 THE CASE OF SMALL ISLANDS

Small islands are identified as territories highly vulnerable to climate change, and with low adaptative capacity, especially in the case of low-lying islands that face the threat of sea level rise. Aside from the expected impacts on islands' resources and habitats, sea level rise will affect deeply the economy of such territories, a problem associated to the fact that settlements and infrastuctures are mainly located in coastal areas (Mimura *et al.*, 2007).

But the assessment of impacts from climate change is surrounded by great uncertainty on such small territories. Aside from the general uncertainty associated to the rate and magnitude of change (Walther, 2004), forecasts on small islands face the challenge of including non-climatic factors on regional circulation models. Although they can be ignored when calibrating global circulatuion models (GCM), they should be considered on such scales, such as topographic conditions, once they have a proeminant role on setting spatial precipitation patterns. Despite the higher resolution, regional circulation models, obtained by processes of regionalization from GCMs, integrate the uncertainties of the source models, and sum others resulting from the process of regionalization itself (Santos & Miranda, 2006).

2.3.1.2 PREDICTED CHANGES AND IMPACTS IN THE MACARONESIA

For the eastern subtropical North Atlantic, an area that includes the Macaronesian archipelagos, projections predict a rise in temperature and general decrease in precipitation, despite seasonal increases (Miranda *et al.*, 2006; Mimura *et al.*, 2007). On these archipelagos, especially those with cloud forests, climate change, combined with past-land use changes and biological invasions, might have deep impacts (Mimura *et al.*, *op. cit.*), creating even conditions prone to extinction of endemic species, as predicted for other oceanic islands (Benning *et al.*, 2002).

The insular condition will very likely support less pronounced climatic changes, comparing to continental areas (IPCC, 2007a). However, small changes on climate and the synergic contribution of the enounced factors may assure high vulnerability and produce significant changes in terms of plant demography and distribution.

The location on the Northern poleward edge of the Hadley circulation might perform a factor that can imply higher vulnerability to climatic changes, namely because of potential readjustements on atmospheric circulation patterns (Sperling *et al.*, 2004). Changes (readjuastements) in the location of the Azores High could interphere in the frequency and intensity of the trade winds, supporting changes in the cloud belt formation. The accepted dependence of the laurel forest from the persistence of cloud cover during summer (see chapter II) makes this type of vegetation especially vulnerable, because of potential changes on the frequency and altitude of the cloud belt. That kind of change was already suggested by studies focused on tropical montane cloud forests (TMCFs) ((Pounds *et al.*, 1999), the tropical counterpart of the subtropical cloud forests (Sperling *et al.*, 2004). There, an upward shift of the cloud base during the dry season is predicted (Still *et al.*, 1999), a shift that might have significant impacts on the demography, and even in the distribution of organisms (Pounds *et al.*, 1999). An opposite trend is forecasted for the Canaries, where a downward shift is projected for the cloud base during the dry season based on a warming trend and an increase in relative humidity, a trend already detected in the last few decades (Sperling *et al.*, 2004). Such projection, in parallel with a drying trend at the upper limit of the cloudbanks (trade winde inversion), suggests a downward shift of the area climatically suitable for the laurel forests (Sperling *et al.*, *op. cit.*). Such results are not supported by predictions for Madeira Island. Without using data about possible changes in length and spatial patterns for the permanence of cloudbanks, and based on the scenarios A2 and B2 (Miranda *et al.*, 2006), Santos & Aguiar (2006) predict a decrease on the area potentially occupied by the heath tree community, in parallel with an upward shift of the temperate laurel forest, which will undergo a contraction at the rear edge.

2.3.2 HOW CLIMATE CHANGE WILL AFFECT ALIEN INVASIVE SPECIES?

Climate change effects and invasion by alien species were identified as two of the major sources of threat to the extant native forests of the Macaroensia (Guimarães & Olmeda, 2008).

In parallel to a wide concern about response of native species to climate change (Bakkenes *et al.*, 2002; Thomas *et al.*, 2004; Botkin *et al.*, 2007), there is a growing interest on forecasting the response of alien invasive species, especially because of their impacts on different domains (Levine *et al.*, 2003; Hellmann *et al.*, 2008; Vilà *et al.*, 2010). Considered an important component of the global environmental change (Mack *et al.*, 2000; MEA, 2005), it is expected that invasion by nonindigenous plants should be favoured by changes on other domains, what might intensify impacts on ecosystems (Dukes & Mooney, 1999). In fact, invasion might act synergistically with other components (Theoharides & Dukes, 2007), namely with climate change (Dukes & Mooney, 1999), strengthening their effects (Hellmann *et al.*, 2008).

Climate change may have complex effects on alien invasive species, very likely favouring them, as suggested by different authors (Dukes & Mooney, 1999; Thuiller *et al.*, 2007; Vilà *et al.*, 2007; Hellmann *et al.*, 2008). It is expected that climate change may increase the potential of invasion of existing invasive species due to reduced climatic and biotic constraints, which should expand areas at risk of invasion (Kriticos *et al.*, 2003). The decrease of the climatic control is mainly associated to the projected increase of minimum temperatures (IPCC, 2007b), and reduced biotic constraints might be determined by a decrease in the capacity to compete by native species. It may also create suitable conditions for new species to became invasive, or diminish impacts on certain areas for species currently considered invasive, changing the effectiveness of control strategies (Hellmann *et al.*, 2008).

The concern about alien plants on islands is related to their higher susceptibility to invasion (Henderson *et al.*, 2006), and current high proportion of non-native species (Vitousek *et al.*, 1996; Sax & Brown, 2000; Lambdon *et al.*, 2008; Sax & Gaines, 2008), a trait detected in the Macaronesian archipelagos (Jardim & Sequeira, 2008).

CAP II – MADEIRA ISLAND IN THE CONTEXT OF THE MACARONESIA

Summary

1 STUDY AREA AND ITS CONTEXT

> “*On a small island, the race for life will have been less severe, and there will have been less modification and less extermination. Hence, perhaps it comes that the flora of Madeira, according to Oswald Heer, resembles the extinct tertiary flora of Europe*.”
>
> (Darwin, 1859, On the Origin of Species, pag. 83)

The archipelago of Madeira is located in the North Atlantic Ocean, between the latitudes 32°24’ and 33° 07’ N and longitudes 16° 16’ and 17° 16’ W. Madeira Island, the largest island (737 km^2) represents approximately 93% of the archipelago’s area. It is a mountainous island of volcanic origin that is associated to an oceanic hotspot (Carvalho & Brandão, 1991), which emerged part dates back to Post-Miocene times (< 5.6 My) (Ribeiro *et al.*, 2005). The island of Porto Santo, also inhabited, is the second biggest (43km^2). In addition to small islets, the archipelago also includes a group of three small islands, known as Desertas Islands (Ilhéu Chão, Deserta Grande, and Bugio).

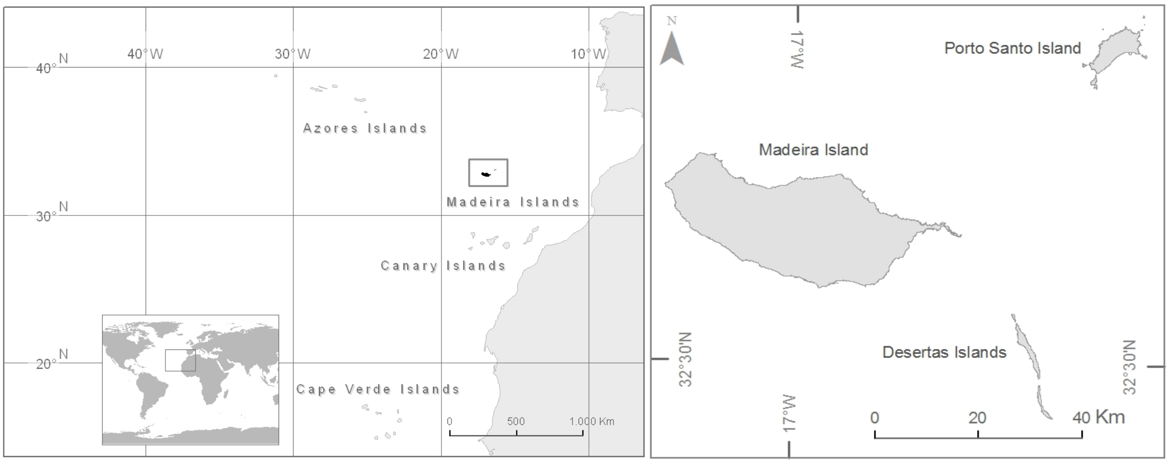


Figure 1 - Geographical position of Madeira Island in the Macaronesia (left) and in the archipelago (right).

The distance between the archipelago and mainland is approximately 900 km to Europe (Ponta de Sagres – Portugal) and about 600 Km to the north-western African coast.

1.1 CLIMATIC CONDITIONS

The subtropical location and the orographic features are relevant determiners for the climatic regime of Madeira Island, which result from contributions associated with factors from different scales.

At the synoptic scale, the location at the subtropical margin on the eastern North Atlantic determines the climatic regime, a fact associated to the specific features of the oceanic and atmospheric circulation. The eastern corner of the subtropical Atlantic is a domain deeply marked by subsidence, a trait derived from the influence of the Hadley and Ferrel cells downward branches', which are in the genesis of the Azores High. The intensity and position of this subtropical high-pressure cell is highly variable among the archipelagos, sustaining the definition of contrasting climatic conditions within the Macaronesia. The Azores archipelago is under the influence of the zonal flow during a significant part of the year, even during summer, when the occasional definition of planetary valleys are responsible for interrupting the influence of the Azores High, a fact that explains the weaker influence of such pressure system in the climate of the archipelago (Ferreira, 1989). In contrast, its influence is critical to the climatic pattern of the Madeiran and Canarian archipelagos, where it is dominant during late spring, summer and early autumn. The Cape Verde archipelago presents a very distinct climatic pattern. The seasonal pattern is clearly determined by an alternation between dry and wet season, an attribute of the tropical domain. In the archipelago the low values of annual rainfall are characteristic of a dry tropical climate.

Madeira Island is positioned under the oscillating influence of the Azores High and the southern belt of the zonal flow of mid-latitudes. The high persistence and related dynamics of the anticyclone cell are key factors on determining the seasonal climatic pattern of the island, once it is an important driving force on controlling the atmospheric and oceanic circulation at these latitudes (Ferreira, 2005). Because of its influence, climate presents a clear mediterranean pattern, with hot, dry summers and wet, warm winters.

From March to October, the reinforcement and northward shift of the high-pressure cells, along with a progressive weakening on the amplitude of the planetary waves and a tendency to set a zonal flow, establishes the influence of the trade winds. During this period Madeira Island is positioned under the meridional border (flank) of the subtropical broad-belt, a position that grants the definition of a dry period.

Because of the seasonal alternation between the polar (winter) and equatorial pulsar (summer), autumn and spring are characterized by significant vertical contrasts in the atmosphere. During such periods the influence of the Azores High is increasingly interrupted by cut-off low circulation systems, which are responsible for heavy rain episodes (Maciel, 2005) a climatic feature common to Azores and Canaries (López-Gómez & López-Gómez, 1979; Ferreira, 1989).

The shelter provided by the Azores high pressure cell places Madeira Island outside the direct influence of cold air ejections on winter, which episodic occurrence is responsible by few days of temperatures lower than 15ºC on areas below 500m m.s.l. and frost events above 1400m. Despite their low frequency (20 days at Bica da Cana (1560m) and 11 days at Pico do Arieiro (1810m)), such events are critical to species distribution, namely for the low cold-tolerant lauraceae species. Because of the lower influence of the Azores High during winter, weather is also influenced by depressions with southward trajectories associated to meridional circulation events, and others of tropical origin, usually with a south-western trajectory, which are responsible for rainy days (Ferreira, 1989).

The previous scale is critical to the climatic regime, the annual pattern; but the analysis of the climatic mosaic of the island must downscale from general atmospheric circulation patterns, and explore spatial patterns at the topographic scale, once altitude and mountains' orientation are determinant for the local climates. The island is characterized by a significant altitudinal range between the highest peaks (Pico Ruivo: 1861m, Pico do Arieiro: 1812m, Bica da Cana: 1560m), disposed with a E-W direction along the centre of the island, and the shoreline Figure 2.

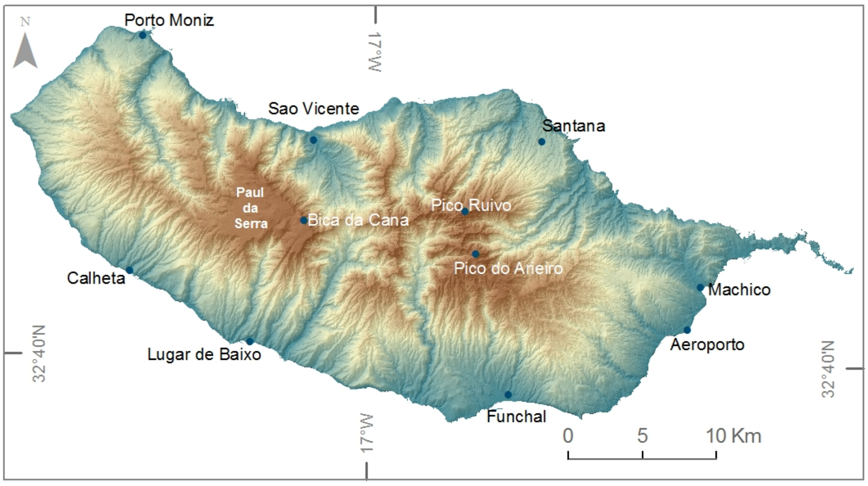


Figure 2 - Topography of Madeira Island

Such configuration promotes clear climatic asymmetries between windward-leeward faces and lowlands-high altitudes; features detected in temperature and precipitation spatial patterns, and subsequently on vegetation (Capelo *et al.*, 2004; Mesquita *et al.*, 2004; Capelo *et al.*, 2007). The E-W mountains' orientation, perpendicular to prevailing trade winds, and the relative position of the island in relation to North Atlantic weather systems are the main causes for the enounced asymmetries (Ferreira, 1989). The combination of such asymmetries and the topographic complexity plays a determinant role in the creation of a complex mosaic of topoclimates. In fact, the highest diversity of topoclimatic conditions in the Macaronesia is found on islands with E-W oriented mountain ranges (Ferreira, 1989).

1.1.1 TEMPERATURE

The marked temperature gradient is a key factor on determining significant differences in terms of ecological conditions for short distances, contributing to set an altitudinal pattern in terms of species distribution (e.g. *Echium* species). Such distribution pattern, supported on the energy and mountains' barrier-shape (local factors), and combined to higher increasing rates in the temperature altitudinal gradient (Demangeot, 2000)[1], supports the definition of vegetation zones of narrow altitudinal range, a feature

---

[1] - Temperature altitudinal gradient has higher rates (temperature goes down faster with increasing altitude) under humid conditions on tropical and subtropical areas.

clearly put in evidence by the natural potential vegetation model proposed for Madeira Island (Capelo *et al.*, 2004).

Despite the low range of annual temperature on significant areas of the island, there is a remarkable spatial variation on temperature. Small areas on coastal areas of the southern face present an annual mean temperature higher than 18ºC (e.g. Aeroporto: 18,8ºC, Funchal (Louros): 18,1ºC, Lugar de Baixo (Ponta do Sol): 19,4ºC). On such areas, tropical nights (minimum temperature > 20ºC) are very common on summer (Santos & Miranda, 2006). On the opposite, on areas above 1400m the annual mean temperature is lower than 10ºC (e.g. Arieiro: 9.1ºC, Bica da Cana: 9.3ºC), indicating the existence of significant periods with low temperatures during winter.

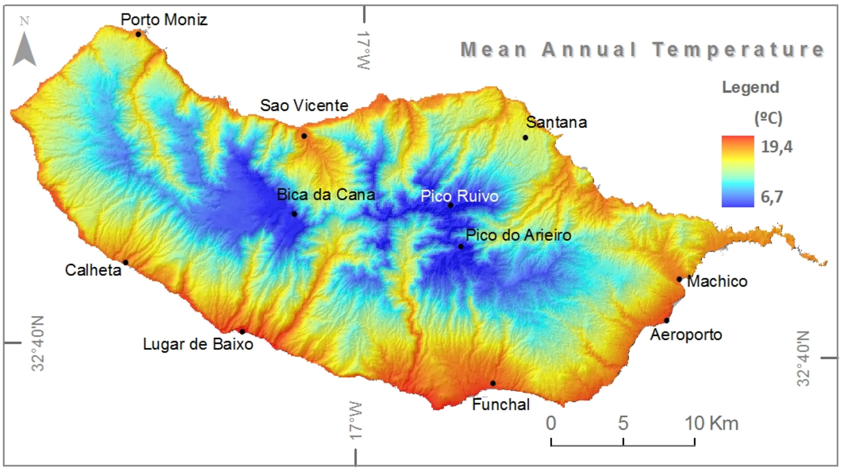


Figure 3 - Spatial variation for mean annual temperature on the island

(Climatic series 1961-1990 - data source: Instituto de Meteorologia, 2010)

The occurrence of frost over night in winter is common, a fact confirmed by the pipcrake formation during nights under anticyclonic conditions after cold air invasion events. The frequency of such events might be the ecological factor that impedes the potential presence of the laurel forest at altitudes higher than 1400 m.

The described scenario for winter at higher altitudes is deeply antagonic if compared to lowlands of the southern face. While higher altitudes (> 1500m) present an average temperature around 5/6ºC (Arieiro, Bica da Cana)[2], lowlands of the southern face (< 200m) register an average winter temperature around 16-17ºC (e.g. Funchal).

Summer is especially hot and dry on the southern face, while on the northern face temperature is usually lower because of cloud belt formation of orographic origin. As a

---

[2] Instituto de Meteorologia – climatic series 1961/1990.

result, the number of days/year with maximum temperature above 25ºC is significantly higher at lowlands of the southern face, especially on the western sector, and is reduced at higher altitudes and on the northern face (Santos & Miranda, 2006).

1.1.2 PRECIPITATION

As expected for a dominant mediterranean climatic pattern, precipitation values are the lowest during summer, especially at coastal areas of the southern face. On such areas the period with climatic water-deficit goes from April to September, which performs a large dry period. Such conditions perform an important source of stress for plants, a feature clearly indicated by the presence of specific physiognomic and physiologic adaptations, such as succulence, leaf reduction, and leaf fall (e.g. *Euphorbia piscatorial*).

Over the island, the higher values of precipitation are registered at the higher summits of the island, above 1400m m.s.l., while the lower values are registered at the lowlands of the southern face (e.g. Lugar de Baixo: 622 mm).

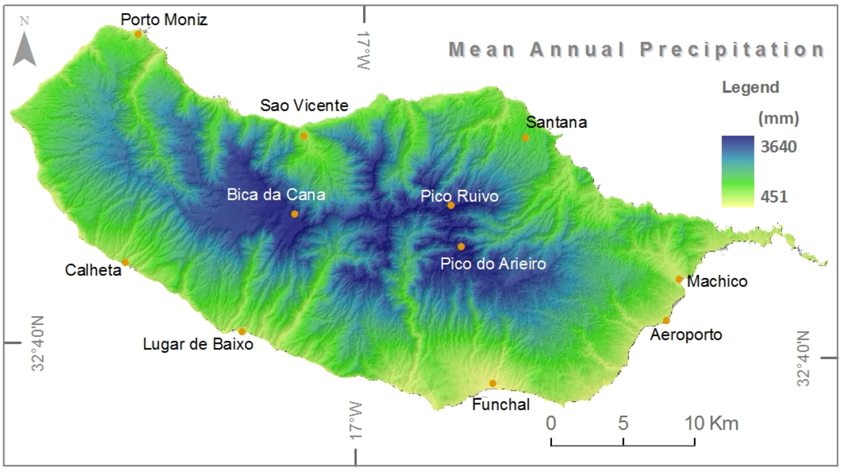


Figure 4 - Spatial variation of mean annual precipitation on the island

(Climatic series 1961-1990 - data source: Instituto de Meteorologia, 2010)

There is a general increase on precipitation with altitude, a trend that is not homogeneous for the entire gradient (Capelo *et al.*, 2007), once there is a slight decrease above 1600m m.s.l. (Bica da Cana: 2966,5 mm (1560m), Arieiro: 2939mm (1810m)).

The asymmetry described for temperature is also identified on precipitation spatial patterns, although inverse. Rainfall is considerably lower at the same altitude in the southern face of the island if compared to the northern face, a feature clearly identified in terms of amount and number of days with precipitation (Santos & Miranda, 2006).

1.1.3 HORIZONTAL PRECIPITATION

One of the climatic variables that highly contribute to the described dichotomy is the number of days with orographic cloud belt formation, which is significantly higher on the northern face of the island. The perpendicular orientation of the island’s mountain range performs a topographical barrier to the lower and humid layer of the trade winds. As result, the adiabatic cooling orographically induced supports the daily definition of a cloud belt on the windward face.

On Madeira Island cloud cover occurs between 600/800m and 1600m m.s.l. on the northward face (Prada *et al.*, 2009). The cloud belt is persistent during summer, when the influence of the Azores High determines higher stability of the temperature inversion, a result from the aerological shelter conditions set on Madeira and Canaries between June and September (Ferreira, 1989). During this period the upper limit of the cloud banks is lower (1300/1400m m.s.l.), controlled by the thermodynamic stability associated to a stronger tradewind inversion. Thickness increases in autumn and winter, associated to an upward shift of the upper limit, showing similar traits (pattern and altitudinal range) to the condition described for Canaries (Sperling *et al.*, 2004). Trade wind influence is reduced in winter, when weather at islands (Madeira e Canarias) is frequently under the influence of northern circulations (López-Gómez & López-Gómez, 1979), a scenario of meridional flow promoted by deep waves sponsored by cold air invasions (Ferreira, 1989).

The persistence of the cloud belt is considered of high importance in terms of ecological conditions, once it creates a semi-humid ambient under a mediterranean dry and hot summer (during the dry season) in Madeira, when it is of frequent occurrence (Prada *et al.*, 2009). That importance could be even higher at the western Canaries (Luis *et al.*, 2005; Ritter *et al.*, 2008; Ritter *et al.*, 2009) under a semi-arid climate (López-Gómez & López-Gómez, 1979).

The dripping-water process associated to the persistent cloud belt, resultant from the coalescence of fog water droplets on vegetation, could work as an important supplementary water source (Prada *et al.*, 2009). Its ecological importance can be very high during summer, a dry season that represent a significant source of stress for vegetation. It is very likely playing a significant role on controlling species and vegetation distribution patterns, namely the altitudinal range of the laurel forest (Sperling *et al.*, 2004), considered a vegetation type with higher demand of water (Ritter *et al.*, 2009). For some areas, low rainfall during summer could be compensated by fog precipitation (Ritter *et al.*, 2009), once the input of water from occult rain can actually double the values recorded for precipitation (Prada *et al.*, 2009). In the Macaronesia, and based on results of fog precipitation collection for Madeira Island (Prada *et al.*, 2009; Prada *et al.*, 2012) and La Gomera (Canary Islands) (Ritter *et al.*, 2007; Ritter *et al.*, 2008; Ritter *et al.*, 2009), the higher values of horizontal precipitation occur mainly on windward areas exposed to the predominant tradewinds at the upper limit of the cloud belt. Several factors contribute to such situation, namely the altitudinal position, structural and morphological aspects of the dominant vegetation, namely the dominance of needle-leaf type species (*Erica arborea*, *Erica maderincola*), wind velocity, direction, and wind turbulence (Prada *et al.*, 2009; Ritter *et al.*, 2009).

On Madeira Island one fact might support the idea of a close relationship between the temperate laurel forest and the occurrence of occult precipitation. This fact is the spatial coincidence in terms of altitudinal range and the definition of a narrow transition and clear floristic differentiation between mediterranean and temperate laurel forest on Madeira Island, a distinction proposed by the natural potential vegetation model (Capelo *et al.*, 2004). And the relationship is not based on the amount of water that drip to the forest floor, once the higher amount of water supplied to the soil is registered at upper areas under the climax heath tree microforest, where the amount of water is a considerable hydrological input for the island (Prada *et al.*, 2009). Nevertheless, and despite the amount of water involved, the cloud belt formation is of great importance for the temperate laurel forest during the dry season. The relative contribution to total soil water may be limited (Ritter *et al.*, 2008), becoming more important to sustain epiphytic communities than vascular plants (Ritter *et al.*, 2009). But even when insignificant amount of water reaches soil, vegetation also benefits from foggy conditions. The immersion on fog, inside a wet and shaded environment, determines a significant decrease on tree transpiration, comparing to summer fog-free days, when higher temperatures support higher values of stand transpiration (Jiménez *et al.*, 1996). The decrease on transpiration is a consequence of the environmental conditions set during cloud immersion, namely a remarkable decrease on mean global radiation and mean ambient temperature. As result, tree sap flow almost ceases during a summer foggy day. Such relationship was demonstrated by different experiments, carried out for needle-like leaf (*Erica arborea* (Ritter *et al.*, 2009), *Pinus canariensis (Luis et al., 2005)*, and broad-leaf trees (*Myrica faya* (Ritter *et al.*, 2009), *Laurus azorica* (*novocanariensis*) (Jiménez *et al.*, 1996); *Persea indica* (González-Rodríguez *et al.*, 2002). For *Erica arborea* and *Myrica faia*, *Ritter et al. (2009)* obtained a reduction on median diurnal tree transpiration of approximately 30 times, almost aproximating the nighttime rates. Such contribution is so relevant that it can encumber the definition of seasonal trends in terms of canopy transpiration for some areas, once summer drought is often mitigated by the higher frequency of orographic cloud formation and associated water-input (Luis *et al.*, 2005).

Although the tolerance of most laurel species to short-duration drought periods (González-Rodríguez *et al.*, 2001, 2002), they have poor stomatal control, so fog immersion may be crucial on reducing the loss of water by transpiration and the profligate use of water under a hot and dry summer (Ritter *et al.*, 2009).

All the arguments support the idea that laurel cloud forests highly benefits from fog, mainly because of the reducing on tree evapotranspiration (Ritter *et al.*, 2008). Being highly shade-tolerant (Morales *et al.*, 1996), laurel species benefit from moist and cool conditions associated to foggy days, reducing the water loss and promoting a significant decrease on the use of soil water resources (López-Gómez & López-Gómez, 1979).

Even[3] considering low water-inputs derived from dripping-water under foggy conditions, it contributes to an effective decrease on water deficit in the soil. For Madeira Island, and considering low storage capacity values for soil moisture (100 mm) (for storage capacity standard values see Fernández-García, 1995), the lower values of deficit are coincident with the temperate laurel forest. In fact, despite the higher values of rainfall registered at the summits, the lowest values for water deficit is obtained for Queimadas, placed within the zone accepted for the potential distribution of the temperate laurissilva.

---

[3] - Out of work after 1982 – Instituto de Meteorologia.

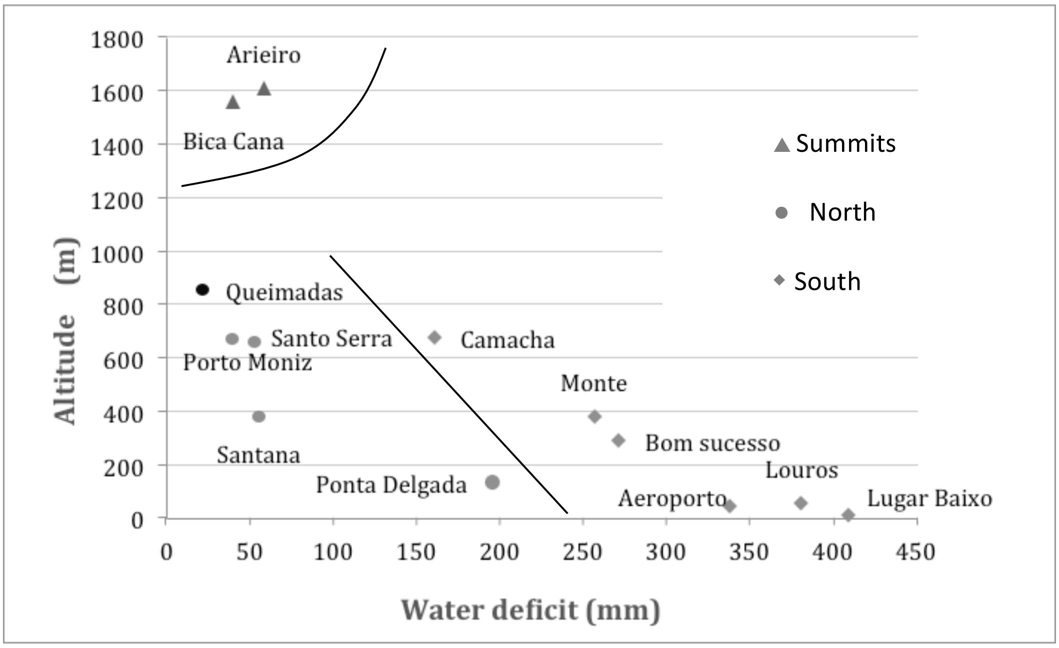


Figure 5 - Water deficit for different sites in Madeira Island

Nota:Results based on values of precipitation and temperature for the 1951-1980 climatic series (Instituto de Meteorologia, 1986) and considering a soil moisture storage capacity of 100mm after the methodological approach of Thornthwaite.

The permanence of the laurel forest under current climatic conditions in the Macaronesia, namely the temperate type, is certainly guaranteed by the indirect effects from the high persistence of the cloud belt during summer, once is very likely associated in the past with a non-seasonal climate with small temperate oscillations and high moisture along the year.

Additionally, the persistence of high transpiration values during winter, indicating mild climatic conditions, and small changes on sap flow along the year, suggesting the existence of water supply even during summer (Jiménez *et al.*, 1996) perform suitable conditions for the permanence of such type of forest under altitudes above which frost occurs.

Although efforts to evaluate water input into island's ecosystems from horizontal rain (Prada & Silva, 1998, 2001; Prada *et al.*, 2009), available data is not yet sufficient to validate a model for all the island, once an extensive monitoring process must be carried out (Cermak *et al.*, 2004), because of a large spatial heterogeneity within different vegetation types, the high topographic complexity of the island, and the inclusion of stemflow in order to guarantee greater accuracy. So, although the undeniable contribution to understand vegetation spatial patterns, namely for the temperate laurel forest, such variable is not included in the group of environmental predictors used on models calibration. The absence of such environmental predictor might perform an additional source of uncertainty on assessing changes on species distributions under future climatic scenarios, namely for species which distribution could be related to such environmental predictor.

1.2 FLORA AND VEGETATION

1.2.1 THE CONTEXT OF MACARONESIA

Different approaches have been proposed to explain the biogeographic attributes of the archipelagos located at the south-eastern sector of the North Atlantic Ocean (Azores, Madeira, Selvagens, Canary Islands and Cape Verde), based on diverse assumptions, proposing different circumscriptions and nomenclatures. The different proposals of circumscription are closely related to the hypotheses used to explain the peculiarities of the flora and vegetation of the islands, namely the origin and relationships of the endemic element.

The discussion about the circumscription for the Macaronesia region ranges from the acceptance of an unit restricted to a "core", which archipelagos present a high level of similarity (Madeira and Canaries), to a larger concept that includes all the archipelagos, or even a larger one that includes enclaves on mainland territories on the west Atlantic coast of the Iberian Peninsula and north-western fringes of Africa.

1.2.1.1 THE ENDEMIC ELEMENT IN THE MACARONESIAN FLORA: ORIGIN AND ASSUMPTIONS

The concept of Macaronesia[4] is introduced in the biogeographic nomenclature to distinguish a territorial unit with specific features in terms of flora and vegetation. One of the attributes that support such distinction is the high proportion of endemics (Médail &

---

[4] - From the Greek *makarios* (meaning fortunate, happy) and *nessos* (meaning islands). The notion of a group of islands with remarkable features close to the African coast comes from Pliny the Elder (Ist century), who did mention to the "fortunate islands", alluding to Juba II, King of Numidia, who makes reference to a group of islands on the left of Mauritania, the current Canary Islands - Pliny, T.E., Rackham, H. (1938). *Natural history / with an English translation by H. Rackham*. W. Heinemann, London. http://citebank.org/uid.php?id=83091.. The term Macaronesia avoids the quick link between the term "fortunate islands" (latin: *fortunatas*) and the current Canaries, recovering the ancient Greek designation, frequent in the classical literature, used to name magnificent islands where gods rest.

Quézel, 1999b; Francisco-Ortega *et al.*, 2000; Jardim & Sequeira, 2008a), among which a high fraction of woody forms (Bramwell, 1972).

Two different assumptions have been used to explain the origin of the endemic element. The *refugium* perspective of Engler faces the endemic taxa as relicts of a former widely distributed subtropical Tertiary flora. Such approach assumes that most part of the distinctive endemic element of the Macaronesian flora is a relict of a formerly widespread subtropical flora that very likely occupied Southern Europe and Northern Africa during the Tertiary (Takhtajan, 1969; Bramwell, 1972; Sunding, 1979; Bramwell, 1985). That flora, extirpated from the nearby continental territories as a consequence of the Plio-Pleistocene climatic crisis, namely the effects of glaciation in Europe and desertification in Africa, found refuge on the oceanic islands (Barber *et al.*, 2002).

Several arguments have been used to support the idea that Macaronesian endemics are palaeoendemics of much older floras (Bramwell, 1972), an hypothesis supported on the existence of disjunct sister group relationships and paleogeographical data (Böhle *et al.*, 1996). One of the main arguments used to support such approach is the existence of plant fossil records on Southern Europe (Bramwell, 1972; Sunding, 1979) related to taxa currently restricted or with a distribution centred on Macaronesia (Vanderpoorten *et al.*, 2007), namely elements of the Macaronesian laurisilva that are accepted as survivals of past widely distributed Tethyan-Tertiary flora (*Ocotea, Apollonias, Persea*, *Clethra, Picconia* (Tenorio *et al.*, 1990; Capelo *et al.*, 2007). Such relicts are of taxonomic nature, once they are living on Macaronesian islands and their extinction is documented from European macrofossils (Miocene and Pliocene), supporting the *refugium* status for the Macaronesian archipelagos (Vargas, 2007). In fact, such explanation is supported on the current existence of endemics (*Laurus novocanariensis, Persea indica, Ocotea foetens, Ilex canariensis, Viburnum rugosum, Viburnum azorica, Picconia excelsea, Picconia azorica, Smilax canariensis, Visnea mocanera, Clethra arborea, Woodwardia radicans, Prunus lusitanica, Myrica faya, Culcita macrocarpa, Davallia canariensis*) that are related to taxa identified in the fossil record (Catalán, 1996).

An additional argument that was used to support the relictual hypothesis is the significant presence of woody-life forms, a common attribute to the floras of Madeira and Canary Islands. The woody habit is considered by Meusel (1952, cit. by Bramwell, 1972) a relict characteristic of the endemic groups, an assumption that supports the idea of colonization of the islands by predominantly woody taxa with origin in the floras of the Tethyan Tertiary forests. Such flora, currently restricted to a small area of their past territory, would arrived in the Macaronesia already as frutescent or arborescent taxa, and integrates elements interpreted as ancestors of many modern Mediterranean taxa Bramwell (1972). In fact, processes of back-colonization between Macaronesian islands and continental territories should have occurred, supporting the idea that Macaronesian islands served as source for continental neo-colonization processes for some taxa (Carine *et al.*, 2004; Caujapé-Castells, 2004; Kim *et al.*, 2008). In addition, other features have been accepted as suggesting a relict distribution for all the endemics, namely distribution patterns, such as disjunct or discontinuous distributions with wide gaps (*Canarina* sp*.,* *Aeonium* sp.*, Jasminum odoratissimum L., Adiantum reniforme L.*), the acceptance of the phanerophites and pteridophytes related to the laurel forests present in the Macaronesian islands as relicts, or the low level of polyploidy of some taxa (see Bramwell, 1972).

But the relict theory is definitely refuted by Carlquist (1974), which perspective is supported by recent studies on phylogenies (Böhle *et al.*, 1996; Kim *et al.*, 1996; Caujapé-Castells, 2004; Mansion *et al.*, 2009). Carlquist (1974) interprets the woody-life forms as the result of evolution from herbaceous founders. Based on knowledge about the Hawaiian Islands' flora, the author postulates that woodiness is the result of radiative adaptation processes undergone by the founders as a strategy to fill empty ecological niches, after colonization based on long-distance dispersal. In addition to the woody habit of some endemic taxa, the taxonomically isolated position of some endemics are also considered as an evidence, namely the significant number of endemic genera and species, which in turn present a significant proportion of woody-growth forms. Such perspective is supported by recent interpretations of phytogeographic patterns and studies on molecular phylogenetic relationships on related groups of woody growth-forms, which testify processes of increasing woodiness associated to radiation, a signal that refutes the relictual nature for endemics that exhibits such trait (Böhle *et al.*, 1996; Kim *et al.*, 1996; Kim *et al.*, 1999; Barber *et al.*, 2002; Carine *et al.*, 2004; Caujapé-Castells, 2004; Kim *et al.*, 2008). The relict theory is also questioned by results for groups not related to the woody growth-forms, which testify the existence of polyploidy among neo-endemics (Díaz-Pérez *et al.*, 2008).

Even the pteridophyte flora, which has been accepted as an element of connection between current and Tertiary vegetation, is no longer totally accepted under the relict approach. Based on bryophyte and pteridophyte floras, Vanderpoorten (2007) concludes that the dynamic interchange provides a better explanation for the observed floristic patterns. Several reasons are mentioned as supportive: i) some elements of the Macaronesian cryptogamic flora have an origin younger than previously thought; ii) some endemic pteridophyte species of Azores and Madeira, considered as indicators of Tertiary relictualism in the cryptogamic flora, have very likely evolved in situ by isolation following long-distance dispersal from the New World; iii) there is some evidence that some of the pteridophytes (e.g. *Adiantum reniforme*) present on Madeira may derive from Canarian taxa, corresponding to a northward colonization rather than ancient vicariance; and iv) the cryptogamic flora of Cape Verde and the Canary Islands moss flora are clearly connected to an interchange of taxa with nearest continental areas. Even Macaronesian pteridophyte and liverwort distributions that are consistent with Engler's refugium approach may reflect a complex mix of relictualism overlaid by more recent evolution and dispersal (Vanderpoorten *et al.*, 2007; Aigoin *et al.*, 2009).

The monophyletic Macaronesia, associated to the relict hypothesis, is challenged by a polyphyletic perspective, which explains the origin of the endemic flora based on a *dynamic interchange approach*, an approach that admits the existence of processes of dispersal and colonization followed by events of speciation. The endemics are the result of an interchange process occurred between mainland territories and archipelagos, among archipelagos, and between islands of the same archipelago, which usually have undergone processes of adaptive radiation as a strategy to fill empty ecological niches in the new territories. Such perspective, previously proposed by Wallace (1881) for the Macaronesian archipelagos, is also considered by Lobin when assessing the relationships among the endemic and native elements of the floras from the different archipelagos (Vanderpoorten *et al.*, 2007). Distinct from the *refugium* model of Engler, such approach is concordant with the dispersalist island biogeographic models, and received strong support from molecular phylogenetic assessments (Vanderpoorten *et al.*, , op. cit.)).

Current spatial patterns and relationships detected for the endemic flora reveal a complexity that outranges the relict assumption associated to the Engler *refugium* approach (Emerson, 2002; Carine *et al.*, 2004; Carine, 2005), and demand the integration of factors associated to dynamic interchanges associated to dispersal events, and recent speciation in order to achieve a full explanation (Vanderpoorten *et al.*, 2007). So, paleogeographical and paleontological data are not providing unquestionable evidences for a clear acceptance of the relict approach. It is only part of the explanation (Vanderpoorten *et al.*, 2007).

Despite the fact that the *refugium* approach is not the full explanation for the flora and vegetation specific traits of Macaronesia, there is no doubt that, because of their geographical conditions, the archipelagos played an important role as refuge for taxa related to the Tertiary flora, which low resistance to low temperatures determined its extinction on Europe during Quaternary glacial periods. Some lauraceae taxa (*Ocotea, Apollonias, Persea,*) (Tenorio *et al.*, 1990) or the moss genus *Echinodium* (Vanderpoorten *et al.*, 2007) are examples of taxa which distribution became restricted to Macaronesian archipelagos after extinction from Europe during the Ice Ages.

1.2.1.2 THE CIRCUNSCRITPION

The term Macaronesia is attributed to the British botanist Philip Barker Webb (1835), and would be likely associated to the archipelagos of Madeira, Selvagens Islands and Canaries (Fernández-Palacios *et al.*, 2011). But the first use of the term with the intent to identify a distinct biogeographic unit is attributed to Engler, who proposes in 1879 a circumscription that includes Azores, Madeira and Canary Islands (Vanderpoorten *et al.*, 2007). Later, other authors expand the limits to include the Cape Verde archipelago (Dansereau, 1961; Bramwell, 1972), creating the classical and widely accepted circumscription of Macaronesia.

The classical circumscription is sometimes expanded to include enclave territories at North Africa and in the Iberian Peninsula (Sunding, 1979). It is suggested that the Macaronesia should include a thin coastal territory facing the Atlantic from the SW of Iberian Peninsula to the North of Senegal, based on biogeographic affinities with the

Macaronesian archipelagos, namely with the eastern Canaries and Cape Verde (Garcia-Talavera, 1999). Or, at least, small enclaves on SW Morocco and at SW Iberian Peninsula, namely the Portuguese Estremadura (Dias *et al.*, 2007b). The acceptance of such territories as repositories for relict taxa from the Tertiary, the existence of similar traits in terms of evolution in the flora with the archipelagos, the existence of common species or taxa with great affinities (*Dracaena draco*, *Diplazium* caudatum, *Asplenium haemionitis*, *Asplenium aethiopicum*), and vicariant or disjunct distributions (Bramwell, 1985) are considered remarkable arguments to support the affiliation of such territories to the Macaronesia region (Garcia-Talavera, 1999).

But such expansion is not widely accepted. An example that illustrates the existence of controversy is found in the affiliation of coastal and subcoastal areas of the south-western Morocco. The existence of affinities in the flora (Kim *et al.*, 1996), an argument considered sufficient to individualize a Moroccan-Macaronesian sector, is not accepted by Médail & Quézel (1999a). Based on a comparative analysis with the Canaries in terms of species life attributes (growth forms, succulence and dispersal), biogeographical spectra, flora traits (presence of succulent species and common endemics to Canary Islands) and landscape features in the lower zones (infra/thermo-mediterranean), they assign the SW Morocco to the Mediterranean sub-region. It is recognized the existence of similarities with some sectors of the Canaries, namely in terms of plant physiognomy (e.g. succulent species) or even by the presence of common and vicariant species. But such attributes are found insufficient to affiliate such territory to the Macaronesia, a position based on the following arguments: i) physiognomic resemblance is supported by climatic and ecologic proximity, ii) a significant proportion of common species are mainly associated to maritime habitats, iii) the significant number of common endemics shared by S.W. Morocco and the Canary Islands, some of them shared with other Macaronesian archipelagos (*Asplenium aethiopicum*, *Davallia canariensis*, *Dracaena draco*), are only indicators for a refuge status for the Tertiary paleoflora, iv) the high percentage of Mediterranean indigenous annuals and phanerophytes, v) the low level of adaptive radiation in the endemic flora when compared to the Canary Islands (Médail & Quézel, 1999a). Even an increase in the number of common taxa after future taxonomic investigations should not justify the affiliation of the S.W. Morocco to the *Macaronesian sub-region*, a territory that is associated to the Mediterranean region in the classification of Rivas-Martínez *et al.* (1993). So, having by reference the phytogeographical spectra and species' life attributes, such territory must be only considered as a specific sector of the North-African Mediterranean domain, and not a Macaronesian enclave (Médail & Quézel, 1999a).

The discussion about the circumscription of the Macaronesia became even more intense when considering data provided by phylogenetic and phylogeographic molecular analyses, contributing to a necessary re-evaluation of the concept of Macaronesia (Vanderpoorten *et al.*, 2007). Several contributions based on new outcomes on molecular phylogenies have been challenging the concept of Macaronesia, not only the circumscription, but also the hypothesis used to explain the origin of the endemic element present in the flora of the archipelagos, and its relationships with mainland territories.

On a first moment the distinct floristic features of the five archipelagos have been considered as sufficient to accept the Macaronesia region as a biogeographic unity (Médail & Quézel, 1999a). Based on phylogenetic analysis on molecular data, recent contributions address the floras of some of the archipelagos to different biogeographic regions. Such change on perspective, which demolishes the classical idea of Macaronesia, is based on the assumption that the specific features of flora and vegetation on such oceanic islands are the result of a more complex contribution of factors and processes than the simple explanation proposed by the *refugium* concept and the relict theory.

Based on the hypothesis of dynamic interchange of taxa, Lobin challenges the concept of Macaronesia addressing the Azores to a submediterranean subregion, the Canaries, Madeira and western Morocco within a Canarian-Mediterranean subregion, and the Cape Verde within the "Saharo-sindian" region (Vanderpoorten *et al.*, 2007). Such perspective is also present in the biogeographic classification of RIVAS-MARTÍNEZ *et al*. (2002, 2007), which resolves the Madeiran and Canarian archipelagos within the Mediterranean region, in a separated sub-region (Canarian-Madeiran sub-region). In fact, the similarities between the Canarian and the Madeiran floras are highlighted when assessing the relationships of the vascular floras within the Macaronesia (Nicolás *et al.*, 1989; Jardim & Sequeira, 2008a). The Azorean archipelago is resolved to the Eurosiberian Region, distinguished in the Atlantic-Central European Subregion as Azorean Province (Rivas-Martínez, 2007), a perspective in harmony with Lobin's proposal. Despite the presence of endemic plants which genera are well represented at Macaronesia (*Picconia, Pericallis, Tolpis, Aichryson, Cedronella*) (Jardim & Sequeira, 2008b), Garcia-Talavera (1999) accepts that the endemic flora of Azores as having higher affiliation to the European flora.

The strong similitude of the Cape Verde to the west-African flora is also mentioned by Garcia-Talavera (1999), who underlines the great affinity to the paleotropical flora, more than to the Mediterranean flora or the floras of the other Macaronesian archipelagos. Nevertheless, some Macaronesian endemic taxa are present in the archipelago, with some shared only with Canaries (e.g. *Launaea*, *Phoenix*, *Limonium*), few with Madeira (e.g. *Sideroxylum*, *Aeonium*, *Echium*, *Teline, Sonchus*), and very few with the Azores (e.g. *Dracaena*), supporting the idea that Macaronesia should not be considered as a single biogeographical region (Jardim & Sequeira, 2008a).

The idea that is difficult to associate all the archipelagos to the concept of Macaronesia is even harder to conceive when other than vascular floras are integrated in the analysis, namely bryophyte and pteridophyte floras. Vanderpoorten *et al.* (2007) assume that an ample Macaronesian concept (Azores, Selvagens, Madeira, Canary Islands, Cape Verde) can be rejected based on the analysis of relationships over bryophyte and pteridophyte floras. The liverwort and pteridophyte analysis supported the identification of an Azorean-Madeiran-Canarian clade, consistent with the Macaronesia's circumscription of Engler, which present higher affinities to Europe. The southern archipelago, Cape Verde, is clearly resolved to sub-Saharan Africa, a relationship that combined with the higher affinities in terms of vascular flora (Duarte *et al.*, 2008), and the larger floristic dissimilarity to the others Macaronesian archipelagos' floras (Nicolás *et al.*, 1989), supports the challenging perspective of assigning the archipelagos to different biogeographical entities.

Such results are consistent with the assumption that the dynamic interchange of taxa with the neighbouring continental territories best explains the origin and relationships among the floras. Such clarification clearly challenges the Engler refugium model and the idea of a relict nature for all the endemic flora of the archipelagos, contributing to reinforce the non-monophyly status of the Macaronesian region (Vanderpoorten *et al.*, 2007).

The idea that the dynamic interchange approach best explains the origin of the endemic element in the flora, supporting the idea of a more polyphyletic Macaronesia, became even clearer on recent outcomes from phylogenetic studies focused on endemic woody growth-forms. Such results refute the monophyletic hypothesis, which is based on the relict nature of the endemic element of the flora.

The discussion about the existence of a solid and homogeneous biogeographic region is going on, benefiting from increasing available data, namely new insights generated by recent outcomes on molecular phylogenies that explore the origin and relationships of the endemic floras of the archipelagos (e.g. Carine & Schaefer, 2010; Schaefer *et al.*, 2011) . It seems that the two hypothesis need to be considered to explain the origin of the endemic element, a perspective postulated by Capelo *et al.* (2007).

1.2.1.3 DIVERSITY PATTERNS IN THE MACARONESIA - FACTORS:

The high level of endemicity is an attribute that is associated to the flora of the Macaronesian archipelagos, accepted as hotspots of biodiversity (Médail & Quézel, 1999b). But the floristic diversity is highly variable among archipelagos and among islands of the same archipelago (Jardim & Sequeira, 2008a; Reyes-Betancort *et al.*, 2008).

As classical issue in biogeography, different models have been proposed to clarify the contribution of different factors on explaining differences on biological richness on oceanic islands (MacArthur & Wilson, 1967; Mueller-Dombois, 1992; Emerson & kolm, 2005; Whittaker *et al.*, 2007; Whittaker *et al.*, 2008). Studies concerning plant diversity in the Macaronesia always list a number of factors that are determinant to explain current richness patterns (Garcia-Talavera, 1999; Fernández-Palacios & Andersson, 2000; Emerson, 2002; Duarte *et al.*, 2008; Jardim & Sequeira, 2008a). The majority of such analyses, based on a comparative approach between islands, are focused on the endemic richness, and factors are mostly valorated as contributors to speciation.

At the archipelago level, the Canary Islands present the higher values of floristic diversity, with a high proportion of endemics (Bramwell, 1972; Fernández-Palacios & Andersson, 2000; Vargas, 2007; Jardim & Sequeira, 2008a; Reyes-Betancort *et al.*, 2008). At the island level, Tenerife, Madeira and Gran Canaria present the higher values of exclusive endemics, while a significant number of islands in the Azores and Cape Verde have no exclusive endemics registered (Jardim & Sequeira, 2008b). Such differences must be associated to factors that affect dispersal, colonization, speciation and extinction, elements that contribute to shape islands' floristic diversity (MacArthur & Wilson, 1967; Whittaker *et al.*, 2008).

The diversity of a territory is dependent on the existence of successful colonization events, which in turn are determined by a trade-off between specific traits of the colonizers (potential ability to dispersal, genetic drift, hybridation) and the conditions of the arrival territories (geographical traits, niche pre-emption, extant diversity).

The ability to dispersal (direct and indirect) affects the diversity of an island but also the diversity within a taxonomic group. In the Macaronesia, the proportion of endemic species is low for taxonomic groups having long-distance dispersal ability, such as bryophytes, and relatively high for angiospermic taxa (Carine *et al.*, 2004). For bryophytes, which distribution is determined by wind connectivity rather than geographic proximity, the dispersal was benefited by trade winds and the prevailing N-S marine current (Nicolás *et al.*, 1989). This is consistently supported by the high levels of homoplasy in the moss group, which may reflect its greater long-distance dispersal ability, necessary for a dynamic interchange with continental areas (Vanderpoorten *et al.*, 2007).

In terms of conditions of the territories, it is undeniable the control exerted from some geographical factors, which have been widely used as explanatory variables, namely the relation between the size of the islands and their distance to propagule source areas, early considered as cardinal factors in the "equilibrium theory", where diversity is the result of a balance between immigration and extinction (MacArthur & Wilson, 1967). Their contribution to explain biological richness depends on the scale (Macaronesia, archipelago, island) and the taxonomic group considered. As example, diversity on low dispersal ability taxonomic groups is dependent on the age and isolation of the islands, while area and habitat diversity are determinant factors at within-archipelago-level (Fernández-Palacios & Andersson, 2000).

The position determines the degree of isolation from propagule source areas (mainland territories or other islands), a key factor to explain differences on diversity among territories and taxonomic groups. The difficulty on dispersing to islands is a limiting factor that definitely should be considered for the number of introductions from other territories, which will regulate the scores for total diversity or endemic richness. When considering total diversity, an increase on distance to propagules source areas (mainland) reduces the chance of colonization, while for short distances a large fraction of the continent species pool has the chance to colonize islands, increasing their diversity. The higher affinities between the Cape Verde and the nearby continental bryophyte and pteridophyte floras (Vanderpoorten *et al.*, 2007), consistent with analyses based on vascular flora (Duarte *et al.*, 2008), underlines the importance of geographic distance.

The scenario is different if considering endemic richness. Oceanic islands (never connected to continents) perform examples of distinct geographical territories which isolation has contributed to reduce genetic interchanges with continental areas. The lower immigration rate, which determines the absence of a regular gene-flow (Borges *et al.*, 2008), perform elementary conditions to speciation, contributing to higher endemic richness. On the opposite, close proximity of propagule source areas has inherent potential for repeated colonisations and lower aptitude to speciation (Barber *et al.*, 2002). The distance to continental shields or other islands is determinant in terms of events of colonization, once the natural entrance of plant species can be related to zoochorian processes, mainly by granivorous and frugivorous birds (ornitocoria), and by arrival of “floating wood/devices/seeds” (hydrochoria) (Dias *et al.*, 2007b). Multiple colonization events for some genera are related to endozoochorus patterns, a process that could have been crucial for long-distance dispersal of fleshy-fruited plants to Macaronesia, namely small (*Ilex*, *Hedera*, *Juniperus* sect. *Juniperus*, *Olea*) or even large trees (*Laurus*, *Ocotea*, *Persea*, *Apollonias*), and for the establishment of ancient lineages in the Tertiary (Tenorio *et al.*, 1990).

However, (Hobohm, 2000) noted that the distance from the source area alone couldn’t explain the levels of endemism in the Canaries. In fact, the Azores, with larger distances to continental source areas[5], present a significantly lower level of endemicity when compared to the Canary Islands[6](Jardim & Sequeira, 2008a). Thus, other variables should be addressed, namely the availability of great diversity of resources in the new territory, an aspect that should be related to habitat diversity. The diversity of habitats

---

[5] - Distance range to Europe: Flores island – 1900 km; Santa Maria island– 1450 km)

[6] - Distance to Africa: Fuerteventura - 97 km)

should have played an important role on controlling diversity patterns, an aspect mainly determined by ranges at different scales: the latitudinal range at the region level and the altitudinal range at the island level. The significant latitudinal range, sometimes considered a feature that challenges the acceptance of all archipelagos as members of the same biogeographic region, is an important contributor for the outstanding diversity found within the Macaronesia. Such remarkable latitudinal extent (Corvo (Azores): 39° 45'N – 31° 17'W; Brava (Cape Verde): 14° 49' N – 13° 20' W) is also supportive to explain differences on plant diversity among archipelagos, namely because of the inherent climatic diversity. The northernmost Macaronesian archipelago has a clear temperate pattern (Azores), while Cape Verde, the southernmost archipelago, is associated to dry tropical conditions. So, while the diversity of habitats associated to latitudinal range is important to understand the high diversity of the region, the position of each archipelago and its consequences in terms of climate are important to explain differences among them.

Besides the control over climate, which is important for the bioclimatic pattern (temperature, precipitation), position also interferes on dispersal. The oceanic (marine currents) and atmospheric (winds) prevailing circulation patterns, besides their contribution on controlling climatic attributes, they also play a critical role on dispersal for some taxonomic plant groups.

In terms of climatic conditions, the position and insular condition promoted the existence of buffered climatic conditions. Such combination of factors played a very important role in the past, when the Macaronesian archipelagos, because of their geographical context, benefited from a sheltered condition in relation to the severe climatic degradation occurred during the Pliocene and Pleistocene on continental areas. The smoother climatic environment performed suitable conditions for sheltering flora (Bramwell, 1972), which got extinct on continents, affected by dryness and cold, especially during the Pleistocene period (Caujapé-Castells, 2004). Despite the likely lower magnitude of climatic fluctuation on the islands of Macaronesia, which supported the survival of palaeotropical taxa, several aspects point to significant direct and indirect impacts on such territories. Changes on sea level modified the configuration and size of the islands (Hewitt, 2000). Those changes very likely affected the conditions to dispersal, namely during the cold periods, when a lower sea level promoted the emersion of current seamounts, promoting the definition of a chain of islands, a necessary condition to support the stepping-stone dispersal scenario (Fernández-Palacios *et al.*, 2011). In fact, and accepting differences to dispersal among taxonomic groups, isolation and dispersal ability were considered not so important limitations in the Macaronesia, once constraints to long-distance dispersion may be less than previously assumed (Carine *et al.*, 2004).

The distance to continental areas can be also contributing to explain differences in terms of climatic conditions between islands of the same archipelago, increasing or smoothing the oceanic influence - the effect of longitude (Duarte *et al.*, 2008). As example, while the easternmost islands of Canaries (Fuerteventura and Lanzarote) present a desert-like climate, exhibiting a deeper influence from continental territories because of higher proximity, the western islands reveal a clear Mediterranean pattern and higher oceanic influence (Sperling *et al.*, 2004).

The existence of significant climatic ranges within archipelagos and within islands, considered a crucial element to habitat diversity, is only part of the equation that explains differences on diversity. Within archipelagos, orographic traits of each island contribute to support differences in terms of habitat diversity, a combination from altitudinal range and topographic complexity. Wide altitudinal ranges, coupled with a rugged topography, are factors that favour higher diversity (Bramwell, 1972). Its contribution goes beyond the definition of higher diversity of habitats, and also contributes to reinforce in some degree conditions to spatial isolation, an elementary factor for speciation (Vargas, 2007). While the diversity of habitats should have been critical to the evolution of many species through adaptive radiation in the Macaronesia (adaptive evolution of form), a strategy to fill empty niches, the evolution into distinguishable species was also supported by vicariant distributions, many of them occurred as a consequence of isolation because of geographical or topographical barriers within islands, assisted by the existence of genetic drift (Bramwell, 1972). The contribution of orography to control floristic diversity is reinforced at the Macaronesia because of deep implications of mountains' range orientation on drawing distinct topoclimatic conditions in association to prevalent winds.

The size of the territory is another geographic feature that shapes island's diversity, namely when combined with other factors. Area interferes with the chance of establishment for new founders, namely because of limited resources, which controls population size and competition rate (MacArthur & Wilson, 1967). It is accepted that higher and larger islands, where ecological ranges are more pronounced and the diversity of habitats is potentially higher, are associated to higher diversity rates (MacArthur & Wilson, 1967; Fernández-Palacios & Andersson, 2000).

Besides the attributes of each island, features of neighbouring islands (size, height, geological age) also contribute to explain diversity patterns (Fernández-Palacios & Andersson, 2000). About the geological age, colonization and speciation have higher chances to occur in older islands, so endemic richness should be higher (Borges & Brown, 1999). However, considering the ontogeny model for oceanic islands (Whittaker & Fernández-Palacios, 2007) older islands are less diverse in terms of habitat. So, species richness and speciation rate are at maximum when an island presents maximum topographic complexity (Whittaker & Fernández-Palacios, 2007; Whittaker *et al.*, 2007). Besides the contribution to its own diversity, the age of an island is also important to shape the biota of neighbouring islands. Such dynamics might have played a decisive role for dispersal and colonization in the Macaronesia in association to stepping-stone processes, where older islands, currently seamounts, worked as sources for dispersal to younger ones, current islands (Fernández-Palacios *et al.*, 2011).

Other factors have been used to explain diversity patterns at Macaronesia, namely the role of the colonization opportunity (Carine *et al.*, 2004; Silvertown, 2004). It is possible that successful colonization into Macaronesia may have been limited to *discrete windows of opportunity* (Carine, 2005). The successful establishment occurred within such colonization windows benefits from the existence of suitable conditions to the founders, namely low saturated habitats (climatic changes), fresh/free habitats (islands emersion, catastrophic volcanic eruptions), vacant niches (increase of altitudinal ranges after volcanic eruptions), and even under contexts of deep climatic and geologic changes over the Mediterranean margins and Atlantic coasts of Africa. The early Pleistocene, characterized by profound climatic changes on northern Africa and Mediterranean, and active volcanism in the Canary Islands, would have created discrete *windows of opportunity*, a combination of factors that could have supported events of colonization and successful radiation for some taxa (Carine, 2005; Kim *et al.*, 2008). In fact, recent molecular phylogenies support the idea that some endemic plant groups on oceanic islands, namely in the Macaronesia, are considered of monophyletic nature, and evolved after a single colonization event, rather than multiple invasions, followed by intense speciation and inter-island dispersion (Böhle *et al.*, 1996; Francisco-Ortega *et al.*, 1996). Such condition must be associated to the low chance of repeated colonization, constrained by dispersal barriers or by the inhibition of later arrivals establishment because of interspecific competition and niche pre-emption carried by first colonizers (Silvertown, 2004). Many Macaronesian endemic plant groups that have experienced single introductions from a continental ancestor (e.g. *Echium*, *Sideritis*, *Argyranthemum, Sonchus*, *Pericallis*, *Bencomia*) present an high level of endemicity, a fact associated to intense radiation after inter-island colonization (Caujapé-Castells, 2004).

Low-saturated habitats or vacant niches (niche pre-emption hypothesis) would favour the establishment and a subsequent adaptive radiation, promoting the diversification of endemic lineages, intense for some of the earlier colonists (Benito-Garzón *et al.*, 2006). Later colonists had less chances to radiate (Kim *et al.*, 2008). Analyses of molecular phylogenies of different plant groups revealed that the mean number of species per endemic group was seven times greater on genera associated to a single colonization event (Silvertown, 2004), comparing to endemic plant groups that might have experienced multiple introductions (e.g. *Euphorbia*, *Ilex*, *Juniperus* sect. *Juniperus*, *Lavatera*, *Olea*, *Hedera*, *Tolpis*, *Saxifraga*, *Convolvulus*, *Viola*) (see Carine *et al.*, 2004; Díaz-Pérez *et al.*, 2008). The possible reason is that groups with many species are more effective at excluding repeating colonisations by relatives than groups with fewer species, since larger groups should pre-empt more of the niche space available for colonization, restricting the number of new colonisations. As consequence, it is expected that events of multiple congeneric colonization in Macaronesia could have occurred only when different archipelagos within the region registered independent colonisations, or in the absence of direct competition because of phylogenetic, morphological and even ecological differences among the colonizing groups (Carine *et al.*, 2004).

In addition to all the arguments mentioned, Emerson & kolm (2005) propose that species diversity itself might be an important driver on promoting speciation, putting on evidence a positive relationship between diversification and species number.

All the mentioned factors are important to explain diversity elementary patterns within Macaronesia, namely for endemic richness. But a full explanation should integrate the use of variables related to disturbance associated to historical land-use by human activities (Jardim & Sequeira, 2008a). Land-use ranges, associated to length and intensity on resources exploitation, might also support the comprehension of differences. The exploitation of resources should have been constrained by topographic features of each island. Thus, it is expected that the higher levels of disturbance would be associated to islands less complex topographically (e.g. Azores islands). There, the expected lower floristic richness could result from synergetic contributions from low diversity of habitats and higher extinction rates determined by human disturbance. Such explanation, combined with the lack of a consistent and critical taxonomic framework for the floras of the Atlantic archipelagos (Schaefer et al., 2011), might be complementary reasons to explain the low diversity of the Azores islands or Porto Santo Island, the late close to Madeira Island. In the case of the Azores Islands, it is clear that isolation played a significant role. The higher distance to continental territories, comparing to Madeira or Canaries, is reinforced by the absence of connection to the line of seamounts that very likely played a significant role on shaping the islands' biota of Madeiran and Canarian archipelagos (Fernández-Palacios *et al.*, 2011), a fact supported by recent phylogenetic studies (Díaz-Pérez *et al.*, 2008). Moreover, atmospheric and oceanic circulation patterns reinforce such isolation, namely the prevalence of westerlies, contrary to potential arrival of colonizers from the European continent, and the existence of an individualized marine current branch (Ferreira, 2005) that reduces the chance of propagules arrival from Europe and other Macaronesian archipelagos by this way.

1.2.2 Flora and vegetation of Madeira Island[7]

The original features of the flora and vegetation of Madeira Island derive from a combination of several factors. The biogeographic isolation, reinforced by geographical circumstances, such as relief conditions, has promoted new ways on evolutionary processes, becoming a major factor on explaining the high rate of endemicity (Capelo et al., 2007).

Its geographic position, determinant for macroclimatic conditions, is also important concerning the distance to propagules source areas (Africa, Europe, America and other archipelagos). The position in the neighborhood of the African and European continents and the proximity to other islands had implications in terms of dispersion,

---

[7] Fernandez-Palacios et al (2004) estrategias de regeneración en la Laurisilva. Makaronesia 6: 90-101.

colonization and speciation. The island benefited from being integrated within a sequential disposition of islands in a line more or less parallel to the European and African continents (Böhle *et al.*, 1996; Barber *et al.*, 2002; Capelo *et al.*, 2007; Dias *et al.*, 2007b).

The existence of older islands in the near proximity (Porto Santo) and the great diversity of habitats, determined by orographic features (significant altitudinal range, perpendicular orientation of the mountains range relatively to the prevalent trade winds, and the high topographic complexity), have been important variables to support the high endemicity rate of the island, one of the richest biota of the Macaronesian islands, a fact clearly accepted when comparing the density of exclusive endemics (Jardim & Sequeira, 2008a).

1.2.2.1 FLORA

Madeira Island is by far the territory with higher floristic richness in the archipelago with the same name, and one of those with higher diversity rate in the Macaronesia, a feature clearly stressed in the analysis presented by Jardim & Sequeira (2008a). The flora of the island includes 1136 taxa of vascular plants (species and subspecies), with a significant number of endemics, exclusive of the island (12%) or shared with other Macaronesian islands (6%). With the largest size and habitat diversity in the archipelago of Madeira, the island presents the highest score for exclusive taxa (687), sharing some with Porto Santo Island (209) and few with Desertas Islands (22). In addition to the high plant diversity, the island presents very singular features considering the small size. One of the most interesting attributes is the existence of exclusive endemic genera (*Sinapidendron* Lowe (Brassicaceae), *Musschia* Dumort. (Campanulaceae), *Monizia* Lowe (Apiaceae), *Melanoselinum* Hoffm. (Apiaceae) and *Chamaemeles* Lindl. (Rosaceae)), attesting the importance of Madeira Island as hotspot of biodiversity in the context of the Macaronesia (Keller *et al.*, 2000; Jardim & Sequeira, 2008a) or even at broader scales (Médail & Quézel, 1999b).

It is accepted that the ancestral taxa of the vascular plants are predominantly of Mediterranean origin (North African or western European) (Panero *et al.*, 1999; Barber *et al.*, 2002; Capelo *et al.*, 2004; Vargas, 2007), considered the main source for dispersal of new evolutionary lineages for the Macaronesian islands (e.g. *Argyranthemum* Webb ex Sch. Bip. (Asteraceae), *Isoplexis* (Lindl.) Loud (Scrophulariaceae), *Sideritis* Tourn. Ex Linn (Lamiaceae)) (for a revision see Carine *et al.*, 2004). The divergence from the respective sister groups must have occurred during the early Pliocene, matching the intensification of glacial activity and major changes in ecological conditions in the northern hemisphere (Carine *et al.*, 2004). A lower number of taxa indicates sister group relationships with the American continent (North America: *Pericallis* D.Don (Asteraceae) and *Sedum* L. (Crassulaceae); South America: *Bystropogon* L'Herit (Lamiaceae)); East (*Solanum* L. (Solanaceae)) and southern Africa (*Phyllis* L. (Rubiaceae)); or with eurso-siberian territories (*Saxifraga* L.) (for a revision see Carine *et al.*, 2004).

The flora of the territory results from the combination of relictual distributions (palaeo-endemics), recent speciation (neo-endemics), processes of dynamic interchange (mediterranean and neo-mediterranean flora), and, more recently, the introduction of taxa associated to human activities (Capelo *et al.*, 2007), a pattern shared with other Macaronesian archipelagos (Kim *et al.*, 1999; Vanderpoorten *et al.*, 2007; Reyes-Betancort *et al.*, 2008; Aigoin *et al.*, 2009).

1.2.2.1.1 PALAEOENDEMICS

The paleo-endemic flora, considered of relictual origin from the subtropical Tertiary Tethysian flora (Mai, 1989; Rodríguez-Sánchez et al., 2009), integrates all the phanerophytes of the laurel forests (*Laurus*, *Ocotea*, *Apollonias*, *Persea*, *Clethra*, *Ilex*, *Picconia*, *Heberdenia*, *Myrica*, *Prunus*), probably *Dracaena* and *Sideroxylon*, and forest-ground and epiphytic pteridophytes. The presence of such taxa in some Macaronesian islands is interpreted as the result of range contraction through extinction of the Palaeotropical geoflora, rather than *in situ* evolution (Cronk, 1997). Those taxa, associated to ancient colonization events from continental areas, survived under a buffered climate in the Macaronesian islands during the climatic degradation associated to the Pliocene-Pleistocene, responsible for their extinction on continental areas.

It comprises both geographic palaeoendemics (Cronk, 1997), taxa extinct from the Mediterranean but present in other parts of the world (*Persea, Ocotea, Clethra*), and taxonomic palaeoendemics, taxa isolated within their clades as result of past continental extinction (Apollonias, Picconia, Visnea) (Cronk, 1992).

The colonization by palaeotropical flora might have undergone two distinct paths (Vargas, 2007): directly from the continent or by a process of stepping-stone from older to new islands, favouring processes of radiation, as pointed by phylogenetic studies (Kim *et al.*, 2008; Aigoin *et al.*, 2009). The stepping-stone process is supported by the existence of older Palaeomacaronesian islands positioned closer to the Iberian Peninsula and North Africa, which are contemporary of the Palaeotropical flora extant at that time in Europe. Such idea is based on the existence of neo-endemic archipelagic species that are older than the islands on which they occur on modern-days. Phylogenetic data for radiations occurred on different archipelagos indicates a progressive pattern of colonization, where younger islands are colonized from older ones, followed by divergence and diversification *in situ* (Keller *et al.*, 2000; Whittaker & Fernández-Palacios, 2007). The stepping-stone dispersal dynamics is considered at different scales in the Macaronesia. It is widely accepted for colonization within archipelagos, among archipelagos, and between European and African mainland territories and the archipelagos. The uncertainties associated to certain plant groups, namely the presence of Lauraceae species on islands far from mainland territories (Flores – AZ), are banished by closer phylogenetic affinities between the Macaronesian and Moroccan populations of *Laurus* (*L. azorica*, L. *novocanariensis*) and the Iberian populations (*L. nobilis*), comparing to the Italian, Greek, and Turkish populations (*L. nobilis*) (Arroyo-García *et al.*, 2001; Rodríguez-Sánchez *et al.*, 2009). Although hard to accept, the importance of the Palaeomacaronesian archipelagos as stepping-stone structures is even considered for the trans-Atlantic long-distance between the American mainland and current European mainland territories. Such role, of special relevance for the time interval between the end-closure of the North Atlantic Land bridge (c. 40 Ma) and the appearance of the oldest extant Macaronesian islands (Selvagem Grande and Furteventura, 30-20 Ma) (see Fernández-Palacios *et al.*, 2011), is challenged by recent results on molecular phylogenies (Schaefer *et al.*, 2012).

1.2.2.1.2 WOODY NEO-ENDEMIC FLORA

The neo-endemic flora is interpreted as resulting from colonisations occurred mainly during late Tertiary and beginnings of the Quaternary by ancestors of continental origin, which undergone intense and rapid processes of radiation on islands, very often associated to events of inter-island colonisation (Whittaker & Fernández-Palacios, 2007). Because of ecological opportunities, namely the existence of empty niches on new habitats, and genetic traits, the processes of speciation were likely faster than on continental areas (Böhle *et al.*, 1996). Probably because founders, usually associated to single events of colonization, only present part of genetics from the original population, and need to adapt quickly to new selecting factors (Francisco-Ortega *et al.*, 1996). One way to solve such handicap is changing their size, a strategy that should have been supported on increasing woodiness. The woody habit is one of the peculiar features associated to neo-endemic flora, which continental ancestors present an herbaceous habit (Carine *et al.*, 2004). The species are shrubs or arborescent forms, monocarpic rosette, caulirosulated or having candelabra habit, with a terminal rosette of leafs at the terminus of long branches formed over several vegetation periods, which often support single inflorescences of several thousands of flowers. Such trend in evolution (woody habit) is present in Boraginaceae species (*Echium*), Asteraceae (*Sonchus* and *Argyranthemum*), Scrophulariaceae (*Isoplexis*), Campanulaceae (*Musschia*), Euphorbiaceae (*Euphorbia*), Plantaginaceae (*Plantagum*), Lamiaceae (*Sideritis*) and Convolvulaceae (*Convolvulus*) (Carine *et al.*, 2004; Capelo *et al.*, 2007).

The exhibition of a perennial and woody growth form by species of predominantly herbaceous genera on mainland territories was identified as an interesting and common trait on oceanic islands (Wallace, 1878). Contrasting theories have been proposed to explain insular woodiness. The relict hypothesis, based on morphological, cytological, and paleogeographical data, interpreted the woody form as ancestral to the herbaceous forms (Bramwell, 1972), a theory rejected by recent studies based on molecular evidences. Such studies confirm that a significant number of island inhabitant species presenting woody habit did evolve from herbaceous Mediaterranean ancestors (Böhle *et al.*, 1996), which satisfies the idea that woodiness is a derived attribute resultant from *in* *situ* insular evolution (Panero *et al.*, 1999), a perspective that follows Carlquist (1974), the author of the *insular woodiness* concept.

Insular woodiness and related forms (candelabra shrub, rosette habits) have arisen independently in many different angiosperm genera (Carlquist, 1974), strongly suggesting that they are selected for, rather than occurring as the result of drift (Böhle *et al.*, 1996). Analysis of character evolution of plant morphology shows extensive morphological differentiation but low genetic variation on Macaronesian plants, an aspect related to the fact that those species undergone a process of "character release" while displaying a similar or identical DNA sequences (Givnish, 1998). In contrast, mainland species of the same group present similar morphologies but remarkable divergent sequences (Böhle *et al.*, 1996).

Different arguments have been used to support the idea that insular woody habit is a new feature, an adaptive response to new selective pressures, namely buffered climatic conditions associated to the release from seasonality, the absence of herbivores, the existence of empty niches on new habitats or the result of successful strategies of reproduction and competition. The climate adaptation hypothesis (constant climates) is not fully supportive, otherwise congeneric species associated with similar climates on mainland (Iberia) would be also woody, a fact not confirmed (Böhle *et al.*, 1996).

According to Böhle *et al.* (1996) such evolution in terms of physiognomy might perform a response to escape from inbreeding depression in geographically isolated founding populations. An answer made possible through a combination of variables, rather than a selection for specific environment-adapted variants of woody forms. To Wallace (1878) perennial woody growth form may reflect selection for longevity of insect-pollinated species within a poor-insect environment, where preference is given to lifelong species with bigger and lasting flowers. Accepting outbreeding as a primary selective factor in island colonization, pollination pressure would favour rare, large and conspicuous inflorescences among outbreeders, which in turn supported the selection of perennial/woody habits capable of producing them. Thus, outbreeding, perennial growth and insular woody habit could represent characters attributable to one selective pressure – the need to escape from inbreeding depression (Böhle *et al.*, 1996).

The existence of empty niches associated to new habitats would have created elementary conditions for successful colonization and radiation. Such scenario is easily accepted after volcanic eruptions, but can be also associated to less catastrophic natural hazards, namely when herbaceous generalists entered into shrubby or even forest communities occupying open spaces created by landslides (Capelo *et al.*, 2007). The perennial growth might have been promoted by the absence of herbivores and a less variable climate, creating the basis for woodiness (Carlquist, 1974), arguments that should be combined with other elements to find a consistent explanation.

The level of endemicity is significant on genera that exhibit woody habit, a trait common to several genera on the island (e.g. *Argyranthemum, Helychrisum, Teucrium, Geranium, Aeonium, Sonchus, Echium, Sinapidendron, Euphorbia, Monizia, Isoplexis, Musschia, Melanoselinum, Plantago, Convolvulus*). In fact, the woody growth forms concentrate a significant number of exclusive endemics.

The woody habitat should perform an advantageous trait. The resulting increase on size benefited woody taxa in niche competition among first colonizers (Wallace, 1878). A good example is presented by the genera *Argyranthemum* Webb (Asteraceae) or *Echium* L. (Boraginaceae), which Macaronesian species potentially inhabit a wide range of habitats, from the coastal cliffs to the highest altitudes, and from semidesert habitats to the domain of the humid laurel forest (Böhle *et al.*, 1996; Francisco-Ortega *et al.*, 1997). It might have been also crucial to the diversification of island forms during the inter-island colonization process, when it is expected that some of the genera underwent significant radiation, suggesting that reproduction rather than adaptation is determinant to insular woodiness (Böhle *et al.*, 1996). Another example that supports the idea that perennial woody forms are very proficient colonizers is associated to their common presence on areas recently affected by landslides within the laurel forest, namely *Argyranthemum pinnatifidum*, *Musschia wollastonii*, *Sonchus fruticosus* and *Euphorbia mellifera*.

1.2.2.1.3 MEDITERRANEAN FLORA

The mediterranen flora present on the island includes Palaeo-mediterranean elements of subtropical origin (xerophytes, sclerophylous, thermophylous) from the circum-mediterranean area (*Olea, Maytenus, Myrtus, Rhamnus, Asparagus*), and neo-mediterranean shrubs (*Genista, Teline*) (Capelo *et al.*, 2004). Such elements occupy mostly the lower altitudes of the island, where dryness is the most significant climatic attribute.

The arrival of plant species well adapted to seasonality associated to the Mediterranean climate is more recent, a fact that can be supported by the existence of several native non-endemic species associated to such climatic conditions, with several examples on Canary Islands (*Juniperus turbinata, Pistacia atlantica, Pistacia lentiscus, Phillyrea angustifolia* (Fernández-Palacios *et al.*, 2008). However, some of the taxa might have arrived earlier, and experienced processes of dispersal by stepping-stone based on bird dispersal (e.g. *Olea*) (Hess *et al.*, 2000).

1.2.2.1.4 ANTHROPIC FLORA

The percentage of plant taxa introduced by human activities is significant in the island (37%) (Jardim & Sequeira, 2008a). A significant number of introductions are voluntary, and are associated to agriculture (e.g. *Castanea sativa, Vitis vinifera, Psidium guajava, Saccharum* sp., *Passiflora molissima*), forestry (e.g. *Pinus pinea*, *Acacia melanoxylon*, *A.* mearnsii, *A. longifolia*, *A. dealbata*, Eucalyptus sp., *Cryptomeria japonica*, *Fagus sylvatica, Acer pseudoplatanus*), and gardening (e.g. *Solanum mauritianum, Hedychium gardnerianum, Cardiospermum grandiflorum*, *Pittosporum undulatum*).

Some of the introduced species are currently considered invasive *(*e.g. *Acacia dealbata, Acacia longifolia, Acacia melanoxylon, Pittosporum undulatum, Solanum mauritianum, Acer pseudoplatanus*), an attribute based on their recent spontaneous increase in terms of area of distribution. Aside from broad climatic tolerance, the success of invasion is associated to fast growth, good dispersal abilities (early and massive production of highly viable seeds, low mass seeds that favour rapid dispersal) (Farrell & Ashton, 1978; Sabiiti & Wein, 1987; Rejmanek & Richardson, 1996; Dukes & Mooney, 1999; Holle & Simberloff, 2005; Marchante *et al.*, 2008), generous vegetative reproduction (Paiva, 1999; Marchante *et al.*, 2008), and fast-growing, an important attribute when competing for resources (Hellmann *et al.*, 2008). Invasion by non-native species is considered to be a major cause for biodiversity loss, species extinction and economic losses (Vitousek *et al.*, 1996; Wilcove *et al.*, 1998; Mack *et al.*, 2000; MEA, 2005;

Pimentel *et al.*, 2005; UNEP, 2010; Vilà *et al.*, 2010). In fact, different types of impacts were described, including effects on the structure and functions of the ecosystems, threatening native biological diversity (Vitousek *et al.*, 1996; Marchante, 2001), interference on fire regime (Mack *et al.*, 2000; Wilgen *et al.*, 2001; Chambers & Wisdom, 2009), and changes on water resources availability (Ehrenfeld, 2003; Henderson *et al.*, 2006).

Alien tree invasive species that cause greatest impacts are those widely associated to planting, and among them *Acacia* species are considered one the most problematic (Richardson, 1998). Different *Acacia* species are considered invasive on different parts of the world, with described impacts in terms of plant communities, soil moisture regimes and soil nutrient levels (Chapman *et al.*, 2001; Adair, 2002; Howell, 2008; Marchante *et al.*, 2008; Fatunbi *et al.*, 2009; Gaertner *et al.*, 2011; Le Maitre *et al.*, 2011). Their capacity to invade and dominate competitive interactions with native species, especially on areas affected by disturbance, is associated to rapid growth (Morris *et al.*, 2011), ability to set large and persistent seed banks, and their capacity to fix nitrogen (Yelenik *et al.*, 2007). Within the genus Acacia, the species *A. melanoxylon* and *A. mearnsii* have the wider distribution on the island today. The introduction of *Acacia melanoxylon* on Madeira Island occurs in the second half of the 19th century, being cited by Lowe in 1862 without being considered as naturalized (Vieira, 2002). The species is used for afforestation on significant areas of the southern face of the island in the fifties and sixties of the last century (Andrada, 1990), a conditions that explains part of its current distribution. The species *A. mearnsii* is introduced in the beginnings of the 20th century to respond to the high demand of firewood and to reduce problems with erosion on low to medium altitudes on the southern face of the island, where it was sowed during the thirties and fourties (Andrada, 1990; Vieira, 2002). Considered as naturalized in the seventies (Vieira, 2002), it is increasing significantly the area of occurrence, mainly on areas close to the sites where it was introduced.

The species *Pittosporum undulatum* is another invasive tree that has a significant distribution today on the island. It is introduced as ornamental during the last quarter of the 19th century, being classified as naturalized and common around Funchal by Menezes in 1984 (Vieira, 2002). The species is considered invasive in different parts of the world (Gleadow & Ashton, 1981; Bellingham *et al.*, 2005), including different Macaronesian archipelagos (Silva *et al.*, 2008; Gil *et al.*, 2013). Although its initial distribution in the island is deeply related to the use as ornamental, its current expansion is very likely associated to bird dispersal, very likely by the European blackbird (*Tordus merula*) (Gleadow, 1982).

1.2.2.2 VEGETATION

The model of Natural Potential Vegetation proposed by Capelo *et al.* (2004), based on a phytosociological approach, identifies six climatophyllous vegetation series in the island, which are represented by the following climax communities: i) the wild olive microforest (*Mayteno umbellatae-Oleetum maderensis*), ii) the community dominated by *Sideroxylon mirmulans* (*Helichryso melaleuci – Sideroxyletum marmulanae*), iii) the mediterranean laurel forest (*Semele androgynae-Apollonietum barbujanae*), the temperate laurel forest (*Clethro arboreae-Ocoteetum foetentis*), iv) the heath tree community (*Polysticho falcinelli-Ericetum arboreae*) and the v) rupicolous community of *Erica maderensis (Parafestuco albidae-Ericetum maderensis*). The spatial distribution of such vegetation series are clearly determined by distinct bioclimatic conditions, associated to a strong altitudinal gradient (Mesquita et al., 2004).

1.2.2.2.1 THE WILD OLIVE MICROFOREST

The driest areas of the island, found on the southern coast until 200 m high, are associated to an open xerophytic micro-forest characterized by the presence of the wild olive-tree (*Olea maderensis* (Lowe) Rivas Mart. & del Arco) (*Mayteno umbellatae-*Oleetum maderensis). Exclusive of the southern coast, such dry inframediterranean community presents a high diversity in terms of endemic species, but it is restricted to very small patches on rocky walls because of an extensive transformation of landscape by human activities, namely agriculture. A significant number of taxa that integrate such community are Mediterranean, namely xerophytic, esclerophyllous and termophyllous paleomediterranean shrubs *(Olea maderensis*, *Maytenus umbellata*, *Chamaemeles coriacea)* (Capelo *et al.*, 2004). Several neo-endemic species with woody habit are also present, associated to different subseral positions (e.g. *Euphorbia piscatoria*, *Sinapidendron angustifolium*, *Echium nervosum, Crambe fruticosa*) or exploring open spaces associated to poor soil conditions (*Sideritis candicans*, *Sonchus ustulatus*).

Table I - Main attributes of the wild olive microforest (Mayteno umbellatae – *Oleetum maderensis*)

Characterisitic species[8]		**Potential distribution**	
Exclusive species	Shared species	Ombrotype / Termotype	Distribution /altitude (m.s.l.)
Olea maderensis *Chamaemeles coriacea* *Echium nervosum*	*Maytenus umbellata* *Globularia salicina* *Euphorbia piscatoria* *Myrtus communis*	Dry inframediterranean	South face: 0 - 200 m

Source: Data adapted from Capelo *et al.* (2004).

1.2.2.2.2 THE COMMUNITY OF *SIDEROXYLON MIRMULANS*

It is accepted that the *Sideroxylon mirmulans* community presents a linear and discontinuous definition. It marginates the island on the north coast to the height of 80 m, and makes the transition, at higher altitudes (200-300), between the domain of the wild olive tree community and the Mediterranean laurel forest on the southern face of the island. As mentioned before for the wild olive tree community, its current distribution is constrained to small and highly disturbed patches.

Because of the very restricted potential distribution and high disturbance, such type of vegetation it is not considered for modelling purposes in this work.

1.2.2.2.3 THE MEDITERRANEAN LAUREL FOREST

The vegetation model identifies two types of laurel forests: the mediterranean laurel forest (*Semele Androgynae–Apollonietum barbujanae*), a thermophillous infra and thermomediterranean, subhumid to humid forest, and the temperate laurel forest

---

[8] - Only species considered for modeling purposes are listed here and in the following tables. For a full description of the communities see Capelo *et al.* (2004). Communities for each series on Annexe 1.

(*Clethro arboreae-Ocoteetum foetentis*), an infra to mesotemperate, humid to hiperhumid forest.

The series of the Mediterranean laurel forest (*Semele androgynae-Apollonio barbujanae* sigmetum) is associated to a significant area o potential distribution on the island, although its low representation on current landscape because of high levels of disturbance (agriculture, urban areas). The climax forest of such series is dominated by *Apollonias barbujana,* a taxon that is accepted as a good bioindicator for the potential presence of such forest, in association to *Semele androgyna*. The vegetation model distinguishes two facies within the series. One facies is associated to the lower and dryer areas of its potential distribution, where *Myrtus communis* and *Hypericum canariensis* area used as indicators. Its potential distribution is restricted to the southern face of the island, from 300-600m m.s.l. At upper areas on the southern face (600-800m) and between 50-300 (450) on the northern one, the community is identified by the presence of a community dominated by *Globularia salicina* and *Erica arborea* (*Globulario salicinae-Ericetum maderincolae*).

Table II - Main attributes of the Mediterranean laurel forest (*Semele androgynae – Apollonietum barbujanae*)

Characterisitic species		**Potential distribution**		
Exclusive species	Shared species	Facies	Ombrotype / Termotype	Distribution /altitude (m.s.l.)
Apollonias barbujana Semele androgyna Ilex canariensis Smilax pendulina Myrtus communis Hypericum canariensis	Laurus novocanariensis Maytenus umbellata Myrica faya Erica maderincola Globularia salicina	*Myrto communis – Hypericetum canariensis*	Upper inframediterranean Termomediterranean Upper Sub-humid	South face: 300 – 600 m
		Globulario salicinae – Ericetum maderincolae	Termomediterranean Lower humid	South face: 600 – 800 m North face: 80 – 300 m

Source: Data adapted from Capelo et al (2004).

1.2.2.2.4 THE TEMPERATE LAUREL FOREST

The temperate laurel forest, the climax vegetation with wider potential distribution on the island, is mainly associated to humid and hyper-humid infra to low mesotemperate areas.

The forest presents outstanding plant diversity, with a remarkable proportion of endemics. The forest community is dominated by paleoendemic taxa, namely lauraceae phanerophytes and pteridophytes, which are considered relicts that establish a link to the Tertiary forests associated to the margins of Tethys Sea. Madeira Island is probably the territory in the Macaronesia where is possible to find the higher fraction of flora elements related to the Tethysian humid temperate forests of the Tertiary (Capelo *et al.*, 2007); Dias *et al.* (2007b). Such connection, based on Medium and Late Tertiary fossil records from Souhtern Europe, testify the existence of communities integrating several phanerophytes (*Ocotea, Apollonias, Persea, Clethra, Picconia*) and pteridophytes (*Culcita, Davallia, Diplazium, Hymenophyllum, Stegnograma*), taxa mostly associated to the temperate laurel forest. The structure and floristic composition of the forest is dominated by three phanerophytes, two Macaronesian endemic of the Lauraceae family (*Ocotea foetens* and *Laurus novocanariensis*) and an exclusive island's endemic of the Clethraceae family. It also integrates other phanerophytes (*Picconia excelsea*, *Heberdenia excelsea, Persea indica*, *Ilex perado)*, some with scarce representation (*Prunus lusitanica* subsp. *hixa*).

Table III - Main attributes of the temperate laurel forest (*Clethro arboreae – Ocoteetum foetentis*)

Characteristic species		**Potential distribution**	
Exclusive species	Shared species	Ombrotype / Termotype	Distribution /altitude (m.s.l.)
Ocotea foetens *Heberdenia excelsa* *Clethra arborea* *Euphorbia mellifera* *Prunus hixa*	*Laurus novocanariensis* *Myrica faya* *Erica maderincola* *Picconia excelsa* *Ilex perado* *Vaccinium padifolium* *Erica maderincola*	Low mesotemperate Humid to low hyper-humid	North face: 300 - 1400 South face: 800 – 1450 m

Source: Data adapted from Capelo *et al*. (2004).

In the margins of the forest or on gaps associated to streams, rocky walls, or created by natural hazards, such as landslides, it is possible to find the woody caulirosulated taxa, the neo-endemics (e.g. *Muschia wollastoni*, *Sonchus fruticosus*, *Isoplexis sceptrum*, *Euphorbia mellifera)*.

On modern days the laurel forest is mainly restricted to hilly slopes at middle elevations of the northern (windward) face of the island. A significant area associated to its potential domain is occupied by subseral stages, namely heath communities.

1.2.2.2.5 THE MICROFOREST OF HEATH TREE

The heath tree microforest (*Polysticho falcinelli-Ericetum arboreae*) is mainly installed under hyper to ultra-hyper-humid conditions of the upper mesotemperate areas above 1400m m.s.l. Dominated by big heaths (*Erica arborea, Erica platycodon* subsp. *maderincola*), such micro-forest is restricted to small areas, a distribution that became even more confined after the big summer forest fires of 2010. The area of potential distribution was deeply disturbed in the past by grazing, cutting and charcoal production. The apparently pauciespecific condition at the tree layer could be a consequence of the high disturbance, once other species might have integrated the community, namely the *Juniperus cedrus* subsp. *maderensis* or the *Sorbus maderensis*, currently reduced to few individuals. Probably, the high level of human disturbance on such areas is very likely masking the natural response of species, and reduces the arguments for a categorical corroboration (Menezes de Sequeira *et al.*, 2007).

The community is structured by species that are shared by other vegetation series.

Above 1650 m, under ultra-hyperhumid and supratemperate conditions, steep slopes and rocky outcrops dominate the landscape. Such scenario is the domain of a different type of vegetation, which is a mosaic of communities organized on the basis of soil conditions. Such pattern should be the result of deep disturbance by grazing during centuries. Perhaps, the diversity of such communities expresses the extirpartion of several taxa because of its natural inadaptance to resist to herbivory.

The most extreme conditions, the rocky outcrops, support a community of rupicolous species (*Erica maderensis, Tolpis macrorhiza, Saxifraga maderensis*), while unacessible areas with deeper soils are associated to a community of hemicriptophytes (*Armeria maderensis, Parafestuca albida*).

1.3 EFFECTS OF LAND-USE ON SPECIES' DISTRIBUTION PATTERNS

In the Macaronesian archipelagos, the biotas have been under great pressure after the human conquest, during the first millennium on the Canaries (De Nascimento *et al.*, 2009), and for the other archipelagos after the 15th century (Dias, 2007; Menezes de Sequeira *et al.*, 2007). The arrival of humans marks a drastic interference on the natural equilibrium of the islands, promoting a significant decreasing of the areas with native vegetation (Bramwell, 1990). Such interference, direct or indirect, is responsible for a significant impoverishment in terms of native elements of the biota (Fernández-Palacios *et al.*, 2011), and the introduction of new ones (Dias *et al.*, 2007a; Jardim *et al.*, 2007). It is very likely that the major cause for the scartered occurrence of some taxa (e.g. *Juniperus cedrus* on Madeira Island), (Menezes de Sequeira *et al.*, 2007), or even extinction of native species (Jardim & Sequeira, 2008a; De Nascimento *et al.*, 2009).

The laurel forest would be widely implanted over Madeira Island before human settlement, only likely absent on the summits and lowlands (Menezes de Sequeira *et al.*, 2007). It should had a more restricted distribution to the most favourable zones (windward mid-elevations) in the Canaries (Fernández-Palacios *et al.*, 2011), and a limited representation in the highest elevations of Porto Santo (Menezes de Sequeira *et al.*, 2007). In the Azores, the laurel forest would occupy all the islands, from the coast to the summit, with the exception of the highest peak (Pico) (Dias, 2007), and no evidence of presence in the Cape Verde at the arrival of the first settlers, although its likely presence on the earlier periods (see Fernandez-Palacios *et al*., 2011).

The deep impacts from human activities are very likely the main factor contributing to the severe reduction of forest cover on the islands, namely the laurel forest, and even further the cause for the extinction for some forest types (De Nascimento, et al. 2009). The area occupied by the laurel forest was significantly reduced because of exploitation for fuel and timber production, and even for agriculture, a pattern found in central and western Canaries (Jiménez *et al.*, 1996), Azores (Dias, 2007), Madeira and Porto Santo islands (Menezes de Sequeira *et al.*, 2007).

Despite differences among the islands, namely associated to specific geographic conditions (e.g. topography), disturbance assumes similar patterns. The level of disturbance is inversely correlated to the complexity of topography, an idea supported by the fact that islands with higher topographic complexity present larger areas occupied by native vegetation (Jardim & Sequeira, 2008a). This association is clear on Madeira Island, where native vegetation is mainly restricted to the northern face, while in the southern face is restricted to few small patches installed on steep slopes (Mesquita *et al.*, 2007). Such pattern is deeply related to accessibility and distance. The lower altitudes (<600/700m a.s.l), where first human settlements were installed, have been associated to agriculture for centuries (Silva & Menezes, 1946). Above such altitudes (700-1000 m) the territory was mainly associated to the exploitation of forest resources, namely timber exploitation and firewood collection; activities that had deep impacts on vegetation (Menezes de Sequeira *et al.*, 2007), and are important to explain current distribution patterns for several taxa, namely those associated to intense exploitation (*Heberdenia excelsa, Apollonias barbujana, Juniperus cedrus, Laurus novocanariensis, Taxus bacatta, Ocotea foetens, Piconea excelsa, Persea indica, Ilex canariensis, Erica arborea, Erica maderincola*) (Andrada, 1990). Because of the intense exploitation of forest resources, significant areas were afforestated during the 20th century, a process based on the use of native and exotic species (Andrada, 1990). Above 1000m m.s.l. firewood collection and grazing contributed to a decisive disturbance of native vegetation, very often reduced to herbaceous communities (Menezes de Sequeira *et al.*, 2007).

The level of disturbance was so intense that the impact of human settlement in Madeira Island is recorded in the sedimentary sequence by a dramatic increment on colluviation processes and enhanced gullying after the 15th century (Goodfriend *et al.*, 1996).

Because of all the mentioned facts, it is clear that current species distribution patterns are deeply shaped by land-use.

CAP III - ASSESSING CLIMATE CHANGE IMPACTS: METHODS, ACCURACY AND UNCERTAINTIES

Summary

1 INTRODUCTION

> *"...uncertainties of model projections must be balanced with the risks of taking the wrong actions or the costs of inaction."*
>
> (Wiens *et al.*, 2009:19729)

> *"Nature is too complex and heterogeneous to be predicted accurately in every aspect of time and space from a single, although complex, model."*
>
> (Guisan & Zimmermann, 2000:150)

The greater than ever concern about the potential impacts of climate change on ecosystems led to an increasing use of different methodologies on their assessment or prediction. In order to evaluate in a more consistent way the implications of projected climatic scenarios different modelling approaches have been developed. The results, although the associated uncertainty level, might work as *starting point* for the definition of adaptation and mitigation measures, suggesting guidelines that can give support to policymakers decisions.

Vulnerability analysis was carried out for different environments and types of organisms, such as fishes (e.g. Lasram *et al.*, 2010), amphibians (Araújo *et al.*, 2006), butterflies (Heikkinen *et al.*, 2010), and plants (Jurasinski & Kreyling, 2007). In the case of plant species, studies have been developed for different territories all over the world, at continental (e.g. Hughes, 2003; Thuiller *et al.*, 2005a; Thuiller *et al.*, 2006a), national (e.g. Iverson *et al.*, 2004; Felicisimo *et al.*, 2012) and regional scales (e.g. González, 2005; Williams *et al.*, 2005). Efforts were mainly focused on areas accepted as highly vulnerable to environmental changes, namely mountain environments (Grabherr *et al.*, 1994; Beniston *et al.*, 1996; Pauli *et al.*, 1996; Beniston & Haeberli, 2001; Theurillat & Guisan, 2001; Gottfried *et al.*, 2012). Such assessments are supported on different methodological approaches, like monitoring current changes on the field (e.g. Pauli *et al.*, 2005) or projecting future changes based on modelling approaches (e.g. Thuiller *et al.*, 2006a).

In the attempt to classify modelling approaches used to assess the potential effects of climate change on biodiversity, Heikkinen *et al.* (2006) assign models into four categories: i) dynamic ecosystem and biogeochemistry models, ii) spatially explicit mechanistic models for single species range shifts, iii) physiologically based, and iv) correlative bioclimatic envelope models / statistical bioclimatic envelope models. Among such types, the correlative/statistical *modelling* approach, also known as *habitat suitability modelling*, *was* widely used for such purpose, despite recognized limitations (Heikkinen *et al.*, 2006).

2 THE PREDICTIVE HABITAT DISTRIBUTION MODELLING APPROACH

> *Models are simplified representations of reality based*
> *on a specified set of conditions*.
> (Korzukhin *et al.* 1996:880).

The distribution of life organisms and their relationship to environmental variables is a central issue for studies carried out on biogeography, conservation and ecology. Especially after the 1980's, the quantification of organism-environment relationships became a central question, with several studies focused on exploring the distribution of plant species in both environmental and geographical spaces (Hill, 1991). Such issue gained an outstanding importance during the last two decades with the development of the habitat predictive modelling approach (Guisan & Zimmermann, 2000), supported on the increasing availability of environmental data, namely high resolution digital maps, and computing advances, namely on GIS technology and statistical techniques (Kearney & Porter, 2009). These advances gave support to a wide range of applications on different domains (Thuiller *et al.*, 2009), such as regional conservation planning (Ferrier *et al.*, 2002a; Ferrier *et al.*, 2002b; Kearney & Porter, 2009), to test biogeographic hypotheses (Leathwick, 1998), guide surveys for rare plant species (Siqueira *et al.*, 2009), assess patterns and vulnerability to invasion from alien invasive species (Thuiller *et al.*, 2005b; Vicente *et al.*, 2010), assess impacts from environmental changes on species distributions, such as climatic changes (Iverson & Prasad, 1998; Thomas *et al.*, 2004; Thuiller *et al.*, 2005a; Araújo *et al.*, 2006; Thuiller *et al.*, 2006a; La Sorte & Jetz, 2010), or application on diseases control (Václavík *et al.*, 2010).

A great achievement of such approach is the ability to evaluate the suitability of a territory to species, even for areas where species data is scarce or do not exist (Guisan & Zimmermann, 2000).

Species distribution modelling, supported on different quantitative modelling approaches, is based on the relationship between a set of environmental variables (predictors) and the known distribution for a given organism (response) (Guisan & Zimmermann, 2000; Muñoz & Felicísimo, 2004; Guisan & Thuiller, 2005; Elith *et al.*, 2006). The attributes of the data used on models calibration, the modelling technique, the theoretical assumptions, and decisions made along modelling procedure determine the type, accuracy, and models usefulness.

Different designations have been used to identify the collection of methods/techniques used, namely Habitat Suitability Models (HSM - Hirzel & Le Lay, 2008), Species Distribution Models (SDM - Zimmermann *et al.*, 2010), Habitat Distribution Modelling (Guisan & Zimmermann, 2000), or Ecological Niche Models (ENM - Peterson, 2001). And those techniques include envelope techniques, regressions, classification trees, Bayesian models, artificial neural networks, and factor analyses (*for a revision see* Guisan & Zimmermann, 2000).

According to Soberón & Nakamura (2009), all methods aim to identify suitable places to species, based on its environmental requirements. But, depending on the method used to set species environmental requirements, and the algorithm used to produce predictions or conceptual theoretical assumptions, results and interpretation may differ. The wide application of such approach supported an exhaustive debate on the limitations, divergences and conceptual problems related to its use, namely on clarifying the conceptual framework associated to niche modelling (Kearney, 2006; Soberón, 2007; Hirzel & Le Lay, 2008; Soberón & Nakamura, 2009), assessing performance of modelling techniques trough comparative analysis (Elith *et al.*, 2006; Peterson *et al.*, 2007; Elith & Graham, 2009), identifying limitations (Barry & Elith, 2006; Heikkinen *et al.*, 2006) and new trends in species distribution modelling (Zimmermann *et al.*, 2010).

2.1 MODELLING SPECIES DISTRIBUTION: THE APPROACH

Apparently no model is appropriate to all questions or scales (Battaglia & Sands, 1998). The most appropriate model should present the simplest structure, meet the purposes of the project, satisfying requirements of resolution and accuracy defined by the user (Battaglia & Sands, 1998).

The attributes of a model are determined by the objectives associated to its end-use. It includes decisions about theoretical assumptions (equilibrium/non-equilibrium), spatial and temporal resolution, processes and parameters to be included in the model, number and type of variables, and type of inputs and outputs.

Different classifications have been proposed in order to classify models according to their attributes (see Guisan & Zimmermann, 2000). According to Levins' classification (1966, cited by Guisan & Zimmermann, 2000), any model is the result of a trade-off between generality, reality and precision. In each model one of those properties is sacrificed when improving the other two, a procedure that is determined by model end-use. According to such approach, a model can be resolved to a category based on its relative position between the three properties: i) **analytical** or **mathematical**, when is designed to predict accurate response within a simplified reality, the model sacrifices reality for generality and precision; ii) **mechanistic**, **physiological**, **casual** or **process-based model,** when a model gives more importance to reality and generality; predictions are based on real cause-effects relationships, and models evaluation is based on the theoretical appropriateness of the predicted response, rather than on predicted precision (Pickett *et al.*, 2007); and iii) **empirical, statistical (correlative) or phenomenological,** models focused on precision and reality, based on empirical facts, and do not describe realistic cause-effect between model parameters and predicted response, or inform about underlying ecological functions and mechanisms.

Resolution of a model is based on the spatial and temporal scales, components that are of special concern on predictive distribution modelling. Complexity is associated to the number of parameters in the model (type and number of environmental variables and processes). An increase in the number of processes and factors determine higher explanatory power, but carry higher levels of uncertainty because of increased complexity and error on predictions (Håkanson, 1995). Model complexity is also dependent on resolution, once increasing resolution often determines higher model complexity. On the opposite, models became simpler and the accuracy of predictor variables less critical decreasing resolution, accepting that complex non-linear processes can be modeled after simple relationships when resolution is reduced (see Battaglia & Sands, 1998). But the decrease on resolution, namely the spatial one, is generally not an option used to reduce complexity, once such approach would compromise the capacity of the model to produce accurate results in terms of distribution patterns. In addition, very often the appropriate resolution is not achieved because of lack of data with higher resolution.

In the case of the *generality* attribute, associated to the diversity of situations (territories, domains) where the model can be applied, it is usually independent in respect to precision, but is deeply dependent on resolution (Battaglia & Sands, 1998). Models structured on high resolution data require higher detail and parameterization, allowing an increase in realism (reality) and a decrease in the potential to generalization, once such models include

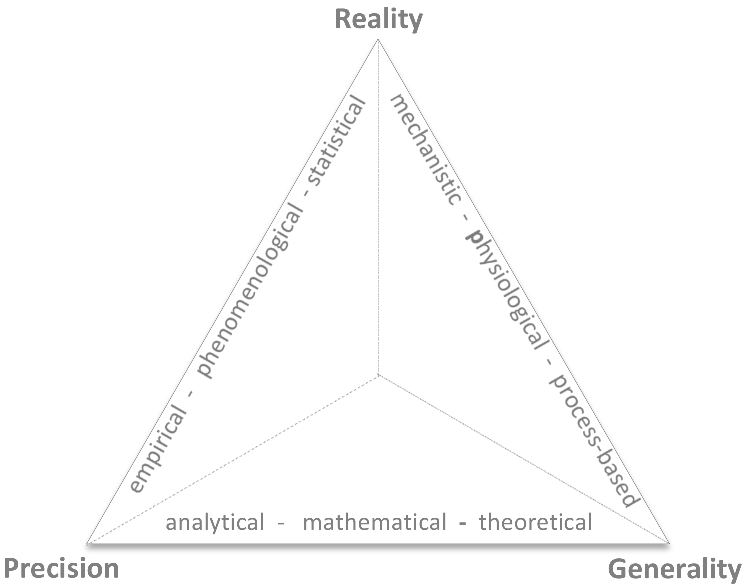


Figure 6 - Classification of a model after its intrinsic properties

Adapted from Guisan & Zimmerman, 2000: 150.

parameters that very often represent only a fragment of the plant-environment system. On the contrary, models that have a high degree of generality can be applied to a wider range of situations, despite the decrease on reality (see Battaglia & Sands, 1998).

Despite helpful, several arguments support the idea that such classification is considered too restrictive and difficult to apply. First, precision and generality are not necessarily in conflict, although most of the predictive vegetation models are the result of a trade-off between these two attributes. Second, both models (empirical / mechanistic) can have high or low degree of generality depending on the organism's attributes (distribution patterns, ecology). So, mechanistic models do not have necessarily to be imprecise. Third, despite the fact that predictive models are generally empirical by nature, they can be based on physiological parameters, being more mechanistic than models based on topographic parameters (Guisan & Zimmermann, 2000). In agreement to such arguments Korzukhin *et al.* (1996) propose a different approach. They accept that pure empirical or mechanistic models do not exist. Those are theoretical concepts associated to opposite edges of a continuum, within which a model can be positioned according to affinities to the attributes assigned to each edge (Mäkelä *et al.*, 2000).

Despite limitations in the application of such classification, a significant number of studies on predictive distribution modelling accepts the dichotomy between mechanistic versus empirical models, regarded as mutually exclusive (Korzukhin *et al.*, 1996; Kearney & Porter, 2009).

Empirical models are usually focused on predicting spatial and quantitative outcomes based on a statistical description of relationships, while mechanistic models are clearly focused on defining rules from the assessment or understanding of key mechanisms that regulate organism-environment relationships (Korzukhin *et al.*, 1996).

In practice, the relative position of a model between the two perspectives is grossly determined by the type o environmental variables used on models calibration, and how data is used to produce predictions. Each perspective is based on different theoretical assumptions, namely the acceptance of *equilibrium or non-equilibrium* in the response on species to environment over time, defining the opposition between *static* and *dynamic* models. Both models are suitable to apply to a range of spatial or organizational scales (tree level, stand level, landscape level). But mechanistic models should be more profitable to improve our knowledge and ability to predict (see Korzukhin *et al.*, 1996).

According to Korzukhin *et al.* (1996), more important than criticize empirical models for being too simplistic and unrealistic, or process models for their abstraction and impracticability, it is necessary to accept that each modelling approach is focused on different purposes. Empirical models have been primarily focused on predicting outcomes, while process models have been primarily directed to understand relationships.

2.1.1 STATIC VERSUS DYNAMIC MODELLING APPROACHES ON SPECIES DISTRIBUTION MODELLING

The great majority of habitat distribution models have an empirical, comparative, static and correlative nature. Predictions rely on empirical relations between known distribution patterns and sets of environmental variables (Iverson & Prasad, 1998; Guisan & Zimmermann, 2000; Thuiller *et al.*, 2008). Based on statistically derived response surfaces, static models assume a time-independent *equilibrium* between species' response and environmental conditions. Such assumption is in opposition to a *dynamic* modelling perspective, which is the support for mechanistic models. In this case, predictions integrate the perspective of dynamic relationships between variables and species distributions (Kearney & Porter, 2009), based on the more realistic concept of *non-equilibrium* (Pickett *et al.*, 2007).

2.1.1.1 MECHANISTIC MODELS OR PROCESS-BASED MODELS

Mechanistic models, also identified as *explanatory*, *process-based*, *biogeochemical*, or *ecophysiological models*, aim to simulate the response of species to environmental predictors based on physiological mechanisms (Woodward & Williams, 1987). The mathematical algorithms used to simulate the biological systems incorporate a mechanistic description of physiological and ecological mechanisms that are critical for species distribution (Kearney & Porter, 2009). The realized response is based on a parameterization of the fundamental niche, coupled with additional rules of competitive behavior (Guisan & Zimmermann, 2000).

The incorporation of range-limit processes on models will expand the potential to application on other time/spatial contexts. The achieved deep understanding about the constraints on limiting distribution and abundance reinforce the robustness of the models when extrapolation is required, a common goal on assessing impacts from climate change on species distribution.

One of the main constraints on the use of mechanistic models is that required data used on parameterization is usually not available and is difficult to obtain, a feature that reduces the applicability of such approach (Battaglia & Sands, 1998). In addition, the development of habitat models of mechanistic nature have been limited by difficulties on linking specific traits of the organisms (physiological, morphological, behavioral) to their environments, namely to climatic and terrain variables (Kearney & Porter, 2009).

Such modelling approach is common on studies about forest management (see Amaro *et al.*, 2003), where growth and productivity, severely affected by physiological constraints, are important features to predict.

2.1.1.2 EMPIRICAL MODELS

Empirical models are a very common approach on species distribution modelling. The wide range of applications associated to such type of models is based on the rapid achieving of quantitative and spatially explicit outputs (Korzukhin *et al.*, 1996), and low requirements in terms of data, namely the use of sparse data in terms of species distribution (Ferrier *et al.*, 2002b). This is an advantage within a context where detailed species-specific information is not available, namely knowledge about the physiological constraints that control the mechanistic links organism-environment (Lischke *et al.*, 1998; Kearney & Porter, 2009). Predictions are based on statistical analyses, which identify interactions between known species distributions (presence or abundance) and fundamental/meaningful environmental predictors (e.g. climate, land-cover, topography) (Guisan & Zimmermann, 2000; Pearson & Dawson, 2003; Guisan & Thuiller, 2005; Araújo & Guisan, 2006; Elith *et al.*, 2006). Such models, also categorized as statistical models, tend to be simple in terms of number and type of environmental predictors, a trait that can be determined either by decision or by the lack of data. Another advantage is their versatility, which permits a relatively rapid analysis for numerous individual species, and gives an important help on extrapolating distributions across large regions (Ferrier *et al.*, 2002b).

Hybrid approaches have also been applied, namely on studies focused on forest management. The hybrid approach, rather than correlate species' distributions to environmental predictors, starts assessing the limitations imposed by specific predictors (e.g. climatic), which impose potential limits in terms of physiological constraints (e.g. photosynthesis) for a selected species. The obtained distribution serves as a reference to obtain the distribution for other species, based on how predictors (e.g. climatic conditions) constrain physiological attributes (e.g. photosynthesis) (Coops *et al.*, 2009).

2.2 ASSESSING CLIMATE CHANGE IMPACTS ON SPECIES DISTRIBUTIONS: ARE STATISTICAL MODELS USEFUL?

A correct interpretation of results from species distribution/habitat suitability models demands a previous clarification about several issues related to such modelling approach. The following discussion aims to clarify the sense that is associated to the use of critical concepts, and provide support to methodological options of this work, namely the pertinence of using habitat distribution models of statistical nature on assessing climate change impacts on species distribution. To achieve such purposes, we focused the discussion on two main topics: **i)** what do habitat distribution models really predict and which interpretation is acceptable for models results, **ii)** how important are the sources and level of uncertainty on habitat distribution models.

2.2.1 WHAT SPECIES DISTRIBUTION MODELS REALLY PREDICT?

There are different perspectives in the interpretation of niche-based modelling results, namely what models' results actually represent (Araújo & Guisan, 2006; Kearney, 2006).

Predictions of species' geographic distributions (actual and potential) based on statistical models are supported on the identification of the species' environmental requirements ("niches" or the ecological profile) from known occurrences (presence/absence or abundance). Such procedure is based on a correlative approach between species' known occurrence within a territory (presences/absences in a geographical space) and related ecological conditions (sets of environmental variables). The derived ecological profile ("niche) is then used to predict areas of distribution (Peterson, 2006). As a critical step for results' accuracy, a question arises: which type of "niche" is achievable using such approach?

The answer to that question will be supported on a discussion about basic concepts that are critical to species distribution modelling in the following text.

2.2.2 CONCEPTS AND ASSUMPTIONS

Species distribution modelling is deeply rooted in the niche theory, namely in the Hutchinson's perspective of fundamental and realized niche concepts (Araújo & Guisan, 2006). Therefore differences in the interpretation of models are very likely related to the existence of different senses associated to the use of critical concepts.

A significant number of studies focused on estimating areas of distribution for different types of organisms were supported on niche-based models of correlative nature (Guisan & Zimmermann, 2000; Peterson, 2006). But the lack of precision and inconsistent use of concepts, such as "niche", "environment" and "habitat", might have supported distorted interpretations of models' results (Whittaker *et al.*, 1973; Kearney, 2006; Soberón & Nakamura, 2009).

2.2.2.1 THE NICHE CONCEPT

Different assumptions have been used to define the niche concept, a divergence that arrives from the type and emphasis given to the variables considered (Chase & Leibold, 2003). According to Whittaker *et al.* (1973), three senses must be distinguished in the use of the niche concept: i) the ***functional*** perspective, related to the role or position of a species within a community; ii) niche as ***habitat***, considering the relationship between the distribution of a species in response to available habitats and other communities; iii) and a combination of both perspectives (***functional* + *habitat***).

Proposed by Grinnell (1917), the niche concept is first associated to a description of environmental conditions for a territory (e.g. food resources) where a species occurs. Such perspective seems to accept "niche" in the "**habitat**" perspective, considering abiotic factors as critical to set the distributional area of an organism (Whittaker *et al.*, 1973). In fact, Grinnell (1914, 1917) was a pioneer on inferring factors that limit distribution based on spatial distribution of species, advancing the idea that species ecological/environmental niche is related to their area of distribution. He also discusses the importance of key issues for species distribution modelling, namely the role of different factors at different scales, such as the contribution of climatic variables to shape species distributions at coarse-grained scales.

The **functional** perspective of niche introduced by Elton (1927), which considers the role of a species in its community, namely in terms of biotic interactions. The importance gave to the biotic environment at the time, namely competition for resources, is very much related to the type of organisms in study (animals), which explains, in part, the importance attributed to role of the organism in the community as determinant for survival, growth and reproduction.

Such discussion about the type of variables that should support the "niche" and their associated spatial resolution was revitalized by Hutchinson (1957, 1978).

2.2.2.2 REALIZED / FUNDAMENTAL NICHE

Hutchinson introduces the concepts of *fundamental* (1957) and *realized* (1978) niches, which must be interpreted as sections of the environmental space (Soberón & Nakamura, 2009). He assumes that the *fundamental niche* is an *n*-dimensional space set by *n* environmental variables (*scenopoetic variables* – e.g. climatic variables and food resources), within which species can survive. But due to biotic interactions (e.g. competition, predation, pathogens) species may be absent from some sections of the fundamental niche. The section of the fundamental niche that really supports the presence of an organism, after considering the biotic interactions is called *realized niche* (Hutchinson, 1978). While the perspective of niche present in the concept of *fundamental niche* of Hutchinson is based on a *Grinellian* prespective, closely similar to the idea of *habitat*, the concept of realized niche reveals more agreement to the perspective associated to niche's *Eltonian* view (Soberón, 2007).

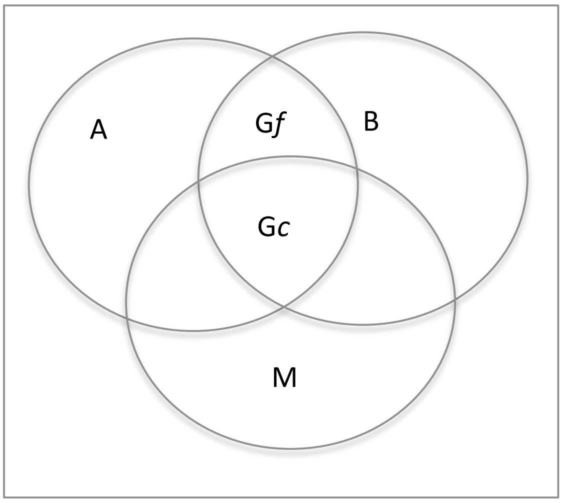
2.2.3 WHAT TYPE OF NICHE DO NICHE-BASED CORRELATIVE SDMS ESTIMATE ?

Most of the studies estimated the "niche" as an intermediate step to predict geographical distributions, and seldom the main concern (Soberon & Peterson, 2005). Depending on assumptions, species distribution models can be regarded as an approximation to species' *fundamental niche* (Soberon & Peterson, 2005), or a spatial representation of the *realized niche* (Guisan & Zimmermann, 2000; Pearson & Dawson, 2003), when assuming that observed distributions used to estimate species-climate relationships are already reproducing the influence of non-climatic factors (Araújo & Pearson, 2005). Such difference on the interpretation of niche models reveals the existence of different perspectives on the formulation of the Hutchinson's *fundamental* and *realized* niche concepts, a condition that might result from a number of difficulties that hamper a full integration of the perspective assigned to such concepts into niche modelling (Araújo & Guisan, 2006).

According to Soberon (2007) the presence of a species on a set of locations is dependent on three main elements:

i) an *intrinsic* and *independent density growth rate,* which is determined mostly by the *scenopoetic* environment variables, defined at coarse-grained resolutions, a view compactible to the *Grinellinan* perspective of niche;
ii) a *resource-interaction component*, which is determined by the biotic context (bionomic variables: competition, predators, pathogens) and the use of resources, their supply and impact of species on them; a fraction of growth associated to *Eltonian* niche processes;

iii) the chance to receive or send propagules (rates of dispersal), a component that determines the metapopulatuion strucuture and source-sink dynamics.



Legend: **A** – areas where scenopoetic variables are suitable to species presence*;* **B** – areas where biotic interactions (competition, predation, disease - *bionomic* variables) are favorable; **M**: accessible areas to species, having by reference dispersal capacity, barriers and distances, for a defined period; **Gc**: current geographic distribution, set by suitable biotic and abiotic conditions, within an area accepted as accessible; **Gf**: potential area of distribution.

Figure 7 - Diagram representing factors that affect distribution in the geographic space (ABM model) (Adapted from Soberón, 2007; Soberon & Nakamura, 2009).

The occurrence of a species on a site indicates therefore that it was accessible, that scenopoetic variables allow a positive intrinsic growth rate, and that species can compete and coexist, or exclude competitors (Soberón, 2007). That perception demands that data for the three elements should be used on species distribution modelling in order to achieve results for actual geographic distribution, based on the estimation of the realized niche. But data for the biotic context and dispersion is usually unavailable, which determines that much of the modelling exercises are based on scenopoetic variables. Once scenopoetic variables are accepted to exert a more determinant influence on shaping distributions at coarse resolutions (Pearson & Dawson, 2003), it is acceptable that studies associated to coarse resolutions, which rely on *scenopoetic* variables (e.g. climatic, topographic), tend to achieve a closer estimation of the fundamental niche. But, admitting difficulties on sampling all the ecological range for a species, it must be accepted that models might not be able to fully capture the “fundamental ecological niche” of a species, underestimating therefore their distribution. Nevertheless, such limitation should have an irrelevant contribution to decrease ability of the models to produce reliable predictions. Based on a *Grinellian* perspective of niche, it is acceptable that the estimation of the fundamental niche is achievable at coarse resolutions (large territories), and predictions based on species distribution modelling approaches can be interpreted as potential distributions. Once variables associated to the biotic context are measured at fine-grained resolutions, whenever they have a major contribution to shape species distribution, it is expected that predictions for such scales, based on the *Eltonian* view of niche, represent the realized niche. But several difficulties contribute to reduce the possibility of using an *Eltonian* perspective of niche on species distribution modelling, and, by consequence, the chance to fully estimate the realized niche. The first obstacle is related to the fact that such variables are very often obtained from a set of parameters that are difficult to obtain. As considered by Soberón (2007), obtaining data for competition on resources, setting a resource-consumer model, would demand available data about spatial and temporal availability of resources, rates and impacts from exploitation. But, it is almost impracticable to measure all the parameters, namely because complex competitive interactions are difficult to predict, and the *Eltonian* processes (biotic interactions) present a fine-grained structure. Consequently, considering the possibility of measuring such variables on the field, it would be necessary to carry out an extensive monitoring process to obtain data to include in the models, with a very detailed scale if compared to scales used on monitoring *scenopoetic* variables, which present lower spatial heterogeneity (Soberón, 2007). Besides the scarcity of bionomic data, ambiguities remain about the influence of biotic interactions with opposite effects (competition/mutualism), the capacity to collect such data because of their very heterogenic spatial patterns, and the spatial resolution at which such interactions are relevant (Araújo & Guisan, 2006). Moreover, it is important to include biotic and dispersal as predictors in modelling, and do not assume that current distribution already reveals its influence, once local biotic factors deeply influence predictions (Meier *et al.*, 2010).

The lack of information about data for bionomic variables, which are expected to be more determinant at fine-grained scales (Soberón & Nakamura, 2009), seems to be an important factor to explain why they are seldom incorporated on niche modelling (Soberón, 2007). In order to reduce such drawback, some authors suggest that bionomic variables and dispersal can be modulated from scenopoetic variables (Leathwick & Austin, 2001). Once the realized niche is difficult to estimate at fine-grained resolutions, are species distribution models able to estimate the fundamental niche at such scales?

Despite being easier to integrate on species distribution modelling, the *Grinellian* perspective of niche faces several limitations when applied at local scales. Even considering the capacity to collect data for the entire geographical range, the fact that distribution is deeply affected by biotic interactions contributes to reduce the chance to fully estimate the fundamental niche. But accepting that current distribution reveals the influence of biotic interactions supports the idea that habitat model predictions are spatial representations of the realized niche (Pearson & Dawson, 2003), a perspective that allows the operationalization of the *Eltonian* perspective of niche. Moreover, it is expected that a calculation of the fundamental niche is unachievable when using correlative models at high spatial resolutions, once a full definition of a species' fundamental niche can be calculated only from experimental approaches (Kearney & Porter, 2009).

Most of the modelling exercises have been supported on the *Grinnellian* perspective of niches. It is a perspective where the duality between environmental and geographical spaces, first discussed by Hutchinson (1957), is easier to set, once correspondence between scenopoetic variables and geographical grids is easily achieved (Soberón & Nakamura, 2009). That is probably the reason, together with the fact that most of the modelling approaches are based on statistical models, why it is more common the use of *habitat suitability models* or *species distribution models* labels, rather than *niche models*, once it is clear that an habitat or a distribution is different than modelling a niche (Soberón & Nakamura, 2009). Habitat suitability models (HSMs) or species distribution models (SDMs) can therefore be seen as operational applications of the ecological niche, using environmental variables to predict the presence/ absence or the abundance of a species throughout the geographical space. Based on such assumption Hirzel & Le Lay (2008) consider that the concept of the ecological niche relates environmental variables to fitness of species, while habitat suitability models relates environmental variables to the likelihood of occurrence of a species. And that distinction could also be based on the type of variables in use. Distribution models based on environmental predictors yield results of *potential habitats* for species (suitable areas), but if combined with spatially factors (e.g. dispersal) results are related to *potential geographical distributions* of species (Araújo & Guisan, 2006). According to (Kearney, 2006) although species distributions can be potentially predicted through modelling of the correlations between organisms known occurrence and habitat conditions, the fully definition of the distribution limits demands the use of a mechanistic approach on modelling the organism's niche. An approach that demands available data about several variables, namely those that include information about the way how morphology, physiology, and response determines the environment features selected when occurring in a particular habitat, and how those environmental conditions affect fitness (survival, growth, reproduction). According to such perspective, "niches" are defined mechanistically, based on physiological experiments, while "habitat" would be predicted trough correlative methods (Kearney, 2006; Kearney & Porter, 2009), a common approach on species distribution modelling that seems to give preference to the *Grinnellian* perspective of niche.

In short, we may assume that fundamental niche is achievable for coarse resolutions, and can be estimated by empirical niche-based models of correlative nature. In the case of fine-grained resolutions a mechanistic approach should be more appropriate, and will support the calculation of the realized niche. While few obstacles are expected for the first scale, a significant number of difficulties is surrounding modelling at high resolution scales, because of the nature of the predictors assumed to be necessary (biotic and abiotic) to capture the set of ecological conditions associated to the survival of a population. A target that becomes even more complex if we consider variables that are ambiguous in terms of contribution or difficult to achieve on niche estimation, such as the impacts of species on the environment (Chase & Leibold, 2003).

2.2.3.1 NICHES AND AREAS OF DISTRIBUTION

While *area of distribution* is associated to the *geographical space*, assumed as the set of grid cells where a species can be actually/potentially detected, the ecological niche is associated to the *environmental space*, a multidimensional volume set by a number of ecological variables (Soberón, 2007).

According to Soberón & Nakamura (2009) there is a clear association between the concepts of niche (fundamental (Hutchinson, 1957), potential (Jackson & Overpeck, 2000), realized (Hutchinson, 1978)) and areas of distribution; where the *area of* *distribution* may be considered the operationalization of the *niche* concept. According to Soberón (2007) the clarification of the "niche" concept in relation to "area of distribution" is dependent on three main distinctions, which he assumes as critical to understand differences between the *Grinellian* and *Eltonian* perspectives of niche: i) niche as "habitat" versus niche as "function" (Whittaker *et al.*, 1973); ii) niche defined at local scales versus niche defined at large spatial extents (Pulliam, 2000); iii) resource versus environmental (e.g. climatic, topographic variables) predictors. The niche as *habitat* is based on the use of non-interactive, non-consumable and less spatially heterogeneous *scenopoetic variables*, to define the associated multidimensional space, which is related to the idea of *fundamental niche* in the case of large territories or coarse-grained resolutions. Under such conditions, niche-based models of correlative nature are appropriate to predict species' potential area of distribution. In the case of assuming niche under the *function* perspective, *bionomic variables* should integrate the group of predictors used on models calibration, because of their influence at the demographic, physiological and behavioral levels. Usually unavailable, such variables are measured at high-resolution spatial scales, where they are expected to be determinant to shape species distribution (Pearson & Dawson, 2003). Integrating such variables, and based on a mechanistic approach, it is possible to calculate the realized niche and predict species potential distribution for fine-grained resolutions. On both perspectives, the use of spatially explicit variables, such as predictors related to dispersal, shall support the calculation of the actual area of distribution (Araújo & Guisan, 2006). Restricting niche definition to the type of variables simplifies the integration of niche theory in niche modelling, and promotes the use of large datasets available for scenopoetic variables (Soberón & Nakamura, 2009).

It is difficult to represent the *Eltonian* factors as static values assigned to a grid, in the same way that it is usually done for the scenopoetic variables when constructing the environmental space. In fact, biological features associated to most species are related to high spatial resolution and are highly dynamic in time and space, which demands a dense sampling design. But, ignoring that environmental space is irregular and changes in time, and neglect the effects of biological conditions (competitors, diseases, pathogens) introduces uncertainty in the interpretation of results of species distribution modelling (Soberón & Nakamura, 2009). In order to overcome such limitations, often habitat models are based on the *Grinnellian* perspective, which niche theory does not include evolutionary factors.

2.2.4 MODELLING GEOGRAPHICAL RANGE SHIFTS UNDER CLIMATE CHANGE SCENARIOS AT HIGH RESOLUTION SCALES: UNCERTAINTIES

Modelling complex relationships in ecosystems always implies a certain level of uncertainty. Thus, results must be interpreted with caution, and always taking into account the assumption that models are a simplification of a more complex reality.

The level of uncertainty using habitat models is a critical issue on assessing climate change impacts on species distribution (Heikkinen *et al.*, 2006), particularly at spatial scales of high resolution, such as the one in use in this work.

Several aspects contribute to generate uncertainty when assessing changes on species distribution based on habitat modelling approach (Fielding & Bell, 1997; Barry & Elith, 2006; Pearson *et al.*, 2006). Those uncertainties are associated to the high variability of results and problems with accuracy, namely the existence of different sources of error that usually are not considered sufficiently (Barry & Elith, 2006).

Uncertainties are of different nature, and can be classified as **intrinsic,** associated to procedures and attributes associated to the habitat modelling approach, or **external.** Among external sources the following can be identified **i)** the magnitude and course of the climatic change, **ii)** uncertainties inherent to climate change scenarios resulting from downscaling processes (regionalization) (Allen *et al.*, 2000), **iii)** uncertainty about species resilience or ability to adapt to projected climatic changes (Thomas *et al.*, 2001), **iv**) impacts on plant productivity from increasing concentration of atmospheric CO2 (Iverson & Prasad, 2002), **v)** changes on predictors not included on calibration because of unavailable data, despite their potential importance to species distributions (e.g. horizontal precipitation), **vi)** uncertainties about changes on relationships between predictors and species under future climatic conditions, namely in the case of non-analog climates (Williams *et al.*, 2007), **vii**), changes on species distribution because of human-induced environmental changes **viii**) and the quality of the data used on models' calibration.

In the group of **intrinsic** sources, different factors contribute to uncertainty, namely **ix**) the inconsistent use of concepts and difficulties on integrate successfully some of the ideas associated to concepts of the niche theory (Araújo & Guisan, 2006; Kearney, 2006), **x**) assumptions in use, **xi**) the variability of models' results, determined by the diversity of modelling techniques in use and parameters used on models calibration, **xii**) or the predictive accuracy of models' results, determined by restrictions or limitations associated to the modelling technique, namely specific traits of the classification algorithm, or caused by features associated to the ecology of the organism, the "algorithmic" and "biotic" errors type according to Fielding & Bell (1997).

Concerning uncertainties about how flora and vegetation might respond to climate change, it is important to have in consideration that response to climate change depends on the specific attributes of the organism and habitat conditions (biotic and abiotic conditions) of a territory. Projected changes on temperature and precipitation regimes might determine opposite impacts, such as an increase on mortality because of higher vulnerability to pests and diseases (Safranyik *et al.*, 2010), or a significant growth in productivity (ACIA, 2004), depending on the territory, the magnitude and sense of the changes, and species attributes. Apart from the variable magnitude of climate change between territories, it is expected that opposite trends occur within a territory, because of differences on species' vulnerability to environmental changes. Some might be favoured while others may suffer deep range contractions or even get extinct (Foden *et al.*, 2007; McKenney *et al.*, 2007; Brook *et al.*, 2008). Moreover, climate change might have deeper impacts because of a synergetic combination of factors, and sometimes some of these factors are not included as environmental predictors on models calibration. For example, populations of fragmented habitats because of human disturbance are likely more vulnerable to changes on climatic conditions. In addition to all uncertainty about plant resilience or ability to adapt, responses of species to environmental predictors may change, once they are typically nonlinear, and are dependent on the spatial, temporal and organizational scales (Lischke *et al.*, 1998). And sometimes the scale used on modelling procedures limit the ability of the model to detect and simulate plant-environment relationships.

The assessment of impacts from climate change on plant species or vegetation communities faces several challenges, namely the wide range of spatial and temporal scales that could be considered. Depending on the spatial scale (small territories/large territories), on the entity considered (species/community), or the domain (phenology, health, distribution), the methodological approach and type of data should differ. And critical data is not always available or is difficult to obtain. In terms of spatial and temporal scales, it is accepted that changes associated to climate change might occur as short-term weather fluctuations (e.g. frosts), or as longer-term changes (e.g. length of the growing season), or in terms of frequency of extreme events (e.g. droughts). Climatic models are able to assure a fully match for large territories and reproduce forecasts of change for a century. But they do not integrate data for topographical scales and trends in terms of extreme events, once frequency and magnitude of extreme events are highly uncertain (Kirschbaum et al., 1996). Extreme events might produce serious impacts at high-resolution scales, being more decisive than changes at coarse spatial resolution. Moreover, at local scales, the response of a species at the margins of its distribution is driven by a combination of factors, such as climate, biotic interactions, fragmentation of the habitat, population dynamics, etc.

The response time is another feature that masks the effects of climate change on species distribution, and reduces our capacity to evaluate accurately the impacts. While expansion could eventually be detected in a short-time period, the contraction might takes longer to be detected (see Woodward, 1987).

2.2.4.1 UNCERTAINTY ESTIMATING RANGE SHIFTS USING SDMS: THE ENDOGENEOUS PROBLEMS

Assessment of future climate change effects on species range limits have been based on habitat modelling approaches of correlative nature (Pearson & Dawson, 2003; Thuiller *et al.*, 2008). The relationships found for current climate, inferred from environmental conditions associated to known geographical range, are projected into the future, in order to assess changes on distributions. It is expected that such changes might be more pronounced at the edges of the environmental range (Anderson *et al.*, 2009), because of their higher sensitivity to environmental changes, conditions mostly associated to the fact that populations are restricted to particular habitats, usually less favourable within a matrix of unsuitable landscapes, and presenting lower number of individuals (Vucetich & Waite, 2003; Hampe & Petit, 2005).

2.2.4.1.1 THE VARIABILITY AND UNCERTAINTY ON MODELS' RESULTS

The high variability on predictions from bioclimatic modelling is considered a weakness and a source of uncertainty, and have been used to challenge the capacity of habitat models to produce accurate results under scenarios of climate change (Thuiller *et al.*, 2004a; Araújo *et al.*, 2005b; Araújo *et al.*, 2006; Pearson *et al.*, 2006). Such variability is associated to the wide variety of modelling approaches in use on predicting species' distributions and the existence of several decision-dependent stages along modelling procedure.

Comparisons among the most used techniques pointed out significant differences on performance and great variance on models' predictions from alternative bioclimatic modelling approaches (Guisan & Zimmermann, 2000; Elith *et al.*, 2006; Pearson *et al.*, 2006). Differences on algorithms for each modelling technique explain the great divergence on models' results, once they are based on different assumptions and mathematical functions. In consequence, there are different degrees of vulnerability among modelling techniques in terms of exposure to spatial and environmental species' traits, which affect their predictive performance (Araújo & New, 2007).

In addition, even small differences on the type and number of predictors can assure significant differences on predictions for future distributions (Thuiller *et al.*, 2004a). In fact, results are highly sensitive to the attributes of the species occurrence data and the environmental predictors used on models calibration, which have great influence on the accuracy of models results.

2.2.4.1.2 THE ACCURACY OF MODELS RESULTS

Despite their common use, habitat predictive models present some limitations assessing shifts on plant distribution under climate change scenarios. As static predictive models, based on empirical field data sets, they are not able to deal satisfactorily with changing environmental conditions (Guisan & Zimmermann, 2000). Their competence to predict species distribution for present environmental conditions at large spatial scales (large territories) is not in question (Ferrier *et al.*, 2002b; Heikkinen *et al.*, 2006). However, their appliance is hampered by limitations when predictions are produced for high resolutions (local scales), projected to other geographical territories or to new ecological conditions. Limitations are mainly determined by the static, empirical and correlative nature of the models, and by the fact that they do not integrate key physiological processes as parameters in the calibration procedure, attributes that constraint their aptitude to assess relationships to species/environment under new environmental conditions (Korzukhin *et al.*, 1996; Battaglia & Sands, 1998; Landsberg, 2003). Besides their correlative basis, the static nature of the models derives also from the assumption that species-specific traits (dispersal, migration, plasticity, adaptation) or biotic interactions will not change under future climatic scenarios, and won't interfere in the relationships between distribution and environmental variables. Such assumption, associated to the idea of "niche conservatism", underlies many applications of habitat models, even when projecting niche predictions across space or time. Niche conservatism refers to the idea that, to some extent, there is a tendency on species to maintain inherited niche characteristics or evolve relatively slowly within lineages, an idea that is supported on empirical and theoretical evidences (for a revision see Soberón & Nakamura, 2009). However, such assumption is surrounded by uncertainties, once there are doubts about the features of the niche that are being conserved and the real meaning of conservatism, and new insights on such domain reveals opposite views (Broennimann *et al.*, 2007).

In terms of projection to other geographical territories, the accuracy of the models could be compromised by the fact that similar conditions in terms of indirect gradients (e.g. topographic position; altitude) can be associated to different conditions in terms of direct and resource gradients (Guisan & Zimmermann, 2000). This is especially important when dealing with models developed for small territories. In these cases, very often calibration is significantly based on indirect gradients, and even direct gradients in use (rain, temperature) express a deeper influence from indirect ones, usually detected on higher correlation scores. In this context, the use of indirect gradients as parameters (e.g. topography, geology, soil conditions) determines that models' applicability is restricted to the scope of the original data (ecological and geographically)(Korzukhin *et al.*, 1996). In case of projections to new ecological conditions, the calibrated model contains no information about the relationship between species and new conditions of the environmental gradient, set outside the current range. So, it is expected that habitat models calibrated from current conditions will not be able to predict accurately the response of species in the context of novel climates (Williams *et al.*, 2007). This is one of the main arguments that support the use of a mechanistic approach. Considering its nature, the mechanistic modelling approach becomes more appropriate to predict the distribution of an organism, especially when it is required the projection of its distribution to a new territory or environmental conditions, as for climate change impacts assessment (Kearney, 2006). Unfortunately, data about species' physiological response to environmental gradients, used on parameterization, is not available for Madeira Island.

Accuracy of predictions are also severely affected by biasing effects derived from attributes of the data used on calibration, once modelling techniques are sensitive to **i**) sample size (number of occurrence records) (Stockwell & Peterson, 2002; Wisz *et al.*, 2008); **ii**) type of occurrence data: presence-absence versus presence-only data (Brotons *et al.*, 2004); **iii**) the ratio presence-absence records (Jiménez-Valverde & Lobo, 2006); or **iv)** errors associated to data collection procedures, namely sampling bias, which is determined by accessibility in the geographical space, and often contributes to introduce bias on sampling the environmental range (Hirzel & Guisan, 2002; Kadmon *et al.*, 2003), and errors on species identification; **v)** failure on including all relevant ecological factors as predictors in the modelling procedure (Fielding & Bell, 1997), **vi)** limited understanding of species dispersal ability (Pearson & Dawson, 2005), **vii)** insufficient knowledge about the mechanisms that rule species distributions (Fielding & Bell, 1997; Barry & Elith, 2006; Pearson *et al.*, 2006), **v)** and lack of data about biotic interactions (Davis *et al.*, 1998). In addition, variability of predictions is highly associated to decisions made along modelling procedures. As example, the selection of a threshold to transform the probability to binary scale will affect results, namely the predicted area.

2.2.4.1.3 CALIBRATION DATA: SPECIES' OCCURRENCES

The attributes of species' occurrence data are very important, not only the type of available data (presence-only, presence-absence, abundance), but also the accuracy. The type of data might limit the options in terms of modelling techniques, which in turn affects the results (Austin *et al.*, 2006; Real *et al.*, 2006; Meynard & Quinn, 2007). In terms of modelling methods it is possible to distinguish between **i**) profile techniques, which only request presence-only data, **ii**) group discriminative techniques, which predictions are based on presence/absence data, with the possibility to generate absences (pseudo-absences or background data) when unavailable (Mateo *et al.*, 2010), and **iii**) quantitative methods, when species abundance data is available (Robertson *et al.*, 2001). Species abundance is rarely available, and most of the modelling methods can be classified as profile or group discriminative. The two groups produce very different results (Loiselle *et al.*, 2003). Profile techniques, based only on presence records, have been used to generate species distribution models based on data from museum and natural history collections, where information for absences is not available (Araújo & Williams, 2000; Barry & Elith, 2006). As first generation of species modelling methods, they were based on simple habitat-matching techniques, preceding the "second generation", the group discriminative techniques, able to fit more complex non-linear relationships between occurrence and environmental conditions (Garske, 2010). The profile techniques include *envelope* (BIOCLIM - Busby, 1991) and *distance based* (DOMAIN - Carpenter *et al.*, 1993) approaches (Barry & Elith, 2006). The *envelope* approaches use presence records and environmental data to set a species profile, which defines the species´ environmental domain in respect to environmental variables. The *envelope* is defined in terms of upper and lower limits of tolerance within a gradient, and doesn't conceive the existence of absences within those boundaries. Each cell is ranked in terms of environmental suitability. The *distance-based* approach calculates the distance between a specific site and the nearest presence in the environmental space. Such approach is focused on distances from adjacent sites associated to presence records, while *envelope* technique is based on the definition of environmental boundaries that enclose all sites assigned to presence records (Barry & Elith, 2006).

In the case of group discriminative techniques, and considering that absences are frequently not available, random "background" or pseudo-absences are generated to calibrate the models (e.g. GARP – Genetic algorithm for rule set prediction; MAXENT), in order to distinguish suitable from unsuitable conditions for species (Elith & Leathwick, 2009; Phillips *et al.*, 2009).

Several studies agree that group discriminative techniques have better performance than profile techniques (Brotons *et al.*, 2004; Segurado & Araújo, 2004; Pearson *et al.*, 2006; Mateo *et al.*, 2010). Most of the group discriminative techniques are regression models, and includes generalized linear models (GLM), generalized additive models (GAM), logistic multiple regression (LMR), multivariate adaptive regression splines (MARS), and maximum entropy (MAXENT). A goodness-of-fit criterion is used to fit a curve using a set of points according to an univariate definition, but accepting variations: i) response can be calculated in respect to many variables, ii) species response to each variable may be linear or non-linear; iii) models are purely additive or admit interactions between predictor variables (Barry & Elith, 2006).

The resolution in use is also a factor that interferes in the accuracy of models' results. Very often resolution is determined by attributes of the available data for environmental variables, and not by species-specific and territory conditions. The sampling effort is determined by sampling design, which in turn is influenced by resolution. But resolution is progressively reducing its importance as a source of bias for predictions, because of improving quality of available data for environmental variables and species occurrence if compared to the recent past, when available data for species occurrence was sparse and very often associated to coarse spatial resolutions, available from natural history museums' collections (Elith *et al.*, 2006).

The sampling design used to collect data must be prudently considered, once an adequate design improve the chance to guarantee a full sampling of the environmental range of the organism. Being correlative models that calculate ecological niche (environmental requirements) from known species occurrences (presence/absence), it is expected that species ecological range be fully recorded, in order to produce accurate predictions. However, very often, it is not easy to evaluate if species' potential range has been fully captured (Pearson & Dawson, 2003; Hampe, 2004; Araujo *et al.*, 2005; Randin *et al.*, 2006), even for species which data was obtained from dedicated surveys and prepared sampling designs. So, it is acceptable that models sometimes only consider part of the “fundamental niche”/ecological profile of the species. Therefore, restricting species environmental range because of incomplete sampling reduces the usefulness of the models for predictive purposes, influencing on the estimation of the response curves, which will produce less accurate results in terms of predicted changes (Thuiller *et al.*, 2004b). On territories of high topographic complexity it is important to account for sampling bias from species data due to limitations on accessing certain areas (Kadmon *et al.*, 2004), an important constraint on Madeira Island. Especially on territories with such geographical constraints, occurrences are often separated by extensive unsurveyed areas, which conditions might be potentially suitable. In order to reduce the impact of such constraint, it is required that areas with rugged topography should be sampled using higher spatial resolutions to obtain accurate results (Lischke *et al.*, 1998). Such issue is of special concern on modelling exercises based on statistical models, once predicted distributions are based on relationships between sampled occurrences and environmental information. Sampling a fraction of the ecological range of the species will produce inaccurate predictions. The error of incorrect sampling is even more important on biasing predictions when the model is projected to new territories or new environmental conditions, such as climate change scenarios.

Another problem that affects the accuracy of models’ results, and is related to the quality of the data, is that species distribution data often is affected by spatial autocorrelation, and biased towards population centres and access routes (Dormann *et al.*, 2007).

2.2.4.1.4 CALIBRATION DATA: ENVIRONMENTAL PREDICTORS

It is expected that models present a certain level of mismatch between their predictions and real distribution patterns. One of the reasons is because distribution patterns are the result of a complex control from a wide group of environmental variables, which are usually reduced to a restricted set in the calibration procedure (Barry & Elith, 2006). A common reason is that data for all the relevant ecological predictors are commonly unavailable. A condition that might hamper the ability to produce accurate results, once species ecological profile is only partially captured, and prediction might represent only a fraction of the suitable habitat. In fact, the type of environmental predictors selected produce important effects in the accuracy of results (Stockwell & Peterson, 2002). Even though, the reduction of variables to a selected subset for calibration purposes is often required, based on the assumption that the enhancement of the predictive power of a model is also dependent on a reduction of the explanatory variables to a reasonable number (Harrell *et al.*, 1996). The selection of factors that might play a major role on controlling species distribution is an important and sensitive task on species distribution modelling, where different procedures have been implemented. The selection can be done by chance, although not recommended (Guisan & Zimmermann, 2000), using statistical approaches (e.g. correlation, standardized regression coefficients, Akaike weights) (Murray & Conner, 2009), or following physiological principles or shrinkage rules, as proposed by Harrell *et al.* (1996). The author propose that the number of predictors included in the final model should be no more than $m/10$, where m is the number of observations, or the number of observations in the least represented category in the case of a binary response (presence/absence). The selection of variables should not rely only on statistical parameters (e.g. use of non-correlated variables) (Guisan & Zimmermann, 2000), and should incorporate relevant ecological theory about species distribution and ecological expert knowledge (Austin, 2007; Meynard & Quinn, 2007).

Although all the efforts addressed to provide the best selection of variables, it is important to take into account that natural systems are not closed, and it is not possible to integrate all potential driving forces implied on controlling species distributions (Araújo *et al.*, 2005b). Thus, it is expected that models should not be able to fully capture reality, a failure that is usually classified as error, uncertainty or lack of performance. In fact, errors are inherent to bioclimatic modelling results, and there is only the possibility of decrease the error as much as possible, but it is impossible to eradicate it. Under such perspective models should be primarily accepted as an heuristic approach (Oreskes *et al.*, 1994).

Results are also dependent on the mode that variables are used. Predictors can be used in the simple way, or after transformation, such as polynomial terms, β-functions, smoothed empirical functions, and significant ordination axes (see Guisan & Zimmermann, 2000). Besides the number and type of environmental predictors

(Stockwell & Peterson, 2002), resolution is another attribute that is critical to models' accuracy (Araújo *et al.*, 2005a). Although resolution should have as reference biological considerations on size and ecology of the species (Soberón & Nakamura, 2009), such decision is usually determined by availability of data (Guisan & Thuiller, 2005) or by constraints to sampling, namely accessibility. The resolution is especially important in the case of evaluating spatial shifts (gain/loss) under climate change scenarios, once it has influence on the niche estimation (Soberón & Nakamura, 2009). Depending on the size of the territory, the selection of an incongruous resolution might overstate predictions. In the case of small territories and specialised species, the capacity of habitat models to produce reliable results is limited by the lack of high-resolution environmental data. In this case, habitat modelling is commonly unable to identify conditions associated to microhabitat scale, which might be important to support species endurance. Except for extreme scenarios, microhabitats, usually associated to microtopography, might act as refuges, and reduce the vulnerability of species otherwise threatened of extinction (Theurillat *et al.*, 1998).

Another weakness associated to habitat models is that they do not integrate data about population structure, population or metapopulation dynamics, attributes that interfere with species distribution, or extinction risk at local scales (Thuiller *et al.*, 2008). That may lead to misleading results in terms of spatial shifts and extinction rates (Akçakaya *et al.*, 2006). Dynamics and dispersal at the limits of species ranges might be important in terms of species' response to climate change, where isolation, population size, release from density-dependent intraspecific competition and limitations in terms of inter-population exchanges might play an important role on determining presence and persistence of a species (Thomas *et al.*, 2001; Thuiller *et al.*, 2008; Anderson *et al.*, 2009) (Keitt *et al.*, 2001; Braunisch *et al.*, 2008). The non-integration of such data is regarded as another source of uncertainty, and supports the idea that habitat models do have problems on predicting accurately changes at the edges of the species ecological range. Such weakness can be considered of great importance, considering that changes are expected to be more significant at the edges of species´ distribution (Hampe & Petit, 2005).

Another type of variables that often is not considered on habitat models is related with biotic interactions, which is considered a limitation and an additional source of uncertainty to models´ results (Davis *et al.*, 1998), considering that its inclusion can improve predictions (Heikkinen *et al.*, 2007). The integration of such data is supported by the idea that the occurrence of a species is determined by physiological responses to environment, but these responses shall reveal the result of interaction with other species (Barry & Elith, 2006). The use of climate-based models is considered sufficient to assess impacts from climate change on species distributions at macroecological scales (Araújo & Luoto, 2007), what is concordant with the idea that such variables are appropriate to estimate potential distributions for large territories (Pearson & Dawson, 2003). Despite that, competitive exclusion might limit poleward spread of species sensitive to low winter temperatures before low-temperature mortality (Woodward, 1987), thus competitive relationships with other species actually limits distribution under the limits of physiological tolerance or competition decreases the capacity to survive, decreasing the level of tolerance for climatic variables; limits to distribution may lie in competitive relationships with other species (Woodward, 1987). But models at high-resolution scales should include data for biotic interactions, otherwise results might overestimate range gains and produce overoptimistic predictions for future distributions (Jaeschke *et al.*, 2012).

At last, developing and applying bioclimatic models involve knowledge in a wide range of methodologies, including the choice of modelling techniques, model validation, collinearity, autocorrelation, biased sampling of explanatory variables, scaling and impacts of non-climatic factors (Heikkinen *et al.*, 2006).

Another issue that introduces uncertainty is related to the fact that validation of models results is not possible when assessing changes associated to environmental changes under future scenarios (Araujo *et al.*, 2005).

2.2.4.2 HABITAT MODELS: DO THEY HAVE PREDICTIVE VALUE FOR CLIMATE CHANGE ASSESSMENTS?

More than an enumeration of weaknesses associated to habitat models, last discussion is a support to understand why such modelling approach stills to be widely used, and an attempt to set bounds for the type of inferences/interpretation that is possible to produce after models results. Predictions must be interpreted not in absolute terms, but as results that are deeply affected by a sequence of decisions.

Despite uncertainties and limitations, species distribution models can be useful (Whittaker *et al.*, 2005). Since only very few species have been studied in detail in terms of their dynamic responses to environmental change, or to biotic interactions, static distribution modelling often remains the only approach for studying the possible consequences of a changing environment on species distribution (Woodward & Cramer, 1996), namely because of the large amount of data needed to support a mechanistic analysis (Lavorel *et al.*, 2007). In fact, they perform an helpful tool to assess potential effects from climate change on biodiversity when range-limiting physiological factors are poorly known, or when absence data for species is not available.

Although the unequivocal advantages using the habitat modelling approach, there are some progresses to be made in order to decrease uncertainty in predictions and solve other methodological issues. Efforts to improve the accuracy of habitat models must be addressed to methodological aspects, such as used statistical techniques, model selection criteria and explanatory variables used in modelling, namely the inclusion of new predictors related to land cover, direct CO2 effects, biotic interactions and dispersal mechanisms (Araujo *et al.*, 2005; Guisan & Thuiller, 2005; Heikkinen *et al.*, 2006).

At local scales, and despite weakness, results from habitat modelling based entirely on scenopoetic variables have considerable predictive value (Peterson, 2001; Feria & Peterson, 2002; Peterson, 2003).

According to Soberon & Nakamura (2009) the *Eltonian Noise Hypotheis* explain, in part, why habitat modelling produces reliable outputs, even only considering scenopoetic variables. One reason is related with the possibility that Eltoniann factors have high correlation to scenopoetic variables, what allows models to capture part of the biotic signature linked to the biological features. Another reason is related to the fact that Eltonian factors are associated to fine-grained resolution. Their influence will be weaken on shaping distributions associated to large geographical extents, where coarse-grained resolutions are usual in terms of data for environmental predictors. But such hypothesis is not acceptable at high-resolution scales, where local interactions might affect distribution (Bullock *et al.*, 2000; Leathwick & Austin, 2001; Hou *et al.*, 2006).

Another fact that difficult the use of bionomic variables on habitat models is the fact that the impacts of such factors (*Eltonian* Factors) may vary significantly within the geographical distribution of a species (Brewer & Gaston, 2003) Accepting that scenopoetic and bionomic variables might have complex spatial structures, namely long ranged-autocorrelations and required fine-grain resolution, it might be difficult to asses the contribution of Grinnellian and Eltonian factors on shaping distributions (Soberón & Nakamura, 2009).

Mechanistic models, providing a more complete description about the role of fundamental environmental predictors, are considered more robust and appropriate to predict shifts on distribution associated to contexts of environmental change (Dormann, 2007). The absence of data about species response on current conditions constrains in a deep way the options on selecting the approach on modelling species distributions. Such constraint is one of the main reasons that explain why static approach remains the most frequent on assessing potential consequences from environmental changes to species distributions (Woodward & Cramer, 1996).

2.2.4.2.1 SDM - USE ON CLIMATE CHANGE

Although critical methodological issues, that may carry some uncertainty on predictions from bioclimatic modelling, the use of single-species bioclimatic “envelope” models is quite common on assessing potential impacts on biodiversity from projected climate changes (Heikkinen *et al.*, 2006). That type of models is based on the assumption that current species distribution is deeply determined by climatic variables. Reducing the amount of variables to be included in the model to the climatic category, these models allow the projection of distributions in face of environmental changes / under future climate change scenarios. However, being sufficient for extensive territories, the only use of climatic data becomes problematic at regional and local scales, where many factors other than climate can influence, sometimes significantly, current and future species distribution and the rate of change or the magnitude of the impacts from climate change.

Despite limitations and uncertainties, which imply that the results obtained using this approach should be interpreted with caution (Pearson & Dawson, 2003; Guisan & Thuiller, 2005; Heikkinen *et al.*, 2006), habitat models are useful to assess how climate change may affect ecosystems, especially providing estimations on potential changes in species' distribution in a given region (Pearson & Dawson, 2003; Beaumont *et al.*, 2005).

Some of the factors that cause uncertainty, namely associated to the variability of models results, received the attention from different contributions, and different methodological approaches were proposed in order to reduce their importance.

Although more often used to assess climate change impacts on the distribution of native species (Bakkenes *et al.*, 2002; Thuiller *et al.*, 2006b), and despite the fact that a fundamental assumption of niche modelling is not achieved (equilibrium), species distribution modelling approach was also applied to forecast potential geographic distribution of alien invasive species (Peterson, 2003; Thuiller *et al.*, 2005b; Hortal *et al.*, 2010), even under climate change scenarios (Thuiller *et al.*, 2007; Vicente *et al.*, 2011).

2.2.5 STRATEGIES TO OVERCOME UNCERTAINTY ON HABITAT MODELS

Predictions are highly sensitive to decisions made at different modelling stages, such as small adjustments on parameters, the threshold selection for producing binary outputs, the average function algorithm used to produce a consensus model, or the method used to select the predictor variables used on models calibration. In fact, correlative techniques are very sensitive to small changes on parameterizations used to describe relationships between species' distributions and environmental predictors.

Once such variability could compromise their usefulness on supporting choices, namely guiding policymakers' decisions (Araújo & New, 2007), different strategies were implemented in order to overcome or reduce the impact of such weakness. In order to reduce uncertainty associated to models results two main strategies were applied: **i)** assessment of models' results based on the calculation of accuracy measures, **ii)** the adoption of ensemble forecasting approaches, in order to produce an output that combine the results of models with better predictive performance.

2.2.5.1 MODELS' PERFORMANCE AND ACCURACY MEASURES

The evaluation of models' performance can be achieved by measuring the accuracy of their predictions. That procedure should be based on independent datasets (Manel *et al.*, 1999; Araujo *et al.*, 2005; Heikkinen *et al.*, 2006), namely those related to different observation times (Fielding & Bell, 1997). Once independent datasets are very often unavailable, different strategies are eligible to evaluate results (Fielding & Bell, 1997; Liu *et al.*, 2005). One approach is testing predictions on a different range in space and time, which will identify the applications for which predictions are suitable (Guisan & Zimmermann, 2000), but few times applied (e.g. Araújo *et al.*, 2005a). A much more common strategy was based on resampling strategies, such as resubstitution, bootstrapping, jackknife sampling, Leave-One-Out procedures, when few records are available, or by partitioning the occurrence set on calibration and evaluation subsets (see Fielding & Bell, 1997). The last approach, a type of cross-validation based on a 2-fold partitioning, is based on a random split of the occurrence data set on subsets applied on models calibration (training) and evaluation (testing) procedures, usually keeping the higher proportion for training purposes (e.g. 70%) and the smaller subset (e.g. 30%) to test predictions (Araujo *et al.*, 2005a). In order to evaluate the decrease in the accuracy of the models, derived from the use of a fraction of the occurrence data on calibration (Fielding & Bell, 1997), the procedure might be carried *n* times. But such has a great advantage, that is to allow the comparision of predictions with observations, a process that can be performed through the calculation of evaluation metrics, which are focused on errors. In fact, the performance or accuracy for binary models (presence/absence or suitable/unsuitable) was mainly focused on their ability to produce results with the lower incidence of errors on predictions, namely errors of type I (false positives) and errors of type II (false negatives) (Fielding & Bell, 1997). The importance of such errors is dependent on the threshold used to convert the probability scale of the models to a binary output (Liu *et al.*, 2005). And the goals of the study may control the weight attributed to the different prediction errors (omission, commission) (Miller *et al.*, 2007).

The use of accuracy measures helps to understand how a specific modelling technique deals with the data used on calibration, evaluating its predictive performance on discriminating suitable from unsuitable conditions, and did not perform an evaluation about how accurately the model can duplicate or be close to reality. So, the evaluation of accuracy of models results is about the capacity of the modelling technique to produce accurate results with the available information. The use of accuracy measures was used not only to evaluate the predictive performance of the modelling methods in use (Elith *et al.*, 2006), but also to support decision about discarding poor models (Vicente *et al.*, 2011). But evaluation is achieved only in relative terms, and predictive value might be questionable (Oreskes *et al.*, 1994).

Despite the possibility of assessing models accuracy trough direct comparison between models probabilistic predictions (continuous scale) and binary observations (Elith *et al.*, 2006), the most common approach is based on the calculation of accuracy measures after the transformation of models predictions (continuous scale) on a binary output. Such transformation is based on a threshold, which selection is critical (Liu *et al.*, 2005). The calculation is based on a two-way contingency table, which scores for the different cells are used to compute measures of agreement between columns and rows, associated to a nominal scale (observed presence, observed absence versus predicted suitable, predicted unsuitable).

2.2.5.2 THRESHOLD-DEPENDENT AND INDEPENDENT ACCURACY MEASURES

The evaluation of predictive accuracy of binary models is based on measures which result might be dependent or not (independent) on the threshold selected to support the conversion from a continuous output.

Different threshold-dependent accuracy measures are available to assess the accuracy of models' results of binary output (percent correctly classified (PCC), omission rate, sensitivity, specificity, precision, Overall prediction success (OPS), Cohens' Kappa (k), Odds ratio, True Skill Statistic (TSS)) (Fielding & Bell, 1997; Guisan & Zimmermann, 2000; Pearce & Ferrier, 2000a; Manel *et al.*, 2001; Allouche *et al.*, 2006; Peterson, 2006; Freeman & Moisen, 2008). As the name says, threshold dependent accuracy measures are those which calculation is dependent on the use of a threshold to convert models' output (habitat suitability, probability of occurrence) from a probabilistic scale to a presence-absence one (0/1). Because of that, such measures were considered less appropriate to assess models' accuracy, and have been substituted by a threshold-independent measure, the Area Under the Curve of the Receiver Operating Characteristic (AUC of ROC), considered more robust.

2.2.5.2.1 AUC OF ROC

Considered as the single most relied-upon measure for accuracy evaluation on species distribution modelling (Peterson *et al.*, 2008), is one of the most used on assessing models´ performance (Lütolf *et al.*, 2006; Brotons *et al.*, 2007; Jewell *et al.*, 2007; Graham *et al.*, 2008).

Models are usually calibrated using a data subset randomly selected (training data) and tested with the remaining subset (test data). ROC curves are calculated for both subsets to obtain the area under the curve (AUC) statistic, which is a measure of predictive ability of the model (Fielding & Bell, 1997). The area under the ROC curve is interpreted as the probability that a randomly chosen presence site gets a higher rank than a randomly chosen background site (Phillips *et al.*, 2006). It relates relative proportions correctly classified (true positive proportion) and incorrectly classified (false positive proportion) cells over a wide and continuous range of threshold levels (Pearce & Ferrier, 2000b; Erasmus *et al.*, 2002) by plotting the false positive fraction values (1-specificity) versus the true positive fraction (sensitivity) (Fielding & Bell, 1997). This makes it a threshold independent measure (Pearce & Ferrier, 2000b). On studies without absence data the curve plots the true positive fraction against the fractional predicted area (Phillips *et al.*, 2006). AUC ranges generally from 0.5 for models with no discrimination ability, predictions are correct only on 50% of the cases, so, areas predicted as suitable have no registered occurrences, to 1.0 for models with perfect discrimination[1] (Engler *et al.*, 2004). Models considered useful must have an AUC higher than 0.7 (Elith *et al.*, 2006; Phillips & Dudik, 2008).

Despite its wide-accepted usefulness to assess overall models ability to predict species distribution, some flaws are pointed out, namely its failure on diagnosing the

---

[1] AUC scale: 0.9-1.0 – excellent; 0.8-0.9 – good; 0.7-0.8 – fair; 0.6-0.7 poor, 0.5-0.6 fail.

factors causing bias on models results (Garske, 2010), or its susceptibility to species-specific traits, namely species extent of occurrence and area of occupancy (Manel *et al.*, 2001; Vanderwal *et al.*, 2009), becoming more a score that gives information about the degree of specialization of a species (Lobo *et al.*, 2008).

Despite the availability of measures to assess the accuracy of predictions produced by the multiplicity of available modelling techniques, the end quality of the model must always be confirmed by knowledge about ecological and distributional features of the species, once high sores could be associated to models showing different results in terms of spatial results (Figueiredo, 2008).

Models' quality and usefulness are dependent on the goals that head the study, and should not be based solely on statistical considerations (Guisan & Zimmermann, 2000).

2.2.5.2.2 ENSEMBLE FORECASTING APPROACH

It's unlikely that a single best habitat modelling approach will ever be identified among modelling techniques, once different aspects/features are valorized depending on the purpose (Segurado & Araújo, 2004; Pearson *et al.*, 2006). Each modelling method has weaknesses and strengths, and it is widely accepted that is not possible to elect a modelling approach that performs better with all kind of data, parameterizations, assumptions, scales and goals (Segurado & Araújo, 2004; Araujo *et al.*, 2005; Elith *et al.*, 2006).

The choice for one modelling approach is determined by several factors, such as the scale of the territory, available data for predictors and species occurrences, the questions to answer, the theoretical assumptions (Pearson & Dawson, 2003; Segurado & Araújo, 2004), and should not depend only on statistical considerations (Guisan & Zimmermann, 2000).

In order to take profit from the strengths of different modelling methods in use and reduce their weaknesses, like differences in accuracy and discrepancies in predictions, a new approach emerged on species distribution modelling. As pointed out by Araújo & New (2007), the variability on results from different modelling techniques can compromise even a simple assessment aiming to predict a contraction or expansion on the geographical range of a given species under certain future climate scenario. So, the selection of an adequate modelling technique is a key decision in the modelling process (Pearson *et al.*, 2006).

Such approach is based on the idea that, instead of selecting a single best model, a difficult choice (Elith *et al.*, 2006), it is rather preferable to use a multi-model ensemble forecasting framework (Araújo & New, 2007; Thuiller *et al.*, 2009). In this case, the final prediction is the result of a consensus forecasting from models fitted with different sets of initial conditions and parameters. The resultant range of forecasts, primarily associated to the variety of modelling approaches in use, and after exploration with appropriate techniques (consensus forecast, bounding box, probabilistic distribution methods), will contribute to improve the robustness of the consensus model (Araújo & New, 2007; Marmion *et al.*, 2009).

This perspective challenges the traditional approach of identifying the model with best performance among an ensemble of models, which is largely based on its capacity to predict the observed data. Several studies comparing alternative models to predict potential shifts on the distribution of species agree on the fact that is not a desirable option relying predictions on a single method (Thuiller, 2003; Segurado & Araújo, 2004; Elith *et al.*, 2006).

The main purpose of using the ensemble forecasting approach is to decrease predictions' error, based on the assumption that individual forecasts contain some independent information, and their combination will provide lower mean error (Araújo & New, 2007). This is of great importance on climate change impacts assessment on species distribution, a topic where the accuracy of predictions is a critical issue (Araújo & New, 2007). When such assessment is developed for conservation purposes, the variability of results might compromise decisions, once projected range shifts could vary significantly in magnitude and direction (Araújo *et al.*, 2005b).

2.2.5.2.3 BIOMOD AND ENSEMBLE FORECASTING

BIOMOD package, a platform implemented in R (R Development Core Team, 2011) that includes several modelling techniques, performs a valuable tool dedicated to maximize the accuracy of species distribution models though an ensemble forecasting approach (Thuiller, 2003; Thuiller *et al.*, 2009). The possibility of producing consensus forecasting allows overcoming some of the limitations associated to species distribution modelling based on statistical models, namely discrepancy on predictions. Once variability on predictions is one of the main weaknesses of the habitat models, which are especially concerning in the case of range shift assessments associated to climate change, several studies of this type have been developed based on the BIOMOD platform, and in a wide range of applications, namely on conservation (Araújo *et al.*, 2004; Vicente *et al.*, 2011), to test methodological approaches(Araujo *et al.*, 2005; Araújo *et al.*, 2005b), assess impacts on different types of organisms (amphibians – (Araújo *et al.*, 2006)), breeding birds (Barbet-Massin *et al.*, 2012), fish assemblages (Buisson *et al.*, 2008), plants (Beaumont *et al.*, 2009), (Engler *et al.*, 2011), butterflies – (Heikkinen *et al.*, 2010)), for different territories (South Africa – (Coetzee *et al.*, 2009), Namibia – (Thuiller *et al.*, 2006b), Europe – (Thuiller *et al.*, 2005a)), on identified vulnerable environments (mountains - (Engler *et al.*, 2011), sub-artic (Fronzek *et al.*, 2011).

The platform allows the use of nine modelling techniques, very common on species distribution modelling, which results are used to build the consensus model.

2.2.5.2.4 MODELLING TECNHIQUES AVAILABLE IN BIOMOD

a) Surface range envelope (SRE)

Modelling technique used to calculate a fitted, species-specific, minimal rectilinear envelope in a multidimensional climatic space (Guisan & Zimmermann, 2000). Such type of modelling technique, bioclimatic envelope, has generally lower performances comparing to others (Brotons *et al.*, 2004; Elith *et al.*, 2006). Despite that, it is very useful when reliable absence data is not available, a condition very common on data from natural history museums collections (Gaubert *et al.*, 2006). Because of the identified lower performance such modelling technique is discarded in this work.

b) Artificial Neural Networks (**ANN**)

Powerful rule-based modelling technique with increasing use in habitat modelling (Pearson *et al.*, 2002; Segurado & Araújo, 2004; Araujo *et al.*, 2005; Elith *et al.*, 2006). This method, able to handle explanatory variables from different sources, such as categorical and boolean data, is considered to be robust and low-sensitive to “noise” associated to the calibration data, and is able to determine climatic envelopes that have nonlinear responses to predictors (Lek *et al.*, 1996; Hilbert & Ostendorf, 2001; Pearson *et al.*, 2002; Heikkinen *et al.*, 2006). As disadvantages**,** it requires a large quantity of data to train, validate and test the network, and allows limited insights into the contributions of the predictors in the prediction process, once it does not allow examining the response curves of species against environmental gradients (Manel *et al.*, 1999; Pearson *et al.*, 2002).

c) Breiman and Cutler’s Random Forest for classification and regression (**RF**)

Considered a very robust technique to predictive mapping (Prasad *et al.*, 2006), random forest analysis (multiple tree analysis) generates hundreds to thousands of random trees, each one grown-based on a randomized subset of predictors (Prasad *et al.*, 2006). The resultant trees are evaluated as a whole, and the smallest (most parsimonious) tree that has a given error level (predictive value) is selected. Several advantages are described on the use of such modelling technique, namely that it overcomes much of the limitations associated to decision trees, namely the lack of stability associated with the structure of trees because of small changes on training data. It is expected that the modelling technique equals or exceeds other current algorithms, produces accurate predictions that do not overfit the data, once the large number of trees produces a limited generalization error (Prasad et al., 2006), it has the capacity to handle thousands of input variables and run efficiently on large datasets, there is no need for cross validation or split a subset to test in order to obtain unbiased estimates, once such procedure is done internally (Breiman, 2001; Breiman & Cutler, 2005).

Although the impossibility of examine the individual trees separately, several metrics support the interpretation, namely variable importance, which makes the results more interpretable than those from other techniques, such as ANN (Prasad *et al.*, 2006).

d) Generalised Boosting Methods (**GBM**)

Because of their recent introduction in ecology, few studies on climate change assessment produced results based on generalized boosted models, also referred as boosting regression trees, an extension of MARS (Multiple Adaptive Regression Splines). Highly efficient in fitting the data, such non-parametric technique, a form of additive logistic regression, combines the strength of different modern statistical technique. Boosting improves predictive accuracy by an iteratively application of a base-learning algorithm (decision tree) to reweighted versions of the training data, and the final boosted classifier's prediction is based upon an accuracy-weighted vote across the estimated classifiers (Friedman *et al.*, 2000).

e) Generalised Linear Models (**GLM**)

Regression modelling technique of parametric nature of frequent use on habitat modelling (Thuiller, 2003; Elith *et al.*, 2006), considered an extension of classic linear regression (Olsson, 2002). GLM models support analysis for non-linear effects among variables and non-normal distributions of the independent variables, and yield predictions (probability values) within the range recorded for the observed values (0/1) (Guisan & Zimmermann, 2000). According to Muñoz & Felicísimo (2004) the use of GLM models on species distribution modelling has important disadvantages. The use of such models assume that the relationships between species response and environmental predictors are linear, an assumption that is difficult to support from real observations; and the use of high-order polynomial functions to deal with multi-modal or skewed distributions can increase the risk of over-fitting, which create models that have low capacity to produce accurate predictions when projecting to other areas or environmental conditions.

f) Generalised Additive Models (**GAM**)

Non-parametric extensions of GLMs that provide a class of models that can cope with linear and complex additive response shapes, being possible to combine both within the same model (Bio *et al.*, 2002). Such modelling technique can cope with regression functions, such as logistic regression, which are forms not easily handled by parametric techniques. Although, potential problems may arise from overdispersion, which must be handled with caution when fitting GAMs (Leathwick *et al*., 1996). Several studies focused on climate change scenarios supported range predictions on the use of GAM models (e.g. Araújo *et al*., 2004; Thuiller *et al*., 2004b).

g) Multiple Adaptive Regression Splines (**MARS**)

Recent technique conceived for flexible regression modelling that has more power and flexibility on modelling relationships that are nearly additive or involve interactions between variables (Friedman, 1991). It combines linear regression, mathematical construction of splines and binary recursive partitioning to create a model where relationships between species response and environmental predictors are either linear and non-linear (Muñoz & Felicísimo, 2004).

h) Classification Tree Analysis (**CTA**)

Also mentioned as Classification and Regression Trees (CART), such modelling technique uses recursive partitioning to split the data into increasingly smaller subsets until a termination is reached (Iverson & Prasad, 1998). In terms o advantages, classification trees allows to capture non-additive response and complex interactions (Thuiller *et al.*, 2003), and numerical and categorical variables can be used together (Iverson & Prasad, 1998). But some limitations are associated to the modelling technique, namely the propensity to produce overly complex models that can support spurious interpretations (Thuiller *et al.*, 2003; Muñoz & Felicísimo, 2004; Araujo *et al.*, 2005).

i) Flexible Discriminant Analysis (**MDA**)

Based on mixture models, it is an extension of linear discriminant analysis for classification. To increase the predictive power of the models, the flexible discriminant analysis running on R-BIOMOD uses a MARS function. A great advantage of the discriminant analysis is the low sensitivity to changes on calibration data associated to random split (Manel *et al.*, 1999).

3 MODELLING: METHODOLOGY AND CALIBRATION DATA

Despite the fact that the main effort of this work is focused on assessing changes on distribution at species level, results about the response of climax communities are also presented. This option is supported on the idea that conservation must be supported on the species level and on the community or landscape level. If conservation at the species level is more appropriate for certain organisms, namely those that are restricted to small areas, the community level is appropriate to conservation at the landscape level, namely when concern is focused on habitats.

The analysis of impacts from climate change is very often focused on the species level, and some of the studies focused on species assemblages/communities are actually based on the species level (Lischke *et al.*, 1998; Ferrier *et al.*, 2002a). Despite the likely adequacy of the assemblage/community level to regional conservation purposes (Ferrier *et al.*, 2002a), several factors contribute to reduce the applicability of such perspective, namely on studies assessing range shifts under climate change scenarios. First, most of the studies are based on the assumption that species might respond to climate change in an individualistic way, a perspective based on fossil records and results based on short-term experimental studies (Baselga & Araújo, 2009). Second, it is expected that individual species-models can provide more precise and realistic predictions than those offered by species assemblage models (Iverson & Prasad, 1998). Third, most of the modelling techniques in use are suitable for individual-species modelling. In addition to such factors, it should be mentioned the high complexity derived from the required integration of variables associated to biotic interactions, or the use of high-detailed environmental variables measured at topographic scales (e.g. climatic, soil conditions) in order to capture the influence of vegetation dynamics in the presence/absence of some species. More concerning than the preparation of the individual-species modelling techniques to cope with data for biotic interactions, which is not trivial (Araújo & Luoto, 2007), is the availability of such data, which is often unavailable or only available for small and specific territories. Another reason that might support the use of models based on individual species as surrogates for vegetation spatial predictions is the apparently good compatibility between such approach and the prevalent ideas on vegetation science - the individualistic (Gleason, 1926) and organismic (Clements, 1916) perspectives. The use of an organismic view might be operable if we accept that a community has a number of species that are exclusive or, at least, are more abundant, attributes that support the individualization of a different entity. Such assumption is fundamental for the phytosociological perspective (Géhu & Rivas-Martínez, 1981). Despite the subjectivity associated to the approach, it is indubitably a useful tool. Namely because of its versatility in terms of scale, once it has different degrees of integration, which are associated to different spatial scales. Such condition supports an useful adaptability to different scales of analysis, from the community to the landscape, or even at continental scales (Rivas-Martínez *et al.*, 1999). Because of that, it performs a proper tool to produce results that are appropriate to support decisions on resources management and spatial planning.

Despite few times used on species distribution modelling, there are modelling techniques available that allow the combination of environmental data with information about species assemblages to enable projections that are expected to duplicate community dynamics, namely multivariate adaptive regression splines for community data (MARS-COMM) (Elith *et al.*, 2006), generalized linear models (GLM), canonical quadratic ordination (CQO) (Baselga & Araújo, 2009).

According to (Ferrier & Guisan, 2006) there are different approaches that can be used on communities' predictive modelling:

i) creating groups of species/community entities and then model their occurrence, which demands a previous classification of the biological data in community types, species groups, ordination axes, or species richness levels;

ii) predicting distribution for each species and then proceed with classification in order to derive the distribution of communities, groups, ordination axes or richness levels;

iii) using a technique (e.g. multiresponse neural networks, vector generalized linear models) that classifies and predict at the same time, based on multiresponse modelling, constrained ordination, constrained classification or through modelling of the compositional dissimilarity.

In this work, results for the communities level are based on the approach “predict first assemble later” (Ferrier & Guisan, 2006). On a first stage models are produced for each species. The results for selected species are then used to derive changes on distribution for the community level.

3.1 SPECIES-LEVEL MODELLING : CALIBRATION AND EVALUATION OF MODELS

During a first stage, models are produced for the species level, based on an ensemble forecasting procedure supported on different modelling techniques (bioclimatic envelope, regression, classification and machine learning methods) and calibration parameters. Modelling and ensemble forecasting procedures are supported on the BIOMOD package (Thuiller *et al.*, 2009), a platform for ensemble forecasting based on habitat modelling techniques, and supported on freeware and open source R software (R Development Core Team, 2011). Aware about the enounced weaknesses, the use of an habitat modelling approach is mainly determined by the lack of data about range-limiting physiological factors and species-specific traits, such as biotic interactions and dispersal, circumstances that very often determine the use of static modelling approaches (Araújo & Guisan, 2006).

Predictions for current and future distributions are based on forecasts from 8 different modelling techniques: regression (Generalised Linear Models, Generalized Additive Models, Multivariate Adaptive Regression Splines), classification (Classification

Tree Analysis, Mixture Discriminant Analysis), and machine learning (ANN, Generalised Boosting Models, Random Forest)[2]. The available bioclimatic envelope technique (SRE – Surface Range Envelope) is discarded, a decision based on the generally low predictive accuracy of such modelling type when compared to others (Elith *et al.*, 2006).

Once independent data to evaluate the models is not available, a procedure of random data splitting was carried out. Species distribution data is randomly split into a calibration (70%) and evaluation (30%) subsets. The calibration data is used during the fitting process of the models, which are evaluated using the remaining subset (Araújo *et al.*, 2005b; Guisan & Thuiller, 2005). Once predictions can present significant variability according to the selected subsets, a cross-validation approach was also implemented, replicating the random splitting procedure 30 times for each modelling technique and for each species. Such procedure gives a better estimation about the predictive performance of each modelling technique, supports further inference about their sensitivity to the attributes of the calibration data, and reduces the biasing effect associated to random selection.

The results from the different modelling techniques and parameters are combined, in order to produce one consensus model for each taxa[3] and climatic context (current climatic conditions, scenarios A2 and B2). Model outputs are converted to a binary scale, based on a ROC-optimized threshold attributing equal importance to sensitivity and specificity. In other words, the selected threshold gives equal importance to the capacity of the model to correctly predict presences and absences (Liu *et al.*, 2005). The combination of the models is supported on a weighted approach, and the weight attributed to each model depends on its capacity to discriminate suitable from unsuitable conditions for the species. Such capacity, designated as accuracy or performance, is assessed by the measure area under the curve (AUC) of a receiver operating characteristic (ROC). In order to improve the accuracy of the consensus model, the ensemble forecasting procedure discarded models that have an AUC value lower than 0.7 (Elith *et al.*, 2006), keeping only those that are considered good or very good in terms of capacity

---

[2] - For details about models parametrisation see Thuiller *et al.*, 2009.

[3] - Taxonomy is according Press & Short (2001) and Jardim & Sequeira (2008b)

to discriminate suitable from unsuitable conditions (AUC > 0.7) (Fielding & Bell, 1997). The remnant models are ranked according to their evaluation score (AUC), and the weight of each model in the consensus one is determined by a decay measure, which reinforces the contribution of the models with higher scores of AUC. As recommended by Thuiller *et al.* (2009), the decay in use is 1.6[4]. The conversion of the ensemble model into a binary output is based on the ROC mean threshold (Liu *et al.*, 2005).

The analysis of changes is based on the spatial comparison of predicted suitable area between current and future climatic scenarios.

3.1.1 SPECIES OCCURRENCE DATA

The high topographic complexity of the island, which has influence on the high variability of ecological conditions, demands that modelling process should be carried using a fine-grained spatial resolution.

Data for species' occurrence was collected between 2008 and 2010, supported on high precision GPS technology and using a reference grid with a 200 x 200 m, a resolution also set for the environmental variables. In order to reduce the sampling bias on species data due to limitations on accessing certain areas, sampling was carried also at distance using prismatic binoculars, despite the fact that such procedure might increase errors related to the identification of species and false absences.

The survey for occurrence data was focused on perennial taxa, including natives and exotics. The selection of native species was based on its importance for conservation purposes, giving privilege to endemic taxa, and their role on the structure of native communities. Although the focus on native and endemic flora, it was found relevant to include results for the response of alien invasive species to projected climatic scenarios, particularly for fast-growing tree species, classified as more competitive (Richardson, 1998; Simberloff, 2000; Morris *et al.*, 2011). The concern about alien plants on islands is related to their higher susceptibility to invasion (Henderson *et al.*, 2006), and their current high proportion of non-native species (Vitousek *et al.*, 1996; Sax & Brown, 2000;

---

[4] If using a decay of 1, all models contribute with the same wheight, performing a situation of committee averaging.

Lambdon *et al.*, 2008; Sax & Gaines, 2008), a trait detected in the Macaronesian archipelagos (Jardim & Sequeira, 2008).

The selection of invasive species was based on **i**) current distribution patterns, selecting taxa with wider distribution, **ii**) exhibition of traits that testify the invasive status on the island, namely spread at the landscape level and spontaneous populations growth (Theoharides & Dukes, 2007; Hellmann *et al.*, 2008), **iii**) arboreal size, which potential for outcompete natives is higher (Simberloff, 2000), **iv**) and the identification of spontaneous stands dominated by one of the selected species. According to such criteria, three taxa were selected: *Acacia mearnsii* De Wild, *Acacia melanoxylon* R. Br., and *Pittosporum undulatum* Vent. Based on the fact that a significant number of occurrences are associated to human plantation/sown, occurrences from sites where cultivation or plantation took place were considered on calibration/evaluation procedures after confirming spontaneous occurrence on adjacent areas, a condition considered as required (Dullinger *et al.*, 2009).

3.1.1.1 ENVIRONMENTAL PREDICTORS

One of the most important steps on species distribution modelling is the selection of the environmental variables that will be used on models calibration, a step that is considered decisive to the accuracy of models' results (Guisan & Zimmermann, 2000).

Although all the efforts addressed to this stage, in order to provide the best selection of variables, it is important to take into account that it is not possible to include all potential driving forces implied on controlling species distribution, a result from the combination of different factors, such as lack of data, inappropriate resolution, or as a strategy to achieve less complex models, factors that are commonly identified as responsible (Araújo *et al.*, 2005b).

The selection of variables was based on the use of zero-order correlation, a technique considered appropriate to detect spurious or less important variables (Liu *et al.*, 2005), and combined with results from multicollinearity diagnostics. In fact, multicollinearity is a frequent issue on non-experimental data, which arises when the independent variables considered for the model are highly correlated, biasing models' result, namely when results are associated to multiple regression analysis (GLM) (Graham, 2003). In order to overcome such issue all environmental variables were tested for pair-wise correlations using Spearman's rho correlation coefficient, and only predictors with correlation scores lower than 0.7 were considered. For those variables highly correlated with several others, we selected the one that is expected to have a direct ecological influence on species distribution (Guisan & Zimmermann, 2000), namely those that can be limiting for plant species distribution (e.g. average temperature of the coldest month; precipitation of the driest trimester - summer). In terms o collinearity diagnostics, based on a standard multiple regression analysis, only predictors with values for Tolerance[5] ≤0.25 and a VIF (Variance Inflation Factor)[6] ≥ 4 were considered (Elith et al, 2006; Wisz and Guisan, 2009, Vicente et al, 2011). Discard independent variables based on a Variance Inflation Factor ≥ 5 is a common, but arbitrary, cut-off criterion for detecting high multicollinearity among variables. There is no formal threshold above which multicollinearity is considered to be present. However, values of VIF that exceed 10 are accepted as indicating multicollinearity problems (Neter *et al.*, 1983). The use of collinearity diagnostics, is supported on the fact that zero-order correlation (simple, bivariate) only considers the relationship between two variables, ignoring the data-redundancy problem, once it does not account for possible overlaps between independent variables. In order to overcome such limitation, zero-order correlations should be followed by the assessment of independent effects in order to rank variables, based on a hierarchical partitioning approach (Murray & Conner, 2009). However such approach is not advisable concerning the number of variables in use, once the resulting ranking is affected by the entering order of variables for models consisting of more than 9 variables (Olea *et al.*, 2010).

---

[5] - Tolerance is the proportion of the variance for the variable in question that is not due to other independent variables. Values close to 1 mean no collinearity, and values close to 0 shows the risk of collinearity.

[6] - Evaluates how much the variances are inflated by multicollinearity (e.g. - ex.: VIF = 5 indicates that multicollinearity is causing the variance of the estimate to be 5 times larger than it would be if the independent variables were uncorrelated. Standard error is doubled when VIF is 4 and tolerance is 0,25.

Table IV -Environmental predictors used on models calibration (Cc) and projections (Fc)

Environmental predictor	Abrev.	Group	Cc	Fcc
Percentage of area that faces North	asp_N	Topographic	✓	
Percentage of area with termophillous exposition – E and S	asp_ES		✓	
Incoming solar radiation – September to March	Rad_sol		✓	
Local diversity of aspect	SWI_asp		✓	
Topographic complexity	SWI_tp		✓	
Percentage of area with slope higher than 50º	Slp_4		✓	
Percentage of area with slope higher than 20º	Slp_34		✓	
Winter precipitation (SCIELO model)	Prec_w	Climatic	✓	✓
Summer precipitation (SCIELO model)	Prec_s		✓	✓
Mean minimum temperature of the coldest month (SCIELO	T_mmcm		✓	✓
Annual range temperature (SCIELO model)	T_ar		✓	✓
Patch size coefficient of variance	PSCOV	Landscape structure	✓	
Patch size standard deviation	PSSD		✓	
Mean shape index	MSI		✓	
Area dedicated to agriculture (%)	P_agr	Landscape composition	✓	
Area occupied by exotic communities (%)	P_exot		✓	
Area occupied by native forest (%)	P_flnat		✓	
Area occupied by urban areas (%)	P_urb		✓	
Area occupied by phaeozems (%)	S_phaeo	Soil conditions	✓	
Area occupied by cambisols (%)	S_camb		✓	

Cc: current conditions; Fcc: future climatic conditions – A2 and B2 scenarios.

It is widely accepted on plant ecology that climate is the main force on determining the distribution of species at global and continental levels (Woodward & Williams, 1987). But at local scales the occurrence of species is determined by their response to conditions defined at the topographic level, which results from a combination from physical and biological factors (Pearson & Dawson, 2003; Retuerto & Carballeira, 2004).

Because of the lack of data about biotic interactions between species, only physical variables are considered. The environmental predictors in use are assigned to five different groups: topographic, climatic, landscape structure and composition, and soil conditions. These groups are mainly reproducing conditions associated to direct and indirect gradients, and do not integrate resource variables (sensu Austin, 2002).

3.1.1.1.1 CLIMATIC VARIABLES

The climatic variables are produced by the CIELO model, which is fitted with climatic data for 1980-1994 (Miranda *et al.*, 2006). Because of the topographic complexity of the island, which supports a wide range of topoclimatic conditions, the variables produced have a small mismatch in relation to the registered values, used to calibrate the model. Nevertheless, the value of correlation is considered good ((Miranda *et al.*, 2006).

Selected variables:

- mean minimum temperature of the coldest month **(T_mmcm)**: on Madeira Island corresponds to February. Frost occurs only at altitudes higher than 1300 m during winter, with a maximum of 20 days/year at Bica da Cana (1560m m.s.l.) and 11 days at Pico do Arieiro (1810m). It is expected that the existence of frost events at high altitudes might act as an ecological barrier for plant species, namely for lauraceae trees, that are low to moderately tolerant to low temperatures (Fernández-Palacios, 1992). Minimum winter temperature is frequently used as predictor in studies aiming to assess the relationship between environmental predictors and species response (Retuerto & Carballeira, 2004), and is accepted as an important predictor on controlling species distribution on mountainous Macaronesian islands (Fernández-Palacios, 1992);
- annual temperature range **(T_ar)**: difference between the average temperatures of the coldest (February) and the hottest month (August);
- winter precipitation **(Prec_w)**: it was obtained summing the mean precipitation values for December, January and February;
- summer precipitation **(Prec_s)**: obtained summing the mean precipitation values for June, July and August. It is a good indicator for drought, playing a very important role on limiting the range of temperate species on lower altitudes.

Discarded variables: annual and seasonal (spring and autumn) precipitation, mean annual temperature, mean maximum temperature of the coldest month (august), seasonal mean maximum (winter, spring, summer and autumn) temperature, mean minimum seasonal temperature (winter, spring, summer and autumn), mean seasonal temperature (winter, spring, summer, autumn), Index of dryness (Verdú & Galante, 2002), annual potential evapotranspiration, potential evapotranspiration for the warmest trimester (JJA) and quadrimester (MJJA), ombrothermic indexes (annual, for the warmest bimonth and for the summer quarter), and Compensated Thermicity Index of Rivas-Martinez (ITc) (Rivas-Martinez, 2004).

3.1.1.1.2 TOPOGRAPHIC VARIABLES

Despite having and indirect effect, topographic variables were included in the group of predictors used on models calibration, a decision that is advisable at such geographical scales (Pearson & Dawson, 2003; Garske, 2010). On Madeira Island, because of the high topographic complexity, there is a great variability of habitat conditions within small distances. The integration of such variables aims to improve the capacity of the models to assess suitability with high detail.

Selected variables:

- percentage of area that faces North (0-22.5º and 337.5-360º)(**asp_N**): derived from aspect calculations based on a Digital Elevation Model. The calculation is based on the percentage of pixels with a resolution of 25x25m that accomplish the basic criteria (faces north) for the pixel size used on modelling (200x200m);

- percentage of area that faces East and South (67.5-202.5º)(**asp_ES**): based on a similar approach than the last variable, their use aims to support a more accurate discrimination of suitable/unsuitable conditions for species that respond to subtle changes associated to topographic features, a trait identified during data collection;

- total incoming solar radiation from September to March **(Rad_sol)**: calculated on a GIS platform after a Digital Elevation Model;

- local diversity of aspect (**SWI_asp**): based on the Shannon-Weaver index:

$$H' = -\sum_{i=1}^{R} pi \ln pi$$

where ***pi*** is the proportion of area occupied by each category of the variable aspect;

- Shannon-Weaver index of topographic complexity (**SWI_tp**): developed by Miller (1986), is based on the summation of diversity values obtained for aspect, slope and altitude;

- percentage of area with slope higher than 20° (**Slp_34**) and higher than 50° (**Slp_4**): the use of such variables is determined by the existence of several species that inhabit steep slopes, namely rocky cliffs. The use of such variables helps to reduce limitations associated to the reproduction of high resolution habitats because of the resolution in use (200x200m);

Discarded variables: altitude, percentage of area that faces westward (SW, W, NW), percentage of area with slope < 20º (**Slp_12**)

3.1.1.1.3 SOIL CONDITIONS

Although important for species distribution (Jones & Reichard, 2009), only few studies have used extensively soil attributes on modelling procedures (Peet *et al.*, 2003). The integration of such variables was supported on a conversion of the categorical variable (type of soil) on a quantitative variable (percentage of area occupied by each soil type). The variables are derived from the Carta de Solos da Região Autónoma da Madeira (Ricardo *et al.*, 1992).

Selected variables:

- percentage of area occupied by phaeozems (**S_phaeo**) and by cambisols (**S_camb**): these are the two most important types of soil in terms of area. The other types present a very restricted distribution:

Discarded variables: percentage of area with steep slopes (redundant information with topographic variables), andosols, arenosols, calcisols, beach deposits, fluvisols, rocky outcrops, vertisols. The rejection of such variables was based on their restricted spatial definition.

3.1.1.1.4 LANDSCAPE COMPOSITION

The integration of variables associated to land-use on models calibration aims to detect if current species distribution reflects any relationship with the different types of land-use. If so, results for predicted changes under future climatic scenarios will be highly biased in the case of the native species. The variables are derived from the Carta de Ocupação do Solo da Ilha da Madeira (COS, 2007).

Selected variables:

- percentage of area dedicated to agriculture (P_agr), urban areas (P_urb), exotic forest (P_exot), and native forest (P_nat).

The variables *percentage of area occupied by exotic forests* (P_exot) and by *urban areas* (P_urb) were removed from the group of predictors used to calibrate models for alien invasive tree species, once such occupations correspond to areas where the species were introduced. Their inclusion might bias models results.

3.1.1.1.5 LANDSCAPE STRUCTURE

This group of predictors includes landscape metrics, which use on models calibration aims to improve the ability of the models to discriminate the presence of complex habitats. Such variables might be especially important in the case of alien invasive trees, in association to areas of high complexity associated to human land-use (Vicente *et al.*, 2010).

Selected variables:

- patch size coefficient of variance (patch density and size metrics) (**PSCoV**)
- patch size standard deviation (patch density and size metrics) (**PSSD**)
- mean shape index (shape metrics) (**MSI**)

Discarded variables: several variables were discarded, a fact supported on the high correlation between metrics (Li & Wu, 2007) – shape metrics (Area Weighted Mean Shape Index, Mean Perimeter-Area Ratio, Mean Patch Fractal Dimension), edge metrics (Edge Density, Mean Pacth Edge), patch density and size metrics (Mean Patch Size, Number of Patches, Median Patch Size).

3.1.1.1.6 FUTURE CLIMATIC SCENARIOS

The climatic scenarios used to project distributions under future conditions are based on the CIELO model (Clima Insular à Escala Local) (Azevedo *et al.*, 1999), a climatic model that uses atmospheric and oceanic parameters calculated by large-scale models to estimate temperature and precipitation on mountainous islands. The scenarios, produced by the Project SIAM II (Climate Change in Portugal. Scenarios, Impacts and Adaptation Measures) (Santos & Miranda, 2006) are projected for 2070-2099 using the CIELO model as support to downscale the A2 and B2 large-scale scenarios from the HadCM3 model (Miranda *et al.*, 2006). In terms of precipitation, the scenarios project a decrease in the annual values (20%-35%). The higher losses in relative terms are predicted for the southern slope of the island, while the higher absolute losses are projected for the higher summits (-800mm). But such average values hide very opposite trends at the seasonal level. In fact, the scenarios project an increase in summer, particularly in the scenario A2 and in the northern face of the island (Figure 8). Despite that, the absolute values are not sufficient to compensate the decrease projected for winter, autumn and spring.

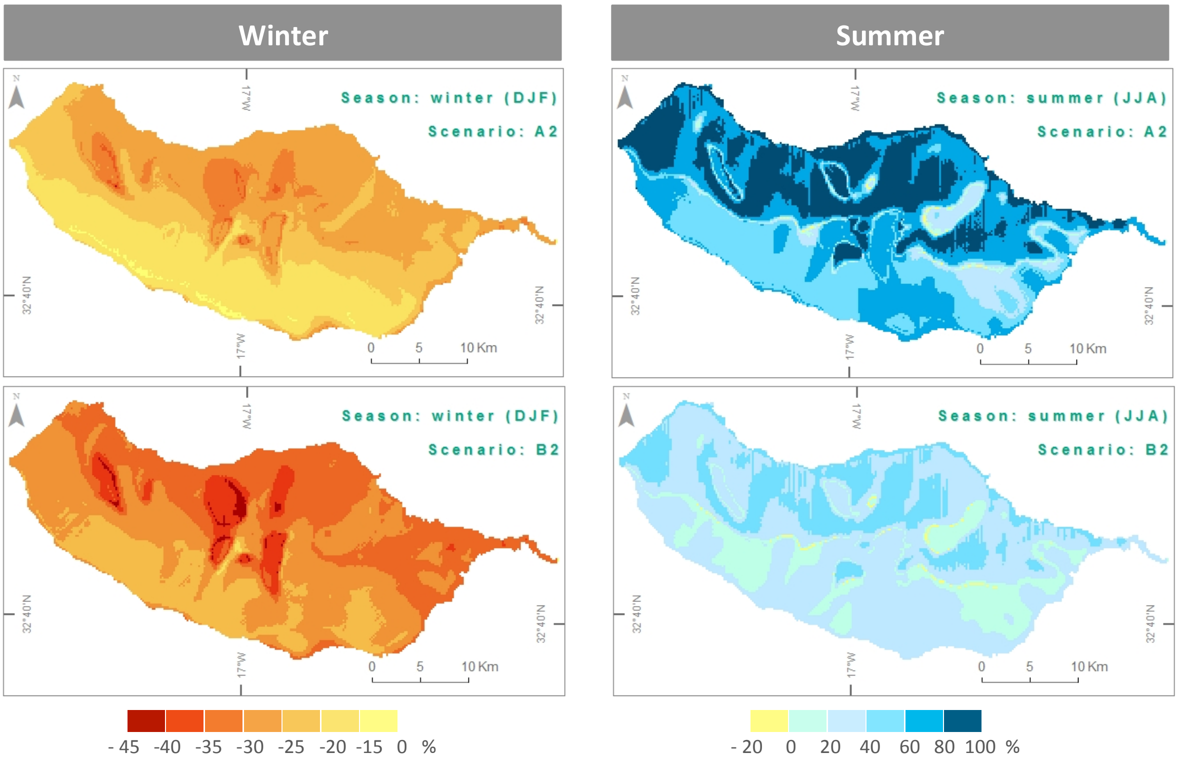


Figure 8 -Relative anomaly (percentage) of seasonal precipitation for the scenarios A2 and B2 at Madeira Island (Source: Project SIAM II)

Both scenarios project a significant decrease in winter precipitation, which is predicted to be more significant in the scenario B2 (20% to 40%) than in the scenario A2 (15% to 35%), despite the fact that the scenario A2 is associated to more extreme changes in terms of SRES emission scenarios. About temperature, it is projected an increase on summer for both scenarios (A2 : 2.4-3ºC; B2: 1.6º-2.2ºC). Such increase is predicted to be higher on coastal areas of the southern face. In winter, the more significant change is projected in terms of minimum temperature, which projections estimate a significant increase (A2: 2.5 - 2.9ºC; B2: 1.5 – 1.8ºC), especially in the upper areas of the island (Miranda *et al.*, 2006). Because of its role on limiting species distribution (Pearson *et al.*, 2002), it was selected the minimum temperature of the coldest month to integrate the group of climatic variables used on calibration.

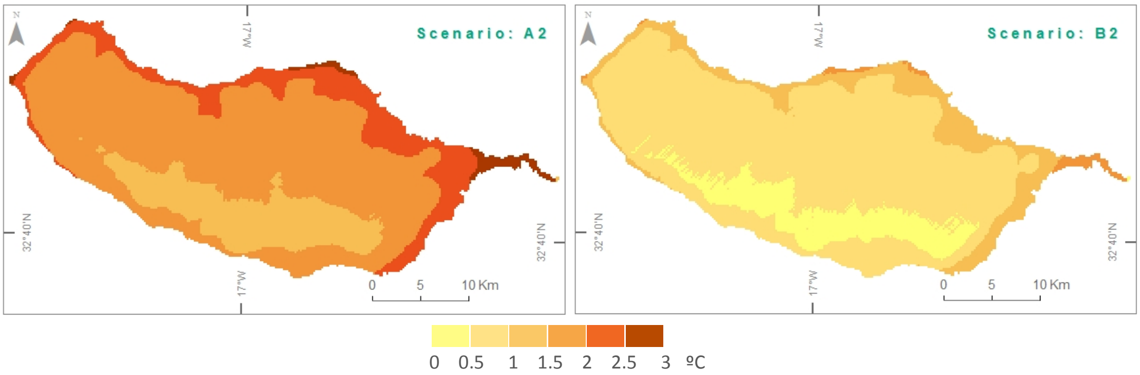


Figure 9 - Anomaly for the mean minimum temperature of the coldest month (February) (Source: Project SIAM II)

3.2 COMMUNITY-LEVEL APPROACH

The assessment of changes on distribution for the community level is carried out only for climax communities of the climatophylous series with significant spatial extent. The definition of each entity (community) is based on the description proposed by Capelo *et al.* (2004), which is based on the perspective of the community concept proposed by the phytosociological perspective (Géhu & Rivas-Martínez, 1981). The selection of species used to represent each climax community is based on the floristic composition of the communities, information gathered both from *rélèves* in the field and published data (Costa *et al.*, 2004).

The area predicted as suitable for each community is based on the combination of modelling results for the species considered as characteristic, being interpreted as representative for each community (Capelo *et al.*, 2004). In the process of combination of results, different weights have been assigned for the selected species. Species accepted as structural and exclusive for a community receive higher scores, while lower scores are assigned to species that are participant on different series of vegetation. Based on that, one of the selected species, considered determinant for the structure and floristic composition of the community, is considered as a direct indicator, and its potential distribution is accepted as sufficient to set the territory as potentially suitable for the community. However, because of the higher disturbance levels exhibited by native vegetation, which could have reduced the area suitable for the species, other taxa are included as support for the definition of the area suitable for the community, despite their lower validity to set the limits of the community alone. In this case, and considered as containing less the predictive power, only areas that register a score higher than a specific threshold are considered as suitable for the community. A table with scores is presented for each community, where it is identified the value below which a territory is not considered as suitable, despite suitable for some of the selected species used in the combination process. In order to improve the results produced for the potential distribution of the communities, species of subseral stages are also included. Such approach is mainly conceived as a strategy to reduce the significant lack of occurrence data for species that are important to the structure of the climax communities, namely trees, a consequence of the high level of disturbance exhibited by native vegetation.

3.2.1 THE ANALYSIS OF CONFLICTS BETWEEN NATIVE COMMUNITIES AND ALIEN INVASIVE TREES

The identification of conflicts is based on the spatial overlay of predicted suitable area for selected tree alien invasive species and native species/climax communities on current and under future climatic scenarios. The integration of non-climatic data (e.g. land-use) on the calibration of models for the alien invasive trees allows the identification of areas with higher susceptibility to invasion.

CAP IV - IMPACTS OF FUTURE CLIMATIC SCENARIOS ON PLANT DISTRIBUTION AT MADEIRA ISLAND: RESULTS

Summary

1 INTRODUCTION

Results about changes on species distribution under climate change scenarios are presented in this chapter, following a structure with three main sections:

i) native species and communities: it includes results for species assigned to some vegetation types, which are correspondent to the climax communities of the climatophylous series best represented on the island, according to the model of potential vegetation proposed by Capelo *et al.* (2004): *Mayteno umbellatae-Oleetum maderensis* (wild olive community), *Semele androgynae-Apollonietum barbujanae* (Mediterranean laurel forest), *Clethro arboreae-Ocoteetum foetentis* (temperate laurel forest), and *Polisticho falcinelli-ericetum aroboreae* (heath-tree community). Results for each community follow the presentation of results for the species selected as characteristic. This section also integrates results for endemic species, with or without protection status, that have not been assigned to the vegetation communities considered;

ii) alien invasive tree species: this section contains results for selected invasive trees: *Acacia mearnsii*, *Acacia melanoxylon*, and *Pittosporum undulatum*;

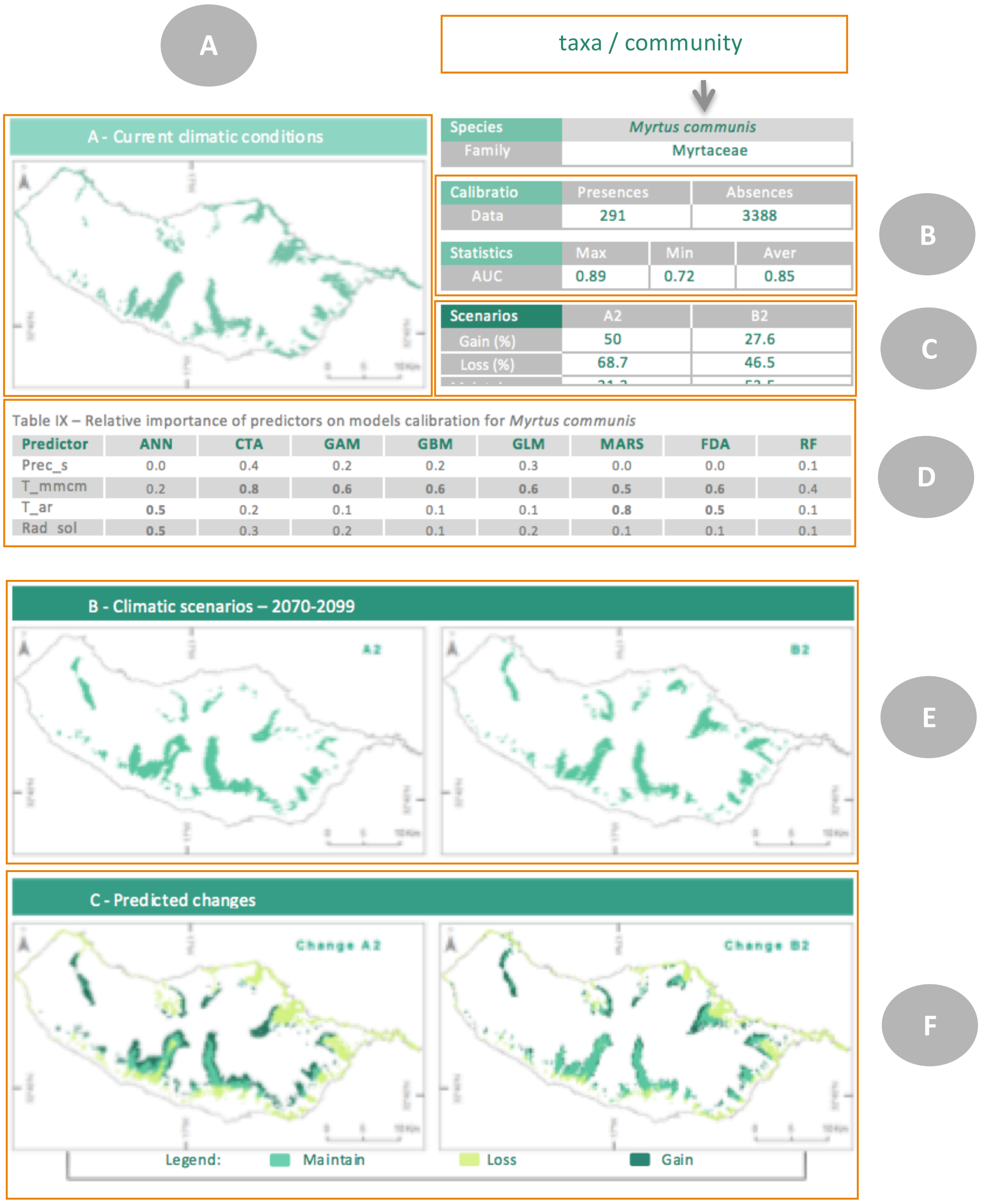
iii) areas of potential conflict: this section includes results for the identification of areas of potential conflict between native communities and alien invasive tree species.

The results are organized on a template page, which includes information for the calibration procedure, such as the number of occurrences used to calibrate models and statistics for the performance of the models (**B**)[1], spatial predictions for suitable area for

---

[1] - The statistics about models' performance are based only on models that were used to produce projections.

current conditions (**A**), relative importance of environmental predictors according the modelling technique, indicating which are most effective on explaining current distribution (**D**); and results for projected climatic changes, namely statistics (**C**) and spatial predictions (**E** and **F**).



Species	*Myrtus communis*
Family	Myrtaceae

Calibratio	Presences	Absences
Data	291	3388

Statistics	Max	Min	Aver
AUC	0.89	0.72	0.85

Scenarios	A2	B2
Gain (%)	50	27.6
Loss (%)	68.7	46.5

Table IX – Relative importance of predictors on models calibration for *Myrtus communis*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
Prec_s	0.0	0.4	0.2	0.2	0.3	0.0	0.0	0.1
T_mmcm	0.2	0.8	0.6	0.6	0.6	0.5	0.6	0.4
T_ar	0.5	0.2	0.1	0.1	0.1	0.8	0.5	0.1
Rad_sol	0.5	0.3	0.2	0.1	0.2	0.1	0.1	0.1

Figure 10 - Template for the organization of results

2 IMPACTS ON DISTRIBUTION FOR NATIVE SPECIES AND COMMUNITIES

2.1 THE DOMAIN OF THE WILD OLIVE MICROFOREST

The wild olive community is an open micro-forest that occupies areas under 200m on the southern face of the island Capelo *et al.* (2004). Because of the high level of disturbance, the community is restricted to small patches confined to steep slopes on rocky walls. Identified by the presence of *Olea maderensis*, the community includes some endemic shrubs, such as *Echium nervosum*, *Euphorbia piscatoria*, *Maytenus umbellata*.

2.1.1 RESULTS FOR THE SPECIES LEVEL

2.1.1.1 *OLEA MADERENSIS* (LOWE) RIVAS MART. & DEL ARCO

Small endemic tree of the Oleaceae family that occurs mainly under 400m of altitude in the southern face of the island. Few occurrences were registered above such altitudes and on the northern face. It also occurs on Porto Santo island.

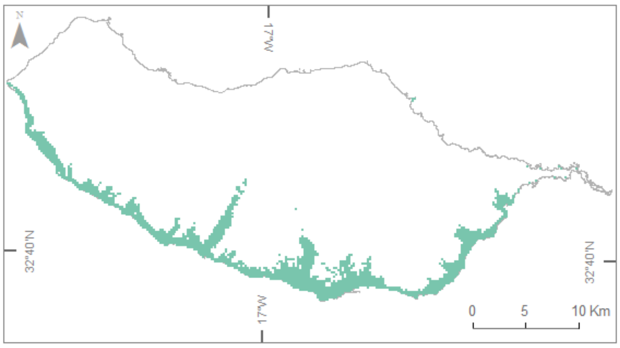
POTENTIAL SUITABLE AREA FOR CURRENT CONDITIONS

Predicted suitable area is highly determined by the influence of the minimum temperature of the coldest month. The variable was elected by all modelling techniques as significant to explain known distribution.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Despite differences in terms of magnitude, models predict an increase in the suitable area for both climatic scenarios. Besides the increase on the southern face, which is very significant for the scenario A2, the models identify as suitable small sections on the coast and valleys on the northern coast.

A - Current climatic conditions



Species	*Olea maderensis*
Family	Oleaceae

Calibratio	Presences	Absences
Data	303	3376

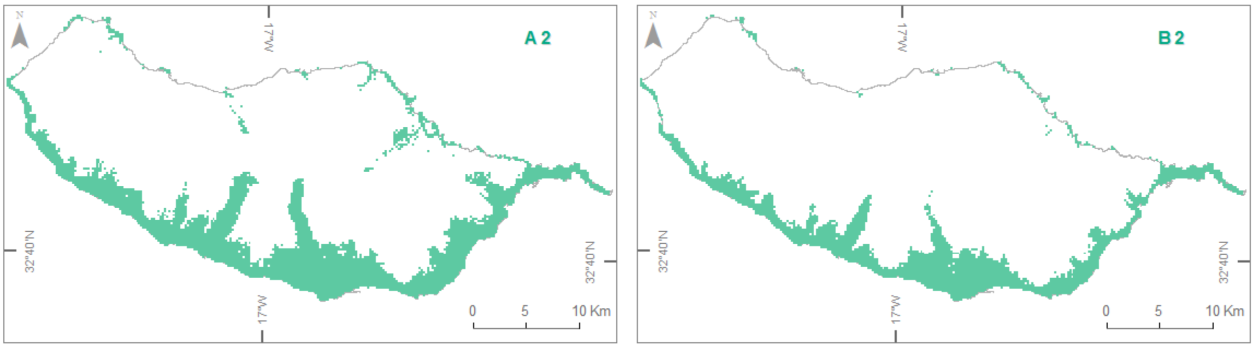
Statistics	Max	Min	Aver
AUC	0.94	0.7	0.8

Scenarios	A2	B2
Gain (%)	142.7	61.4
Loss (%)	0.2	4.8
Maintain	99.8	95.2

Table V – Relative importance of predictors across models for *Olea maderensis*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_w	0.1	0.1	0.2	0.1	0.3	0.4	0.0	0.1
Prec_s	0.3	0.0	0.0	0.0	0.0	0.0	0.1	0.0
T_mcm	**0.6**	**0.9**	**1.0**	**0.9**	**1.0**	**1.0**	**1.0**	**0.6**
T_ar	0.0	0.3	0.2	0.2	0.1	0.3	0.4	0.1

B - Climatic scenarios – 2070-2099



C - Predicted changes

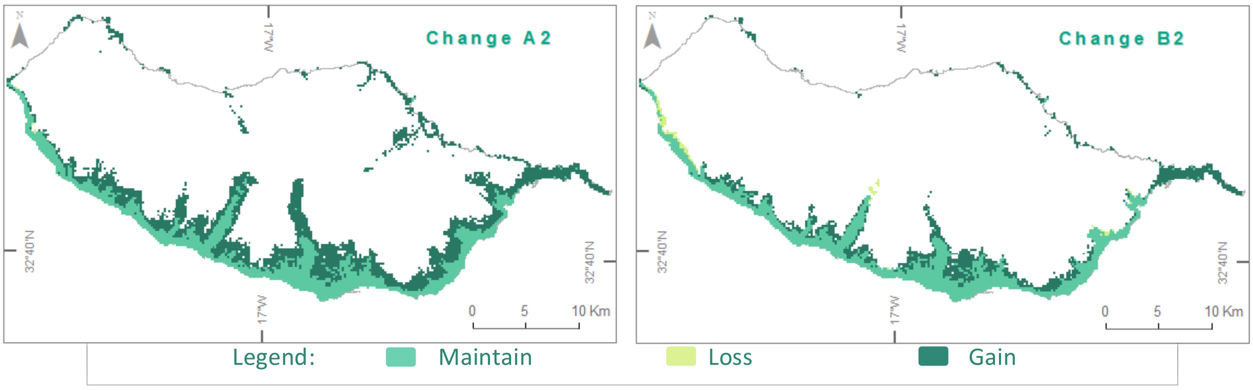


Figure 11 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Olea maderensis*

2.1.1.2 *MAYTENUS UMBELLATA* (R. BR.) MABB.

Evergreen endemic shrub of the Celastraceae family that inhabits the coastal cliffs and end-sections of valleys on both faces of the island. It is quite common on rocky outcrops, a position that is associated to refuge conditions considering the high disturbance level of the surrounding territories.

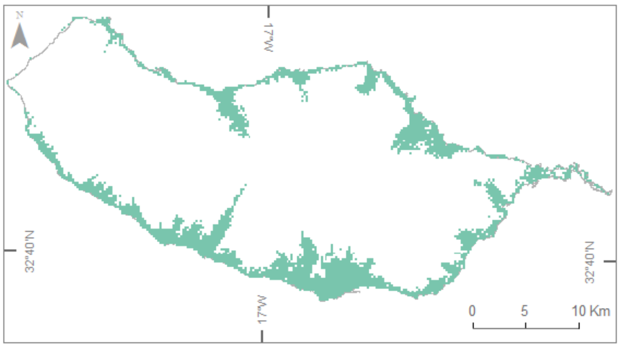
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The area predicted as suitable is highly associated to the influence of the minimum temperature of the coldest month, a predictor identified as determining by different modelling techniques. The high level of disturbance associated to the areas of potential distribution is identified in the fact that models based on ANN technique identify variables related to structure (PSSD) and landscape composition (A_urb) as having a contribution on the explanation of current distribution patterns.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Models predict a significant increase on suitable area on both scenarios, along with a conservation of the current suitable area. The forecasted increase is structured by topographic conditions, mainly along valleys, an association that explains the substantial expansion of suitable area in the eastern sector of the island, where topographic conditions are more associated to the existence of large valleys.

A - Current climatic conditions



Species	*Maytenus umbellata*
Family	Celastraceae

Calibration	Presences	Absences
Data	350	3329

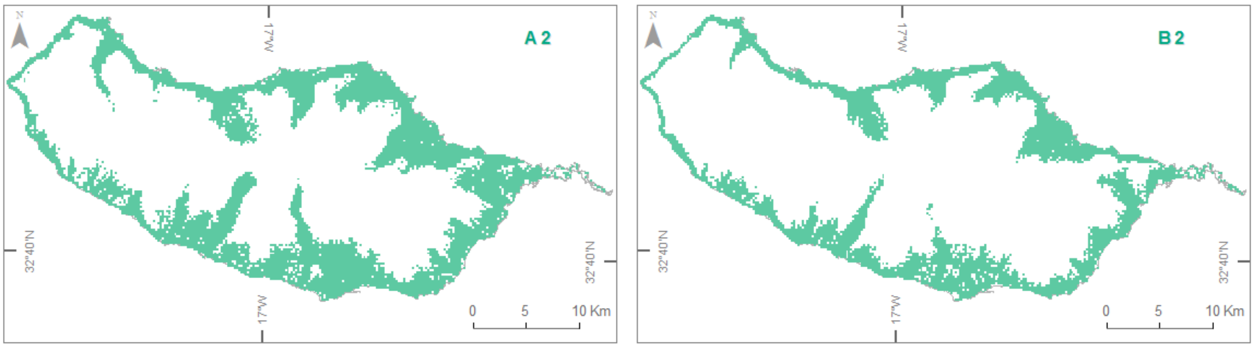
Statistics	Max	Min	Aver
AUC	0.87	0.73	0.83

Scenarios	A2	B2
Gain (%)	115.4	55.6
Loss (%)	5.1	5
Maintain	94.9	95

Table VI – Relative importance of predictors across models for *Maytenus umbellata*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_w	0.3	0.2	0.2	0.1	0.4	0.4	0.1	0.1
T_mmcm	0.2	**0.8**	**0.9**	**0.8**	**1.0**	**1.0**	**0.9**	**0.6**
PSSD	**0.5**	0.0	0.0	0.0	0.0	0.0	0.0	0.0
A_urb	0.2	0.3	0.1	0.0	0.1	0.1	0.1	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes

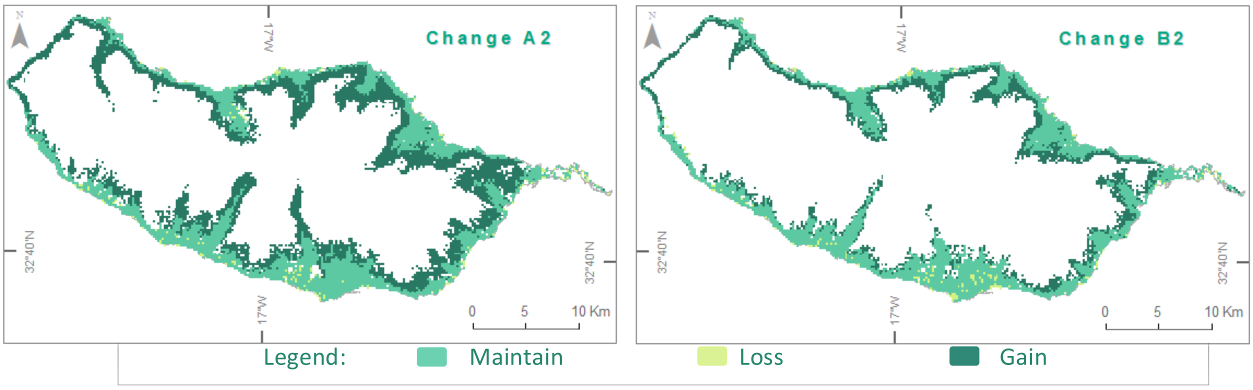


Figure 12 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Maytenus umbellata*

2.1.1.3 *EUPHORBIA PISCATORIA* AITON

Endemic succulent shrub that occurs in the exposed and driest sectors of the island, up to 300m, where it can reach dense communities. Its occurrence on inner locations on valleys, at altitudes above 200m (máx. 600m) in the southern face of the island, and in the northern face is usually associated to small isolated populations occupying rocky outcrops. On the northern coast it is restricted to few sites at very low altitudes (< 100m) in the end-section of valleys. The occurrence data for *Euhphorbia piscatoria* was obtained using a different methodological approach. The presence-absence data was obtained from interpretation of aerial photography. The sampling effort is the same in all grid cells. It is one of the species that seems to recover well after the abandonment of agriculture. However, the invasion of its potential habitat by alien invasive species (*Cardiospermum grandiflorum* Sw., *Arundo donax* L.) is appreciable.

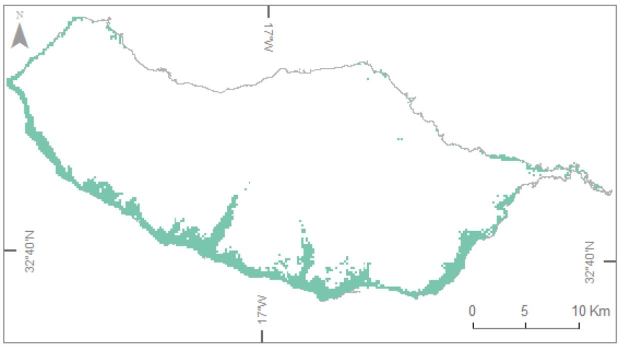
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The area predicted as suitable by the models present a high coincidence with the current distribution. The minimum temperature of the coldest month is the variable that is considered with higher relative importance on explaining current distribution patterns.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Models predict a significant increase in terms of suitable area for both scenarios, but concentrated on the southern face of the island. Only inner sections of valleys are predicted to become suitable on the northern face under the A2 scenario.

A - Current climatic conditions



Species	*Euphorbia piscatoria*
Family	Euphorbiaceae

Calibratio	Presences	Absences
Data	402	3277

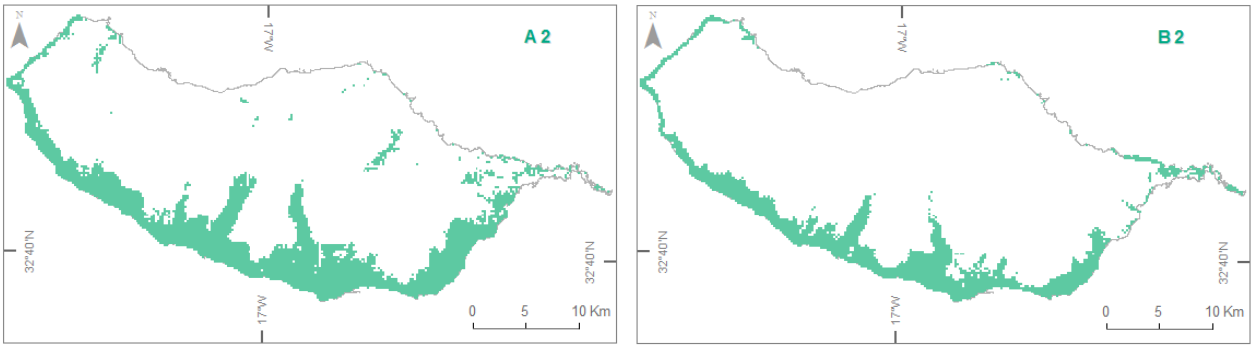
Statistics	Max	Min	Aver
AUC	0.97	0.78	0.9

Scenarios	A2	B2
Gain (%)	122.2	44.9
Loss (%)	1.4	6.2
Maintain	98.6	93.8

Table VII – Relative importance of predictors across models for *Euphorbia piscatoria*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_w	0.2	0.1	0.1	0.1	0.2	0.2	0.1	0.1
Prec_s	0.1	0.0	0.2	0.0	0.3	0.0	0.1	0.0
T_mmcm	**0.7**	**0.9**	**1.0**	**0.9**	**1.0**	**1.0**	**1.0**	**0.7**
T_ar	0.0	0.4	0.4	0.2	0.3	0.3	0.3	0.2

B - Climatic scenarios – 2070-2099



C - Predicted changes

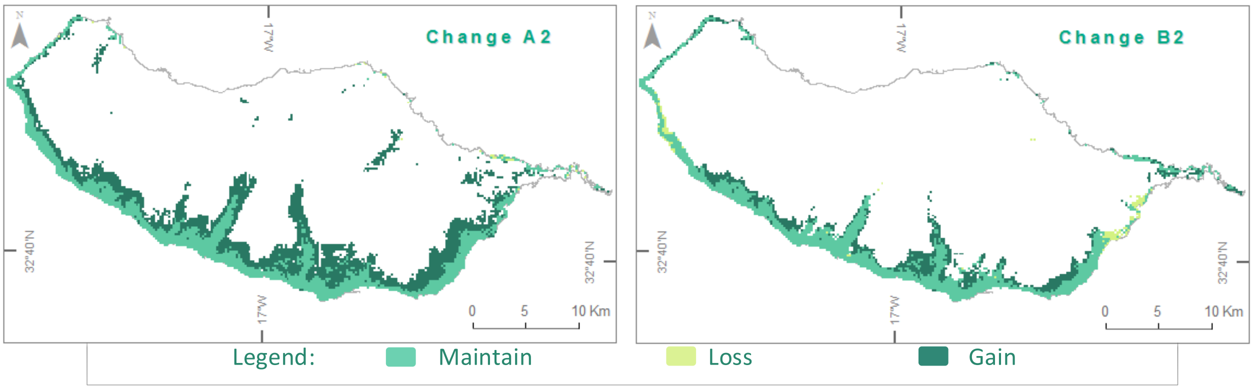


Figure 13 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Euphorbia piscatoria*

2.1.1.4 *ECHIUM NERVOSUM* DRYAND.

Endemic shrub of the Boraginaceae family that occurs mainly on coastal areas under 200m. It is a common species within its area of potential occurrence, despite the high disturbance by human activities. It is a species that has a significant rate of recover on parcels abandoned by agriculture, but is negatively affected by the competition by alien invasive species (*Cardiospermum grandiflorum* Sw., *Arundo donax* L.).

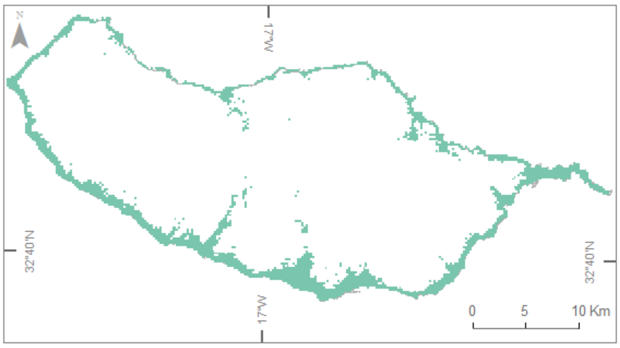
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The area predicted as suitable is very restricted to coastal areas. As verified for the last species, the models identify the minimum temperature of the coldest month as decisive to explain known distribution. With low contribution, and only for models based on the ANN modelling technique, winter precipitation and the existence of areas that face South and East are also identified. Also with low contribution, but identified by almost all modelling techniques, the area occupied by exotic communities is identified as a predictor that helps to explain current distribution, in a negative way. So, the presence of exotic communities is already conditioning the distribution of such species.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The increase in area predicted as suitable is more significant for conditions associated to the A2 climatic scenario. Despite differences on magnitude among scenarios, there is a similar trend in terms of spatial pattern.

A - Current climatic conditions



Species	*Echium nervosum*
Family	Boraginaceae

Calibratio	Presences	Absences
Data	329	3350

Statistics	Max	Min	Aver
AUC	0.93	0.78	0.9

Scenarios	A2	B2
Gain (%)	145.7	62.7
Loss (%)	0	1
Maintain	100	99

Table VIII – Relative importance of predictors across models for *Echium nervosum*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_w	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
T_mmcm	0.3	**1.0**	**0.9**	**0.9**	**0.9**	**0.9**	**1.0**	**0.7**
A_exot	0.4	0.0	0.2	0.1	0.2	0.1	0.1	0.1
aspES	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0

B - Climatic scenarios – 2070-2099

C - Predicted changes

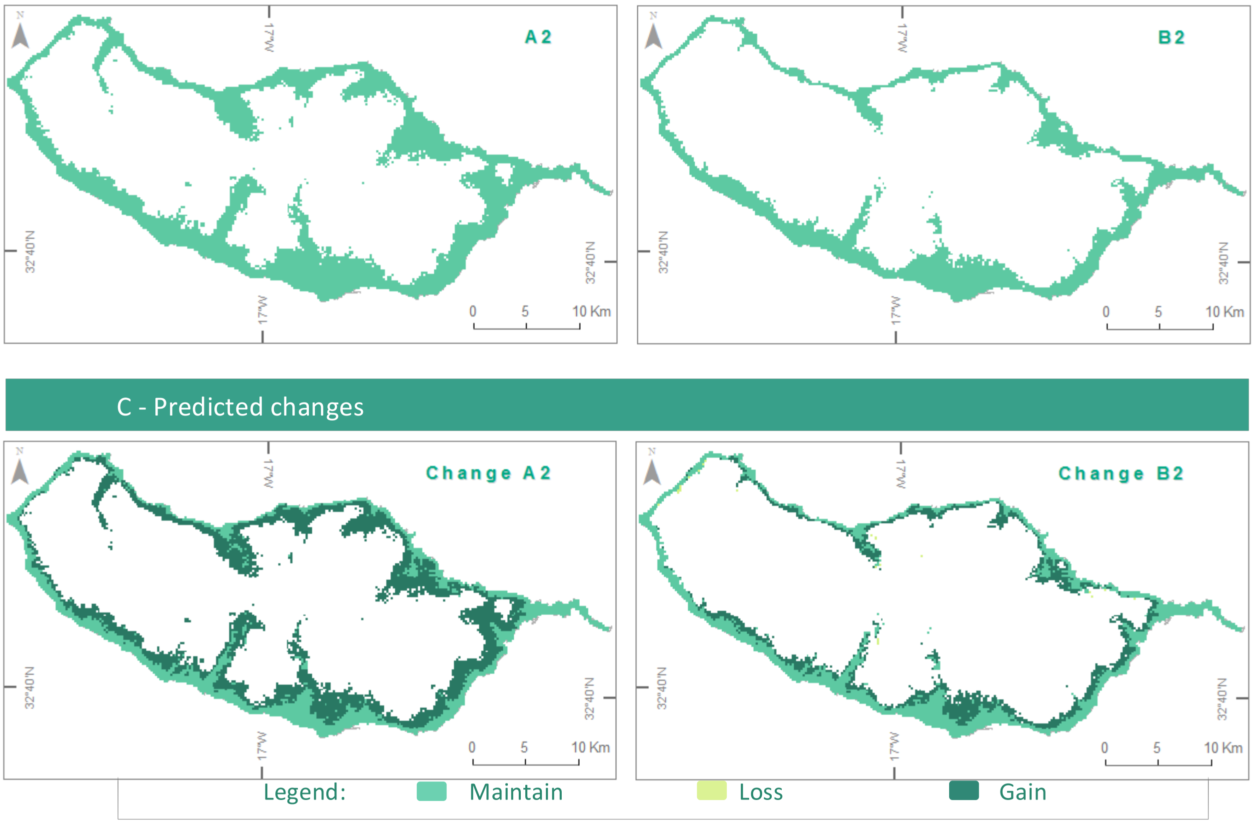


Figure 14 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Echium nervosum*

2.1.2 RESULTS FOR THE COMMUNITY LEVEL

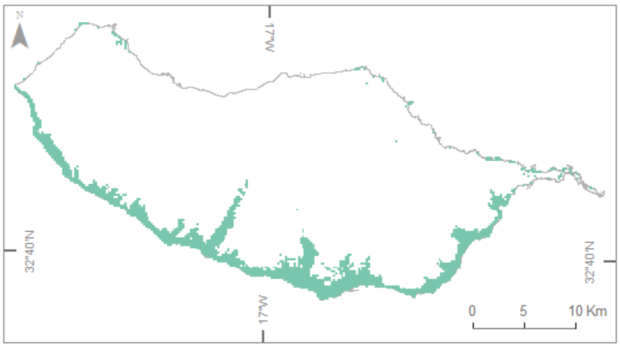
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The area predicted as suitable for the wild olive community is mainly restricted to southern face of the island. Such results are deeply associated to the higher score attributed to the taxa *Olea maderensis*. Despite the conservative perspective associated to such option, it is based on the assumption that species have a different importance as indicators for the community. So, species shared by different types of vegetation (*Echium* nervosum, *Maytenus* umbellata) should not be used as only indicator for a community.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Both scenarios predict a maintenance in the suitable area, and an increase associated to an expansion to upper areas in the southern face and along valleys on the opposite face, a change that is more clear in the scenario A2. Projections for scenario B2 reveal higher importance in terms of loss of suitable area, namely in the inner section of valleys and upper limits of potential distribution.

A - Current climatic conditions

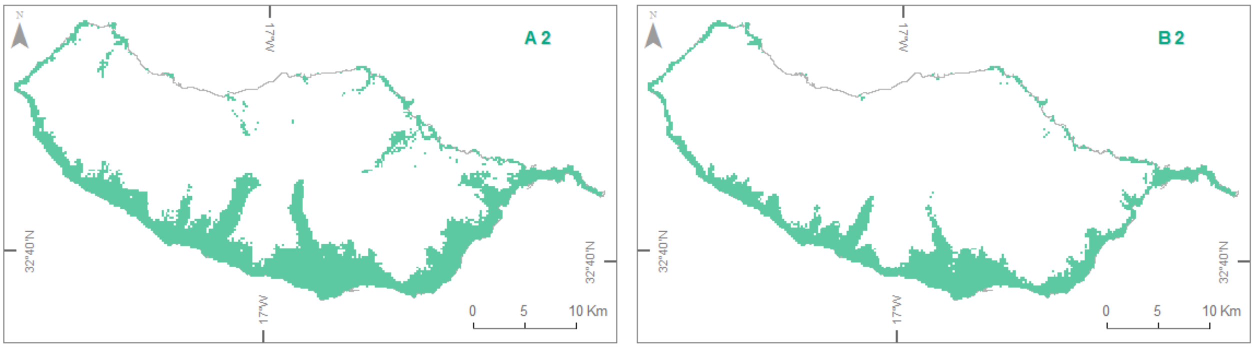


Community	Wild olive microforest (>=4)

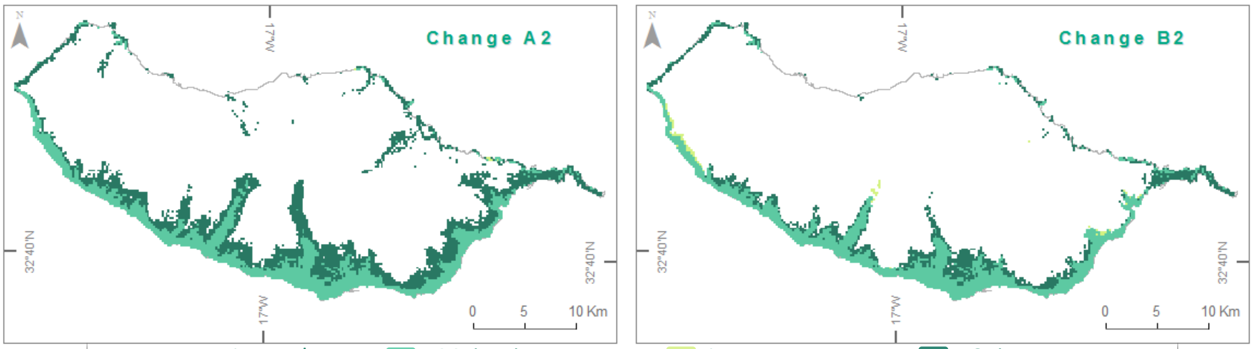
Species	Score
Olea maderrensis	4
Maytenus umbellata	1
Euphorbia piscatoria	2
Echium nervosum	1

Scenarios	A2	B2
Gain (%)	137.7	59.3
Loss (%)	0.3	3.7
Maintain (%)	99.7	96.3

B - Climatic scenarios – 2070-2099



C - Predicted changes



Legend: 🟩 Maintain 🟩 Loss 🟩 Gain

Figure 15 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for the wild olive microforest

2.2 THE DOMAIN OF THE MEDITERRANEAN LAUREL FOREST

The Mediterranean laurel forest occupies sub-humid to humid territories, pontually infraMediterranean areas with deeper soils. Its potential area of distribution is within 300 to 800 m on the southern coast and within 50 to 300 m in the northern face (Capelo *et al.*, 2004). Based on floristic composition Capelo *et al.* (2004) consider two different versions for this forest. Currently the community is restricted to small patches on rocky walls, a consequence of the intense use by human activities on its potential area of distribution.

2.2.1 RESULTS FOR THE SPECIES LEVEL

2.2.1.1 *APOLLONIAS BARBUJANA* (CAV.) BORNM.

Endemic Macaronesian tree of the Lauraceae family that dominates the tree layer of the Mediterranean laurel forest. Its distribution is severely affected by land-use, and occurs mainly on valleys' rocky walls.

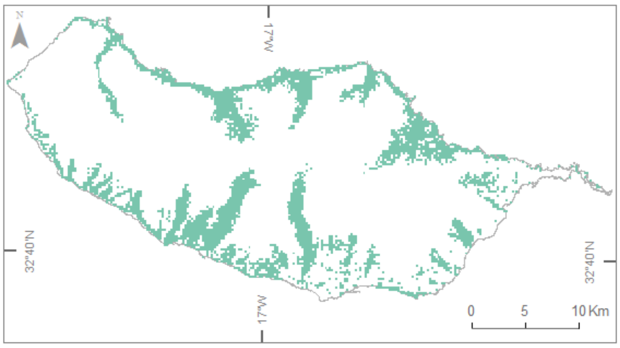
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The predicted area clearly shows a scattered distribution, mostly associated with valleys. Such forecast is clearly biased by the influence of disturbance by human activities. Despite that, the predictor variables selected for its explanatory power are only climatic (incoming solar radiation, minimum temperature of the coldest month).

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Models predict an upward shift for the species, which is based on the loss of suitable area in the rear edge (low altitudes) and a gain on areas close to upper current margin (upper altitudes). The loss of suitable area is predicted to be more important along the coastal areas, while gain is predicted to occur at inner sections of the valleys.

A - Current climatic conditions



Species	*Apollonias barbujana*
Family	Lauraceae

Calibratio	Presences	Absences
Data	768	2911

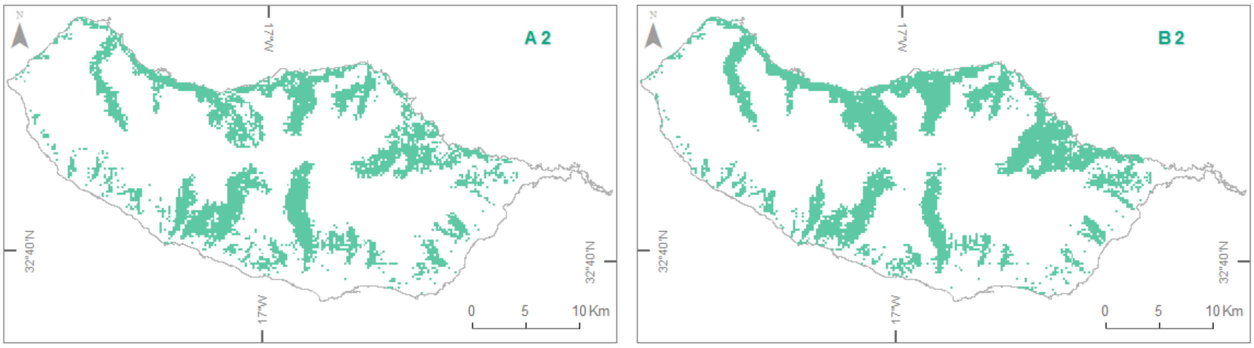
Statistics	Max	Min	Aver
AUC	0.87	0.81	0.86

Scenarios	A2	B2
Gain (%)	42.7	40.5
Loss (%)	29.3	17.5
Maintain	70.7	40.5

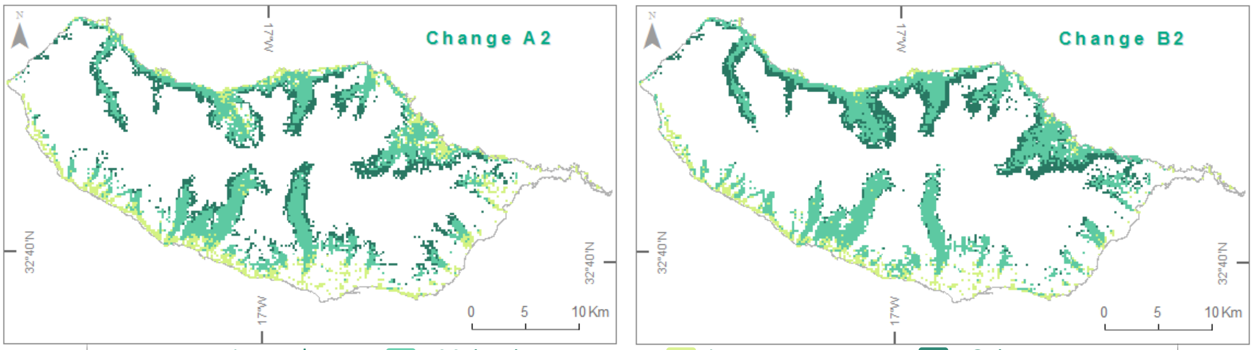
Table IX – Relative importance of predictors across models for *Apollonias barbujana*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Radsol	0.3	0.3	0.3	0.3	0.3	0.3	0.2	0.2
T_mmcm	0.5	0.6	0.4	0.5	0.4	0.6	0.4	0.4
T_ar	0.0	0.1	0.1	0.0	0.2	0.4	0.3	0.0
Prec_s	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes



Legend: 🟩 Maintain 🟨 Loss 🟩 Gain

Figure 16 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Apollonias barbujana*

2.2.1.2 *SEMELE ANDROGYNA* (L.) KUNTH

Endemic Macaronesian liana of the Liliaceae family that occurs mainly in the potential area of the Mediterranean laurel forest.

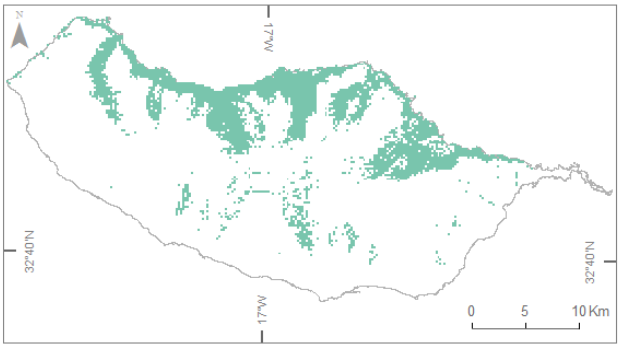
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

Predicted suitable area is mainly associated to the northern face of the island. On the southern face suitable areas are restricted to small patches at higher altitudes. The predictors identified as having more relative importance are climatic (annual temperature range, winter precipitation) and topographic (incoming solar radiation), which confirms the thermophyllous character of the species. Despite only considered for one modelling technique (ANN), the percentage of area with step slopes (slp_34) was considered relevant to explain current distribution. That reveals a strategy of the species, but also the condition of refuge associated to a significant number of sites where the species is found.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Suitable area is predicted to increase for both scenarios. Such increase is spatially concentrated on the northern face of the island, and is predicted to be more important under the scenario B2. Despite the fact that only a small fraction of the potential suitable area is lost, it is is very much restricted to the southern face, which is important in relative terms, once will reduce drastically the area suitable on such part of the island.

A - Current climatic conditions



Species	*Semele androgyna*
Family	Liliaceae

Calibration	Presences	Absences
Data	143	3536

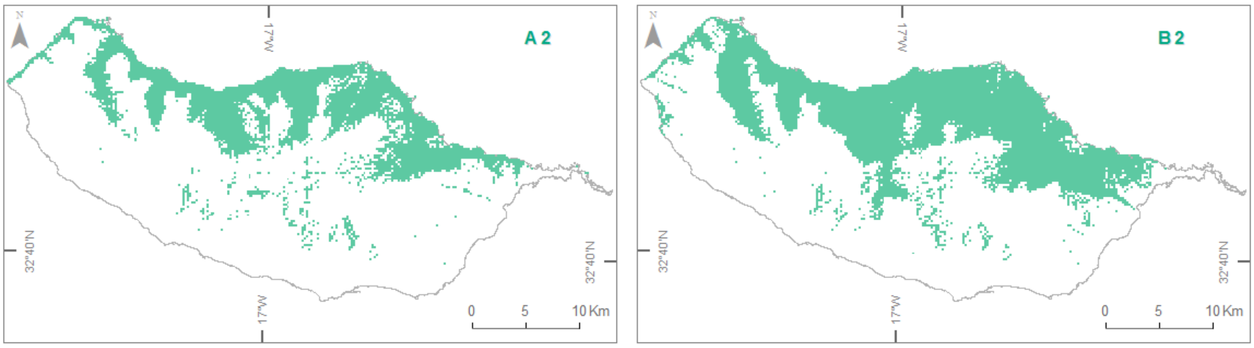
Statistic	Max	Min	Aver
AUC	0.87	0.7	0.8

Scenarios	A2	B2
Gain (%)	37.3	105
Loss (%)	5.5	3.2
Maintain (%)	94.5	96.8

Table X – Relative importance of predictors across models for *Semele androgyna*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Rad_sol	0.1	**0.5**	0.4	0.3	0.4	0.3	0.2	0.2
Prec_w	**0.7**	0.2	0.1	0.0	0.1	0.3	0.0	0.1
T_ar	0.0	**0.9**	**0.6**	**0.7**	**0.6**	**0.8**	**0.7**	**0.5**
Slp_4	**0.5**	0.0	0.0	0.0	0.0	0.0	0.1	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes

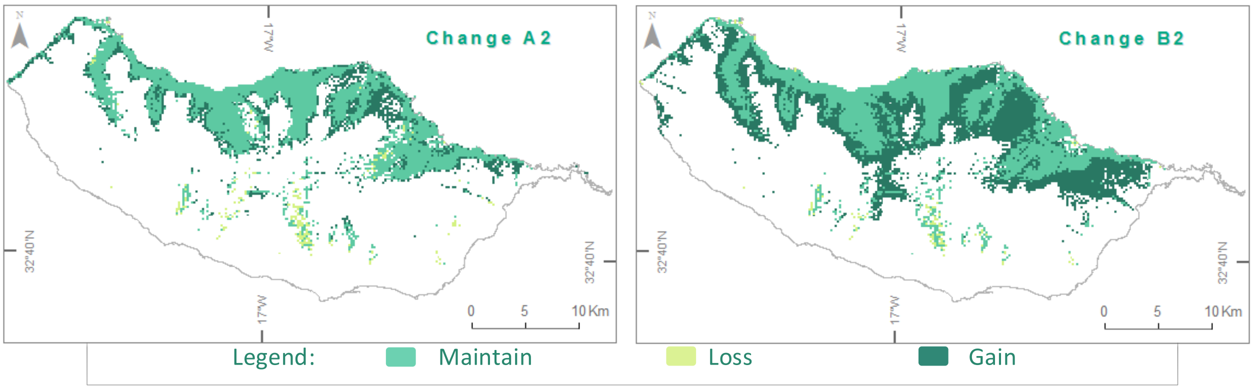


Figure 17 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Semele androgyna*

2.2.1.3 *HYPERICUM CANARIENSE* L.

Endemic Macaronesian shrub of the Theaceae family that occurs on low-altitude territories of the southern face of the island, within the potential area of distribution of the Mediterranean laurel forest. Despite its restricted distribution, it is frequent, and can be dominant on shrubby communities.

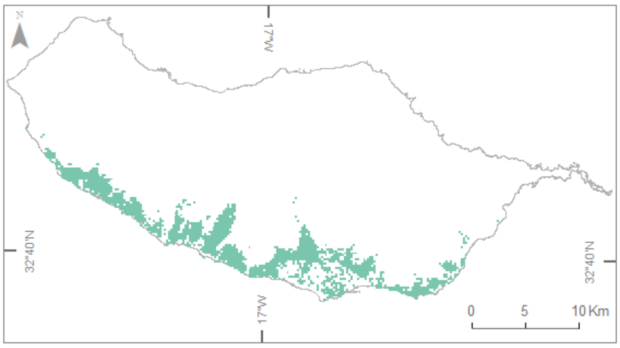
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The area predicted as suitable is characterized by the low values of precipitation and high average temperatures. The minimum mean temperature of the coldest month and annual temperature range are identified as important predictors to explain current distribution. Despite its lower relative importance, several modelling techniques identify the existence of areas facing north as a predictor. That conditions shows the importance of including topographic variables on species distribution models at such spatial scales.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The models predict a clear upward shift for the species, supported on a balanced loss of suitable area at lower altitudes (rear edge) and a gain at upper areas that are defined in the neighborhood of the potential distribution for current climatic conditions.

A - Current climatic conditions



Species	*Hypericum canariense*
Family	Theaceae

Calibration	Presences	Absences
Data	83	3596

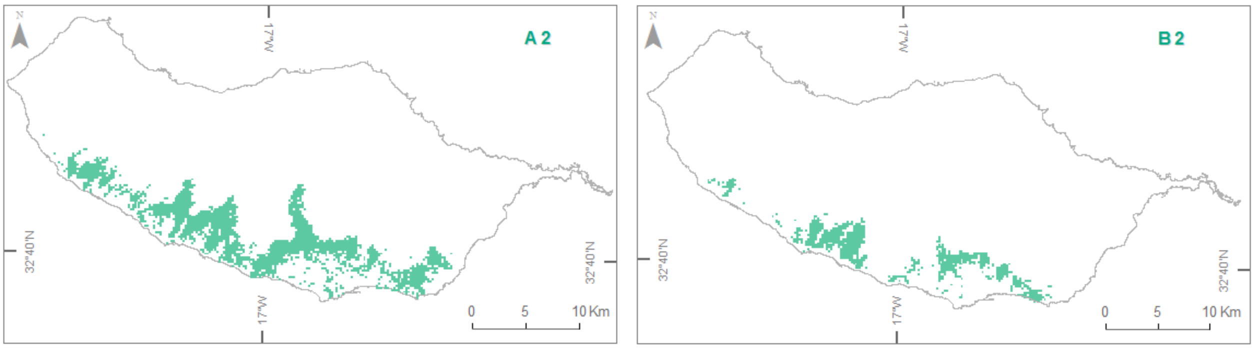
Statistics	Max	Min	Aver
AUC	0.87	0.7	0.82

Scenarios	A2	B2
Gain (%)	61.5	10.3
Loss (%)	41.8	63
Maintain (%)	58.2	37

Table XI – Relative importance of predictors across models for *Hypericum canariense*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_w	-	0.0	0.3	0.0	**0.6**	**0.6**	0.0	0.1
T_mmcm	-	**0.6**	**0.9**	**0.4**	**1.0**	0.3	**0.5**	0.3
T_ar	-	**0.8**	**0.5**	**0.6**	0.4	**1.0**	**0.7**	0.3
asp_N	-	0.0	0.3	0.1	0.3	0.3	0.2	0.1

B - Climatic scenarios – 2070-2099



C - Predicted changes

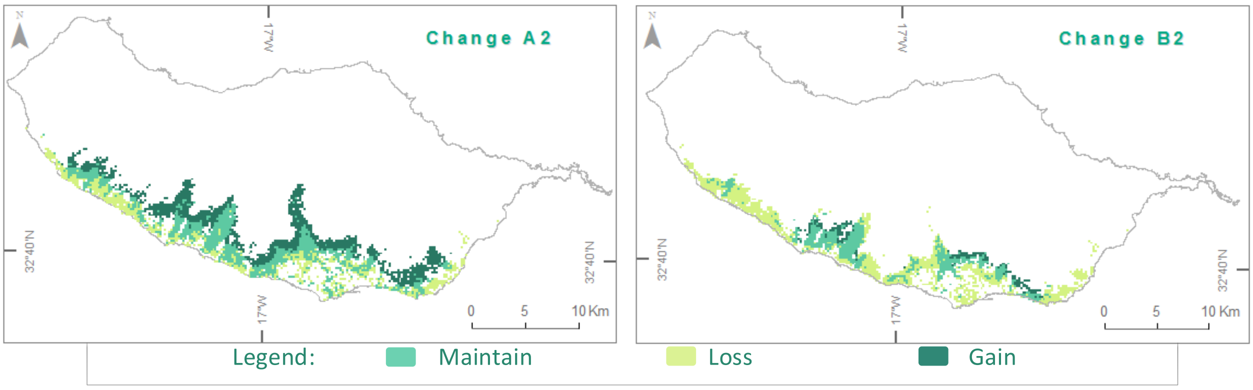


Figure 18 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Hypericum canariense*

2.2.1.4 *MYRTUS COMMUNIS* L.

Native shrub of the Myrtaceae family that occurs mainly in the western part of the island, where it is associated to large valleys. As a mesophytic shrub, Its current distribution seems to be deeply restricted by the practice of agriculture.

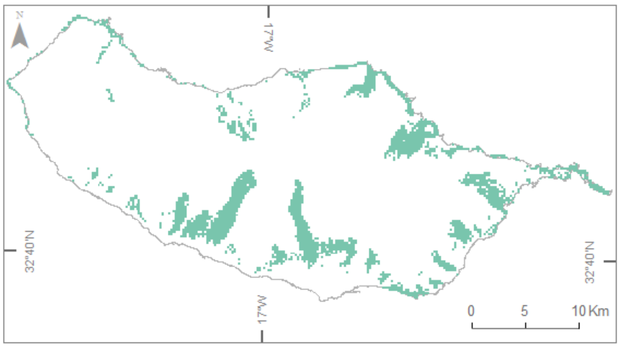
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The models present a good fit between known distribution and predicted suitable area. The minimum mean temperature of the coldest month and the annual temperature range are identified as the predictors with higher contribution to explain current known distribution.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

It is predicted a significant loss in terms of suitable area, which is of higher importance than the projected gain for both scenarios. The loss of suitable area, which occurs in the lower altitudes, is especially evident in the projections for the scenario A2.

A - Current climatic conditions



Species	*Myrtus communis*
Family	Myrtaceae

Calibratio	Presences	Absences
Data	291	3388

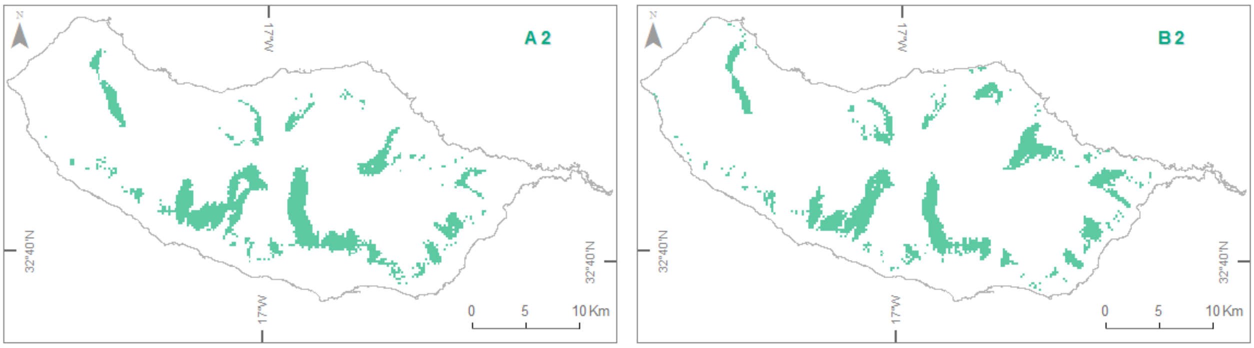
Statistics	Max	Min	Aver
AUC	0.89	0.72	0.85

Scenarios	A2	B2
Gain (%)	50	27.6
Loss (%)	68.7	46.5
Maintain	31.3	53.5

Table XII – Relative importance of predictors across models for *Myrtus communis*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
Prec_s	0.0	0.4	0.2	0.2	0.3	0.0	0.0	0.1
T_mmcm	0.2	**0.8**	**0.6**	**0.6**	**0.6**	**0.5**	**0.6**	0.4
T_ar	**0.5**	0.2	0.1	0.1	0.1	**0.8**	**0.5**	0.1
Rad_sol	**0.5**	0.3	0.2	0.1	0.2	0.1	0.1	0.1

B - Climatic scenarios – 2070-2099



C - Predicted changes

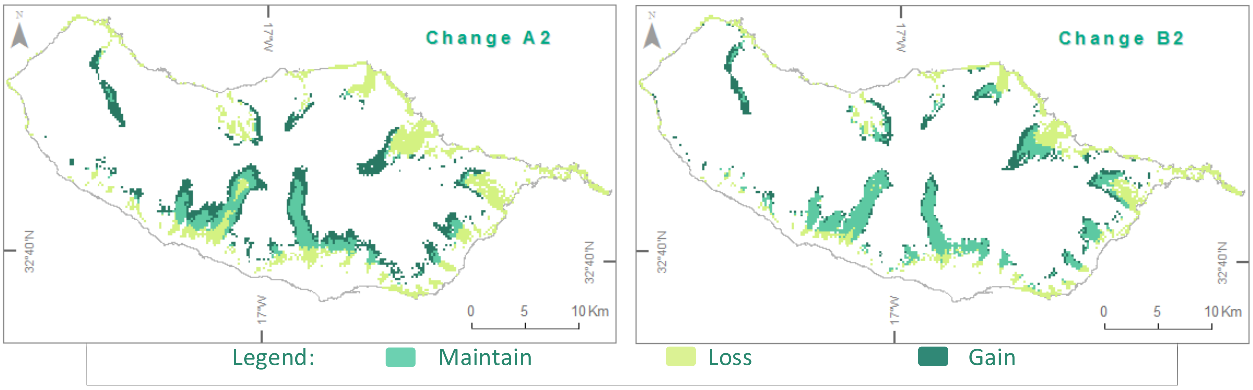


Figure 19 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Myrtus communis*

2.2.1.5 *Smilax pendulina* Lowe

Endemic macaronesian liana of the Smilacaceae family that is mostly restricted to the northern face of the island. Despite the wide area where it can be found, it is a rare plant. It is found on areas near the coast, in the territory potentially associated to the Mediterranean laurel forest, but it can enter on deeper areas of the valleys, where the potential vegetation is associated to the temperate laurel forest, occupying mainly termophyllous positions, namely associated to open communities installed on steep slopes facing from NE to SW.

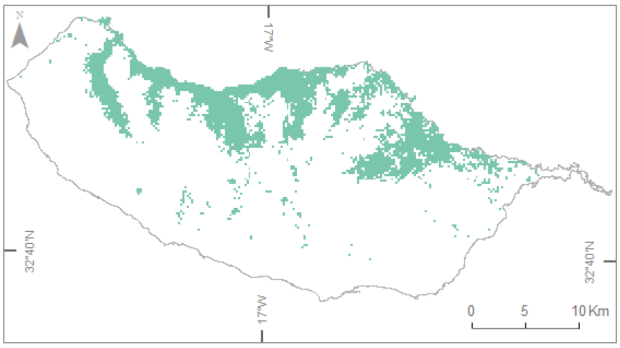
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

Only a small fraction of suitable area is detected by the models in the southern face of the island, which corresponds mainly to the inner section of valleys. Such prediction is very likely determined by the fact that models identify the presence of native forest as determinant to explain current distribution, and those areas have associated small patches of native forest. However, the annual temperature range is identified as the predictor with higher explanatory power for known distribution.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

In terms of projected changes models predict a maintenance of the current suitable area and a significant increase, especially for the A2 scenario. That condition might be associated to a decrease in the annual temperature range for the climatic scenarios, and low sensitivity to a decrease in the amount of precipitation.

A - Current climatic conditions



Species	*Smilax pendulina*
Family	Smilacaceae

Calibratio	Presences	Absences
Data	72	3607

Statistics	Max	Min	Aver
AUC	0.79	0.7	0.72

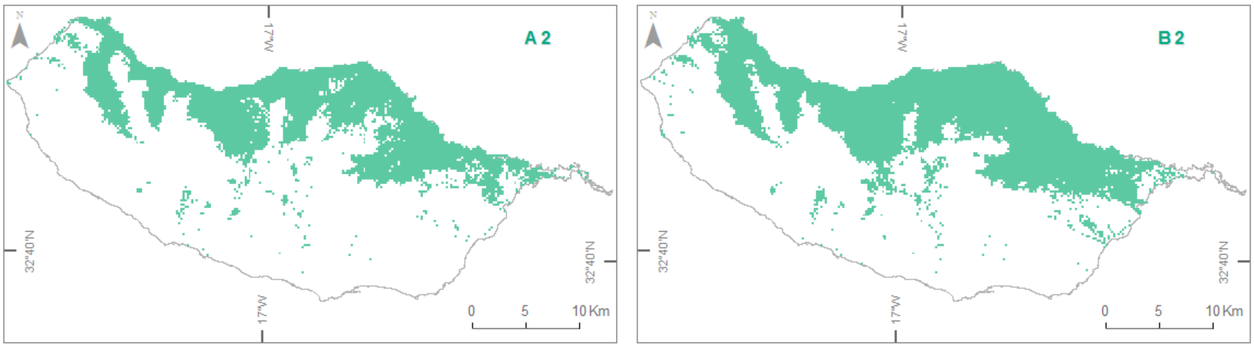
Scenarios	A2	B2
Gain (%)	57.9	102
Loss (%)	0.2	0
Maintain	99.8	100

Table XIII – Relative importance of predictors across models for *Smilax pendulina*

Predictor	**ANN**	**CTA ***	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_w	0.3	-	0.0	0.0	0.1	**0.5**	0.0	0.1
T_ar	0.2	-	**0.5**	**0.8**	0.4	**0.6**	**0.5**	0.3
A_flnat	**0.6**	-	0.2	0.2	0.2	0.4	0.3	0.2
PSCOV	0.3	-	0.1	0.2	0.1	0.4	0.0	0.1

* - The absence of values indicates that models produced by the modelling technique are no used because of low AUC (<0.7).

B - Climatic scenarios – 2070-2099



C - Predicted changes

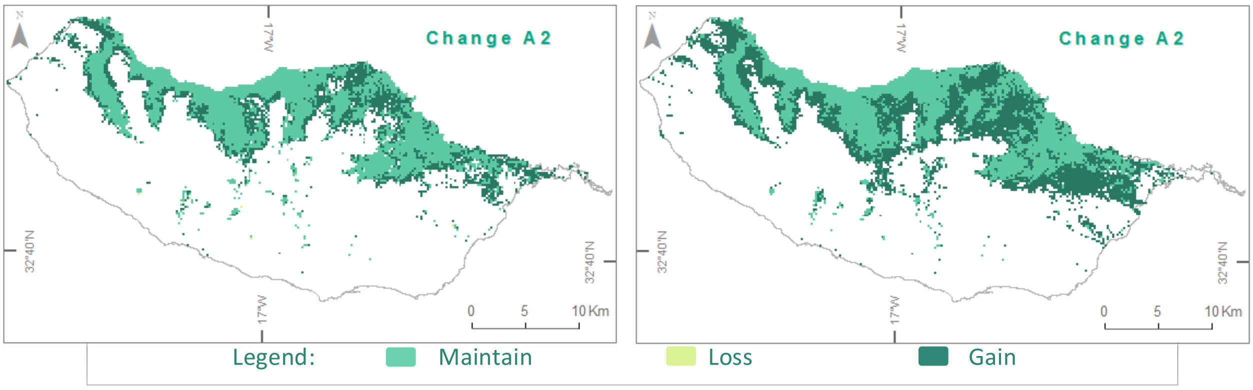


Figure 20 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Smilax pendulina*

2.2.1.6 *ILEX CANARIENSIS* POIR

Endemic macaronesian tree of the Rosaceae family that presents a low representativity within its area of distribution. Among the species associated to the Mediterranean laurel forest this one might be the one that occupies inner sections in the valleys and higher altitudes. In the field it seems to mark the transition between the Mediterranean and temperate laurel forest, where it is replaced by the congener taxa *Ilex perado*. In terms of ecology, is very common on rocky outcrops.

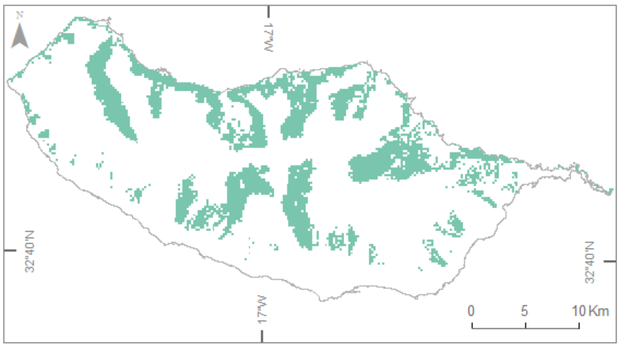
POTENTIAL SUITABLE AREA FOR CURRENT CONDITIONS

Predictions identify a clear topographic pattern in the distribution of the species, namely in the southern face of the island. Most of the suitable area is associated to valleys, and their upper limits of distribution seems to match with the lower predicted geographical range of the temperate laurel forest.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The projected changes reveal a timid upward shift, based on a small gain at upper neighbouring areas, and a significant loss at lower altitudes, which is far more important than the projected gain, especially for the scenario A2.

A - Current climatic conditions



Species	*Ilex canariensis*
Family	Aquifoliaceae

Calibration	Presences	Absences
Data	272	3407

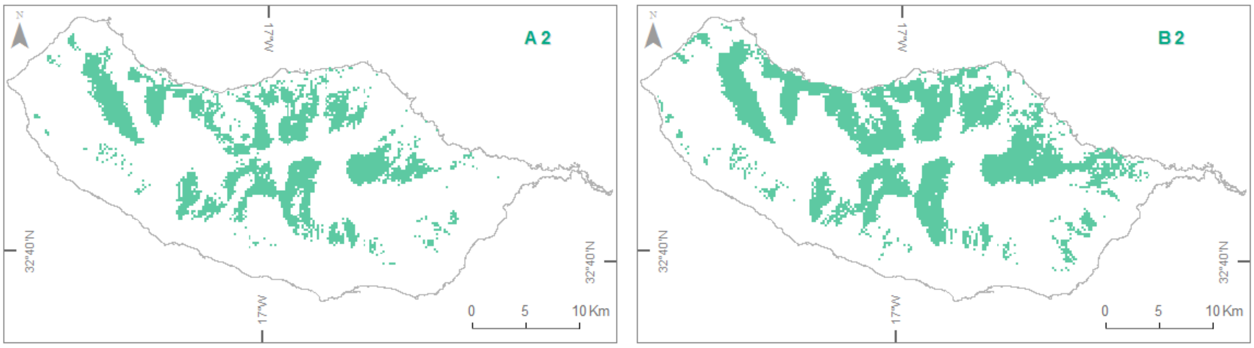
Statistics	Max	Min	Aver
AUC	0.86	0.7	0.79

Scenarios	A2	B2
Gain (%)	25.8	36.1
Loss (%)	41.9	12.5
Maintain	58.1	87.5

Table XIV – Relative importance of predictors across models for *Ilex canariensis*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
Prec_w	**0.6**	0.2	0.1	0.2	0.1	0.2	0.2	0.1
T_mmcm	0.0	**0.6**	**0.5**	0.4	**0.5**	0.4	0.4	0.2
T_ar	0.0	0.2	0.3	0.1	0.3	**0.5**	0.2	0.1
Rad_sol	0.1	**0.6**	0.3	0.3	0.2	0.4	0.3	0.2

B - Climatic scenarios – 2070-2099



C - Predicted changes

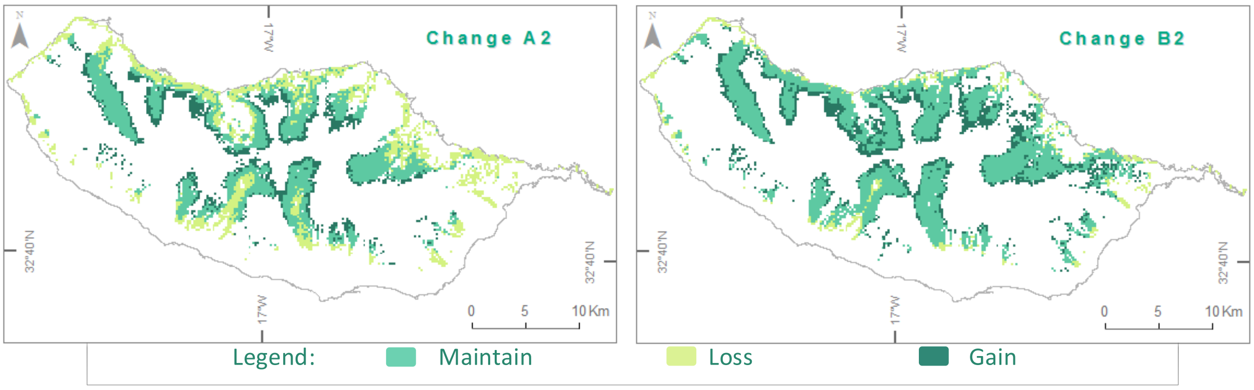


Figure 21 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Ilex canariensis*

2.2.2 RESULTS FOR THE COMMUNITY LEVEL

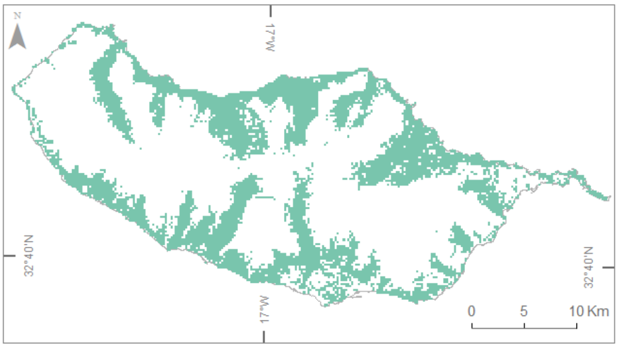
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

Predicted distribution of the Mediterranean laurel forest is mainly structured by topographic conditions, and is clearly associated to medium and end-sections of valleys, an association that might reveal the refugee condition that most of the characteristic species exhibit. In fact, most of the area that is expected to be suitable for such forest was deeply disturbed by human activities, namely agriculture, reducing the area to small patches.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Predictions under future climatic scenarios forecast an increase in terms of suitable area, which is more pronounced in the northern face of the island under the scenario B2. The predicted increase is based on a significant gain associated to the expansion at the upper edge, and is far more important than the projected loss. The predicted loss on suitable area presents a remarkable coincidence for both scenarios, both spatially and in terms of magnitude, electing the lower altitudes of the southern face as more susceptible.

A - Current climatic conditions

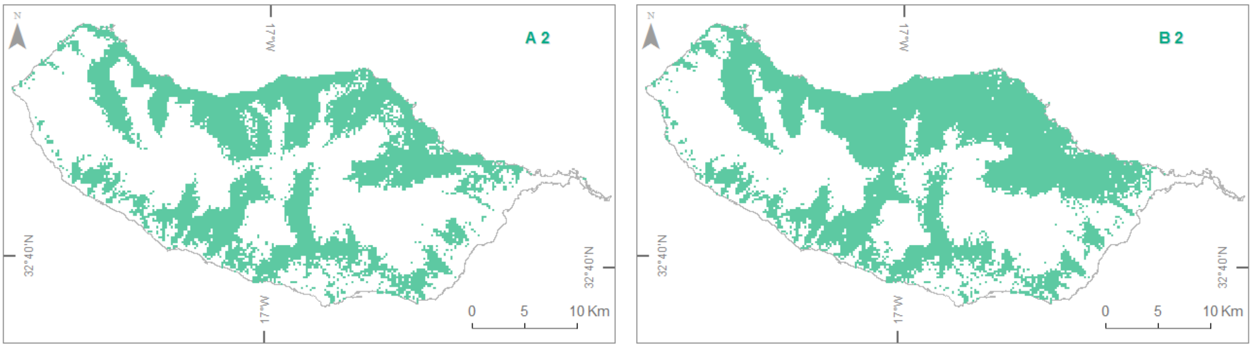


Community	Mediterranean laurel forest (>=3)

Species	Score
Apollonias barbujana	4
Semele androgyna	2
Hypericum canariense	4
Myrtus communis	4
Smilax pendulina	2
Ilex canariensis	2

Scenarios	A2	B2
Gain (%)	35.2	55.9
Loss (%)	18.6	15.5
Maintain (%)	81.4	84.5

B - Climatic scenarios – 2070-2099



C - Predicted changes

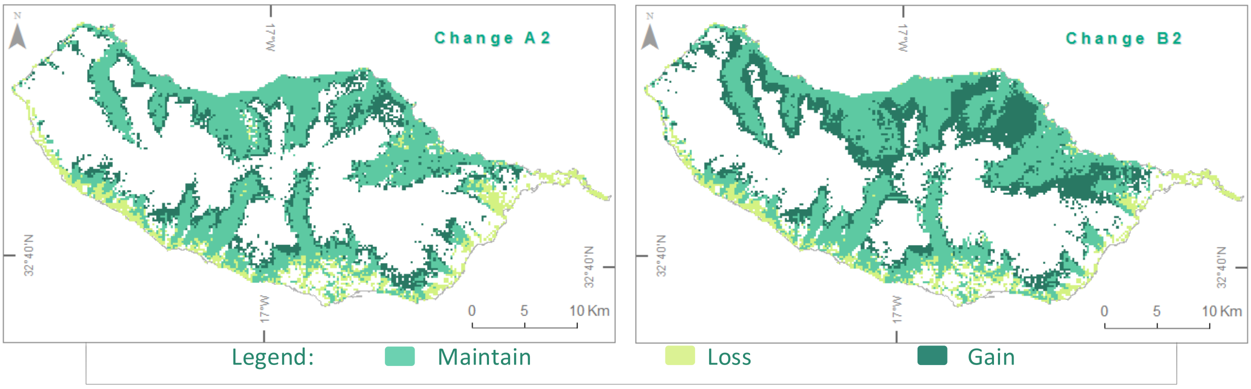


Figure 22 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for the Mediterranean laurel forest

2.3 THE DOMAIN OF THE TEMPERATE LAUREL FOREST

According to the vegetation model proposed by Capelo *et al.* (2004), a significant portion of the island is potentially suitable to the temperate laurel forest. Their distribution seems to be controlled by precipitation on the lower altitudes and by temperature at the summits of the island. The tree layer is dominated by lauraceous species (*Ocotea foetens, Laurus novocanariensis, Persea indica*), which are generally, despite differences among them, high water-demanding (Ritter *et al.*, 2009) and low tolerant to drought and low temperatures (González-Rodríguez *et al.*, 2001).

There are few records of occurrence on the southern face of the island, a consequence clearly associated to the high level of disturbance exhibited by the native vegetation. That condition contributed to reduce the capacity of the models to predict accurately

2.3.1 RESULTS FOR THE SPECIES LEVEL

2.3.1.1 *LAURUS NOVOCANARIENSIS* R. MART., LOUSÃ, F. PRIETO, E. DIAS, J. C. COSTA & C. AGUIAR

Macaronesian endemic tree of the *Lauraceae* family, native to Madeira and Canaries. It is widely distributed on the island, from low altitudes near the coast to the 1400 m m.s.l. It is the lauraceous species with wider ecological range. Its distribution is mostly associated to the temperate laurel forest, but it can reach lower altitudes on west and north-facing slopes, where it can be detected in fragments of the Mediterranean laurel forest. Historical and recent disturbance (charcoal production, cutting, fire, grazing) contribute to mask their limits of distribution, namely on the southern face of the island and on areas above 1200 m. Their presence in the high plateau of Paul da Serra (>1450 m), with very few individuals, is dubious in terms of spontaneous occurrence, once afforestation plans have been implemented on such areas.

PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The models predict as unsuitable the driest areas of the island, corresponding to the low altitudes, especially on the eastern sector of the island, and areas above 1400 m m.s.l. In terms of environmental predictors, such results are determined by the average minimum temperature of February, which is the variable that presents the higher importance on models produced by different modelling techniques (GAM, GLM, MARS, FDA)[2]. Models exhibit the lowest average scores in terms of performance or predictive accuracy (AUC) concerning all the species considered. Some of the modelling techniques were actually discarded in the production of the final model because of the low quality of the models (AUC < 0.7 – ANN, CTA). The models that have been considered in the production of the final model for potential distribution, produced by the other modelling techniques, present also low scores of AUC, most of them presenting a value equal to the 0.7, below which models are discarded (see discussion and conclusions chapter). The low values exhibited by all techniques must be related to the wide distribution of the species. Such fact determines a wide ecological range and higher difficulties to distinguish between suitable and unsuitable conditions.

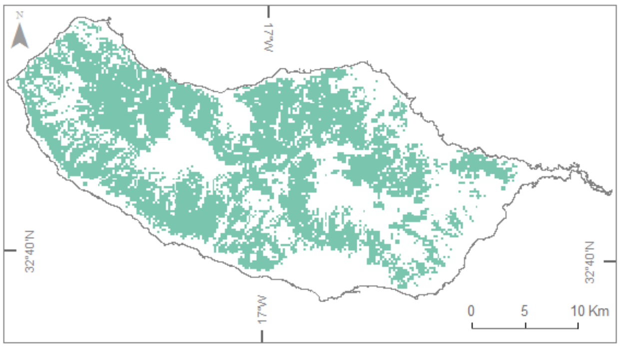
CLIMATIC SCENARIOS AND PREDICTED CHANGES

The models predict a significant lost in terms of suitable area for both climatic scenarios at the lowest areas of potential distribution, a trend that is not compensated by the predicted gain. Such lost is more significant in the scenario A2. Despite the low contribution of precipitation variables to define the potential distribution model for current climatic conditions, changes on precipitation in the climatic scenarios should likely contribute to predicted changes.

---

[2] - The importance of the variable is obtained by **1 – correlation score.** The correlation score is calculated between the original prediction and the prediction made with a permuted variable, or the correlation between the results produced with and without the variable in question. High values mean high importance while zero (0) means that the variable is not important to the produced model.

A - Current climatic conditions



Species	*Laurus novocanariensis*
Family	Lauraceae

Calibratio	Presences	Absences
Data	1498	2181

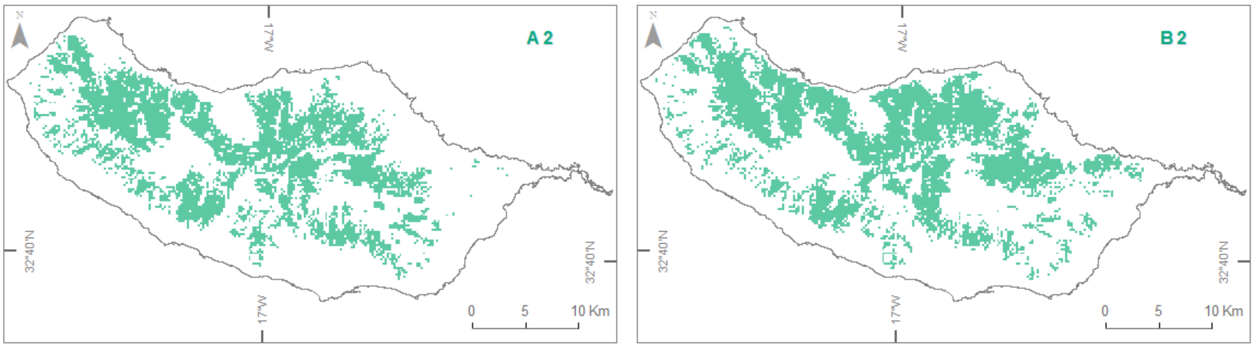
Statistics	Max	Min	Aver
AUC	0.71	0.7	0.7

Scenarios	A2	B2
Gain (%)	1.7	2.9
Loss (%)	41.4	34.3
Maintain	58.6	65.7

Table XV – Relative importance of predictors across models for *Laurus novocanariensis*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
Prec_S	0.2	0.4	0.0	0.0	0.0	0.0	0.0	0.0
T_mmcm	0.0	0.4	0.5	0.3	0.5	0.8	0.5	0.2
T_ar	0.0	0.3	0.2	0.1	0.2	0.4	0.2	0.1
PSSD	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes

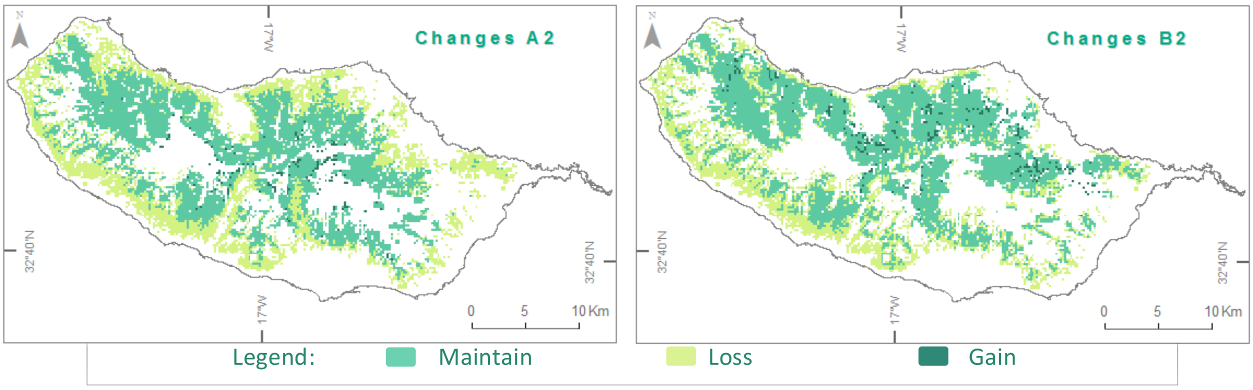


Figure 23 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Laurus novocanariensis*

2.3.1.2 *ILEX PERADO* AITON

Endemic tree of the Aquifoliaceae family that occurs mainly on the northern slope of Madeira Island and highest summits of the island. In the last location it survives on rocky outcrops, once the territory was deeply disturbed by fire, cutting and grazing. It is deeply associated to the temperate laurel forest, but it is also present above its area of potential distribution, reaching the summits of the island. On its lower distribution sets contact with the distribution of *Ilex canariensis*, which might be used as indicator for the transition between the temperate and the meditteranean laurel forests.

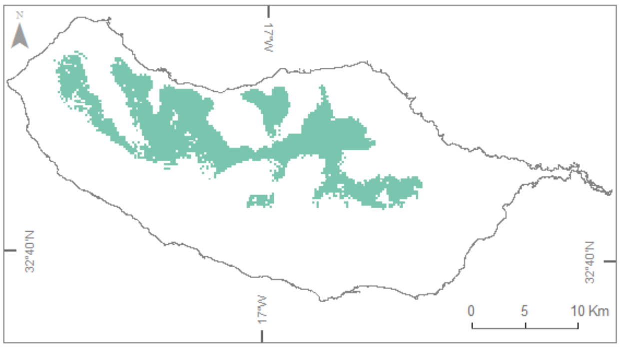
POTENTIAL SUITABLE AREA FOR CURRENT CONDITIONS

The predicted suitable area reveals that models were able to capture the main features associated to current distribution patterns. Models identify the minimum mean temperature of the coldest month and summer precipitation as the two most determining predictors to explain known distribution.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Predictions for the species reveals an unusual trend in terms of spatial response. The curious response is not associated to the fact that models predict a maintenance of the suitable area, with just a small decrease. What it is not expectable is that the gain in terms of suitable area is projected for the lower altitudes, in opposition to a likely upward shift.

A - Current climatic conditions



Species	*Ilex perado*
Family	Aquifoliaceae

Calibratio	Presences	Absences
Data	242	3437

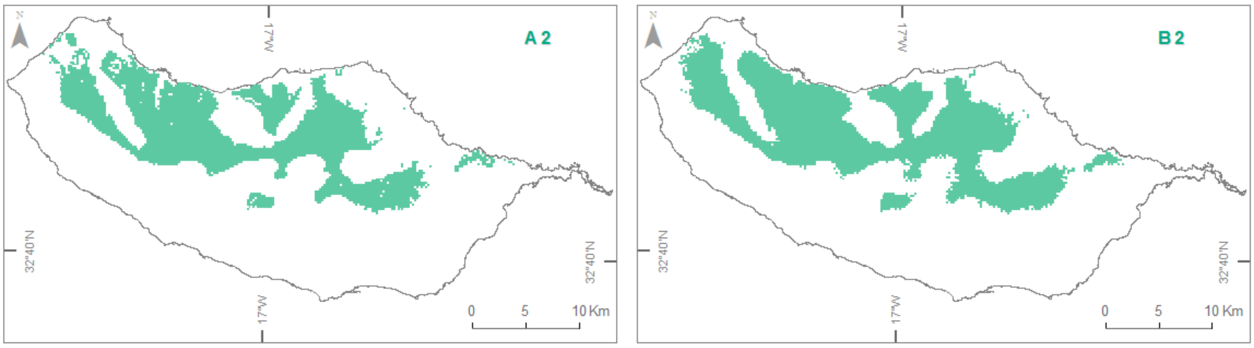
Statistics	Max	Min	Aver
AUC	0.93	0.81	0.89

Scenarios	A2	B2
Gain (%)	32.5	48.8
Loss (%)	5.3	0.4
Maintain	94.7	99.6

Table XVI – Relative importance of predictors across models for *Ilex perado*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_s	**0.6**	**0.5**	0.0	0.3	0.0	0.3	**0.7**	0.3
T_mmcm	0.1	**0.7**	**0.9**	**0.5**	**0.9**	**0.6**	0.3	0.3
T_ar	0.0	0.1	**0.5**	0.0	0.4	0.2	0.0	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes

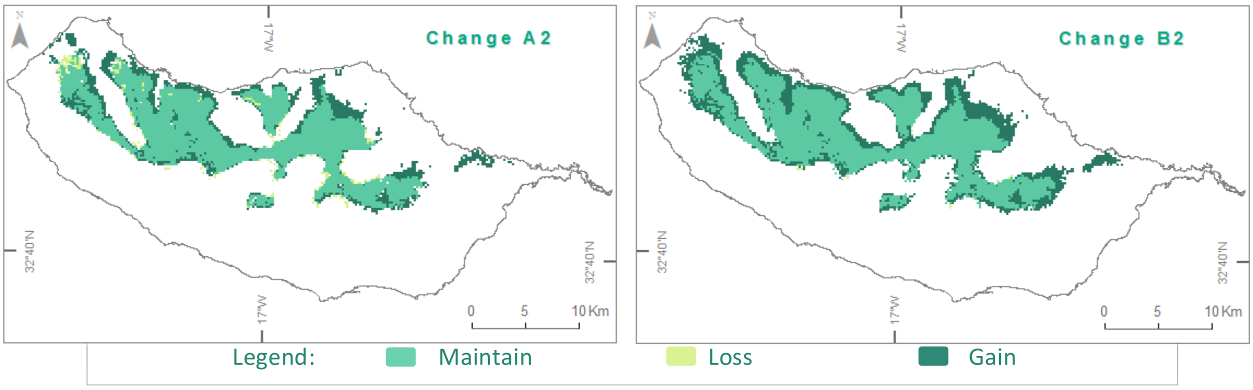


Figure 24 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Ilex perado*

2.3.1.3 *OCOTEA FOETENS* (AITON) BAILL.

Endemic Macaronesian phanerophyte present on Madeira Island and some of the islands of the Canarian archipelago. It is a big tree (30-40 m) that very often is dominant in the temperate laurel forest. Its presence is interpreted as a good indicator for such type of vegetation. Its current distribution is mostly restricted to the northern face of the island, a fact that is controlled by the high intensity, length and diversity of types of disturbance that encompass the southern face. Only few groups of individuals were identified on the southern face.

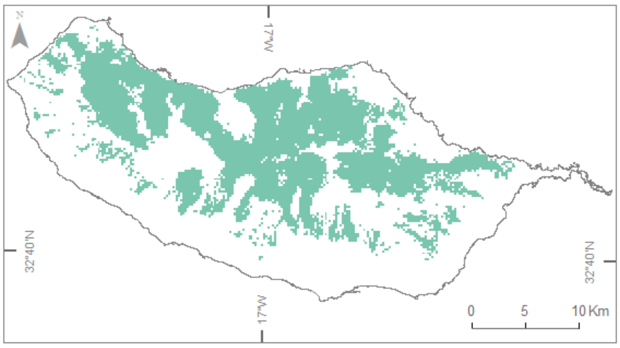
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The predicted suitable area clearly exhibits the contribution of the average minimum temperature of the coldest month (February), as environmental predictor, and the lack of presences on the southern face of the island, a biasing effect derived from the almost extirpation of the species. In terms of environmental variables, the average minimum temperature of February is the predictor with higher importance among different modelling techniques, a situation similar to the one described for *Laurus novocanariensis*. Such result is well matched with the assumption that *Lauraceae* species are cold sensitive.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The predicted changes are significantly different between the climatic scenarios. The scenario A2 predicts a significant loss of suitable area, while the results for the scenario B2 present a significant gain and a very restricted loss. Such predictions might reveal an high susceptibility of the species to small changes in terms of climatic conditions.

A - Current climatic conditions



Species	*Ocotea foetens*
Family	Lauraceae

Calibratio	Presences	Absences
Data	764	2915

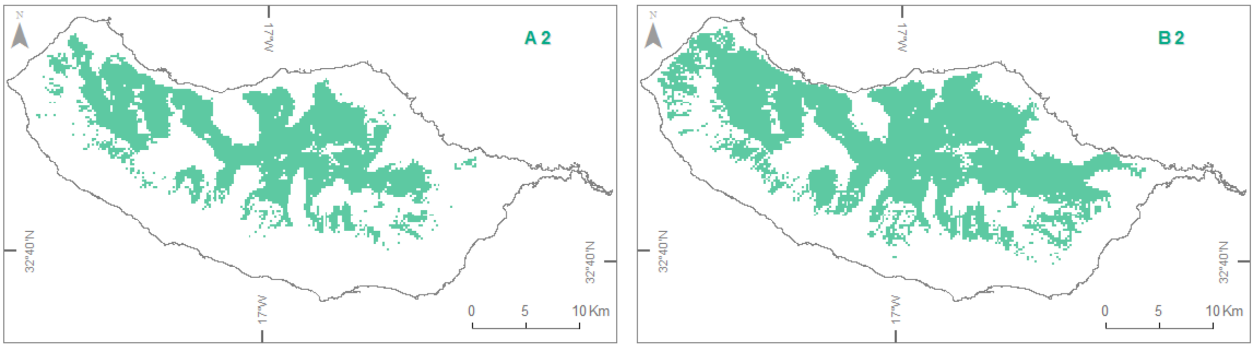
Statistics	Max	Min	Aver
AUC	0.84	0.7	0.79

Scenarios	A2	B2
Gain (%)	6.7	18.5
Loss (%)	30.7	5.9
Maintain	69.3	94.1

Table XVII – Relative importance of predictors across models for *Ocotea foetens*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
Prec_w	0.3	0.0	0.0	0.0	0.1	0.2	0.1	0.1
T_mmcm	0.1	0.3	**0.8**	**0.6**	**0.8**	**0.6**	**0.6**	0.4
Prec_s	0.2	0.0	0.0	0.0	0.0	0.3	0.0	0.1

B - Climatic scenarios – 2070-2099



C - Predicted changes

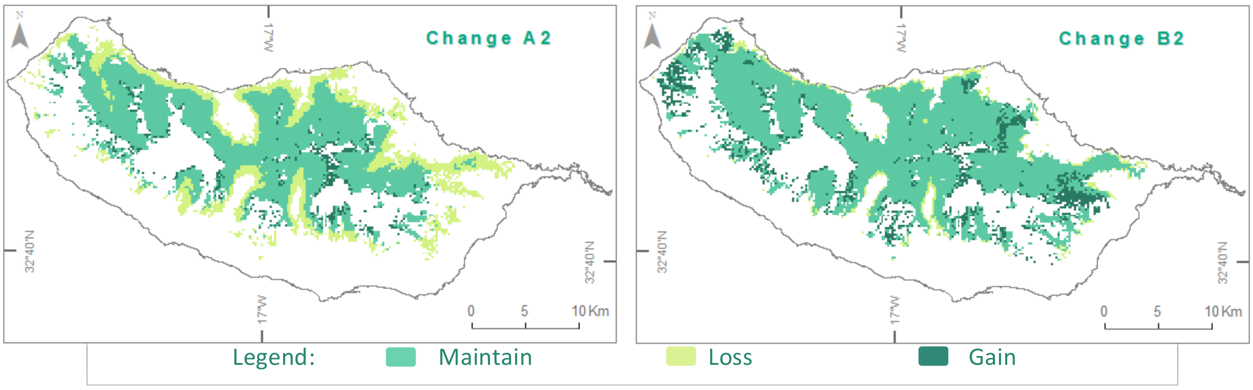


Figure 25 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Ocotea foetens*

2.3.1.4 *CLETHRA ARBOREA* AITON

Endemic evergreen tree of Madeira Island and only representative of the Clethraceae family. Very common in the temperate laurel forest. Together with *Myrica* faya Aiton, it is a pioneer in the installation stage of the temperate laurel forest, namely in the definition of a tree layer, on areas affected by disturbance, contributing very often to degrade the extant shrubby communities, usually heath communities. However, on mature versions of the forest is very frequent as shrub.

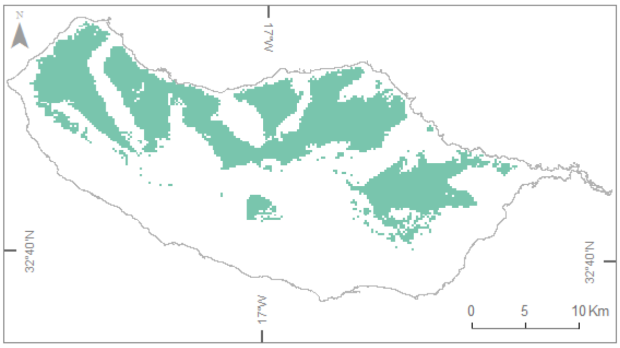
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

Just as mentioned for the previous species, the potential distribution of Clethra arborea in the southern face of the island might be underestimated by the models, a fact that is associated to the lack of occurrence data. The valleys of the northern face and the summits of the island are predicted as unsuitable. That potential distribution is supported on the fact that the ecological niche of the species is largely structured on the contribution of three main predictors: summer precipitation, average minimum temperature of the coldest month and annual temperature range. In fact, species are not tolerant to dryness and high temperature range. As example, during the summer of 2012, because of unusual low values of precipitation during previous winter, it was very frequent to see individuals in the forest exhibiting fading-leafs.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The loss of suitable area is very significant for the scenario A2, a trend that is in opposition to the results obtained for the scenario B2, where the gain in terms of suitable area is higher than the loss.

A - Current climatic conditions



Species	*Clethra arborea*
Family	Clethraceae

Calibratio	Presences	Absences
Data	378	3301

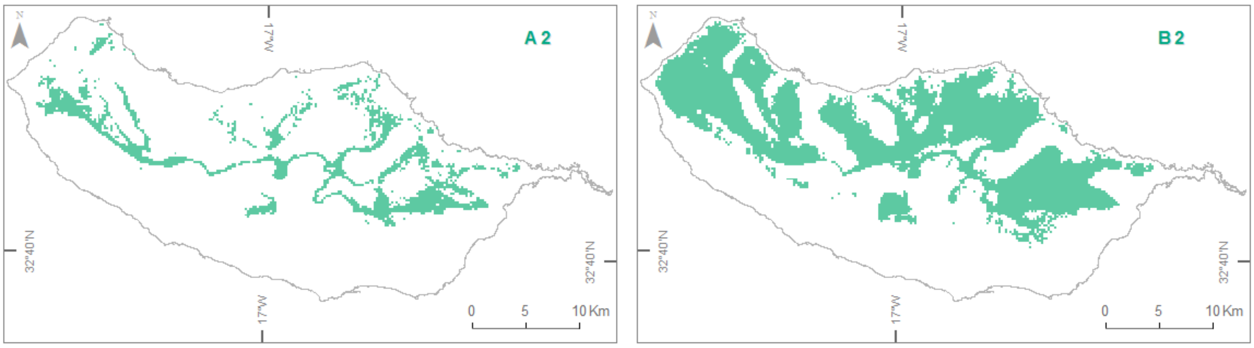
Statistics	Max	Min	Aver
AUC	0.88	0.7	0.8

Scenarios	A2	B2
Gain (%)	13.2	24.2
Loss (%)	78.4	11.0
Maintain	21.6	89.0

Table XVIII – Relative importance of predictors across models for *Clethra arborea*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
Prec_s	**0.5**	**0.7**	0.1	**0.5**	0.1	**0.5**	**0.6**	0.3
T_mmcm	0.0	**0.5**	**0.7**	0.4	**0.8**	**0.7**	0.4	0.3
T_ar	0.0	0.5	0.5	0.0	0.6	0.5	0.1	0.1
Prec_w	0.1	0.1	0.0	0.0	0.0	0.4	0.0	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes

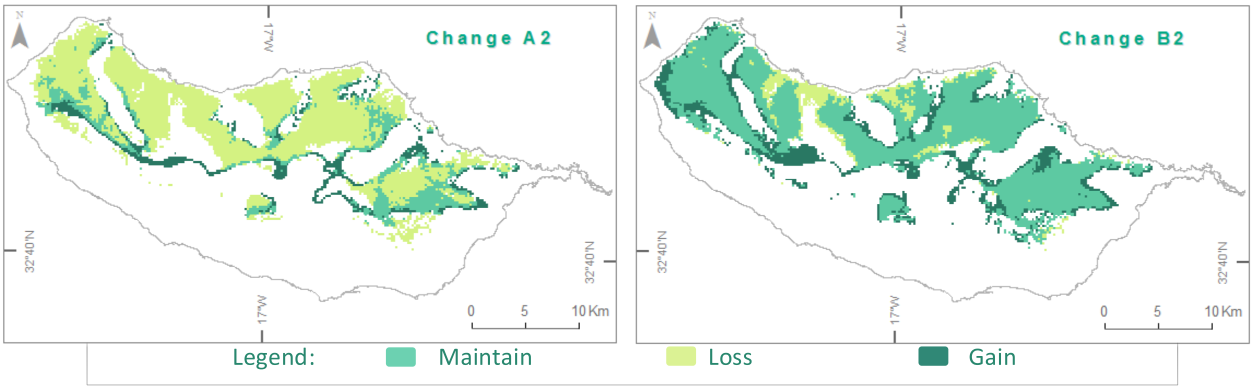


Figure 26 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Clethra arborea*

2.3.1.5 *PICCONIA EXCELSA* (AITON) DC.

Macaronesian endemic evergreen tree of Madeira Island and Canaries. In the Azores the genus is represented by *Picconia Azorica.* In Madeira Island it is a wide distributed species with low frequency within its area of distribution. Clearly related with the temperate laurel forest, it occupies the more termophyllous areas, being more common at altitudes below 1000m. Its low frequency might reveal a negative selection from human activities, a fact related with the quality of the wood.

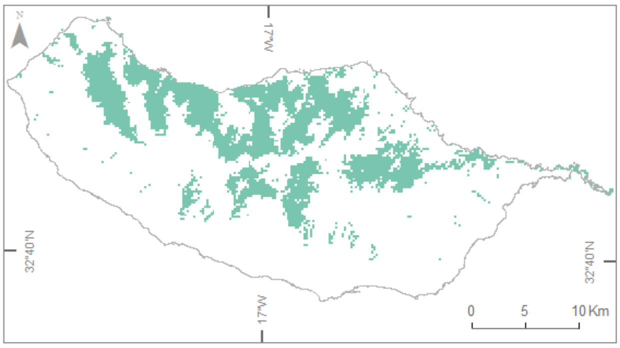
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The more termophyllous aptence of the species is clearly captured by the models, which identify valleys and low altitudes of the northern face as privileged areas to the occurrence of the species. That attribute would very likely favour a significant presence also on the southern face of the island; an idea that is derived from the significant presence on deeply disturbed remnant patches of temperate laurel forest in this section of the island. That explains the prediction of suitable areas on inner sections of larger valleys. In terms of environmental variables, a significant number of modelling techniques identify winter precipitation, annual range of temperature and minimum average temperature of the coldest month.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Despite generally weak, predicted changes are more significant for the scenario B2, with gains for higher altitudes and a significant maintenance of the area identified as suitable for current conditions. Higher losses are predicted under the scenario A2, and mainly detected on the lower section of the current altitudinal range.

A - Current climatic conditions



Species	*Picconia excelsa*
Family	Oleaceae

Calibratio	Presences	Absences
Data	196	3483

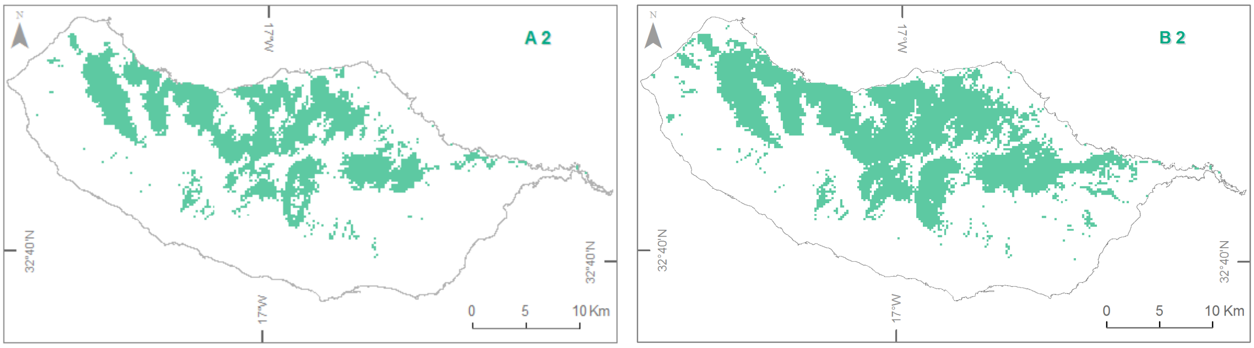
Statistics	Max	Min	Aver
AUC	0.87	0.7	0.81

Scenarios	A2	B2
Gain (%)	9.1	39.7
Loss (%)	12.6	2.5
Maintain	87.4	97.5

Table XIX – Relative importance of predictors across models for *Picconia excelsa*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
Prec_W	**0.6**	**0.5**	0.2	0.2	0.2	0.4	0.1	0.1
Prec_S	0.0	**0.4**	**0.5**	0.1	**0.6**	**0.6**	0.3	0.1
T_Mmcm	0.0	**0.4**	**0.5**	0.1	**0.6**	**0.6**	0.3	0.1
T_ar	0.0	**0.4**	0.4	0.1	0.3	0.6	0.1	0.1
PSSD	**0.6**	0.1	0.1	0.0	0	0.1	0.0	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes

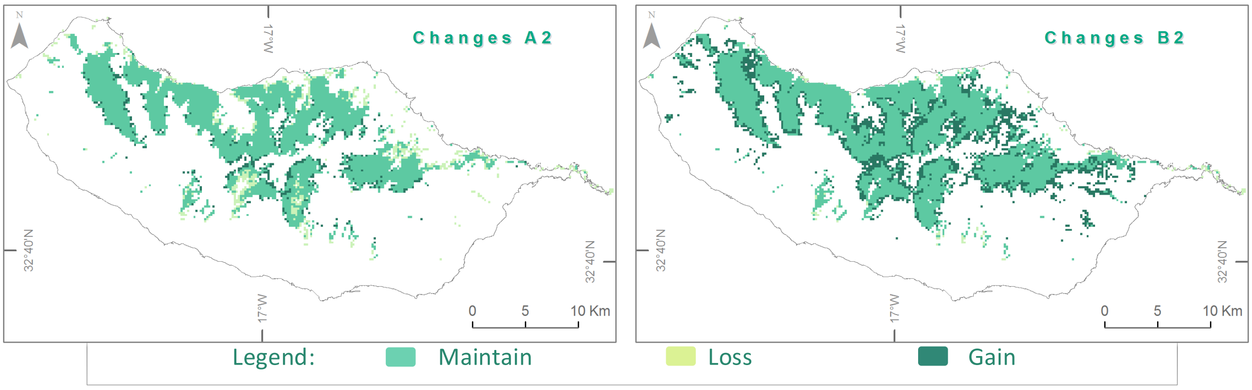


Figure 27 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Picconia excelsa*

2.3.1.6 *HEBERDENIA EXCELSA* (AITON) BANKS EX DC.

Endemic Macaronesian tree of the Myrsinaceae family that occurs in the temperate laurel forest. It is a species of rare occurrence within its area of distribution. The known distribution seems to indicate a preference by very humid conditions, once it was mostly detected at altitudes above 800 m . Among the trees of the temperate laurel forest, this is one of the most tolerant to low temperatures, once occurrences where detected on areas above 1300m. At such altitudes, its distribution is clearly masked by the deep disturbance from human activities.

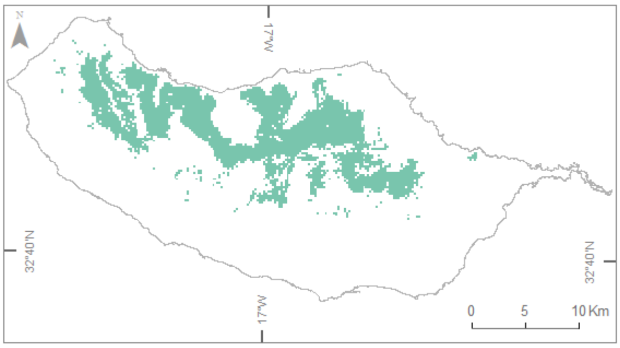
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The predicted area for the species is entirely restricted to the northern face of the island, which reveals a preference for very humid conditions. As example, it is clear the definition of unsuitable areas the lower sections of the larger valleys. Some of the modelling techniques actually identify summer precipitation as an important variable to explain the potential distribution. Nevertheless, the higher explanatory power is attributed to the average minimum temperature of the coldest month, a pattern that is similar to all trees of the temperate laurel forest.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

It is predicted a considerable gain in terms of suitable area for both scenarios, a pattern that is especially favorable in the case of the scenario B2. A significant gain is associated to altitudes above current distribution, revealing an upward shift.

A - Current climatic conditions



Species	*Heberdenia excelsa*
Family	Myrsinaceae

Calibratio	Presences	Absences
Data	76	3603

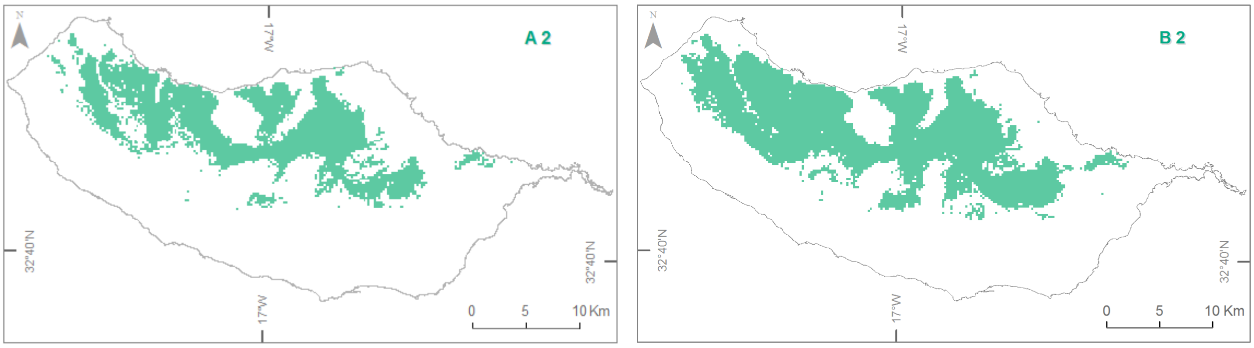
Statistics	Max	Min	Aver
AUC	0.87	0.7	0.81

Scenarios	A2	B2
Gain (%)	26.5	63.8
Loss (%)	14.2	1
Maintain	85.8	99

Table XX – Relative importance of predictors across models for *Heberdenia excelsa*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
Prec_w	0.3	0.1	0.0	0.1	0.2	**0.7**	**0.5**	0.1
T_mmcm	0.1	0.1	**0.9**	**0.6**	**1.0**	**0.7**	0.4	0.4
T_ar	0.0	0.2	**0.6**	0.2	**0.8**	0.4	0.0	0.1
PSSD	**0.8**	0.0	0.0	0.0	0.0	0.1	0.0	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes

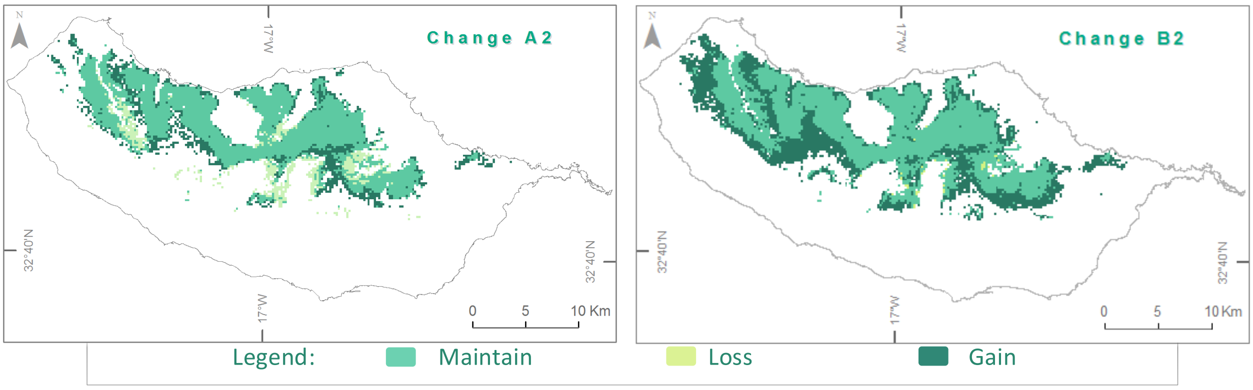


Figure 28 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Heberdenia excelsa*

2.3.2 RESULTS FOR THE COMMUNITY LEVEL

The potential distribution of the temperate laurel forest was derived from the predicted distribution of 5 trees, which have been considered characteristic of the community. Considering that species distributions outrange or present a more restricted distribution than the community, different weights have been attributed to the selected trees.

The species with higher scores are considered better indicators of the community.

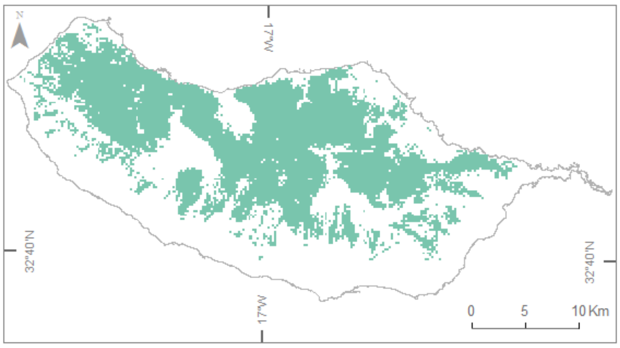
POTENTIAL SUITABLE AREA FOR CURRENT CONDITIONS

Predicted suitable area presents a high level of spatial agreement with the proposed model of potential vegetation by Capelo *et al.* (2004), although supported on different methodological perspectives (Mesquita *et al.*, 2004).

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The loss of suitable area is particularly small in the scenario B2, whereas predicted gain is significant. In this case, there is a clear gain at higher altitudes, indicating an upward shift that is also detected in the scenario A2, despite the lower magnitude. But such assessment might underestimate the real change in the case of any of the scenarios. This is because there is no available data about spatial and time series for fog precipitation, one of the variables with higher explanatory power in relation to the distribution of such vegetation type. The high correlation between topography and cloud banks formation, or the low density and highly asymmetric distribution of the weather stations, reduce the pertinence of using data from weather stations in order to calculate the spatial patterns of such variable, namely using the number of foggy days.

A - Current climatic conditions

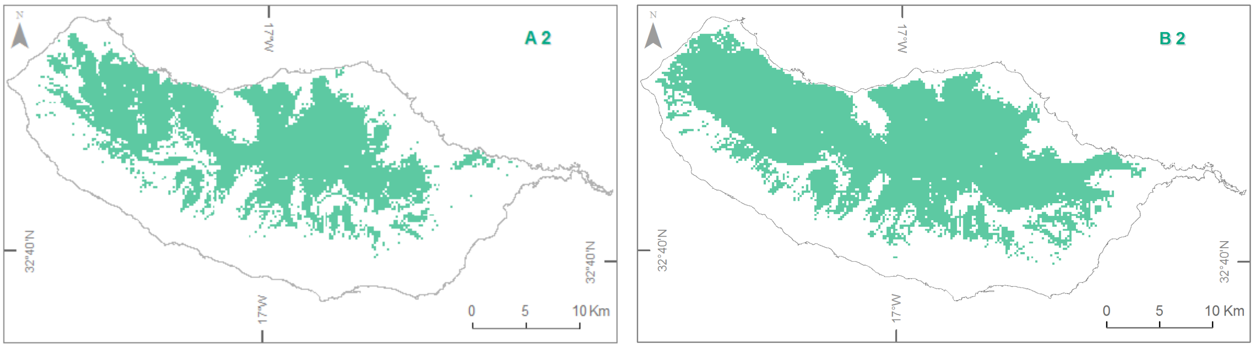


Community	Temperate laurel forest (>=3)

Species	Score
Laurus novocanariensis	1
Ocotea foetens	3
Clethra arborea	2
Picconia excelsa	2
Heberdenia excelsa	2
Ilex perado	1

Scenarios	A2	B2
Gain (%)	9.0	23.4
Loss (%)	25.5	5.3
Maintain	74.5	94.7

B - Climatic scenarios – 2070-2099



C - Predicted changes

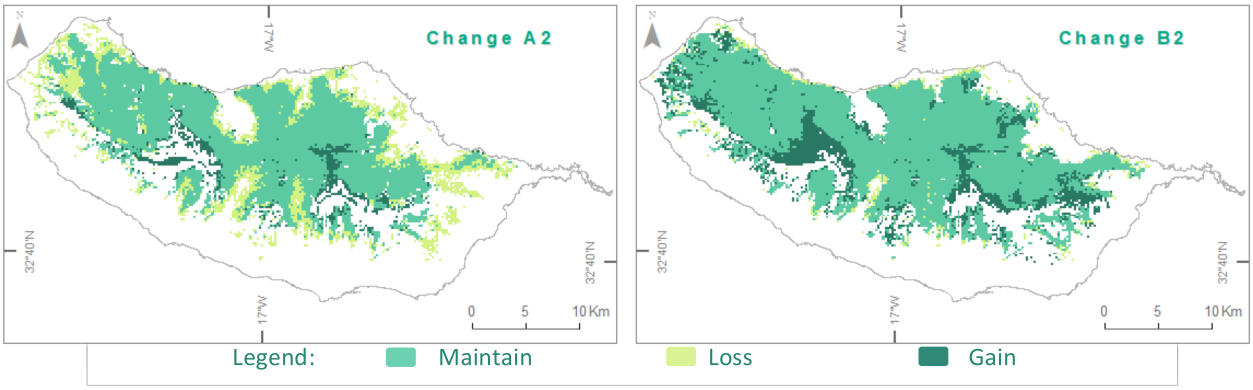


Figure 29 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for the temperate laurel forest

2.4 THE DOMAIN OF THE TREE HEATH MICROFOREST

The meso-supratemperate hyper to ultra-hyperhumid areas above 1400m that are not associated to particular topographic conditions (very steep slopes, rocky walls) are potentially associated to a microforest dominated by *Erica arborea* (Capelo *et al.*, 2004).

2.4.1 RESULTS FOR THE SPECIES LEVEL

2.4.1.1 *ERICA ARBOREA* L.

Native micropharenophyte of the Ericaceae family that presents a frequent occurrence in the northern face of the island, from the coast to the highest summits. On the southern face is frequent in the easternmost sector.

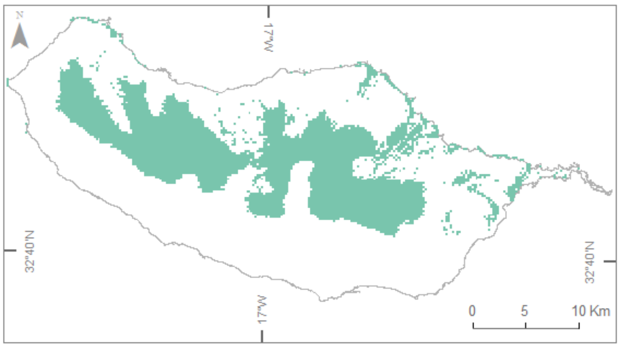
POTENTIAL SUITABLE AREA FOR CURRENT CONDITIONS

Predicted suitable areas for *Erica arborea* are mainly associated to territories above 900 m high. Although less important, models also predict low-altitude areas as suitable in the northeast fraction of the island. Because of the high dissimilarity in terms of ecological conditions associated to the territories, such results support the idea that it could be the case of two different taxa (see Désamoré et al., 2011).

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Projected distributions for future climatic scenarios predict a significant decrease in the suitable area for medium altitudes, and an opposite trend for the lowest areas. Such prediction reinforces the idea of two distinct taxa, with different ecological requirements.

A - Current climatic conditions



Species	*Erica arborea*
Family	Ericaceae

Calibratio	Presences	Absences
Data		

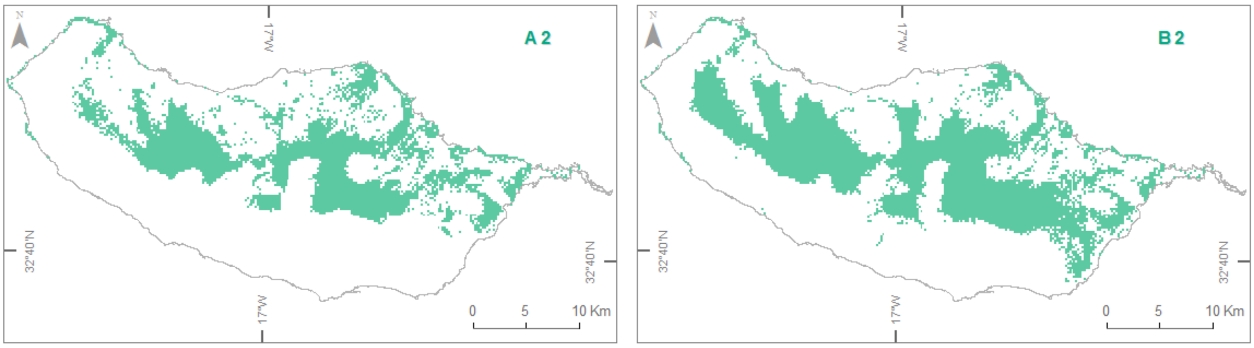
Statistics	Max	Min	Aver
AUC			

Scenarios	A2	B2
Gain (%)	15.4	21.9
Loss (%)	35.4	8.3
Maintain	64.6	91.7

Table XXI – Relative importance of predictors across models for *Erica arborea*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
T_mmcm	**0.6**	**0.9**	**0.7**	**0.8**	**0.7**	**0.7**	**0.9**	**0.5**
T_ar	0.0	0.0	0.2	0.1	0.3	0.3	0.0	0.1

B - Climatic scenarios – 2070-2099



C - Predicted changes

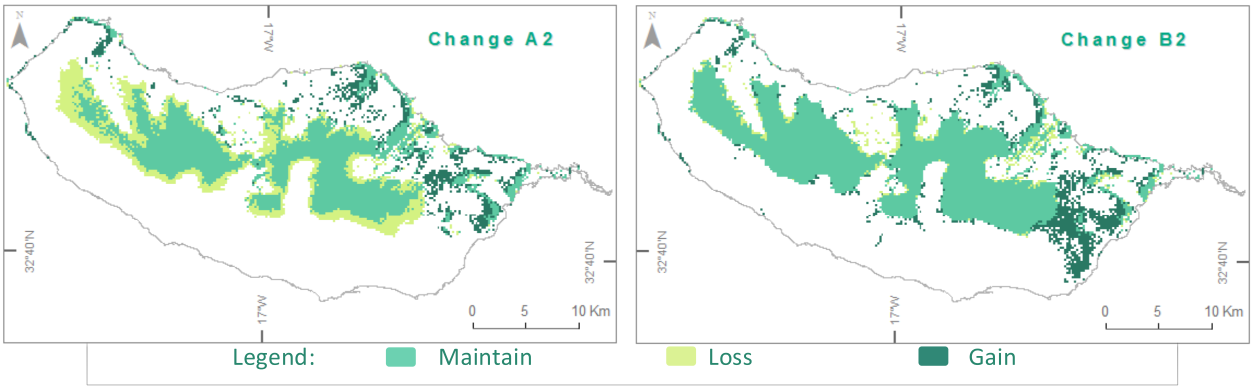


Figure 30 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Erica arborea*

2.4.2 RESULTS FOR THE COMMUNITY LEVEL

The tree heath community (*Polysticho falcinelli-Ericetum arboreae*) is a microforest that is potentially associated to territories above 1400 m m.s.l. on Madeira Island. At such altitudes, the climax community is structural and floristically dominated by *Erica arborea*, which reduces our chance to use other species to achieve the potential distribution of the sintaxa. Once few occurrences were collected for *Polistichum falcinelli,* it was not possible to use such taxa, despite its status of characteristic taxon for such community (Capelo *et al.*, 2004). So, instead of adding species to obtain the final model, the potential distribution of the community was derived from a process of intersection considering the potential distribution of other vegetation types (temperate and Mediterranean laurel forests, wild olive microforest). Thus, the model is based on the assumption of exclusion, where it is only possible to assign one vegetation type (climax community) a territory (cell).

The current distribution of such community is considerably restricted considering their potential area of distribution, a consequence mainly associated to grazing and charcoal production, activities currently forbidden. In fact, the length and intensity of such disturbances might have masked the natural ecotone with the temperate laurel forest, contributing to biasing predictions in the sense of estimate reduced areas for such forest. On modern days, other sources of disturbance remain active, namely summer wildfires, which were responsible for a massive reduction in the area occupied by such community in the last three years.

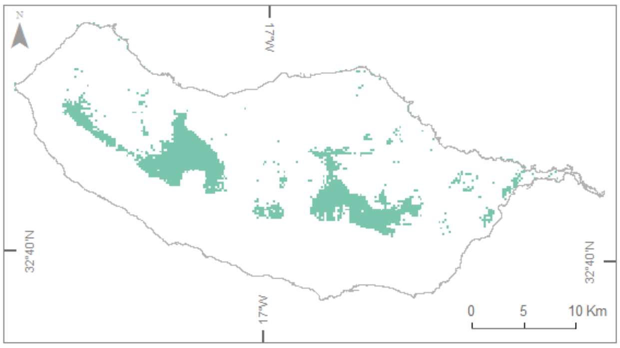
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The predictions clearly show the association between the heath tree community and the highest summits of the island. Based on the knowledge about current distribution of such community, it is possible to assume that such approach perform an acceptable way to predict the distribution of such community, despite some flaws. The model identifies as suitable territories under altitudes (<1400m m.s.l.) above which the community has its climax domain. Once such areas are potentially associated to other types of forest (Capelo *et al.*, 2004), such prediction should represent a situation of over-prediction. Such results are clearly determined by the fact that the dominant *Erica arborea*, used to model the distribution of the community, has a wide distribution in the island. In fact, the heath tree integrates the floristic composition of shrubby communities associated to sub-seral stages, namely forms of degradation, from other vegetation series, namely the *Globulario salicinae-Ericetum maderincolae*, associated to the series of the Mediterranean laurel forest (*Semele androgynae-Apollonio barbujanae sigmetum)*; and the *Vaccinio padifoli-Ericetum maderincolae*, related to the temperate laurel forest series (*Clethro arborea-Ocoteo foetentis sigmetum*) (see Capelo *et al.*, 2004; Costa *et al.*, 2004). The wide distribution of the *Erica arborea* is evident in the model representing its potential distribution for current conditions (Figure 20). So, the models clearly reveal the need of using species that have distribution more consistent with the potential area for the community. Two species that should accomplish such criterion exhibit a distribution deeply restrained by disturbance, namely *Sorbus maderensis* and *Juniperus cedrus* subsp. *maderensis*. The method used to overcome such difficulties, the intersection process with results for other climax communities, is also biased by the fact that models are vey likely underpredicting the area suitable for the temperate laurel forest at its upper limit, where disturbance should have favoured heath tree species.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The predicted changes estimate a significant loss in terms of suitable area, namely in the scenario B2. Despite the contribution from changes on environmental predictors, the loss in terms of area is grossly determined by the upward shift of the temperate laurel forest. In fact, those are the only results that integrate information that we can consider that are reproducing the influence of biotic interactions by an indirect way. The new predicted area (gain) is detected mainly at altitudes under 1400m, which reflects the idea of two distinct taxa. Once such areas are associated to other climax communities, it is possible to assume that such community presents highly to projected climatic changes.

A - Current climatic conditions

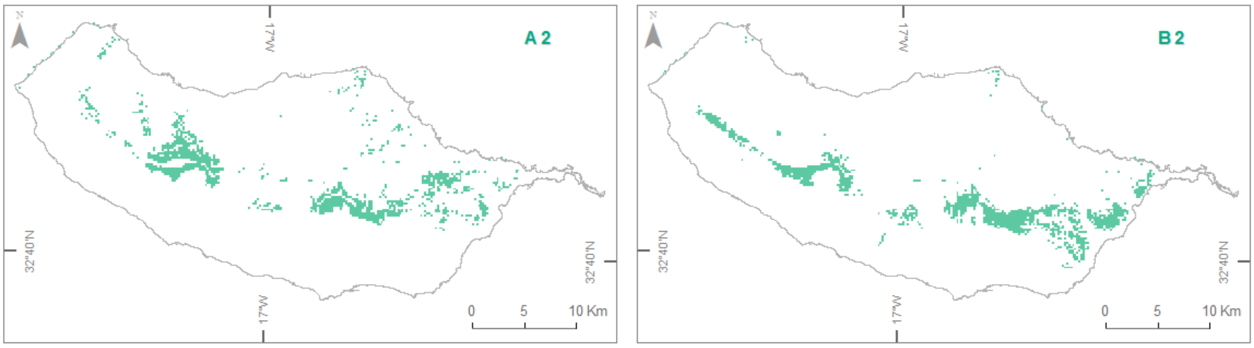


Community	Tree heath community

Species	Process
Erica arborea	Intersection
Temperate laurel forest	
Mediterranean laurel forests	
Wild olive microforest	

Scenarios	A2	B2
Gain (%)	17.9	17.6
Loss (%)	59.3	58.7
Maintain	40.7	41.3

B - Climatic scenarios – 2070-2099



C - Predicted changes

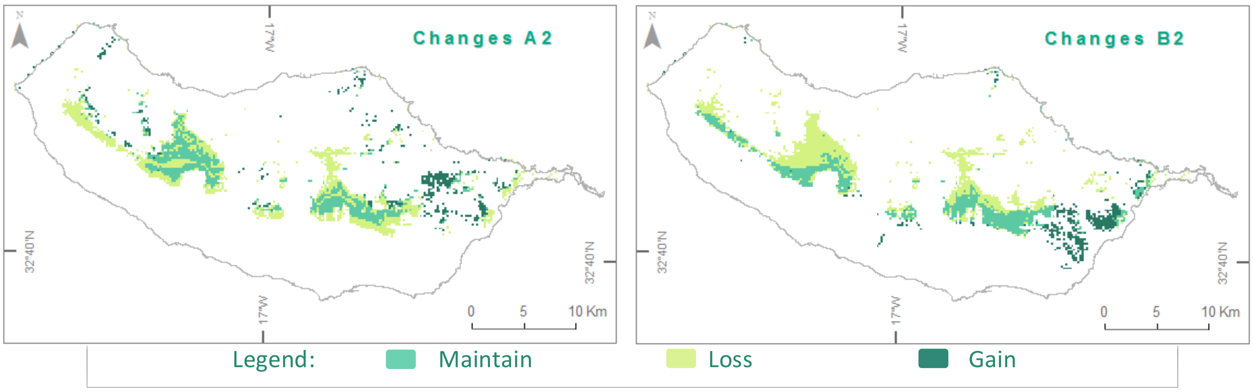


Figure 31 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for the tree heath community

2.5 PREDICTING IMPACTS ON ENDEMIC FLORA

Impacts from climate change on species distribution are expected to be more concerning in the case of species with restricted occupancy areas and small populations. Rare endemic species that have restricted ecological and geographical ranges fit such criteria very well (NSR - Figure 32), and are already presenting important challenges in terms of conservation. Despite the especial interest on assessing potential impacts for conservation purposes for such species, such aim is not always achievable using habitat modelling approaches. This is mainly because of low number of occurrences associated to the restricted distribution, and the resolution associated to environmental predictors available, attributes that hinder the capacity of the models to produce accurate results. That usually occurs because models are not able to capture habitat conditions accurately.

HABITAT SPECIFICITY		GENERALIST		SPECIALIST	
ABUNDANCE - ISLAND		ABUNDANT	RARE	ABUNDANT	RARE
GEOGRAPHICAL RANGE	WIDE	WGA	WGR	WSA	WSR
	NARROW	NGA	NGR	NSA	NSR

Figure 32 - Classification of species according the frequency and size of the area of distribution
Adapted from Rabinowitz (1981) and Espeland & Emam (2011).

WGA	abundant species, present on different habitats and with a wide distribution on the island
WGR	abundant species over a large range but associated to specific habitat conditions
NGA	species that are abundant in several habitats but restricted geographically
NGR	rare species associated to different types of habitat in a narrow area of distribution
WSA	abundant species associated to specific habitat conditions on a wide geographical range
WSR	rare species that are restricted to a type of habitat on a wide area of distribution
NSA	species that are habitat specialists and have a small geographical range, but are abundant in the area of occurrence,
NSR	specialist species that have a rare occurrence within a narrow geographical distribution.

2.5.1 ENDEMIC SPECIES WITH PROTECTION STATUS

This section is dedicated to the assessment of changes on distribution for protected species under the Bern Convention (B) and Habitats Directive (H) (Jardim & Sequeira, 2008). The following table presents the species with registered occurrences, identifies those (green bold) with modelling results, and present the classification according to Figure 32.

Table XXII - Endemic species with interest for conservation

Taxon	Protection status	Type	Nr.
Argyranthemum pinnatifidum subsp. succulentum	B, H-IV	NER	7
Berberis maderensis	**B, H-IV**	**NER**	**10**
Calendula maderensis	B, H-II, IV	NER	3
Chamaemeles coriacea	**B, H-II ***	**NGR**	**37**
Cirsium latifolium	H-II, IV	NEA	15
Convolvulus massoni	**B, H-II, IV ***	**NGR**	**46**
Echium candicans	**H-II, IV**	**NGR**	**117**
Goodyera macrophylla	B, H-II, IV	NGR	4
Marcetella maderensis	B, H-II, IV	NGR	3
Maytenus umbellata	**H-II, IV**	**NGA**	**350**
Melanoselinum decipiens	**H-II, IV**	**WGR**	**95**
Musschia aurea	**B, H-II, IV**	**NER**	**21**
Musschia Wollastonii	**B, H-II, IV ***	**NER**	**17**
Scilla maderensis	H-IV	NER	3
Sideroxylon marmulano	**B, H-IV**	**NGR**	**219**
Sorbus maderensis	**H-II, IV**	**NGR**	**10**
Teucrium betonicum	**H-II, IV**	**WGA**	**191**
Viola paradoxa	B, H-II, IV	NER	3

Protection status: **B** – Bern Convention, **H** – Habitats Directive (**II**: Annex II – Animal and plant species of community interest whose conservation requires the designation of special areas of conservation; **IV**: Annex IV – Animal and plant species of community interest in need of strict protection. Deliberate picking, collecting, cutting, uprooting or destruction of such plants in their natural range in the wild is prohibited; **V**: Annex V – Animal and plant species of community interest whose taking in the wild and exploitation may be subject to management measures); **Nr.**: number of occurrences; ***** priority species; **text in green bold**: species with modelling results.

2.5.1.1 *BERBERIS MADERENSIS* LOWE

Endemic Macaronesian shrub of the Berberidaceae family that presents a distribution restricted to the higher summits of the island. It is a very rare species within its potential area of distribution.

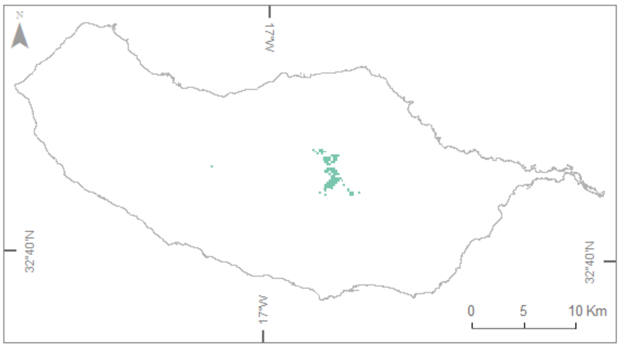
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The predicted area is severely restricted to the highest summits of the island. The incoming solar radiation and the minimum temperature of the coldest month are clearly identified by most of the modelling techniques as determining as useful to explain current distribution.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The projected climatic changes are deeply harmful for such species, once predictions support a drastic reduction of the suitable are for the scenario B2 and the absence of suitable areas in for the scenario A2, which means the extinction of the species.

A - Current climatic conditions



Species	*Berberis maderensis*
Family	Berberidaceae

Calibratio Data	Presences	Absences

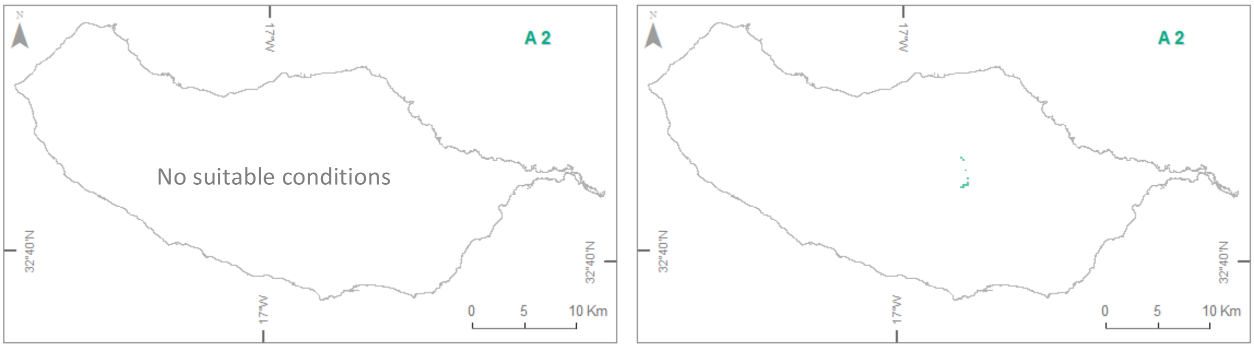
Statistics	Max	Min	Aver
AUC	0.9	0.7	0.8

Scenarios	A2	B2
Gain (%)	0	0
Loss (%)	100	89.2
Maintain	0	10.8

Table XXIII – Relative importance of predictors across models for *Berberis maderensis*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
Rad_sol	**1.0**	**0.9**	**0.8**	0.4	**0.8**	**0.8**	0.3	0.3
Prec_s	**0.6**	0.0	**0.8**	0.0	**0.8**	0.2	0.2	0.0
T_ar	0.1	**1.0**	**0.8**	**1.0**	**1.0**	**1.0**	**1.0**	**0.7**
SWI_asp	0.0	0.0	0.2	0.0	**0.5**	0.0	0.0	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes

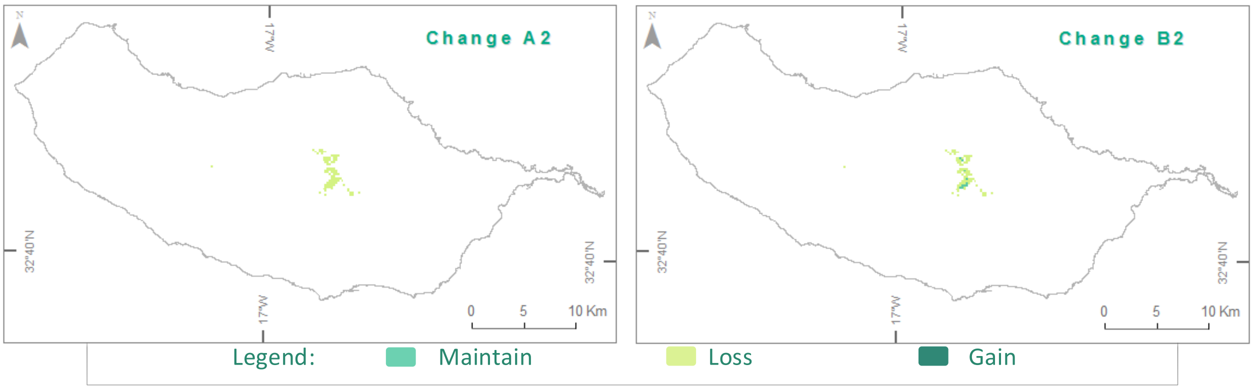


Figure 33 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Berberis maderensis*

2.5.1.2 *CHAMAEMELES CORIACEA* LINDL.

Endemic evergreen shrub of the Rosaceae family, with coriaceous leaves, that occurs on coastal areas, mainly in the southern face of the island up to 200m, where it integrates the wild olive community (*Mayteno umbellatae-Oleetum maderensis*). In terms of habitat, it inhabits coastal rocky cliffs, but can also be found on inner sections of the valleys.

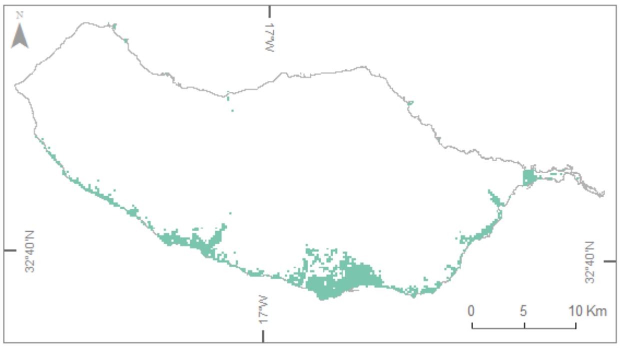
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The predicted area is restricted to coastal areas and low altitudes in the center of the southern face of the island. The minimum mean temperature of the coldest month is elected by several modelling techniques as critical to explain current distribution. More interesting than the expected contribution of topographic variables (Slp_34) is the fact that models identify the percentage of urban area as an important predictor, which reveals that fact that its habitat is under great pressure. Such condition, combined with a low frequency within its area of distribution, explains the status of rare species.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Models results predict an increase in terms of suitable are, that is more evident in the scenario A2. A very interesting feature, shared by other species that have a restricted distribution on coastal areas, the models are unable to predict the response under the scenario A2 (in orange), which can be interpreted as resultant from the incapacity of the models to discriminate the response of the species under new climatic conditions, once novel climatic conditions are not currently present, and do not integrate calibration.

A - Current climatic conditions



Species	*Chamaemeles coriacea*
Family	Rosaceae

Calibratio	Presences	Absences
Data	37	3642

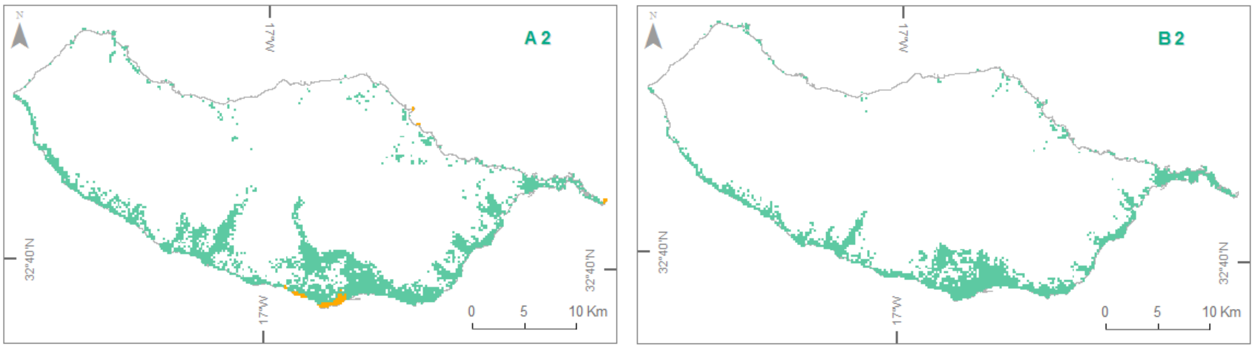
Statistics	Max	Min	Aver
AUC	0.9	0.7	0.8

Scenarios	A2	B2
Gain (%)	133.9	60.6
Loss (%)	11.2	3.6
Maintain	88.8	96.4

Table XXIV – Relative importance of predictors across models for *Chamaemeles coriacea*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
Slp_34	0.3	**0.6**	0.0	0.0	0.1	0.0	0.0	0.0
T_mcm	0.1	**0.7**	**0.9**	**0.6**	**0.9**	**0.7**	**0.7**	0.4
T_ar	**0.7**	**0.7**	0.2	0.2	0.2	**0.6**	**0.5**	0.1
Asp_N	0.4	0.0	0.2	0.0	0.2	0.0	0.0	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes

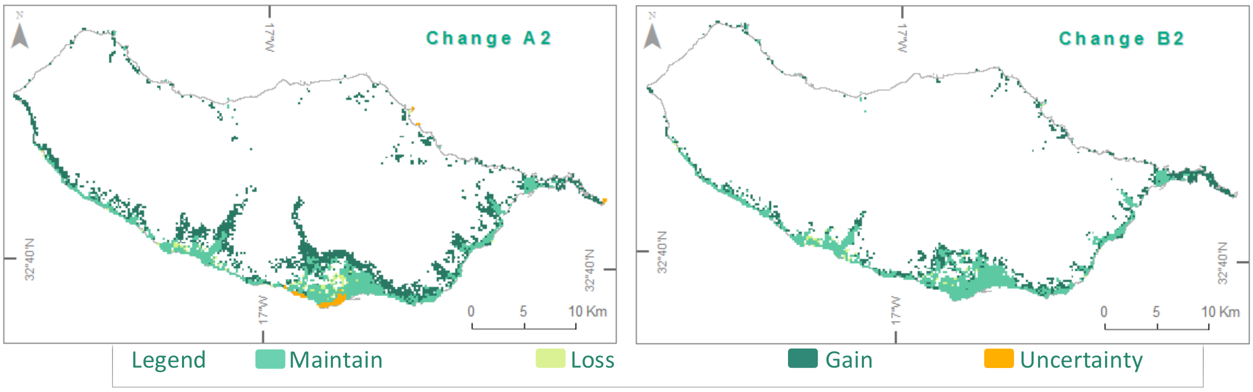


Figure 34 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Chamaemeles coriacea*

2.5.1.3 *CONVOLVULUS MASSONII* F. DIETR.

Endemic climbing shrub of the Convolvulaceae family that occurs mainly in the climacic domain of the Mediterranean laurel forest. On the southern face of the island, on few localities, it is possible to find individuals on lower altitudes, reaching territories associated to the wild olive microforest domain.

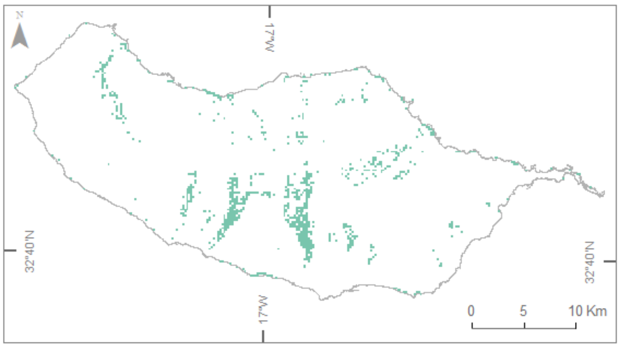
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The area predicted as suitable presents a scattered pattern, and is greatly coincident to large valleys, namely on the southern face. The contribution of topography on controlling species distribution is detected by the models, which select incoming solar radiation (Rad_sol) as an important predictor to explain current distribution.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The trends in terms of gain and loss of suitable area is very equivalent in terms of magnitude on both scenarios. However, despite new suitable areas are mostly detected in the northern face of the island, the gains are not spatially coincident. While the scenario A2 predicts gains mainly at medium altitudes, the scenario B2 detects new suitable areas at low altitudes.

A - Current climatic conditions



Species	*Convolvulus massonii*
Family	Convolvulaceae

Calibratio	Presences	Absences
Data		

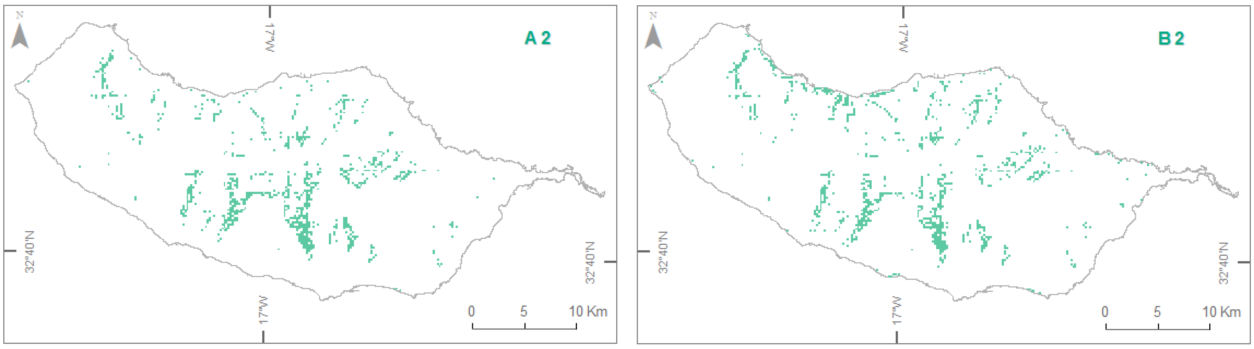
Statistics	Max	Min	Aver
AUC	0.9	0.7	0.82

Scenarios	A2	B2
Gain (%)	26.9	33.6
Loss (%)	31.4	28.2
Maintain	68.6	71.8

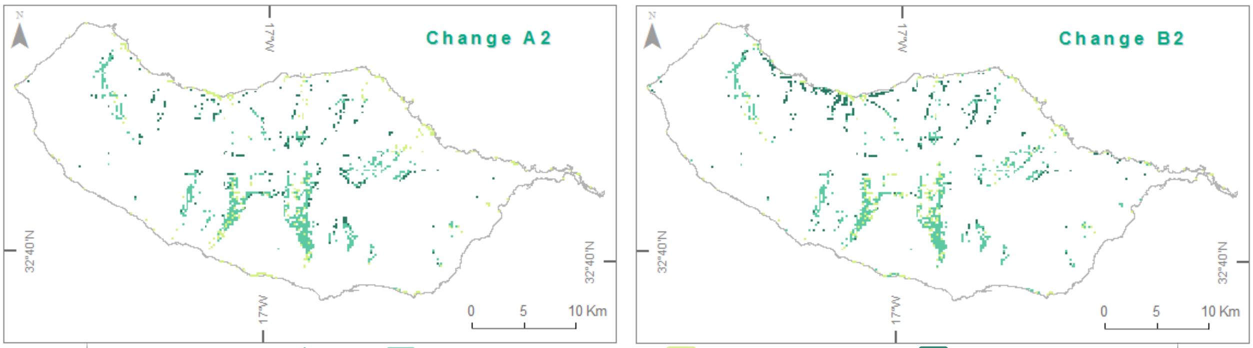
Table XXV – Relative importance of predictors across models for *Convolvulus massonii*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Rad_sol	**0.7**	**0.9**	0.4	**0.7**	0.4	**0.8**	**0.5**	0.3
Prec_w	**0.7**	0.0	0.3	0.1	0.2	0.2	0.3	0.0
Prec_s	0.1	**0.8**	0.3	**0.5**	**0.6**	0.1	0.2	0.2
T_mmcm	0.0	**0.6**	0.2	0.1	0.3	0.2	0.2	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes



Legend: 🟩 Maintain 🟨 Loss 🟩 Gain

Figure 35 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Convolvulus massonii*

2.5.1.4 *ECHIUM CANDICANS* L. F.

Endemic shrub of the Boraginaceae family that inhabits open areas from 800m up to the highest peaks. Within its area of distribution presents a low frequency.

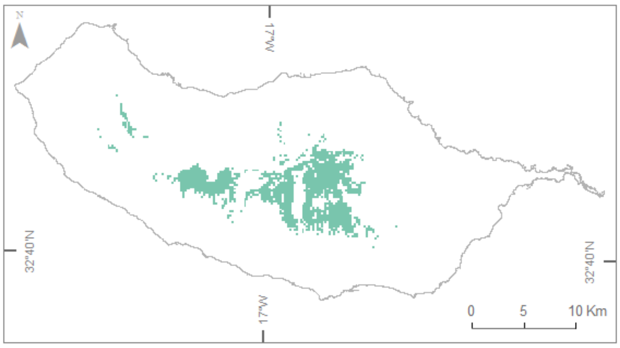
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

Models results have captured the main pattern associated to the distribution of such species. The minimum mean temperature of the coldest month is the predictor identified with higher relative importance to explain current distribution.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Forecasts for future scenarios estimate a significant decrease in the suitable area, a trend that is equivalent in terms of magnitude and spatially coincident. Predictions identify the lower ranges of the potential distribution as more vulnerable to projected climatic changes, a trend common among species that occupies the higher summits of the island.

A - Current climatic conditions



Species	*Echium candicans*
Family	Boraginaceae

Calibratio	Presences	Absences
Data	117	3562

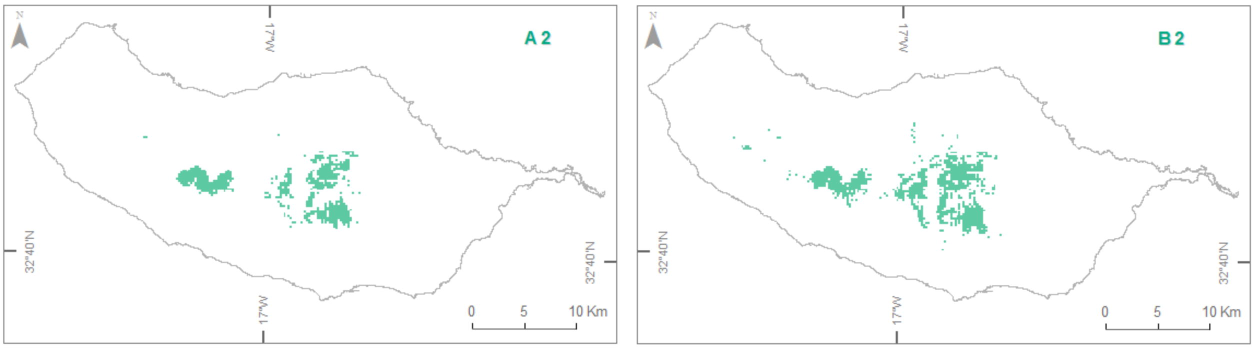
Statistics	Max	Min	Aver
AUC	0.95	0.73	0.9

Scenarios	A2	B2
Gain (%)	0.4	1.1
Loss (%)	56.4	38.3
Maintain	43.6	61.7

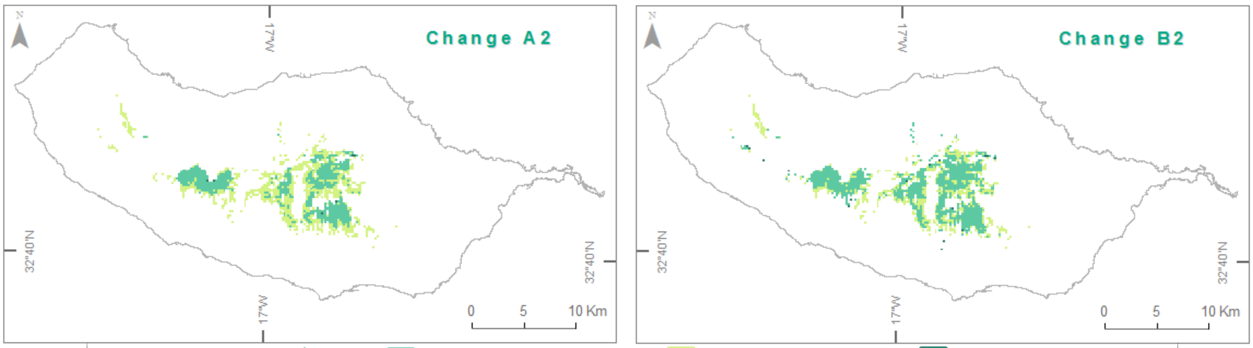
Table XXVI – Relative importance of predictors across models for *Echium candicans*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
Slp_34	0.2	0.1	0.3	0.1	0.3	0.0	0.0	0.0
Prec_jja	0.1	0.0	0.4	0.2	0.4	0.2	0.4	0.2
T_mcm	**0.8**	**0.6**	**0.8**	**0.6**	**0.8**	**0.7**	**0.9**	0.4
T_ar	0.4	0.4	0.1	0.2	0.0	0.2	0.2	0.2

B - Climatic scenarios – 2070-2099



C - Predicted changes



Legend: 🟩 Maintain 🟨 Loss 🟩 Gain

Figure 36 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Echium candicans*

2.5.1.5 *MELANOSELINUM DECIPIENS* (SCHRAD. & J.C. WENDL.) HOFFM.

Shrubby monocarpic endemic species of the Apiaceae family, reaching up to 3m in height, which occurs between 800m and 1600 m m.s.l. The genus is endemic of Madeira Island, with only one species described. Despite the wide territory that is associated to the identified altitudinal range, the species is found on few locations. It was used in the past to feed animals, a fact that explains its cultivation.

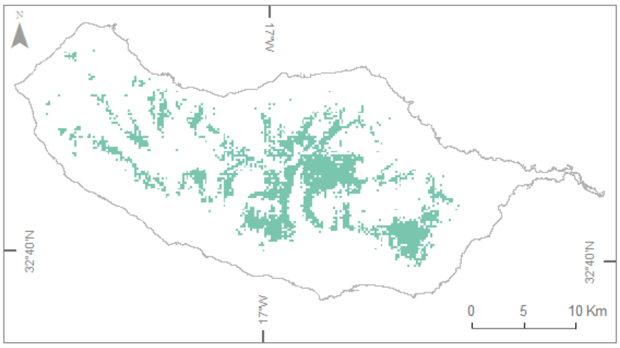
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

Predicted area for *Melanoselinum decipiens* reveal an asymmetric shape in the island. Such result is determined by the fact that few occurrences were detected on the western sector of the island. In terms of environmental predictors, the minimum average temperature of the coldest month is elected as the variable with higher influence to explain the known distribution. An interesting feature revealed by the models, and despite the non-registration of presences when there is an evident association to human use, is the identification of variables related with land-use (percentage of area associated to agriculture use – Perc_agr) and landscape metrics (Patch Size Coefficient of Variance) as revealing importance to current distribution. That reveals the possible interference of the human use on the current distribution of the species. The species occurs mainly on open areas, namely those associated to disturbance in the recent past (e.g. grazing). Such condition might favour the species on areas recently abandoned by agriculture, where the seed bank might have been reinforced because of the human use of that species.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The predicted changes under the future climatic scenarios are visibly distinct. Predictions for the scenario A2 reveal a common trend among the species that have a distribution associated to territories of temperate termotype, an upward shift, with losses on the rear edge and new suitable areas (gain) at higher altitudes. The predicted gains are more significant in the scenario B2, and are mainly concentrated on the northern face of theisland.

A - Current climatic conditions



Species	*Melanoselinum decipiens*
Family	Apiaceae

Calibratio	Presences	Absences
Data	95	3584

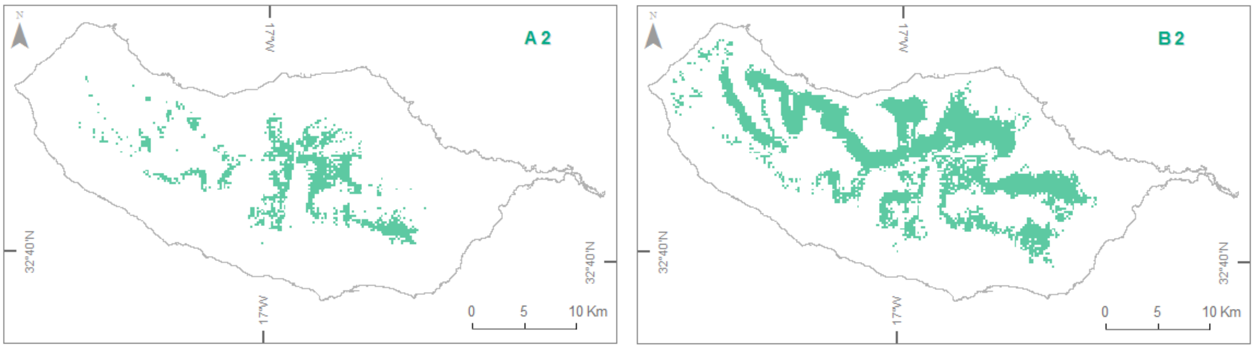
Statistics	Max	Min	Aver
AUC	0.88	0.7	0.81

Scenarios	A2	B2
Gain (%)	12.4	81.3
Loss (%)	59.4	27.9
Maintain	40.6	72.1

Table XXVII – Relative importance of predictors across models for *Melanoselinum decipiens*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
T_mmcm	-	**0.8**	**0.9**	**0.9**	**0.8**	**0.9**	**0.7**	**0.7**
PSCOV	-	0.0	**0.5**	0.0	0.4	0.1	0.3	0.0
Perc_agr	-	0.0	0.2	0.3	0.1	**0.8**	0.1	0.2
T_ar	-	0.0	0.3	0.1	**0.7**	0.0	0.2	0.1

B - Climatic scenarios – 2070-2099



C - Predicted changes

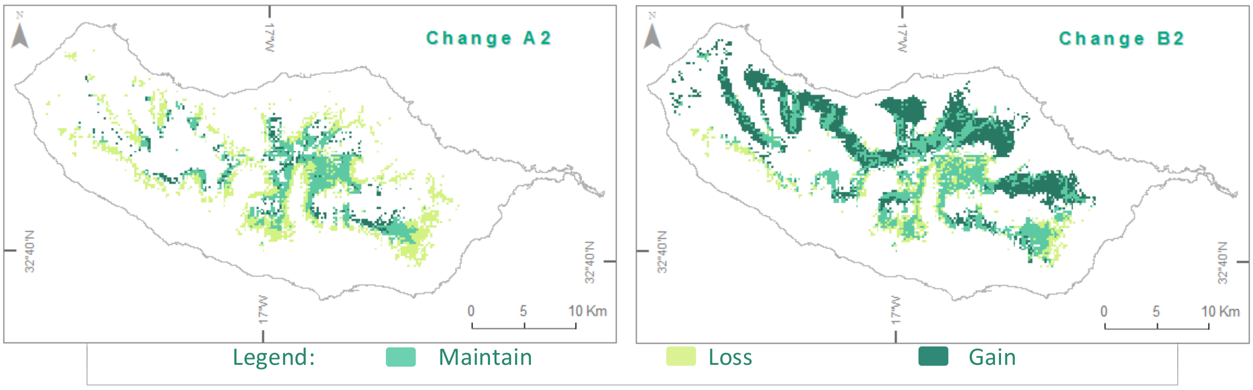


Figure 37 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Melanoselinum decipiens*

2.5.1.6 MUSSCHIA AUREA (L. F.) DUMORT.

Herbaceous perennial endemic species of the Madeiran archipelago, that occurs mainly on a very restricted area along the coast, and on few sites. It is found on rocky cliffs, exploring rock fissures, poor environments in terms of nutrients availability. The genus *Musschia* is endemic of the archipelago, with three species described. The human pressure, namely the process or urbanization, is a major source of threat, causing habitat loss and fragmentation.

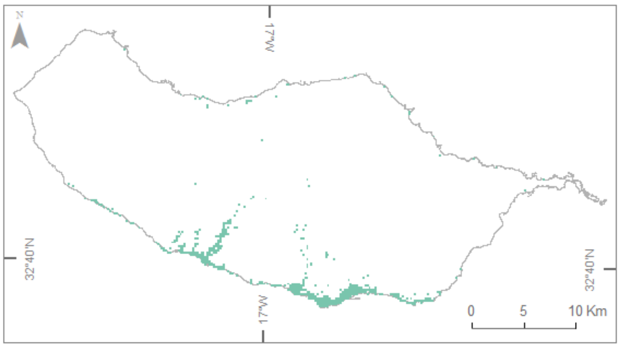
POTENTIAL SUITABLE AREA FOR CURRENT CONDITIONS

Models predict a very restricted area for current conditions, which is centred on the southern face of the island. The low number of occurrences and the type of habitat, which conditions are difficult to reproduce at the resolution used on modelling (200x200m), explain the variability shown by the modelling techniques in terms od predictors that reveal a major contribution on determining current distribution.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The type of habitat makes the species very vulnerable to changes on climatic conditions. Because of the low number of occurrences and the projected definition of novel climatic conditions at the low altitudes of the island, the models are not able to predict the response of the species on areas currently suitable. So, results reveal a great uncertainty, despite increase in terms of suitable area based on upward shift. Predicted increase is more significant on the northern coast, especially on the scenario A2.

A - Current climatic conditions



Species	*Musschia aurea*
Family	Campanulaceae

Calibratio	Presences	Absences
Data	21	3658

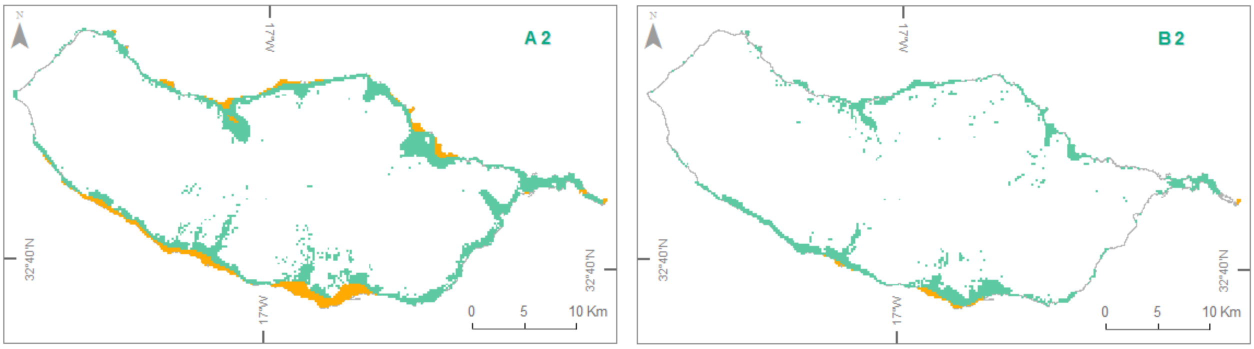
Statistics	Max	Min	Aver
AUC	0.8	0.7	0.74

Scenarios	A2	B2
Gain (%)	428.3	204.3
Loss (%)	1.2	11.7
Maintain	44.9	78.3
Uncertainty	53.9	10

Table XXVIII – Relative importance of predictors across models for *Musschia aurea*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_w	**0.6**	-	0.2	0.0	0.0	0.2	0.0	0.1
T_mmcm	0.0	-	0.0	0.4	0.3	**0.8**	**1.0**	0.2
T_ar	0.0	-	**0.6**	0.4	0.4	**0.5**	0.0	0.3
Rad_sol	0.3	-	**0.5**	0.0	**0.6**	**0.6**	0.1	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes

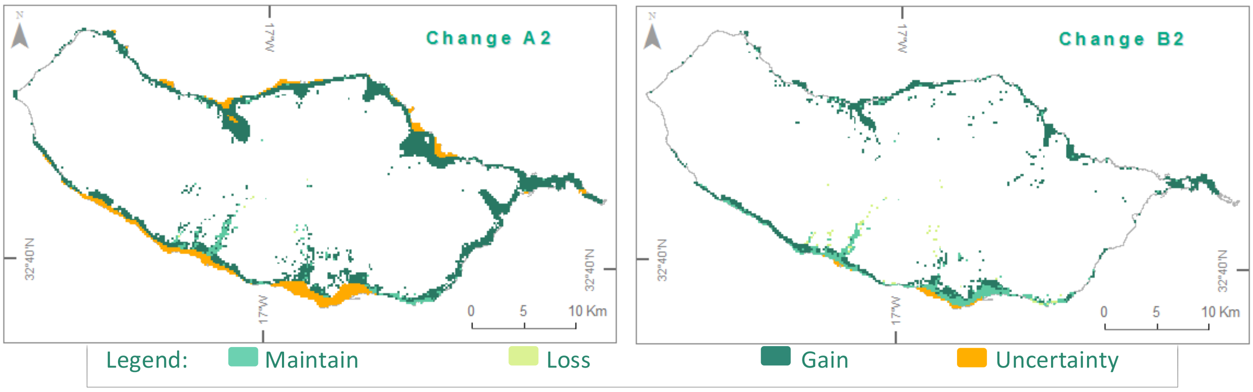


Figure 38 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Musschia aurea*

2.5.1.7 MUSSCHIA WOLLASTONI LOWE

Shrubby monocarpic plant of the endemic genus *Musschia* that can reach 2 m in height. It is a very rare plant that lives on small forest gaps and very moist areas in the temperate laurel forest, namely in the margins of small streams or areas affected by landslides, where it can occur with other shrubby caulirosulated endemic species (e.g. *Sonchus fruticosus*, *Euphorbia mellifera*).

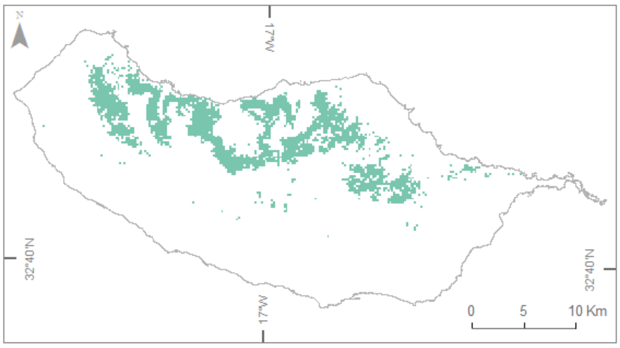
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

Predicted suitable area is mostly associated to the northern face of the island, a fact that is very likely related to the absence of native forest on the southern part of the island. Another variable that might have influence on this distribution is the very high frequency of foggy days on the northern coast, which supports the permanence of a moist environment.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Predictions for future climatic scenarios reveal a maintenance of the area predicted as suitable for current conditions and a significant expansion to new areas. That response might be deeply related to the rise in the mean minimum temperature of the coldest month, which will support the projected decrease in the temperature annual range, both predictors elected as more determinant to current distribution. For the other variable, winter precipitation, both scenarios project a decrease. Although definitely associated to a contraction response, such forecast is not perceived by the models as a possible cause for significant losses on suitable area.

A - Current climatic conditions



Species	*Musschia wollastonii*
Family	Campanulaceae

Calibratio	Presences	Absences
Data	17	3662

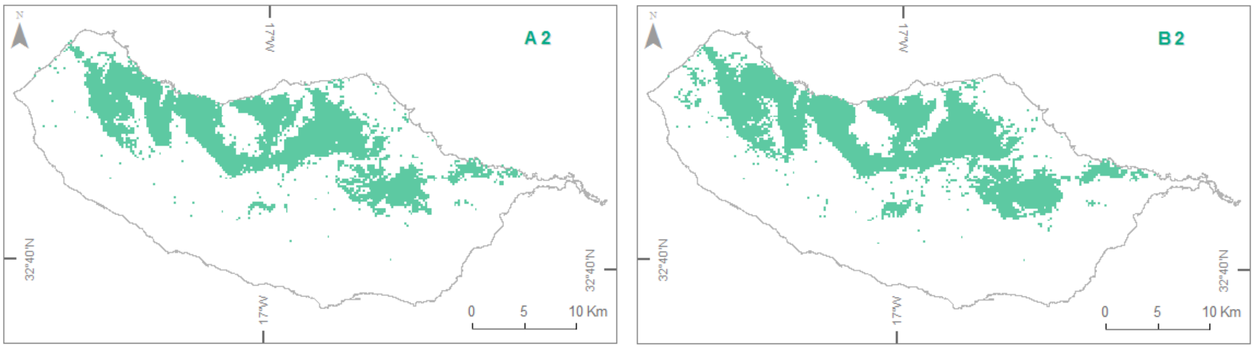
Statistics	Max	Min	Aver
AUC	0.77	0.7	0.73

Scenarios	A2	B2
Gain (%)	77.3	98.5
Loss (%)	2.8	0.2
Maintain	97.2	99.8

Table XXIX – Relative importance of predictors across models for *Musschia wollastonii*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
Prec_w	**0.5**	-	**0.8**	0.3	0.3	0.0	0.1	0.2
T_mmcm	0.0	-	0.4	0.0	**0.7**	0.1	0.1	0.1
T_ar	0.3		0.0	0.5	0.0	0.8	0.9	0.2

B - Climatic scenarios – 2070-2099



C - Predicted changes

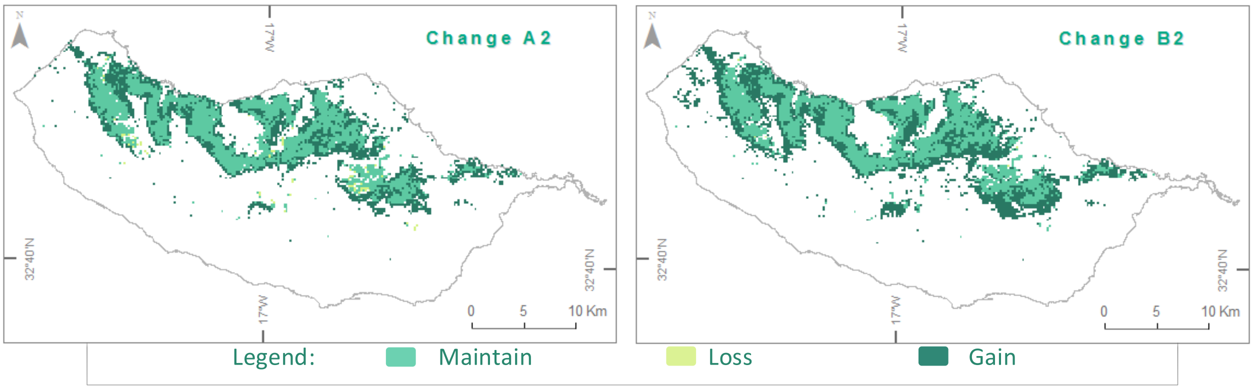


Figure 39 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Musschia wollastonii*

2.5.1.8 *SIDEROXYLON MIRMULANS* R. BR.

Shrub to small tree of the Sapotaceae family that is endemic of the Macaronesian archipelagos (Canaries, Cape Verde, Madeira), and inhabits the costal territories of both faces of Madeira Island, but with higher frequency on the northern one. Common on coastal rocky cliffs, it is also found on inner sections of the large valleys, where it occupies the same ecology.

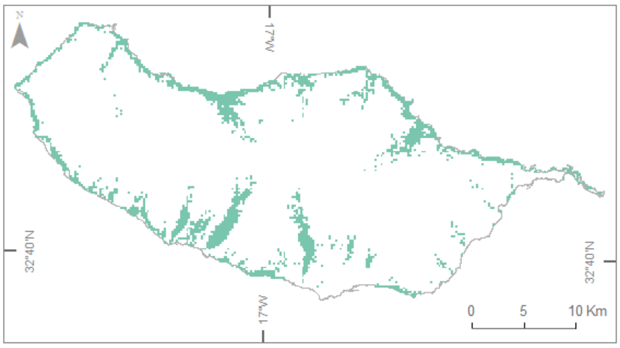
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

Predicted area for current conditions show that models clearly capture the main patterns associated to expected and known distributions for the species. The association to coastal areas and valleys indicates a preference for termophyllous areas. This conclusion is also supported by the fact that most of the modelling techniques in use elected the minimum average temperature of the coldest month as the predictor with higher relative importance. Notwithstanding the common occurrence on steep slopes and rocky cliffs, only one modelling technique (CTA) identifies a topographic variable (Slp_34) as determinant to explain current distribution.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Predictions for future climatic scenarios present a spatial dichotomy in terms of losses and gains. Significant gains are predicted in terms of suitable area for the northern face of the island and for the scenario B2, namely on inner sections of the largest valleys. In terms of predicted loss, the models identify the coastal areas of the southern face as highly vulnerable.

A - Current climatic conditions



Species	*Sideroxylon mirmulans*
Family	Sapotaceae

Calibration	Presences	Absences
Data	219	3460

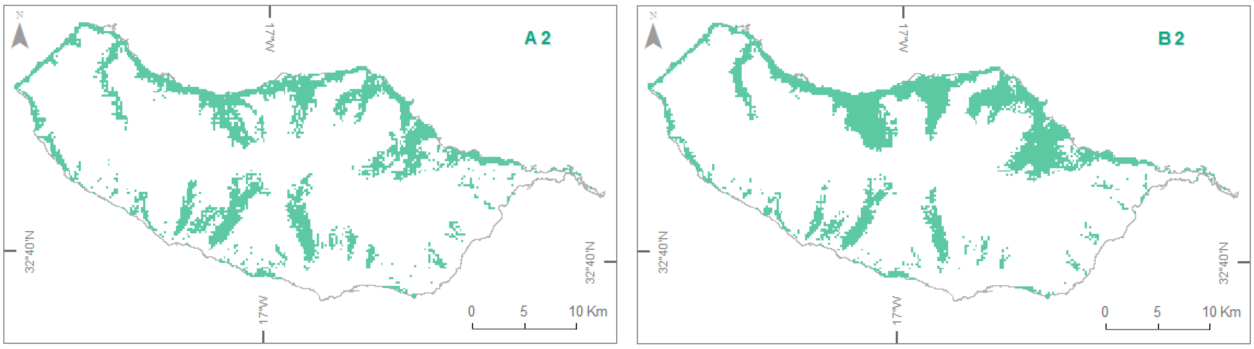
Statistics	Max	Min	Aver
AUC	0.88	0.74	0.84

Scenarios	A2	B2
Gain (%)	87.5	89.9
Loss (%)	13.3	10.1
Maintain (%)	86.7	89.9

Table XXX – Relative importance of predictors across models for *Sideroxylon mirmulans*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_w	0.1	**0.7**	0.1	0.1	0.1	0.3	0.1	0.1
T_mmcm	**0.5**	**0.7**	**0.5**	**0.5**	**0.5**	0.4	**0.5**	0.4
T_ar	0.4	0.0	0.1	0.1	0.1	**0.5**	0.1	0.1
Slp_34	0.1	**0.7**	0.1	0.1	0.1	0.3	0.1	0.1

B - Climatic scenarios – 2070-2099



C - Predicted changes

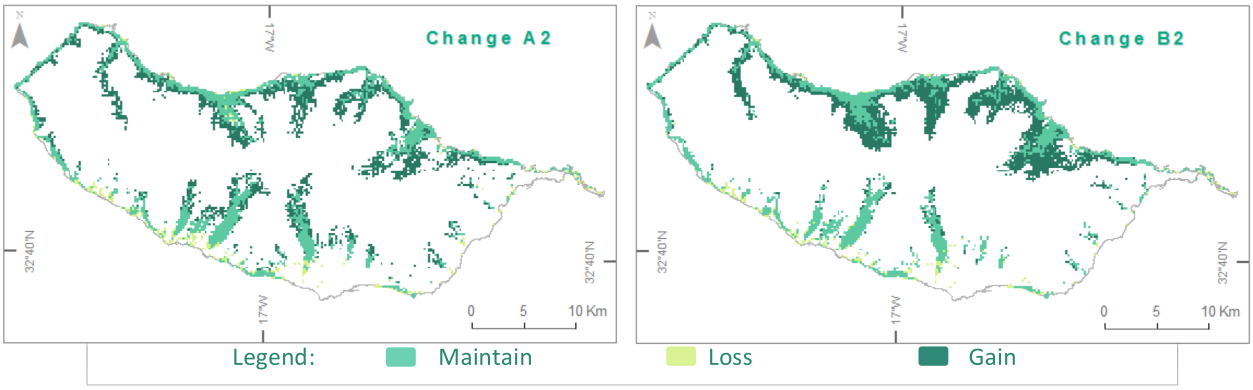


Figure 40 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Sideroxylon mirmulans*

2.5.1.9 *SORBUS MADERENSIS* (LOWE) DODE

Endemic tall shrub of Madeira Island that presents a distribution restricted to the highest summits. In fact, almost all population was extirpated by the big wildfires of 2010. Despite the low number of occurrences registered (10), it was considered acceptable to carry on with modelling, a decision based on the limited geographical range, which reduces the change of producing highly biased results. Nevertheless, it is expected that such limited occupancy area is deeply determined by land-use, a fact that might contribute to underestimate suitable area.

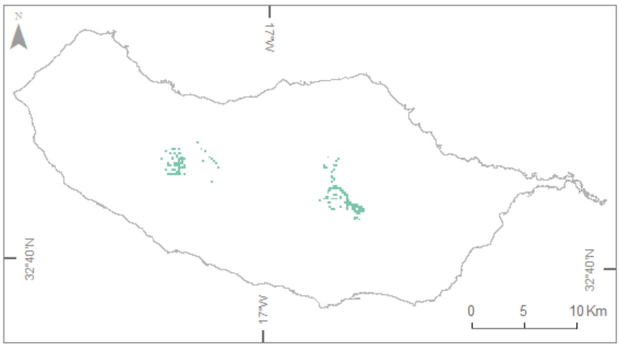
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The area predicted as suitable is restricted to the highest summits of the island. As expected, models predict the existence of suitable areas at Bica da Cana (western area), where the species was not found. In this case, it puts in evidence that species' current distribution is deeply affected by land-use. The mean minimum temperature of the coldest month is the predictor that assumes higher importance across the models.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Similarly to other species that present a current distribution restricted to small populations at the summits of the island, predictions project a significant loss of suitable area. The loss of suitable area implies a significant reduction on both scenarios, almost extirpation in the scenario A2. Such fact is clearly related to the rise on the minimum temperature, which prompts an upward shift of the species climatic envelope. Because of the topographic position, available area should reduce significantly.

A - Current climatic conditions



Species	*Sorbus maderensis*
Family	Rosaceae

Calibratio	Presences	Absences
Data	10	3669

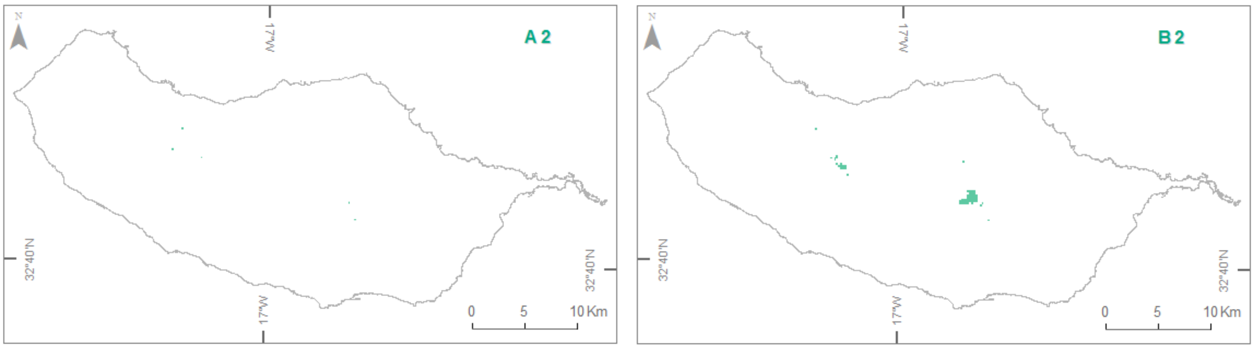
Statistics	Max	Min	Aver
AUC	0.93	0.7	0.85

Scenarios	A2	B2
Gain (%)	1.3	30.9
Loss (%)	98	90.6
Maintain	2	9.4

Table XXXI – Relative importance of predictors across models for *Sorbus maderensis*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_w	**0.5**	0.0	0.1	**0.8**	0.3	**0.5**	0.1	**0.5**
Prec_s	0.2	**0.7**	0.1	**0.8**	**0.7**	0.2	0.0	0.2
T_mmcm	0.0	**1.0**	**0.9**	**1.0**	**0.8**	**0.6**	**0.7**	0.0
T_ar	0.0	**0.9**	0.3	**0.9**	**0.6**	0.0	0.1	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes

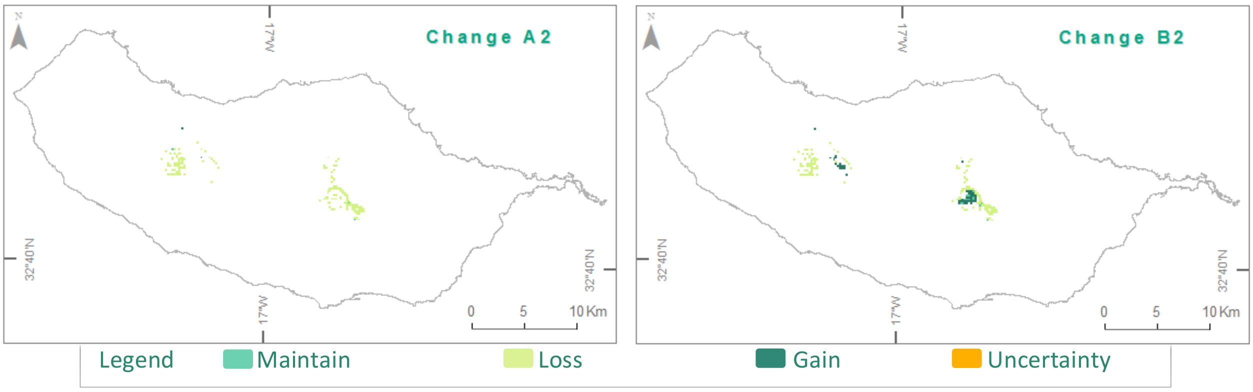


Figure 41 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Sorbus maderensis*

2.5.1.10 *TEUCRIUM BETONICUM* L'HER.

Small perennial endemic shrub of the Lamiaceae family that inhabits open spaces, namely areas that registered a disturbance in the recent pats. It is very common on parcels abandoned by agriculture, where it is easy to detect when flowering because of the purplish corolla.

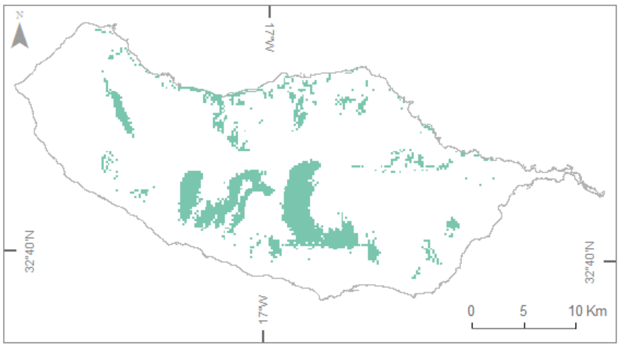
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

According to predictions, suitable areas are mainly associated to medium altitudes of valleys located on the southern face of the island and. With less significance, predicted area is also associated with valleys, but with a larger altitudinal range – coast to medium altitudes. Despite the significant number of registered occurrences on parcels abandoned by agriculture in the recent past, all the variables elected by the modelling techniques as playing a significant role to explain known distribution are of climatic type.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Two very different results are predicted among the climatic scenarios. The climatic changes projected by the scenario A2 support a significant decrease in terms of suitable area, which is mainly associated to the lower fraction of the altitudinal range. And predicted gain is of low significance, namely if compared with the predicted gain for the scenario B2. In this scenario, a significant increase on suitable area is predicted for the northern face of the island, and a less significant loss on the lower sections of the altitudinal range on the southern face, where the gain is almost neglectable.

A - Current climatic conditions



Species	Teucrium betoniucum
Family	Lamiaceae

Calibration	Presences	Absences
Data	191	3488

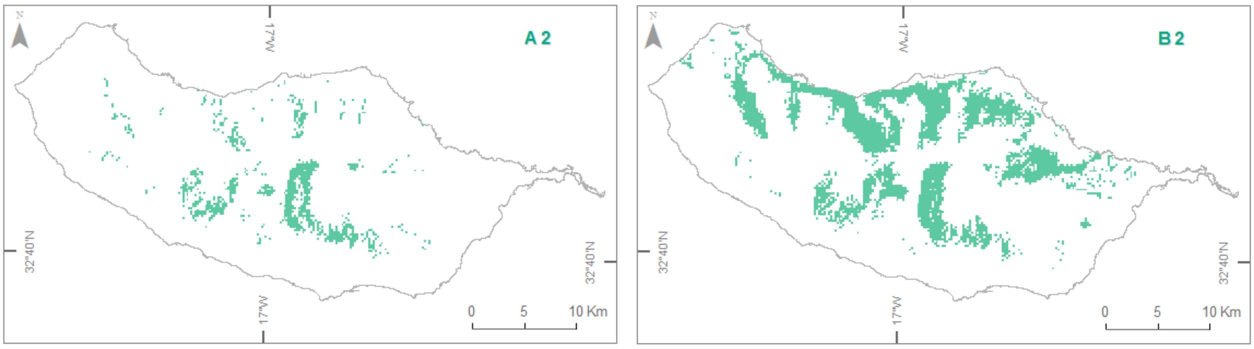
Statistics	Max	Min	Aver
AUC	0.87	0.7	0.82

Scenarios	A2	B2
Gain (%)	6.6	92.7
Loss (%)	62.5	28.8
Maintain (%)	37.5	71.2

Table XXXII – Relative importance of predictors across models for *Teucrium betonicum*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_w	0.4	0.0	0.2	0.0	0.2	**0.9**	**0.6**	0.1
Prec_s	0.3	**0.8**	0.2	0.3	0.3	0.0	0.2	0.3
T_ar	0.0	0.3	0.3	0.1	0.4	0.0	**0.6**	0.1
T_mmcm	0.0	**0.6**	**0.5**	0.3	**0.5**	0.0	**0.6**	0.2

B - Climatic scenarios – 2070-2099



C - Predicted changes

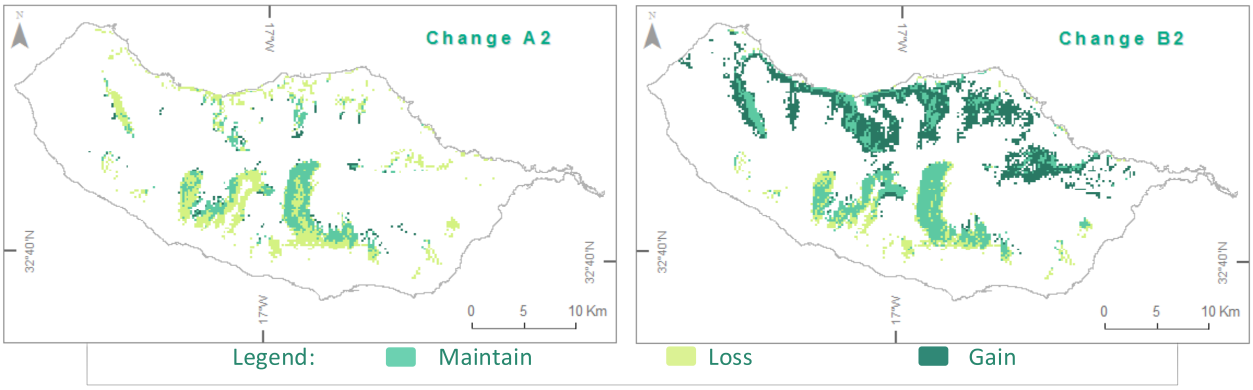


Figure 42 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Teucrium betonicum*

2.5.2 ENDEMIC SPECIES WITHOUT PROTECTION STATUS

This section is dedicated to the assessment of changes on distribution for endemic species that have no protection status under the future climatic scenarios considered.

Most of the species included in this section present a wide geographical range, are able to colonize different habitats and can be locally abundant (WGA). But few of them are associated to narrow geographical ranges, are restricted to habitats of low spatial extent and can be rare (type NER - Figure 32).

Table XXXIII – List of species considered in this section

Taxon	Type of distribution	Nr.
Armeria maderensis	NGR	21
Argyranthemum pinnatifidum subsp. pinnatifidum	WGA	176
Bupleurum salicifolium	WGR	49
Carlina salicifolia	WGA	110
Euphorbia mellifera	WEA	88
Erica maderensis	NEA	31
Erysimum bicolor	WGR	50
Matthiola maderensis	NEA	40
Pericallis aurita	WGA	154
Rosa mandonii	WGA	104
Sonchus pinnatus	WER	158
Sonchus fruticosus	WGA	275
Sonchus ustulatus ssp. *ustulatus*	NER	31
Sonchus ustulatus ssp. *maderensis*	NER	11
Sideritis candicans	WGR	112

WGA	abundant species, present on different habitats and with a wide distribution on the island
WGR	abundant species over a large range but associated to specific habitat habitat conditions
NGA	species that are abundant in several habitats but restricted geographically
NGR	rare species associated to different types of habitat in a narrow area of distribution
WSA	abundant species associated to specific habitat conditions on a wide geographical range
WSR	rare species that are restricted to a type of habitat on a wide area of distribution
NSA	species that are habitat specialists and have a small geographical range, but area abundant in the area of occurrence,
NSR	specialist species that have a rare occurrence within a narrow geographical distribution.

2.5.2.1 *ARMERIA MADERENSIS* LOWE

Herbaceous and perennial endemic of the Plumbaginaceae family, forming small tussocks, which inhabits the highest summits of Madeira Island, above 1500m m.s.l. On modern days present a low frequency within its geographical range, a fact that might be associated to centuries of grazing. Its occurrence is mainly associated to small inaccessible patches of deep organic soil, the so-called *mangas*, which may be considered as topographic refugees. A significant number of populations were extirpated during the wildfires of 2010.

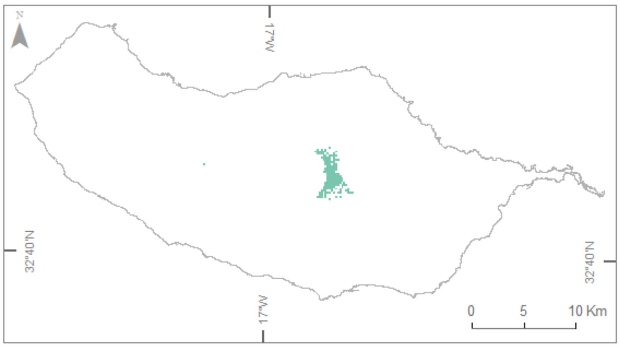
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The predicted area is restricted to the central massif of Madeira, corresponding to the highest peaks of the island. The tolerance to low temperatures is an attribute that explains its distribution, a relationship clearly detected by the different modelling techniques by selecting the mean minimum temperature of the coldest month as a significant limiting factor. The context of refuge that characterizes the locations where the species was recorded is patent in the fact that a topographic predictor (topographic complexity) is selected as an environmental variables that must be considered to explain current distribution.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The loss of suitable area under the projected scenarios is especially concerning, once suitable area becomes deeply restricted, in the case of the scenario B2, or the island has no longer suitable conditions for the species, considering the results for the scenario A2. Such vulnerability is reinforced by the low frequency of the species, which is very likely associated to centuries of grazing. Another important source of threat is the invasion by exotic shrubs, namely *Cytisus* sp., that is promoting the reduction of available habitat.

A - Current climatic conditions



Species	*Armeria maderensis*
Family	Plumbaginaceae

Calibration	Presences	Absences
Data	21	3658

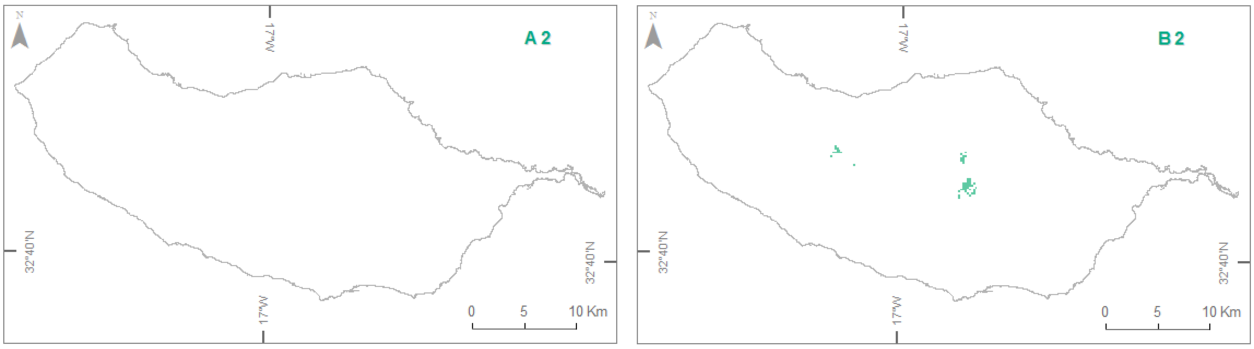
Statistics	Max	Min	Aver
AUC	0.99	0.7	0.87

Scenarios	A2	B2
Gain (%)	0	8.7
Loss (%)	100	75.8
Maintain (%)	0	24.2

Table XXXIV – Relative importance of predictors across models for *Armeria maderensis*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_w	**0.8**	0.2	**0.5**	0.0	0.0	0.1	0.2	0.2
Prec_s	**0.5**	0.1	0.0	0.0	**0.5**	**0.7**	0.2	0.0
T_mmcm	0.4	**0.9**	**0.8**	**1.0**	**1.0**	**1.0**	**1.0**	**0.8**
SWI_tp	0.0	**0.8**	0.4	0.4	**0.7**	0.1	0.0	0.2

B - Climatic scenarios – 2070-2099



C - Predicted changes

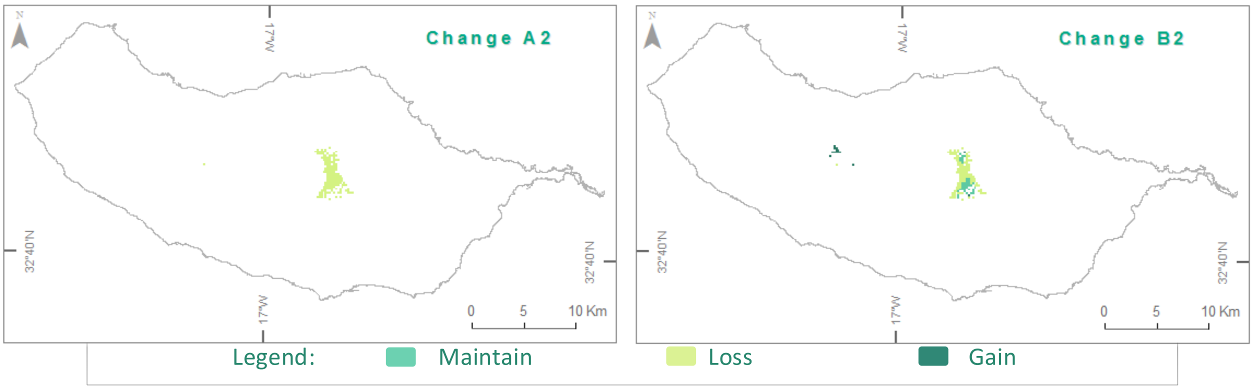


Figure 43 – Predicted suitable area distribution for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Armeria maderensis*

2.5.2.2 *ARGYRANTHEMUM PINNATIFIDUM* (L. FIL.) LOWE SUBSP. *PINNATIFIDUM*

Perennial woody shrub of the Asteraceae family, reaching 1.5m in height, that presents a wide distribution in the island. It is more common on the northern face of the island, from very low altitudes (300m) to upper areas (1600 m). It inhabits mostly small openings associated to rocky outcrops in the laurel forest, or small gaps associated to tree fall and small recent surface landslides. The association to rocky outcrops, on areas with difficult accessibility, have granted its survival at the upper areas of its range on the southern face of the island, a territory affected by intense grazing during centuries.

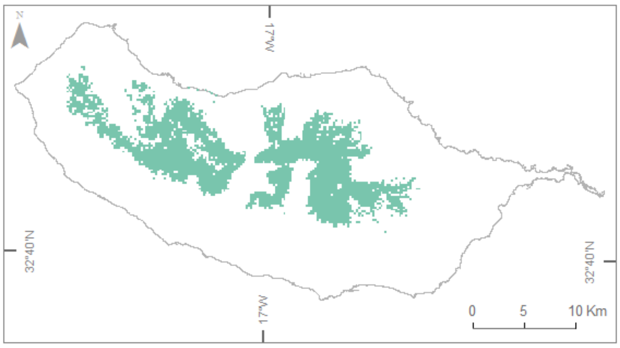
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The area predicted as suitable is associated to altitudes between 800m m.s.l. and 1600m m.s.l.. Despite the resolution used (200x200m), the models were able to capture the association between the species and topographic predictors, namely areas with high slopes (Slp_4), or exhibiting complex structure in terms of landscape composition. But the factor with more relative importance to explain current distribution is the mean minimum temperature of the coldest month, a predictor identified by all modelling techniques. The identification of suitable areas near the coast are possibly related with biasing effects from the inclusion of occurrences for the species *Argyranthemum haematoma*.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The predicted changes for the scenario A2 reveal the interference of possible misleading on the identification of taxa. It is not expected that a species has opposite responses, namely a loss suitable area on the rear edge (lower altitudes), and gains on even lower altitudes. Occurrence data for the lower altitudes should be confirmed in the field.

A - Current climatic conditions



Species	*Argyranthemum pinnatifidum*
Family	Asteraceaee

Calibration	Presences	Absences
Data	176	3503

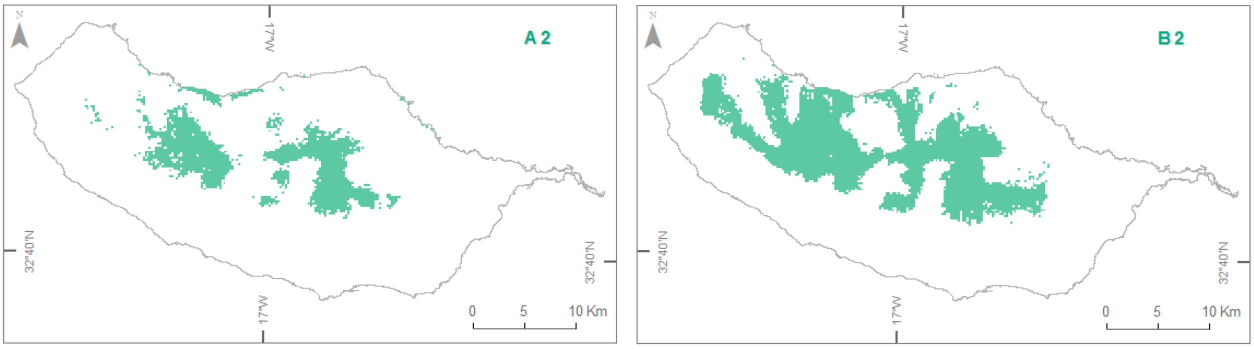
Statistics	Max	Min	Aver
AUC	0.89	0.81	0.86

Scenarios	A2	B2
Gain (%)	5.9	30.2
Loss (%)	47.2	5.9
Maintain (%)	52.8	94.1

Table XXXV – Relative importance of predictors across models for *Argyranthemum pinnatifidum*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Slp_4	0.3	**0.6**	0.1	0.1	0.1	0.3	0.2	0.1
T_mmcm	**0.7**	**0.9**	**0.9**	**0.9**	**0.9**	**0.9**	**0.9**	**0.6**
PSCOV	0.3	0.0	0.0	0.0	0.0	**0.5**	0.0	0.0
PSSD	**0.5**	0.0	0.0	0.0	0.0	**0.5**	0.1	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes

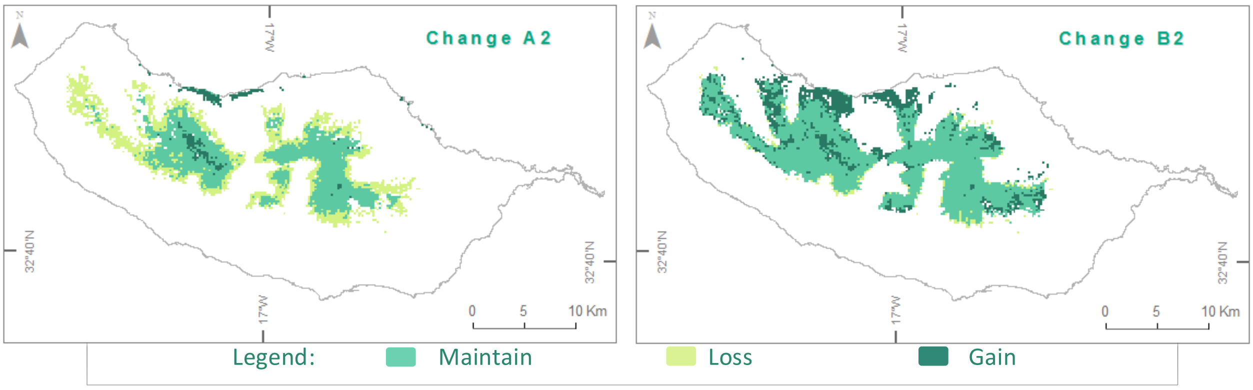


Figure 44 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Argyranthemum pinnatifidum*

2.5.2.3 *BUPLEURUM SALICIFOLIUM* R. BR. EX BUCH SUBSP. *SALICIFOLIUM*

Endemic plant of Macaronesia that presents a low frequency on Madeira island. It is a small perennial herbaceous plant, with woody basal stem, of the Apiaceae family, that inhabits exposed rocky areas, with thin soils, on the higher summits of the island.

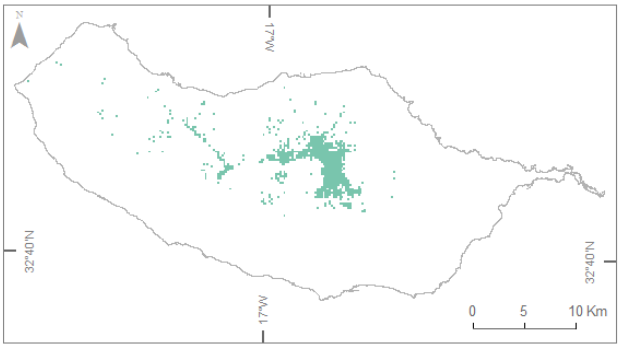
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

Suitable conditions are mainly associated to the highest peaks of the island, a fact that is related to cold-tolerance of the species. The models also captured the association between species occurrence and topographic features, a fact that explains why predicted area on the western summits (Paul da Serra area) is more restricted, a prediction that reveals the lower availability of habitat, despite similar climatic conditions.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Results expose a significant decrease in suitable area, namely for the scenario A2, which almost determines the extirpation of the species, a feature associated to the fact that it occupies summit areas. Such response is deeply related to the projected rise of the minimum temperature, which shall be more impacting than the upward shift of lower-altitude species.

A - Current climatic conditions



Species	*Bupleurum salicifolium*
Family	Apiaceae

Calibratio	Presences	Absences
Data	49	3630

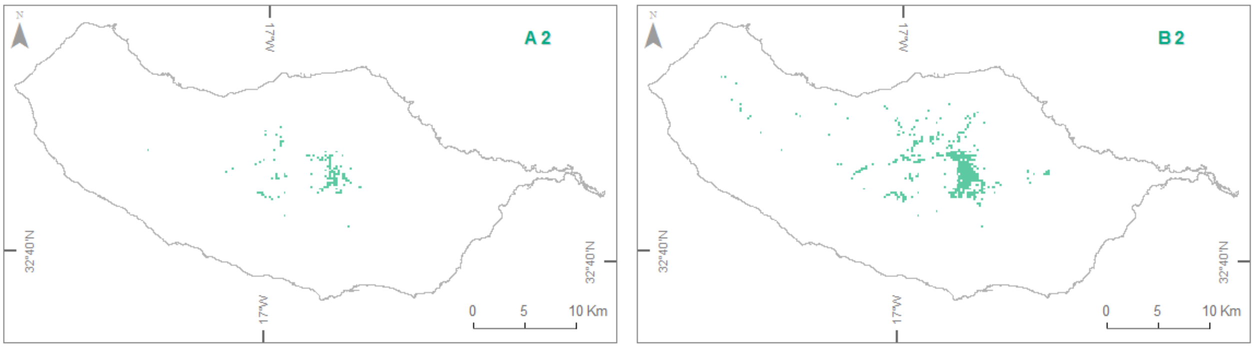
Statistics	Max	Min	Aver
AUC	0.9	0.72	0.83

Scenarios	A2	B2
Gain (%)	2.4	9.8
Loss (%)	85.9	53.6
Maintain	14.1	46.4

Table XXXVI – Relative importance of predictors across models for *Bupleurum salicifolium*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Slp_34	0.3	0.2	**0.7**	0.0	**0.7**	0.0	0.0	0.0
Prec_s	0.1	0.1	0.2	0.0	**0.7**	0.0	0.2	0.0
T_mmcm	**0.7**	**0.9**	**0.6**	**0.9**	**0.6**	**0.8**	**0.9**	0.4

B - Climatic scenarios – 2070-2099



C - Predicted changes

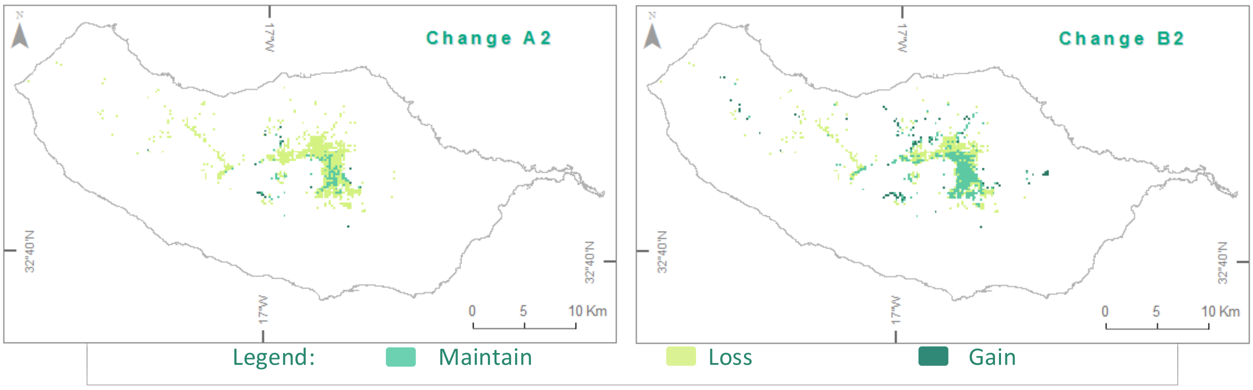


Figure 45 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Bupleurum salicifolium*

2.5.2.4 *CARLINA SALICIFOLIA* (L. F.) CAV.

Macaronesian endemic shrub of the Asteraceae family that exhibits a wide distribution in the island. It is more frequent in the centre of the island, namely on hilly slopes associated to the highest peaks and valleys.

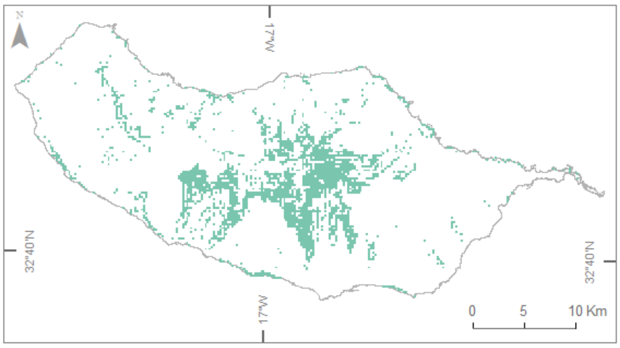
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

Models detect a significant relationship between the presence of the species and the existence of steep slopes (slope_4) or areas of higher topographic complexity (SWI_tp). The wide predicted geographical range and the association to specific topographic conditions suggest that its distribution is less determined by climatic conditions, an assumption supported by the low importance of climatic variables to explain current distribution. In fact, the predicted suitable area has a pattern that follows the steep slopes associated to deep valleys.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Projections predict similar values in terms of gain and loss for suitable area under the scenario B2. For such scenario predicted loss has a diffuse pattern, such as in the scenario A2, but the predicted gain, more significant than in the scenario A2, is concentrated in the northern face of the island.

A - Current climatic conditions



Species	*Carlina salicifolia*
Family	Asteraceae

Calibration	Presences	Absences
Data	110	3569

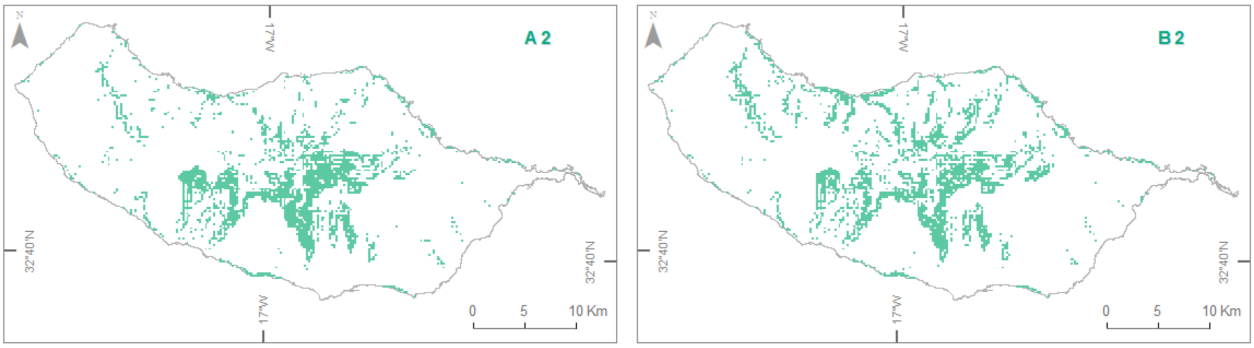
Statistics	Max	Min	Aver
AUC	0.83	0.7	0.77

Scenarios	A2	B2
Gain (%)	4.6	19.9
Loss (%)	14.3	19.5
Maintain (%)	85.7	80.5

Table XXXVII – Relative importance of predictors across models for *Carlina salicifolia*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Rad_sol	**0.5**	0.4	0.0	0.0	0.0	0.2	0.0	0.1
Slope_4	**0.6**	**0.9**	0.4	**0.5**	0.4	0.3	0.3	0.3
Prec_w	0.7	0.2	0.1	0.0	0.2	0.1	0.1	0.0
SWI_tp	0.0	0.0	0.0	0.1	0.0	**0.7**	**0.6**	0.1

B - Climatic scenarios – 2070-2099



C - Predicted changes

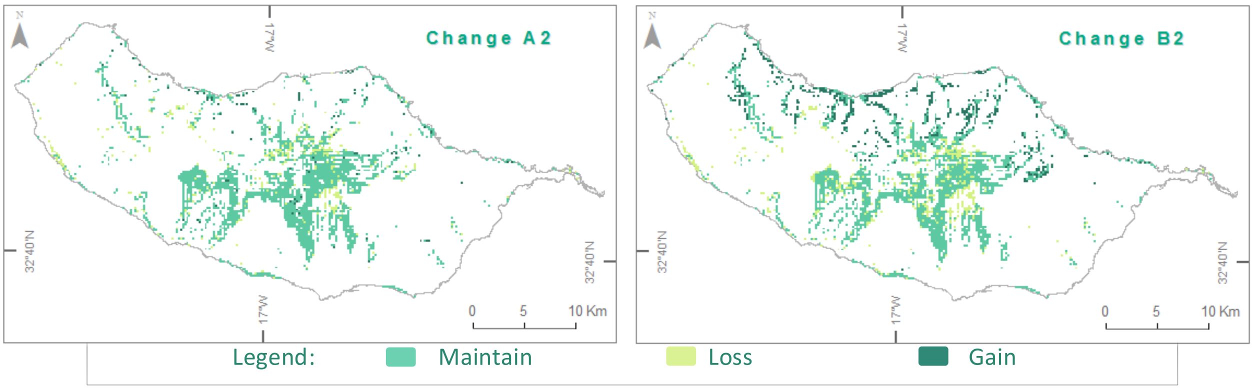


Figure 46 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Carlina salicifolia*

2.5.2.5 *EUPHORBIA MELLIFERA* AITON

Tall shrub to small tree of the Euphorbiaceae family, endemic to Madeira and Canaries. On Madeira Island it is a characteristic species of the temperate laurissilva, where it inhabits moist places, namely the margins of streams.

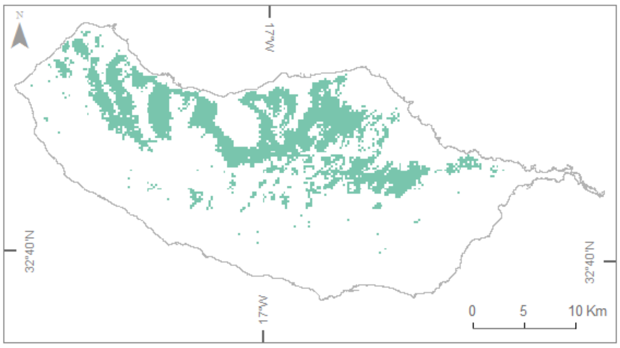
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The potential distribution reveals a significant match to the area currently occupied by the temperate laurissilva. The distribution is mainly constrained by the low tolerance to low temperatures and drought, what gives higher importance to the spatial pattern of the mean minimum temperature of the coldest month and summer precipitation.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The decrease on suitable area is mostly identified on the lower margin of the altitudinal range, a response associated to the decrease on summer precipitation. Such results are spatially compatible with the predicted response of the temperate laurisilva, which lower areas should be occupied by the Mediterranean laurel forest.

A - Current climatic conditions



Species	*Euphorbia mellifera*
Family	Euphorbiaceae

Calibration	Presences	Absences
Data	88	3591

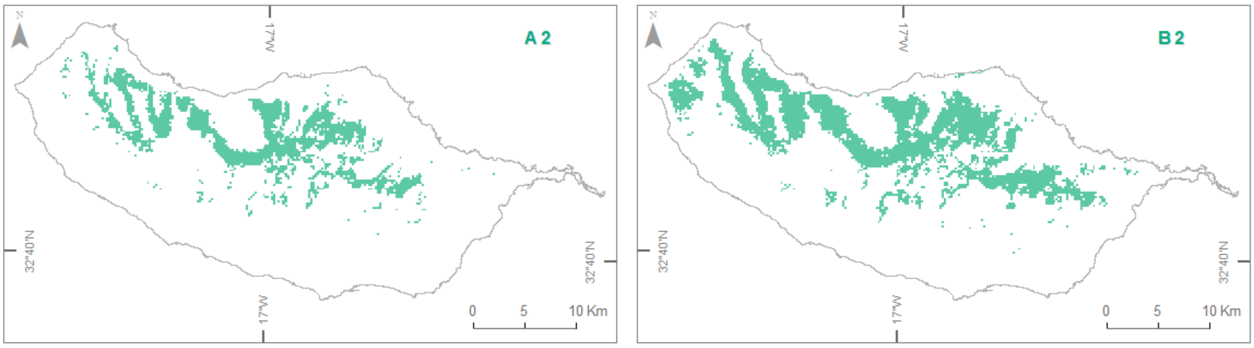
Statistics	Max	Min	Aver
AUC	0.87	0.7	0.78

Scenarios	A2	B2
Gain (%)	11.4	28.5
Loss (%)	49	23.9
Maintain (%)	51	76.1

Table XXXVIII – Relative importance of predictors across models for *Euphorbia mellifera*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
Prec_s	**0.7**	0.1	0.3	0.1	0.2	**0.6**	**0.5**	0.1
T_mmcm	0.1	**0.6**	**0.5**	**0.5**	**0.7**	**0.7**	0.4	0.3
T_ar	**0.6**	**0.6**	0.2	0.3	0.2	0.4	0.2	0.2
PSSD	**0.9**	0.0	0.0	0.0	0.0	0.0	0.0	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes

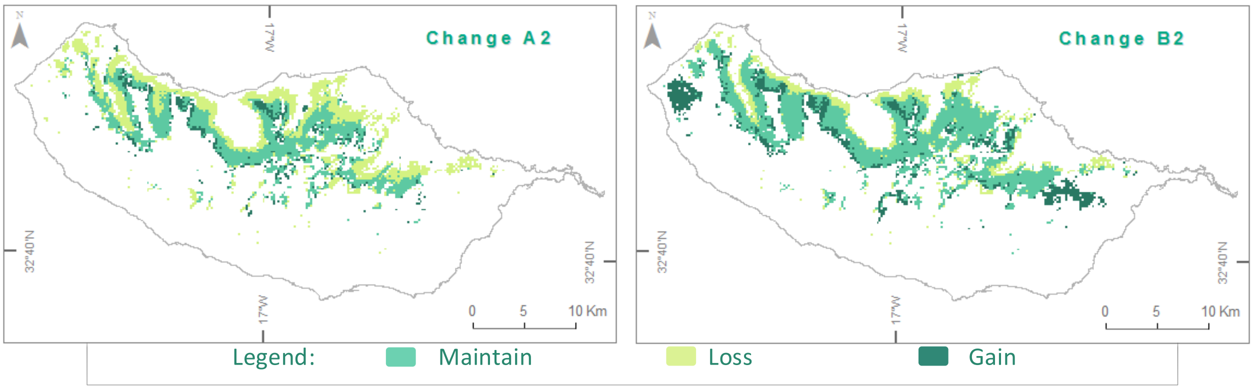


Figure 47 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Euphorbia mellifera*

2.5.2.6 *ERICA MADERENSIS* (BENTH.) BORNM.

Small prostrate shrub of the Ericaceae family that inhabits the highest peaks of Madeira Island. It is found on rocky outcrops and walls at altitudes above 1500m.

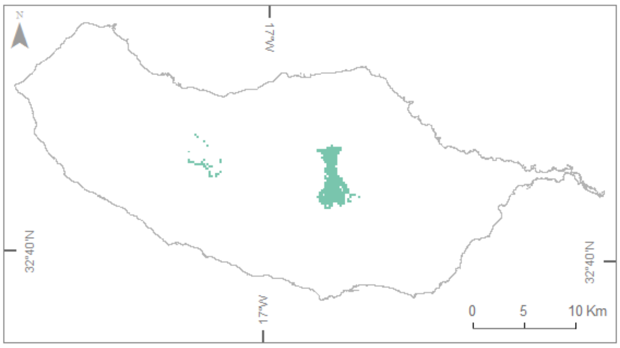
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The suitable area is restricted to a small territory, deeply disturbed in the past by intense grazing and on recent years by fire. The habitat occupied by the species reveals its resistance to extreme conditions, namely the capacity to explore nutrient-poor environments and tolerate negative temperatures during winter nights.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The predicted lack of suitable conditions according the scenario A2, or significant reduction on suitable area for the scenario B2, are mainly determined by the projected decrease on winter precipitation, which is expected to be more significant on the summits of the island.

A - Current climatic conditions



Species	*Erica maderensis*
Family	Ericaceae

Calibration	Presences	Absences
Data	31	3648

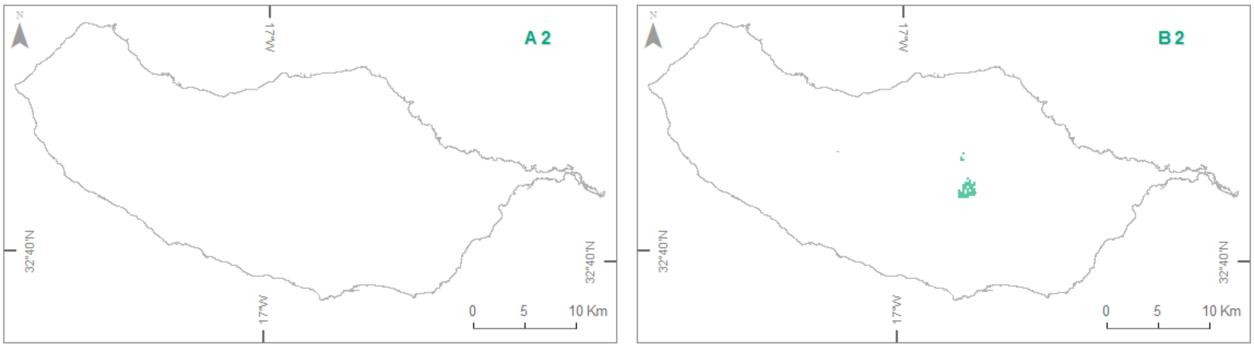
Statistics	Max	Min	Aver
AUC	0.95	0.82	0.89

Scenarios	A2	B2
Gain (%)	0	0.3
Loss (%)	100	82.9
Maintain (%)	0	17.1

Table XXXIX – Relative importance of predictors across models for *Erica maderensis*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_s	0.0	**0.6**	0.0	0.2	0.0	**0.6**	0.2	0.1
Prec_w	0.0	0.0	**0.5**	0.0	**0.5**	0.2	0.1	0.1
T_mmcm	0.0	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**	**0.8**
T_ar	0.0	0.0	**0.6**	0.0	**0.6**	**0.6**	0.0	0.2

B - Climatic scenarios – 2070-2099



C - Predicted changes

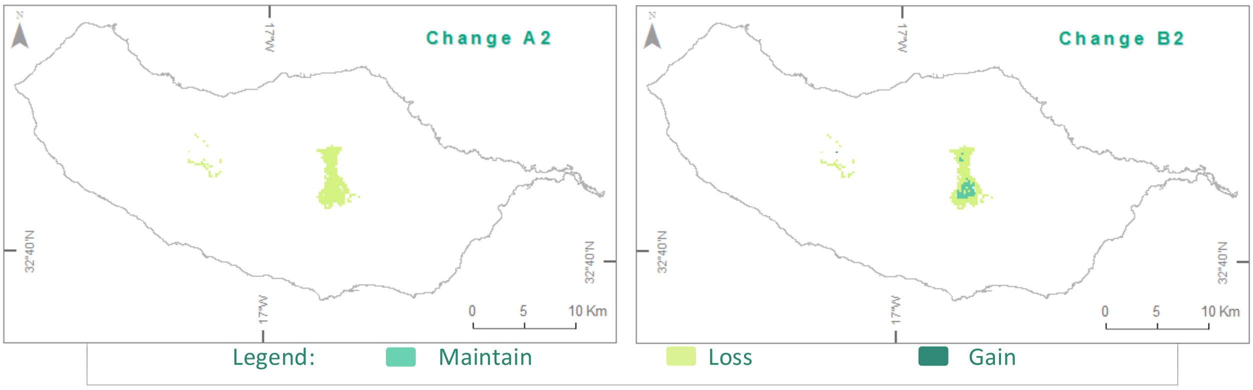


Figure 48 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Erica maderensis*

2.5.2.7 *ERYSIMUM BICOLOR* (HORNEM.) DC.

Small endemic shrub of the Cruciferae family present on different archipelagos of the Macaronesia (Madeira, Canaries, Cape Verde). Despite its wide distribution on Madeira Island, it is not a common plant, preferring shady places in the laurissilva or on areas occupied by heath tree communities under the altitude of 1600m m.s.l.

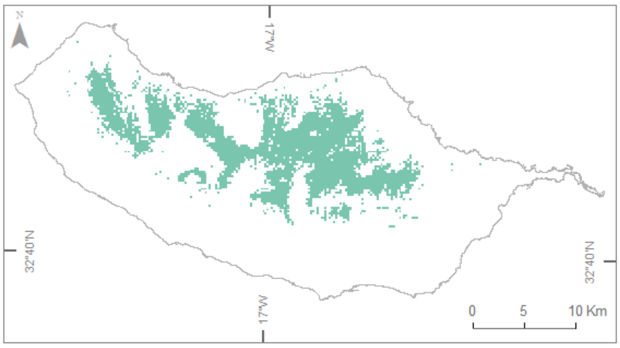
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The area accepted as suitable is associated to the presence of the temperate laurel forest, corresponding to the areas with the lower values of annual evapotranspiration in the island. That is mostly favoured by the high frequency of the cloud banks, that support the permanence of a moist environment, what reveals a low tolerance to drought and low temperatures.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The comparison of results for both scenarios reveal an opposite response. The scenario A2 supports an important decrease in terms of suitable area, while results for the scenario B2 predict a significant expansion of the suitable area. Such gain is detected along the margin of the area identified as suitable for current climatic conditions, which spatial range is predicted to be very similar under the climatic conditions projected for the scenario B2.

A - Current climatic conditions



Species	*Erysimum bicolor*
Family	Brassicaceae

Calibratio	Presences	Absences
Data	50	3629

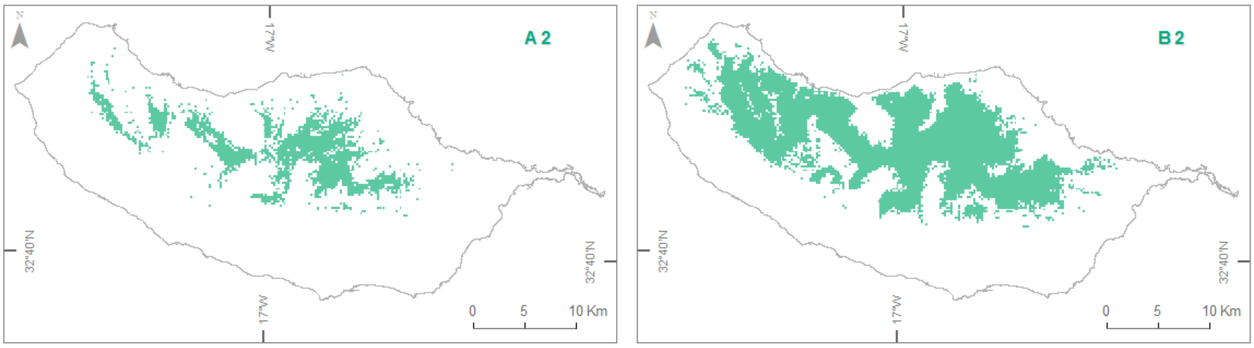
Statistics	Max	Min	Aver
AUC	0.87	0.7	0.78

Scenarios	A2	B2
Gain (%)	0.4	66.7
Loss (%)	45	1
Maintain	55	99

Table XL – Relative importance of predictors across models for *Erysimum bicolor*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_w	**0.7**	0.0	**0.5**	0.3	0.4	**0.5**	0.1	0.2
T_mmcm	0.0	**0.8**	**0.9**	**0.8**	**1.0**	0.3	**0.5**	0.4
T_ar	0.0	0.4	**0.7**	0.2	**0.6**	0.1	0.0	0.1
SWI_tp	0.0	**0.6**	0.0	0.2	0.0	0.8	0.0	0.1

B - Climatic scenarios – 2070-2099



C - Predicted changes

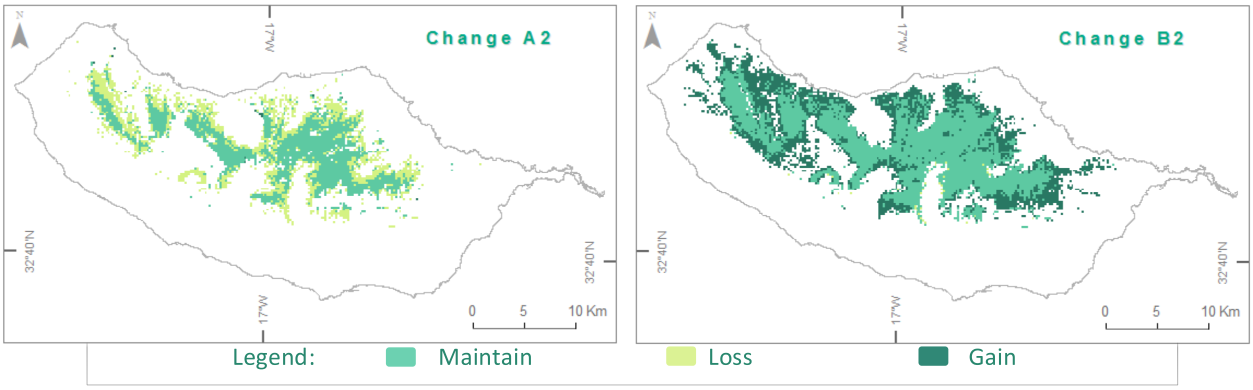


Figure 49 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Erysimum bicolor*

2.5.2.8 *MATTHIOLA MADERENSIS* LOWE

Herbaceous biennial or perennial plant of the Brassicaceae family that has a distribution restricted to areas exposed to the sea, namely rocky walls. It is very common within its area of distribution, where it is easily to detect when flowering because of the violet to purplish color of the flowers. The species presents a high capacity to support disturbance by human activities, as confirmed in the field.

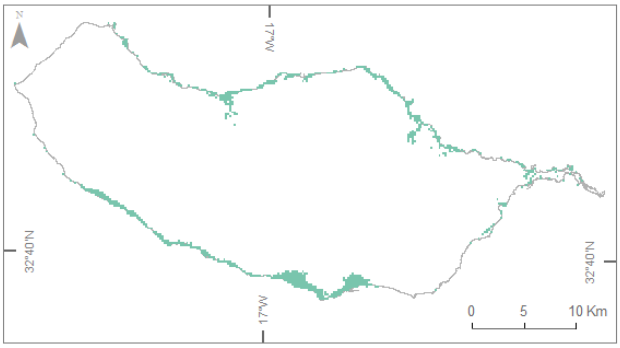
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The mean minimum temperature of the coldest month is the limiting factor that contributes significantly to constrain its distribution, which reveals a high tolerance to drought and intolerance to low temperatures.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The predictions reveal a trend also detected for species that present similar ecological requirements, namely the resistance to drought. Such condition explains the predicted changes, which are based on the decrease of the summer and winter precipitation on both scenarios. The models predict the maintenance of the current suitable area and a significant increase under the future climatic scenarios.

A - Current climatic conditions



Species	*Matthiola maderensis*
Family	Brassicaceae

Calibration	Presences	Absences
Data	40	3639

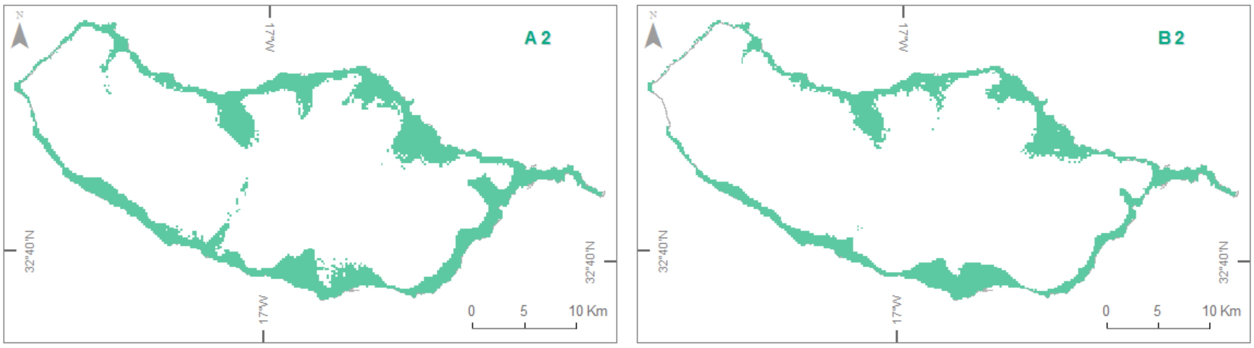
Statistics	Max	Min	Aver
AUC	0.96	0.7	0.84

Scenarios	A2	B2
Gain (%)	444.7	308
Loss (%)	0	0
Maintain (%)	100	100

Table XLI – Relative importance of predictors across models for *Mathiola maderensis*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_w	**0.6**	0.3	0.0	0.1	0.0	0.2	0.0	0.1
Prec_s	0.5	0.0	0.0	0.0	0.6	0.1	0.0	0.0
T_mmcm	**0.6**	**1.0**	**1.0**	**0.8**	**1.0**	**1.0**	**0.9**	**0.5**
T_ar	0.1	**0.5**	0.4	**0.5**	0.4	0.4	0.3	0.3

B - Climatic scenarios – 2070-2099



C - Predicted changes

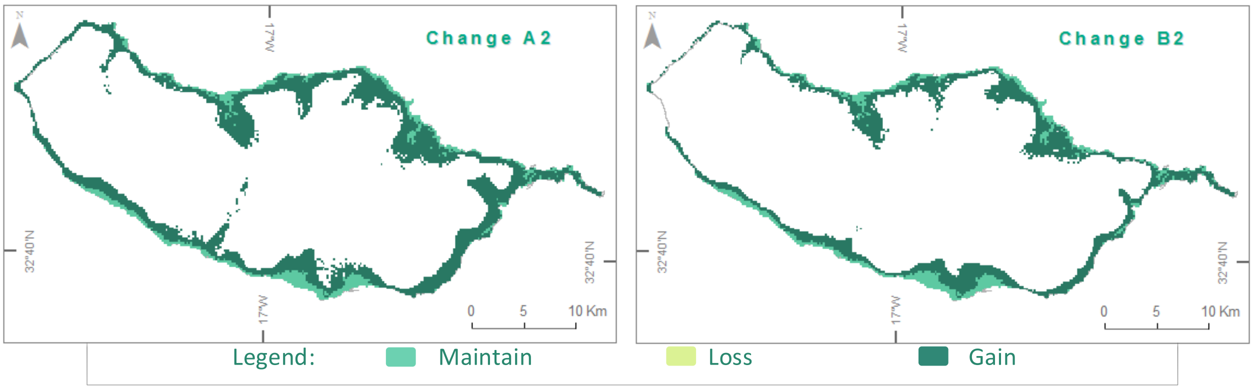


Figure 50 – Predicted area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Matthiola maderensis*

2.5.2.9 *PERICALLIS AURITA* (L'HÉR.) B. NORD.

Perennial endemic shrub (Madeiran archipelago) with prostrated habit of the Asteraceae family with wide distribution range and high frequency. It has preference for open areas from 800m to 1700m m.s.l., avoiding forest environments with tree dense cover.

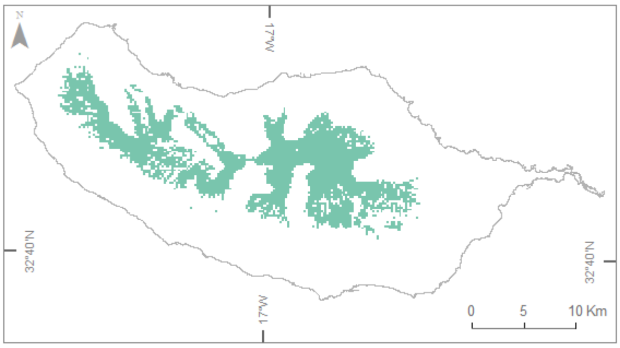
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

Topographical conditions, namely steep slopes (Slp_34), and mean minimum temperature of the coldest month, are the two predictors identified by the models as having an important contribution to current distribution. Such distribution reveals a tolerance to low temperatures and the common presence of the species on small gaps within shrubby communities or in the forest, which are usually associated to steep slopes or slope discontinuities, some of them created by human intervention (levadas, pathways, roads).

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Climatic conditions associated to both scenarios support a significant decrease on suitable area, especially within the scenario A2, and a timid or unappreciable gain. Once it is a very common species at the upper range of distribution, the potential loss suitable area doesn't put the species in risk.

A - Current climatic conditions



Species	*Pericallis aurita*
Family	Asteraceae

Calibration	Presences	Absences
Data	154	3525

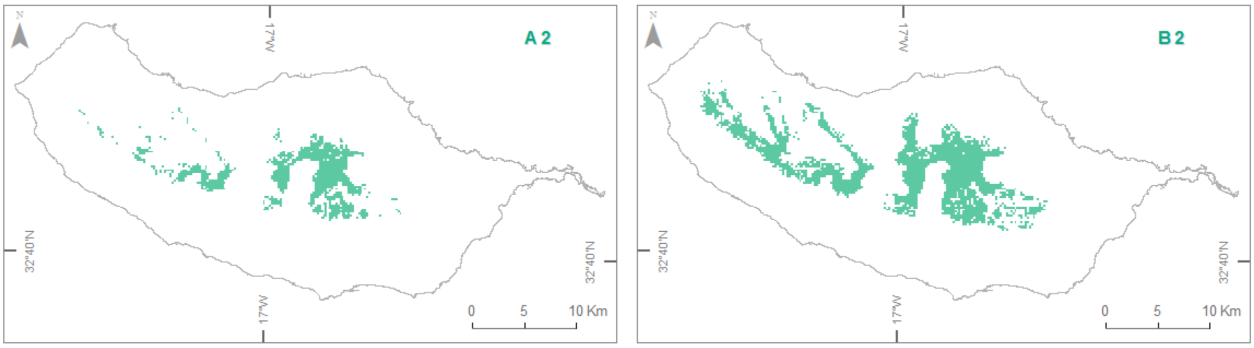
Statistics	Max	Min	Aver
AUC	0.87	0.77	0.84

Scenarios	A2	B2
Gain (%)	0.1	2.4
Loss (%)	72.4	41.3
Maintain (%)	27.6	58.7

Table XLII – Relative importance of predictors across models for *Pericalis aurita*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Slp_34	**0.5**	0.4	0.3	0.1	0.3	0.2	0.1	0.1
T_mmcm	**0.7**	**0.9**	**0.7**	**0.9**	**0.7**	**0.8**	**0.9**	**0.7**

B - Climatic scenarios – 2070-2099



C - Predicted changes

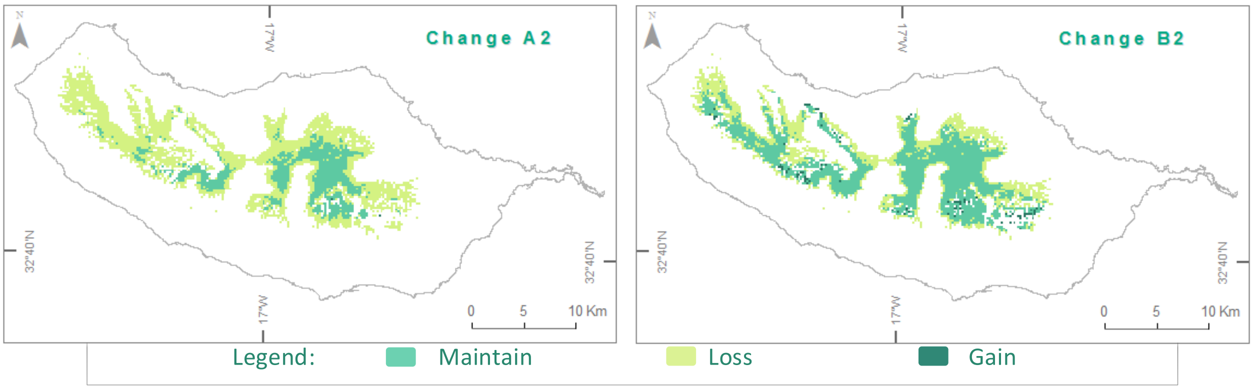


Figure 51 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Pericallis aurita*

2.5.2.10 *ROSA MANDONII* DÉSÉGL.

Endemic perennial (Madeira Island) and creeping shrub of the Rosaceae family with a wide distribution, from 600 to 1600m m.s.l. It is not very common, but it can be found on different types of habitat and vegetation types. It is easily detected because of the large white flowers grouped on terminal corymbs.

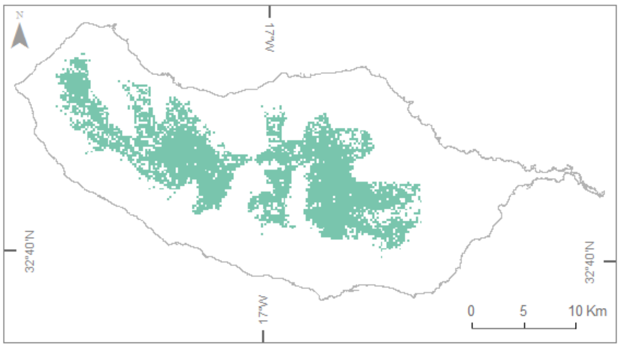
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

Models forecast a wide suitable area, defined above 800m m.s.l. Climatic variables are determinant for the distribution of the species, especially the mean minimum temperature of the coldest month.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The predicted changes are very identical for both climatic scenarios. There is a significant decrease in terms of suitable area, which is detected on the lower altitudes, the rear edge of the potential distribution for current conditions.

A - Current climatic conditions



Species	*Rosa mandonii*
Family	Rosaceae

Calibration	Presences	Absences
Data	104	3575

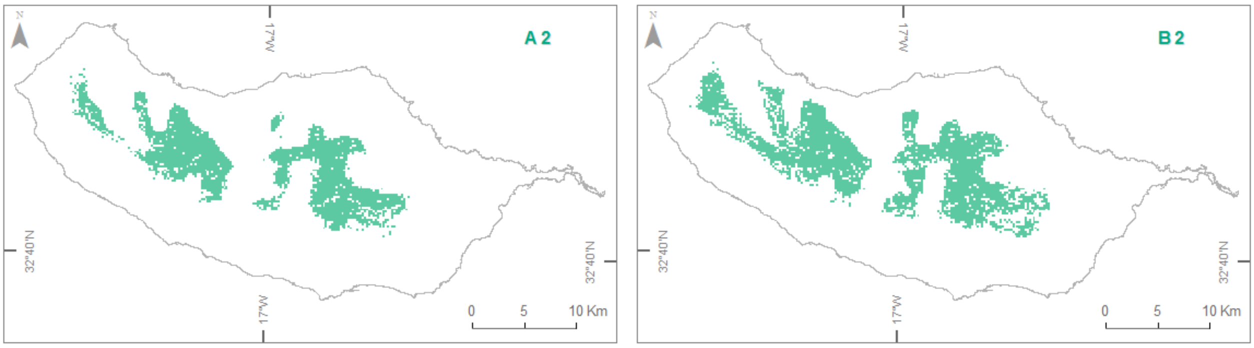
Statistics	Max	Min	Aver
AUC	0.83	0.7	0.77

Scenarios	A2	B2
Gain (%)	5.2	7.8
Loss (%)	47	33.5
Maintain (%)	53	66.5

Table XLIII – Relative importance of predictors across models for *Rosa mandonii*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_w	**0.8**	0.0	0.0	0.0	0.0	0.0	0.0	0.1
T_mmcm	0.2	**1.0**	**0.9**	**1.0**	**0.8**	**0.9**	**0.9**	**0.7**
T_ar	0.0	**0.5**	0.0	0.4	0.4	**0.5**	0.1	0.2

B - Climatic scenarios – 2070-2099



C - Predicted changes

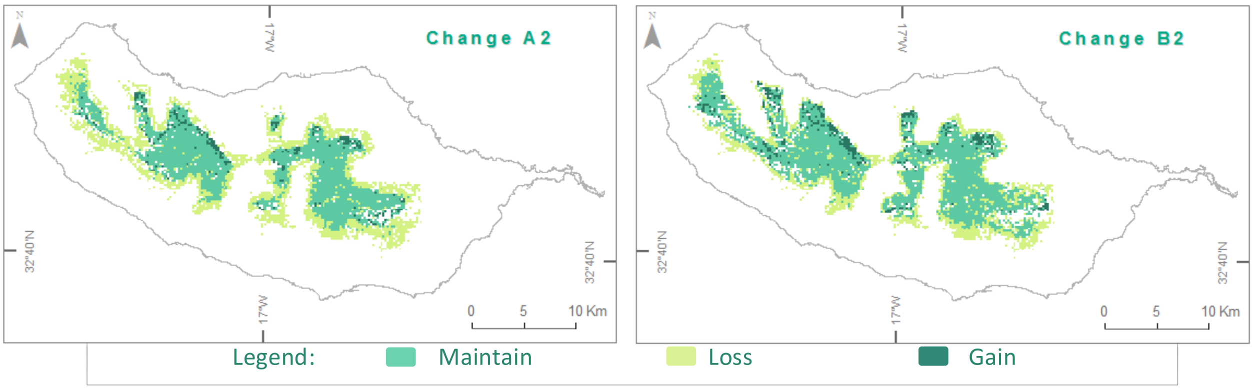


Figure 52 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Rosa mandonii*

2.5.2.11 *SONCHUS PINNATUS* AITON

Perennial endemic shrub (Madeira Island) of the Asteraceae family, with pinnatisect or pinnatipartite leaves, that inhabits rocky outcrops and walls. On such habitats is easily detected by its shape, reaching 2m in height, and when flowering, by the large terminal corymb cyme of yellow flowers.

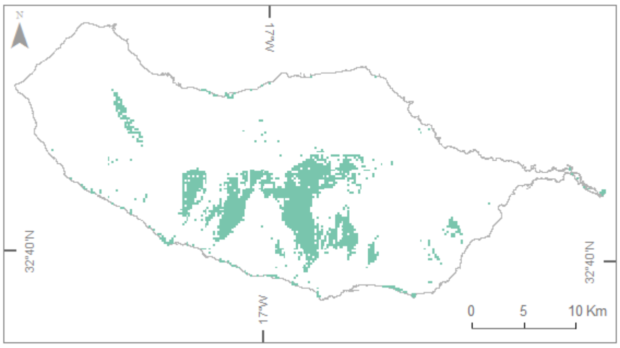
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The area predicted as suitable is mostly associated to large valleys of the southern face of the island, where the distribution of the species is dependent on the combination of climatic and topographic variables. The species seems to avoid areas that are more susceptible to drought, namely those with low values of summer precipitation, associated to altitudes below 800m on the southern face. Because of its low cold-tolerance, the upper limit of the suitable area is positioned at 1400m, altitude above which is frequent the occurrence of frost events during winter.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The projected scenarios support similar predictions in terms of loss and maintenance, both in terms of magnitude and spatial coincidence. But the results are very much different in terms of gains. Predicted new area for the scenario A2 is less important and is mainly detected on the southern face of the island, while in the case of the scenario B2 the higher gain is significantly associated to new areas on the northern face of the island. Such results are supported on the projected increase of summer precipitation, which should be more significant on the northern face of the island.

A - Current climatic conditions



Species	*Sonchus pinnatus*
Family	Asteraceae

Calibration	Presences	Absences
Data	158	3521

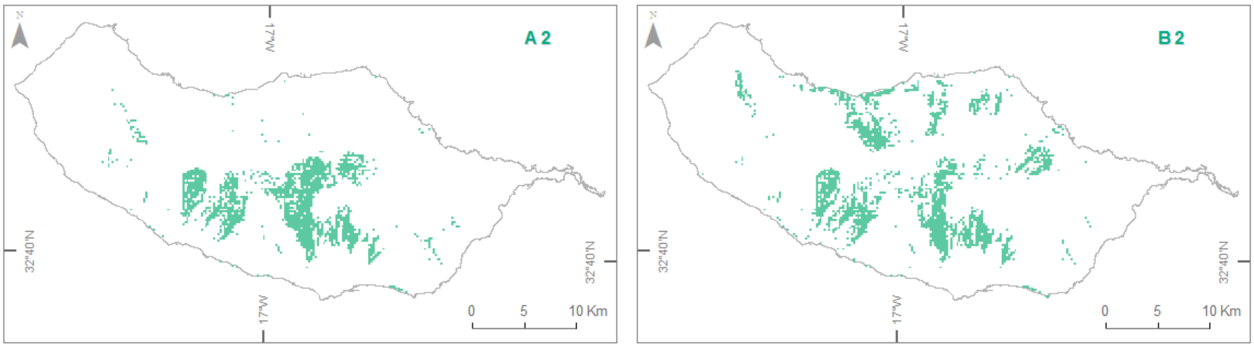
Statistics	Max	Min	Aver
AUC	0.86	0.71	0.8

Scenarios	A2	B2
Gain (%)	7.8	37.2
Loss (%)	31.6	45.4
Maintain (%)	68.4	54.6

Table XLIV – Relative importance of predictors across models for *Sonchus pinnatus*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_w	**0.6**	0.0	**0.6**	0.1	**0.5**	0.1	0.4	0.1
Prec_s	**0.5**	**0.8**	0.0	0.4	0.2	0.2	0.0	0.3
T_mmcm	0.0	0.1	0.4	0.0	**0.5**	0.1	0.1	0.1
Slp_34	0.1	**0.5**	0.2	0.2	0.1	**0.5**	0.3	0.1

B - Climatic scenarios – 2070-2099



C - Predicted changes

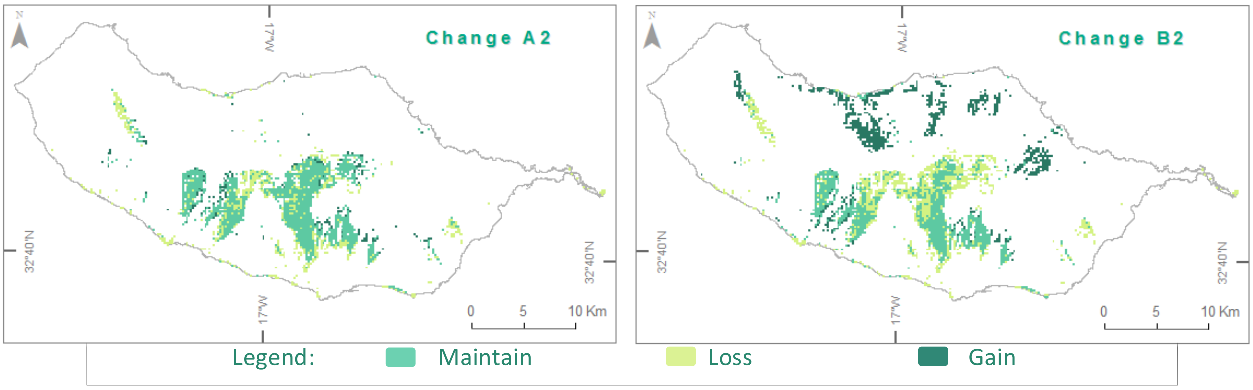


Figure 53 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Sonchus pinnatus*

2.5.2.12 *SONCHUS FRUTICOSUS* L. F.

Robust perennial endemic shrub (Madeira archipelago) of the Asteraceae family, reaching 4m in height, with sizable heads of yellow flowers disposed on a large cyme. It is a common plant, distributed within the area associated to the temperate laurel forest, which inhabits open areas or gaps in the forest associated to tree fall, rocky outcrops or areas affected by recent landslides.

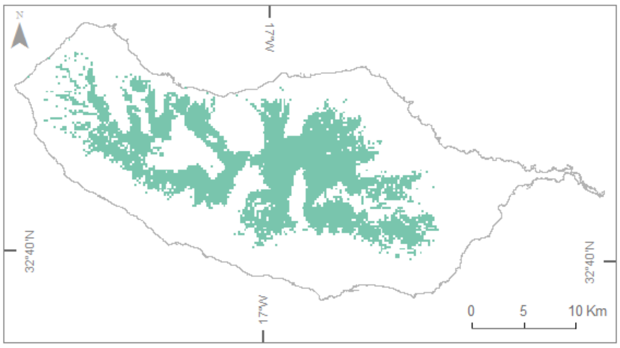
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The results show a significant match between to the area identified as suitable for the temperate laurel forest. It is clear the constrain imposed by the occurrence of frost events, which is detected on the absence of suitable conditions on the high plateau of Paul da Serra, where frost events occur at altitudes above 1400m. On the eastern peaks the limiting altitude is higher, a fact that is related too the differences in terms of topographic conditions. The Paul da Serra, an high plateau, is favourable to the accumulation of cold air during the night, what promotes frost at lower altitudes. Despite only revealed by one modelling technique, the preference of the species for open areas is detected by the association of current distribution with areas with higher heterogeneity in terms of types of vegetation, a conclusion inferred from the selection of the variable PSSD (Pacth Size Standard Deviation) as influencing current distribution.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Projected climatic conditions support a significant decrease in the suitable area for the scenario A2. Such loss is predicted to occur on the lower altitudinal range, on both faces of the island on the scenario A2, and mostly affecting the southern face, and with lower magnitude, on the scenario B2.

A - Current climatic conditions



Species	*Sonchus fruticosus*
Family	Asteraceae

Calibration	Presences	Absences
Data	275	3404

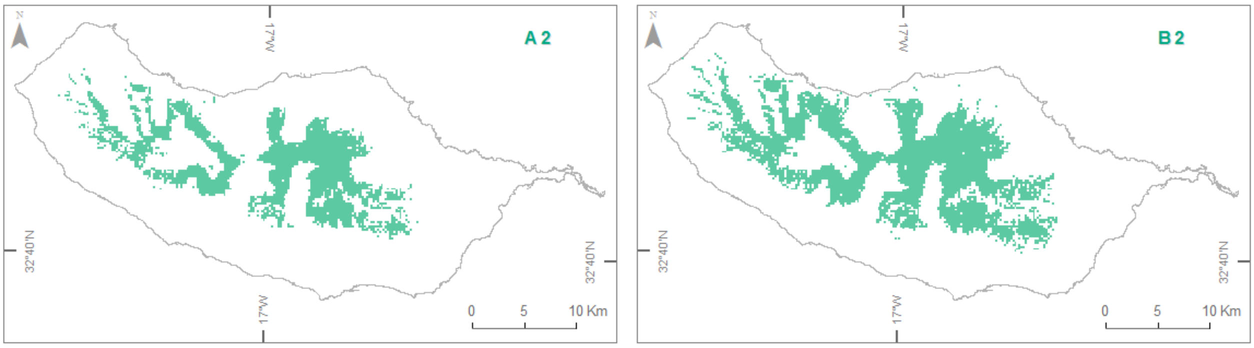
Statistics	Max	Min	Aver
AUC	0.83	0.72	0.8

Scenarios	A2	B2
Gain (%)	1.4	3.1
Loss (%)	45.7	18.5
Maintain (%)	54.3	81.5

Table XLV – Relative importance of predictors across models for *Sonchus fruticosus*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Rad_sol	**0.6**	0.0	0.1	0.0	0.1	0.4	0.3	0.1
T_mmcm	0.0	**0.7**	**0.6**	**0.8**	**0.6**	**0.9**	**0.8**	**0.6**
Prec_w	**0.6**	0.0	0.1	0.0	0.1	0.1	0.1	0.0
PSSD	**0.9**	0.0	0.3	0.0	0.0	0.0	0.1	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes

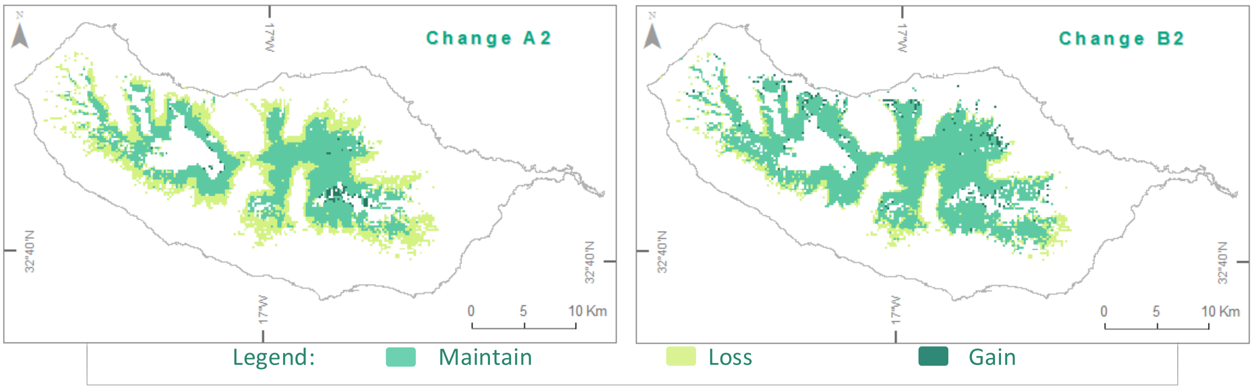


Figure 54 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Sonchus fruticosus*

2.5.2.13 *SONCHUS USTULATUS* LOWE SSP. *USTULATUS*

Small herbaceous perennial of the Asteraceae family that is endemic of Madeira Island. It inhabits rocky outcrops and walls exposed to the sea on the southern face of the island.

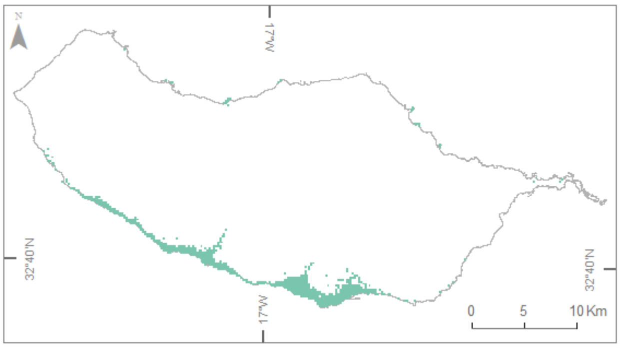
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The area identified as suitable is associated to the driest sections of the island. Such prediction is significantly structured by the minimum temperature of the coldest month (T_mmcm), the environmental variable with higher contribution to explain known distribution patterns. Models are also capable to identify specific topographic features, namely steep slopes (Slope_4), as important to set the ecological profile of the taxa.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Predictions present relevant gains in terms of suitable area for future climatic scenarios, especially in the scenario A2. Such predicted increase is more important in the northern sector of the island, a territory currently associated to the taxa *Sonchus ustulatus* ssp. *maderensis*. For this scenario, models are not able to discriminate environmental suitability on a small area that is currently identified as suitable, a situation associated to the definition of new climatic conditions, which are out of the climatic range set during models calibration.

A - Current climatic conditions



Species	*Sonchus ustulatus*
Family	Asteraceae

Calibration	Presences	Absences
Data	31	3648

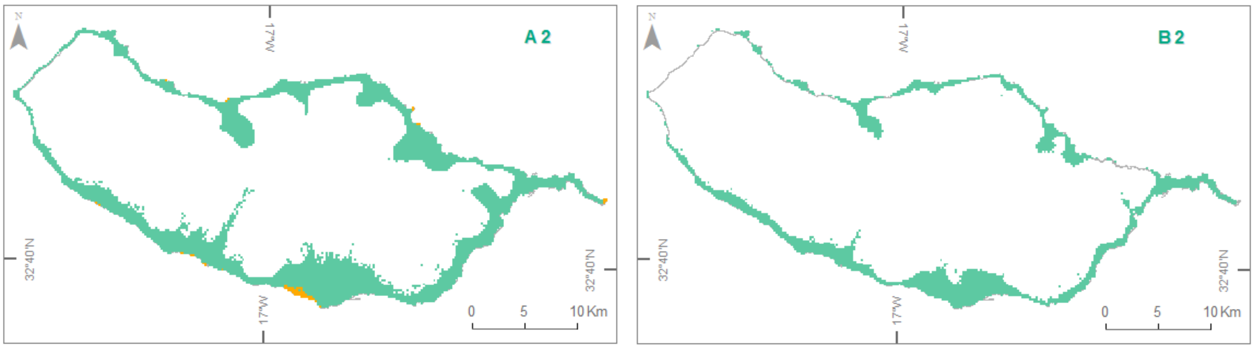
Statistics	Max	Min	Aver
AUC	0.92	0.7	0.8

Scenarios	A2	B2
Gain (%)	535.6	238.7
Loss (%)	0	0
Maintain (%)	92	100

Table XLVI – Relative importance of predictors across models for *Sonchus ustulatus*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Rad_sol	**0.9**	0.2	0.2	0.0	0.2	0.3	0.0	0.0
T_mmcm	0.0	0.3	**0.8**	**0.8**	**0.8**	**1.0**	**1.0**	**0.5**
Prec_s	0.0	0.0	0.4	0.0	0.4	0.0	0.0	0.0
Slp_4	0.0	**0.6**	0.4	0.1	0.3	0.3	0.0	0.1

B - Climatic scenarios – 2070-2099



C - Predicted changes

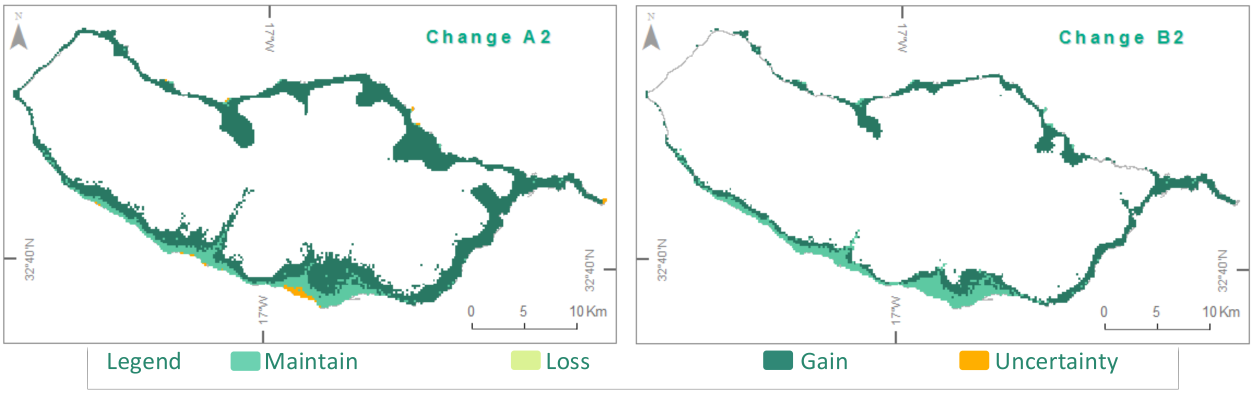


Figure 55 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Sonchus ustulatus*

2.5.2.14 *SONCHUS USTULATUS* LOWE SSP. *MADERENSIS* ALDR.

Small herbaceous perennial of the Asteraceae family that is endemic of Madeira Island. It is a rare plant that inhabits rocky walls and outcrops, and occurs on a small coastal fringe in the northern face of the island.

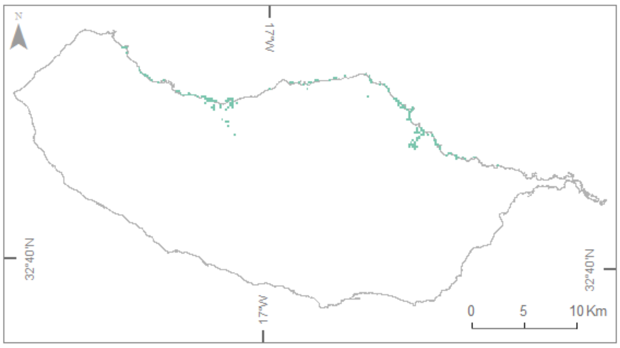
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

Models predict a very restricted area as suitable for the occurrence of the species, which is mainly determined by mean annual range of temperature. The results might be partially biased by different factors, namely the low number of occurrences, associated to the high difficulty on collecting data for current distribution, and because of the spatial resolution in use.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Models predict a substantial increase on suitable area for future climatic scenarios, registering the higher increase among all the species considered for the scenario B2.

A - Current climatic conditions



Species	*Sonchus maderensis*
Family	Asteraceae

Calibration	Presences	Absences
Data	11	3668

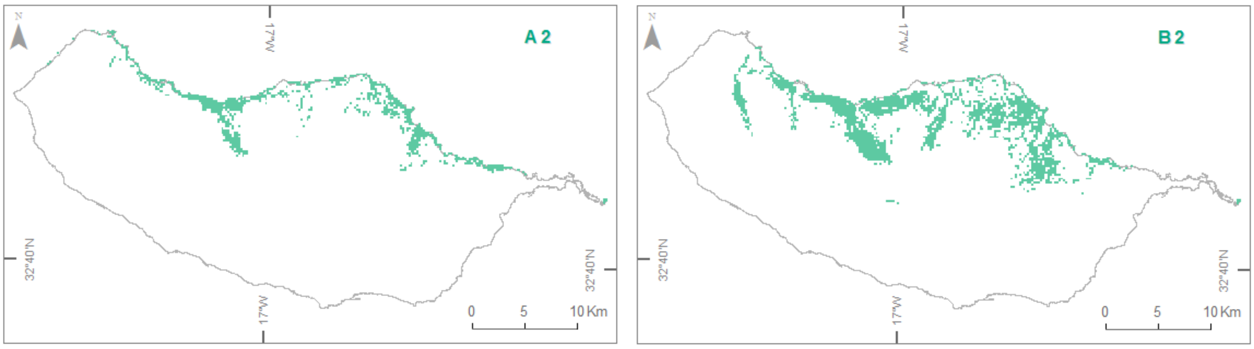
Statistics	Max	Min	Aver
AUC	0.94	0.7	0.81

Scenarios	A2	B2
Gain (%)	407.8	1006
Loss (%)	0	1.2
Maintain (%)	100	98.8

Table XLVII – Relative importance of predictors across models for *Sonchus maderensis*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Rad_sol	**0.7**	-	0.4	0.0	**0.6**	**0.7**	0.1	0.2
T_ar	0.0		**1.0**	**0.9**	**1.0**	**1.0**	**0.8**	**0.5**
P_agr	**0.5**		0.4	0.1	**0.5**	0.1	0.1	0.0

B - Climatic scenarios – 2070-2099



C - Predicted changes

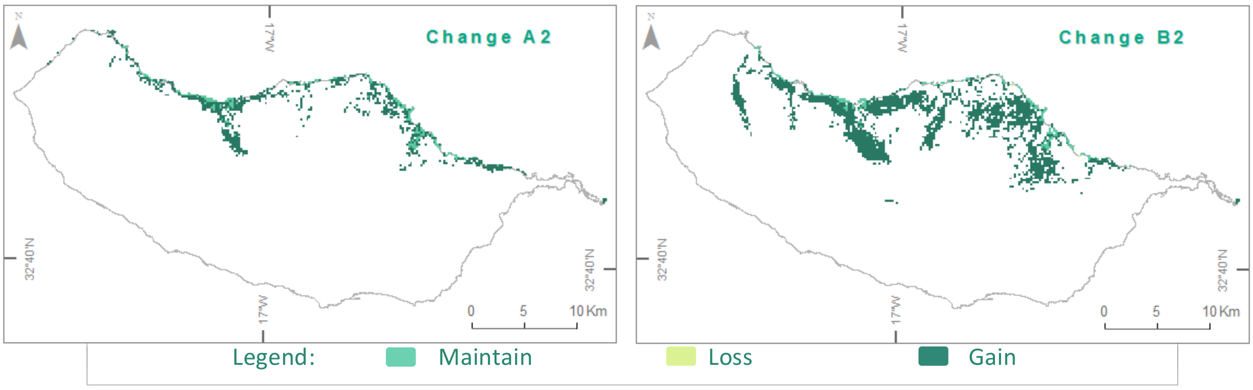


Figure 56 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Sonchus maderensis*

2.5.2.15 SIDERITIS CANDICANS AITON

Small perennial shrub of the Lamiaceae family endemic to Madeira Island. It is a common plant that has a wide distribution, but it is more frequent on areas of complex topography in the center of the island.

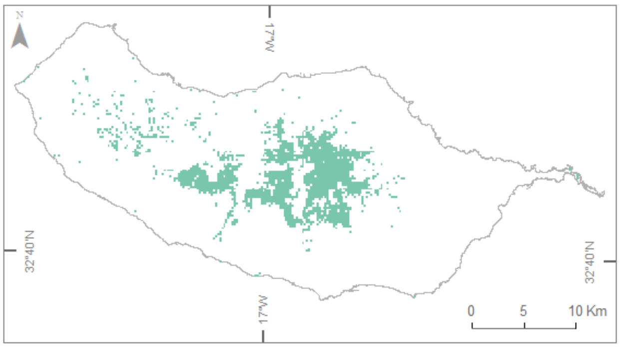
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

Predictions for suitable area are spatially associated to the area of the island with higher topographic complexity, especially to the eastern buttresses of the Paul da Serra and slopes around the highest peaks. Such association is identified by the models when selecting slope (Slope_34) as a predictive variable. In terms of climatic variables, models select the mean minimum temperature of the coldest month and summer precipitation as determining variables to set current distribution patterns, attributing higher relative importance to the first one.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Predictions project a loss on suitable area at lower altitudes, with higher incidence on the northern face of the island, and irrelevant or no gains. Once a significant percentage of occurrences are associated to shrubby formations associated to human disturbance, it is expected that a recovery of native forests after ongoing abandonment of traditional activities will reduce significantly the area where the species really occurs.

A - Current climatic conditions



Species	*Sideritis candicans*
Family	Lamiaceae

Calibration	Presences	Absences
Data	112	3567

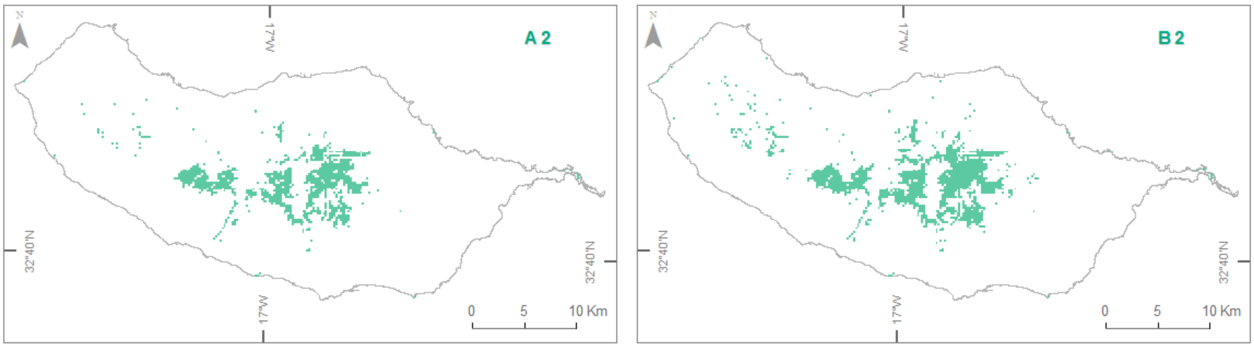
Statistics	Max	Min	Aver
AUC	0.9	0.74	0.84

Scenarios	A2	B2
Gain (%)	0	1.5
Loss (%)	46.5	30.3
Maintain (%)	53.5	69.7

Table XLVIII – Relative importance of predictors across models for *Sideritis candicans*

Predictor	**ANN**	**CTA**	**GAM**	**GBM**	**GLM**	**MARS**	**FDA**	**RF**
Prec_s	0.4	0.2	0.2	0.0	0.3	0.1	0.0	0.1
T_mmcm	0.3	**0.6**	**0.6**	0.4	**0.6**	0.4	0.4	0.3
Slp_34	0.1	**0.5**	0.0	0.0	0.0	0.1	0.1	0.1

B - Climatic scenarios – 2070-2099



C - Predicted changes

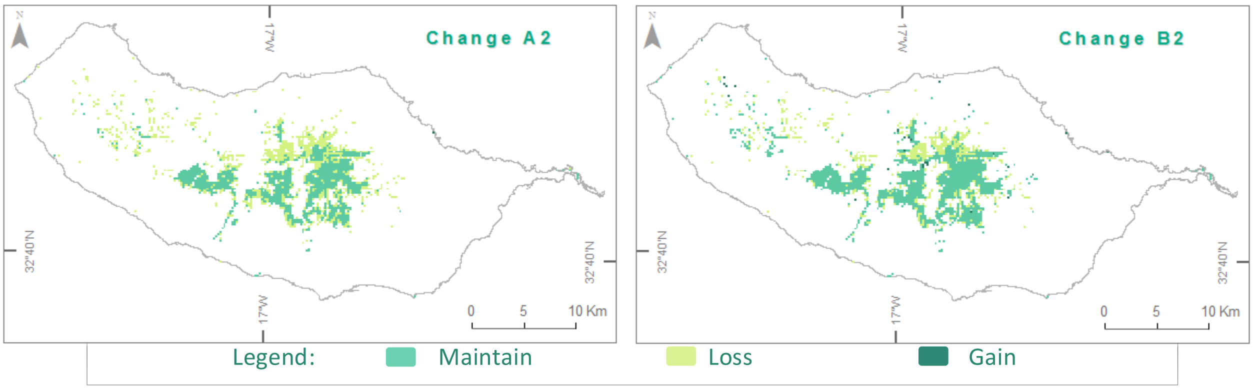


Figure 57 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Sideritis candicans*

3 PREDICTED RESPONSE OF ALIEN INVASIVE SPECIES TO PROJECTED CLIMATE CHANGE

This section integrates the results for predicted changes on suitable area for selected alien invasive tree species under future climatic scenarios: *Acacia mearnsii*, *Acacia melanoxylon, Pittosporum undulatum*.

3.1 CHANGES ON SUITABLE AREA FOR TREE ALIEN INVASIVE SPECIES

The identification of areas that are suitable for alien invasive species aims to support the discussion about the existence of factors that might interfere on the dynamics of native species under future climatic scenarios, particularly in the case of taxa for which predictions forecast an increase on suitable area or simply significant range shift. Their distribution on the island reflect in general a human-driven pattern, especially in the case of the *Acacia* species, which have been used on afforestation campaigns on steep slopes (Andrada, 1990). Because of that, current geographical range seems to be more constrained by propagules availability than by habitat limitations, a common feature on territories affected by invasion (Rouget & Richardson, 2003).

3.1.1.1 *ACACIA MEARNSII* DE WILD.

Fast-growing leguminous tree of the Fabaceae family native to SE Australia and Tasmania (Paiva, 1999). On Madeira Island was significantly introduced on the southern face of the island, where dryer conditions are more similar to ecological conditions found on its native area . Today it is colonizing successfully areas affected by disturbance (fire), areas abandoned by agriculture, streams and open exotic forests of *Pinus pinatser* and

Eucaliptus sp. Its capacity to invade new areas affected by disturbance in regions where it was introduced is well documented (Dye *et al.*, 2004; Howell, 2008; Fatunbi *et al.*, 2009).

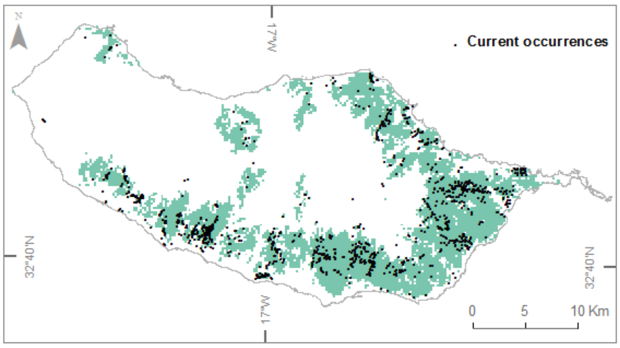
POTENTIAL SUITABLE AREA FOR CURRENT CONDITIONS

Projected suitable area exhibits a pattern clearly associated to species introduction by forestation campaigns on the eastern sector of the island (Andrada, 1990). Such circumstance, aside from the recent introduction of the species, helps to explain the identification of unsuitable conditions on the western sector. Some of the modelling techniques identify the presence of exotic forests (*Eucalyptus* sp. and *Pinus pinaster* forests) as a predictor with importance to explain current distribution, a detail associated to the on-going invasion of open exotic forests by *Acacia mearnsii.* A reason that reveals that species distribution is not in equilibrium with climate is the fact that none of the climatic variables has significant explanatory power.

CLIMATIC SCENARIOS AND PREDICTED CHANGES

Projections for invasive species have a high level of uncertainty. The main reason is because species are not in equilibrium with present ecological conditions, what determines that absences are not determined by environmental constraints (climatic), but by availability of seeds. That condition might explain the projected decrease in terms of suitable area at the lower edge of the current , determined by the predicted expansion of ecological conditions where the species is currently absent. That condition is also supporting an underevaluation of the predicted expansion.

A - Current climatic conditions



Species	*Acacia mearnsii*
Family	Fabaceae

Calibration	Presences	Absences
Data	809	2870

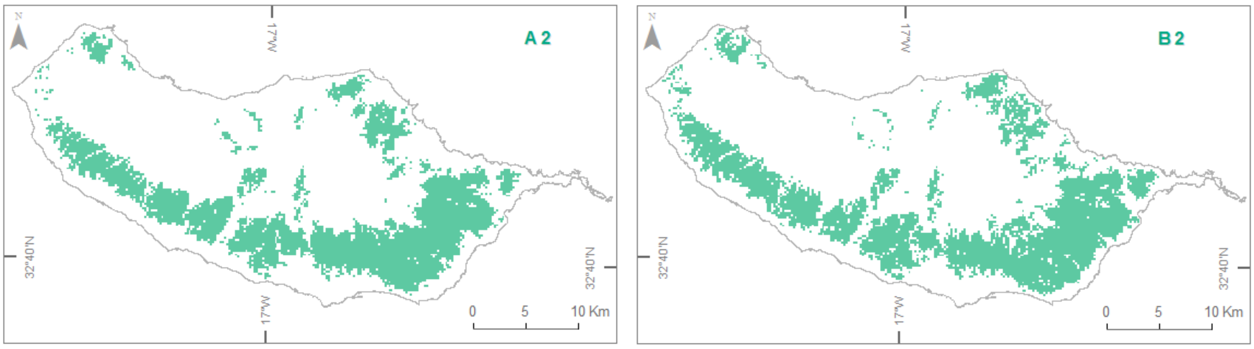
Statistics	Max	Min	Aver
AUC	0.9	0.72	0.81

Scenarios	A2	B2
Gain (%)	26.3	26.6
Loss (%)	32.2	26.3
Maintain (%)	67.8	73.7

Table XLIX – Relative importance of predictors across models for *Acacia mearnsii*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
T_ar	0.0	0.3	0.1	0.1	0.1	0.4	0.2	0.1
Flt_exot	0.2	**0.7**	0.2	0.4	0.2	0.3	0.3	0.3
Prec_w	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1

B - Climatic scenarios – 2070-2099



C - Predicted changes

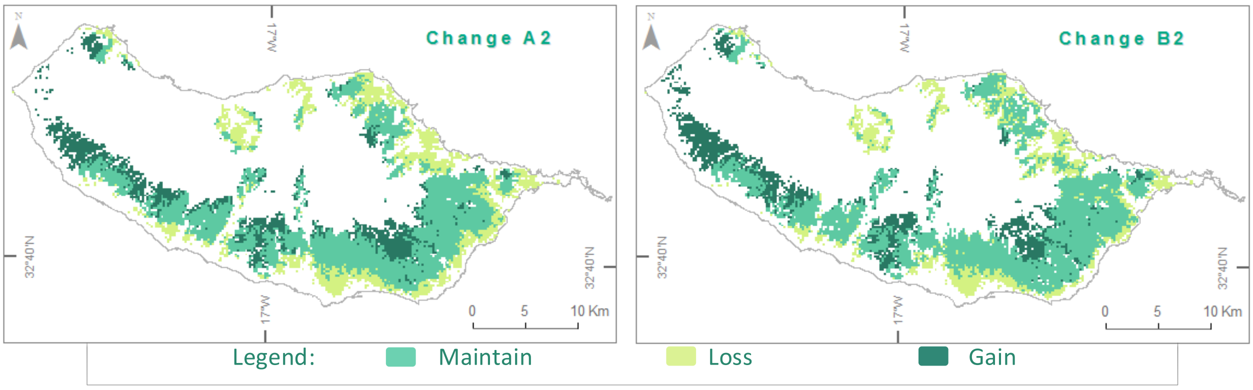


Figure 58 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Acacia mearnsii*

3.1.1.2 ACACIA MELANOXYLON R. BR.

Naturalized fast-growing tree of the Fabaceae family native to SE Australia and Tasmania that is considered invasive in different parts of the world, namely South Africa and Iberian Peninsula (Paiva, 1999; Marchante *et al.*, 2008). On Madeira island was used as forestry tree or as ornamental along roads (Andrada, 1990; Vieira, 2002). Several isolated young individuals were recorded on areas far away (> 2 km) from sites of introduction, some already producing seeds.

PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

Predicted suitable area reveals a pattern associated to plantations, a trait already described for *Acacia mearnsii*. Results reveal a conservative performance of the models, a result determined by methodological options[3] and distribution traits. Methodological options lead to results that over-fit calibration data, but reinforces confidence on results; and absence on significant areas of the island is very likely associated to recent introduction and insufficient time to allow propagules to reach all suitable ecologies.

The significant contribution of the variable *percentage of area occupied by exotic forests* (mainly eucalyptus and pine forests) indicates that such forests present higher susceptibility to invasion.

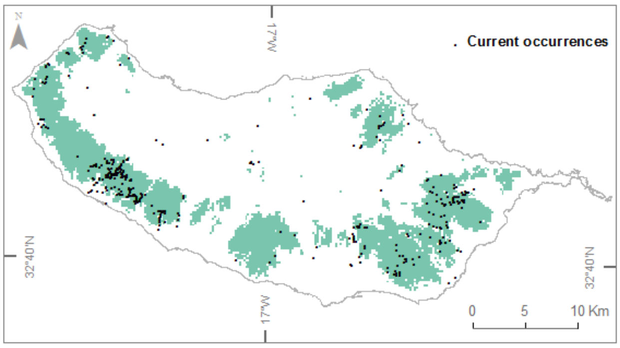
CLIMATIC SCENARIOS AND PREDICTED CHANGES

Models predict a reduction on suitable area, mainly at lower altitudes; and a small predicted gain on upper areas.

---

[3] - A pixel is considered suitable if at least half of the models consider it as so. In the case of ecological conditions with very few occurrences, models very likely consider such ecologies as unsuitable. In the case of native species, that approach helps to reduce the importance of outliers. But, in the case of alien invasive species such occurrences might be considered as indicators for invasion pathways. The option for this methodological approach is based on the higher confidence on results.

A - Current climatic conditions



Species	*Acacia melanoxylon*
Family	Fabaceae

Calibration	Presences	Absences
Data	309	3370

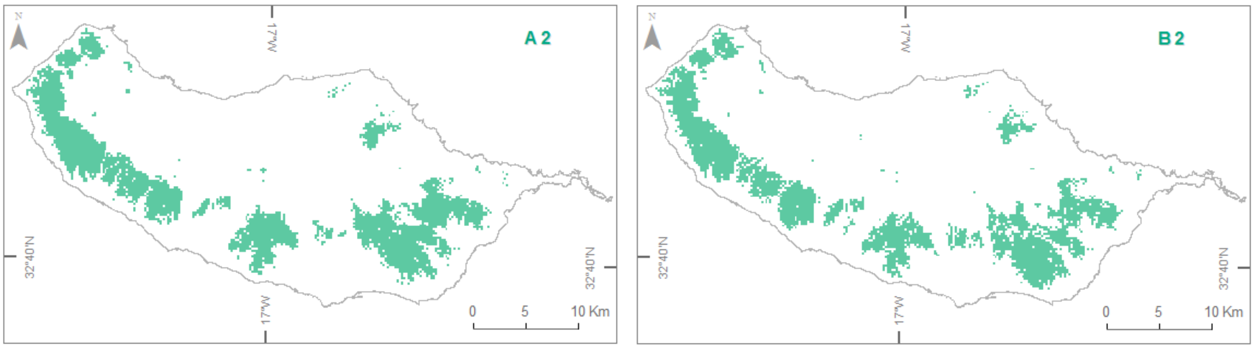
Statistics	Max	Min	Aver
AUC	0.9	0.7	0.8

Scenarios	A2	B2
Gain (%)	4.3	1.9
Loss (%)	30.5	29.8
Maintain (%)	69.5	70.2

Table L – Relative importance of predictors across models for *Acacia melanoxylon*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
Prec_w	0.4	**0.6**	0.1	0.1	0.1	0.2	0.1	0.1
Prec_s	**0.5**	0.4	0.0	0.0	0.2	0.4	0.0	0.0
T_mmcm	0.0	0.4	0.2	0.1	0.4	0.4	0.3	0.1
Flt_exot	0.3	**0.6**	0.1	0.4	0.1	0.1	0.2	0.3

B - Climatic scenarios – 2070-2099



C - Predicted changes

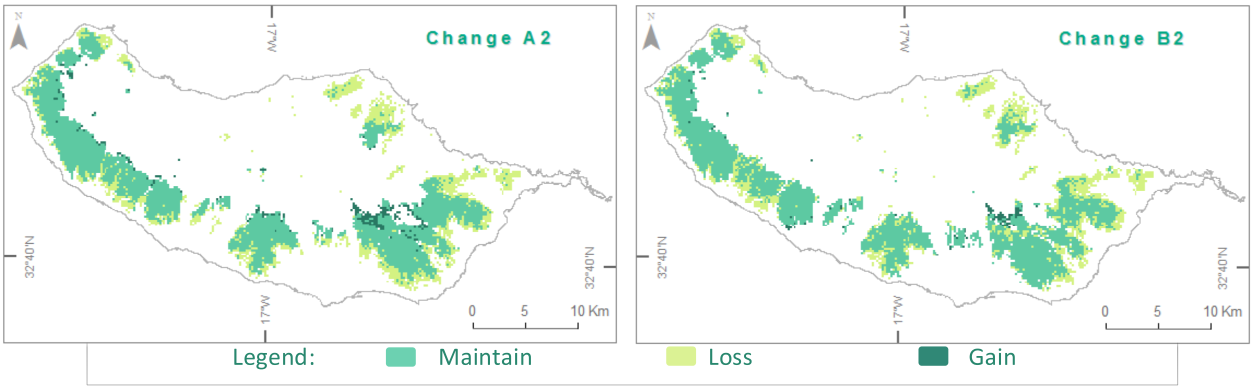


Figure 59 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Acacia melanoxylon*

3.1.1.3 PITTOSPORUM UNDULATUM VENT.

Large evergreen tree of the Pittosporaceae family native to south-east Australia (Paiva, 1997). Current distribution on Madeira Island is mainly associated to urban areas of low density, where it is usually colonizing areas abandoned by agriculture close to gardens where it was introduced as ornamental. The fact that such species was not used in wide plantations, and the use as ornamental is not that common, may reveal a high potential to invasion.

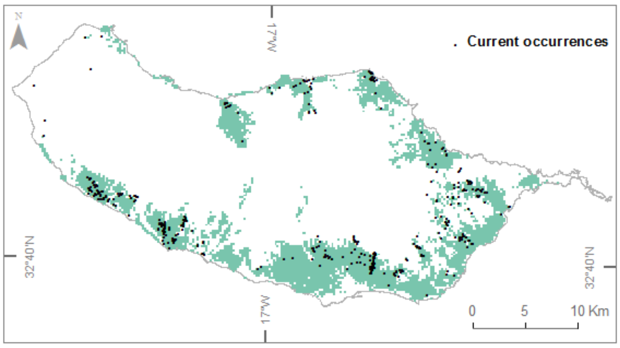
PREDICTED SUITABLE AREA FOR CURRENT CONDITIONS

The area predicted as suitable is deeply associated to the proximity to propagules source. In fact, one of the modelling techniques assigns significant explanatory power to the existence of urban areas, which identifies the areas that worked as sources for dispersal (gardens).

CLIMATIC SCENARIOS AND PREDICTED CHANGES

The models predict a significant expansion to upper areas, which present conditions that are more similar to those found on its native area, namely higher values of rain (Gleadow & Ashton, 1981). Its preference by humid areas explains the predicted loss in terms of suitable area in the scenario A2, once very pronounced dry season should act as a limiting factor. Once again, the predicted expansion is very likely supported on current distribution patterns.

A - Current climatic conditions



Species	*Pittosporum undulatum*
Family	Pittosporaceae

Calibration	Presences	Absences
Data	312	3367

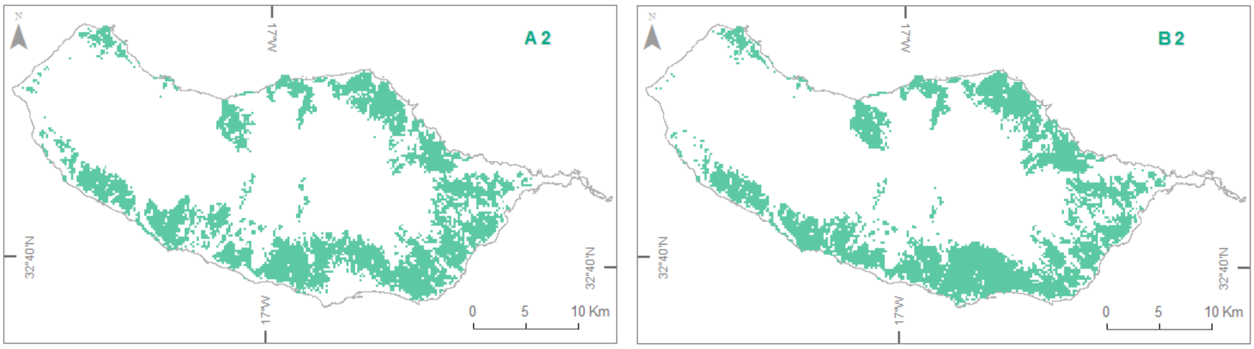
Statistics	Max	Min	Aver
AUC	0.81	0.7	0.77

Scenarios	A2	B2
Gain (%)	40.3	35.6
Loss (%)	16.7	9.5
Maintain (%)	83.3	90.5

Table LI – Relative importance of predictors across models for *Pittosporum undulatum*

Predictor	ANN	CTA	GAM	GBM	GLM	MARS	FDA	RF
T_ar	0.0	**0.5**	0.0	0.1	0.2	**0.7**	0.4	0.1
T_mmcm	0.4	0.0	0.4	0.1	0.3	0.1	0.2	0.1
P_urb	0.2	**0.8**	0.1	0.2	0.1	0.2	0.4	0.2

B - Climatic scenarios – 2070-2099



C - Predicted changes

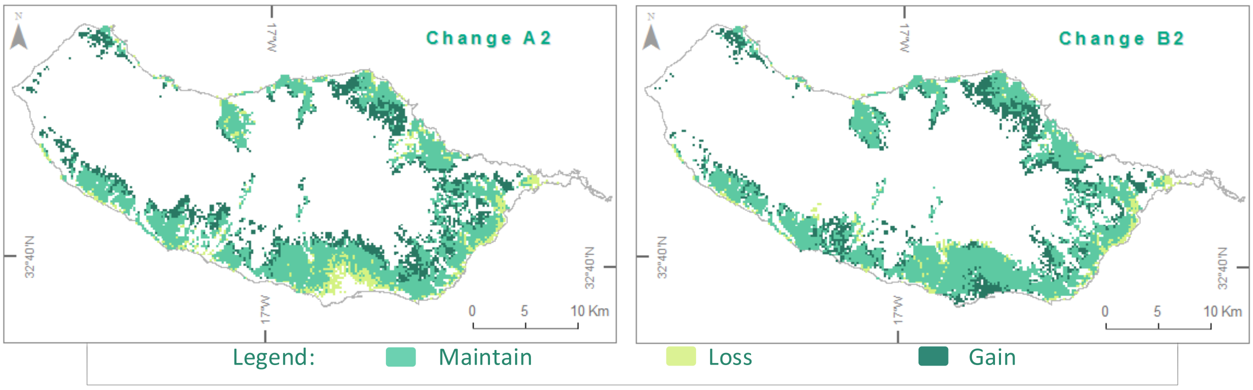


Figure 60 – Predicted suitable area for current climatic conditions (A), climatic scenarios (B) and predicted changes (C) for *Pittosporum undulatum*

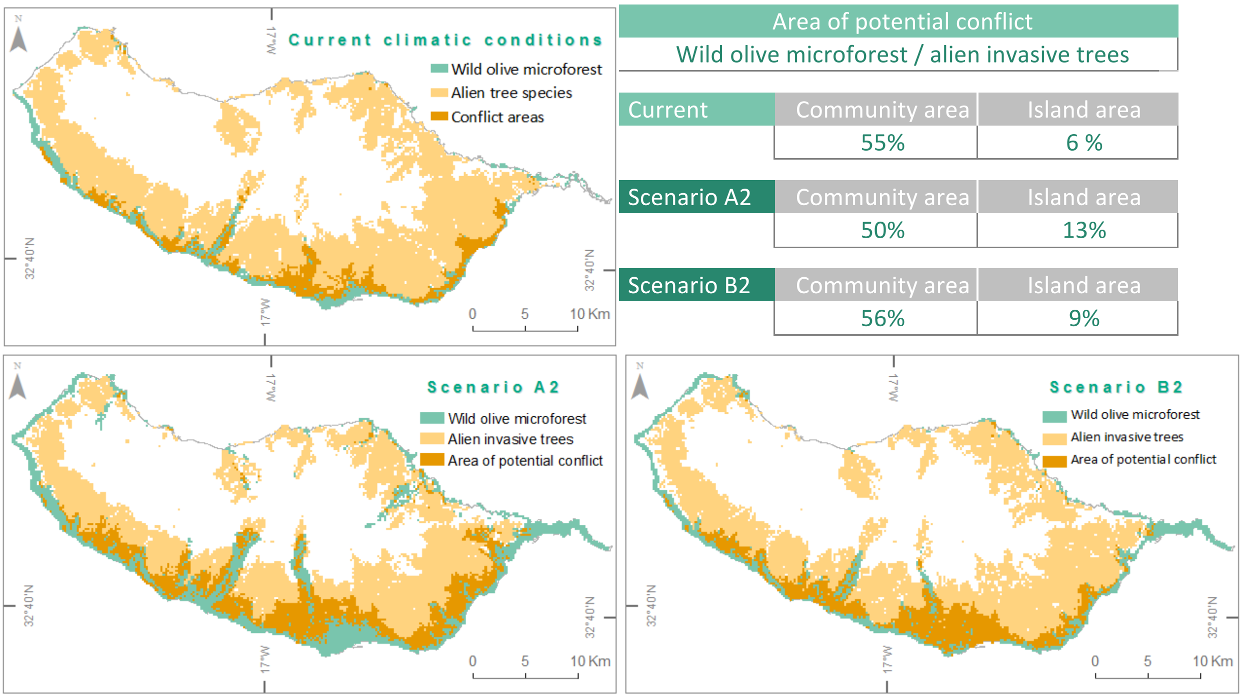
4 AREAS OF POTENTIAL CONFLICT BETWEEN ALIEN TREE INVASIVE SPECIES AND NATIVE FORESTS

Based on the assumption that projected climatic change might favour alien invasive species, it is expected that such species could contribute to interfere on the dynamics of the native species (Dukes & Mooney, 1999; Thuiller *et al.*, 2007; Vilà *et al.*, 2007; Hellmann *et al.*, 2008). This is remarkably important on areas disturbed by human activities. Because of the strategies and ecological range recognized to alien invasive species (Rejmanek & Richardson, 1996), such areas are highly susceptible to invasion (Vicente *et al.*, 2010), a fact that will reduce the capacity of native species to install, compromising dispersal to new areas under future climatic scenarios. As observed on Madeira Island, the areas where alien invasive trees established spontaneous communities present very low plant diversity, very often presenting a significant impoverishment if compared with native communities (Figueiredo *et al.*, unpublished data). Such condition of exclusion performs a situation of conflict, and supports the idea that the installation of communities dominated by alien invasive trees will reduce the chances of the native species to install.

This section aims to identify the areas of potential conflict between the selected alien invasive tree species and native communities, based on the spatial overlap of areas predicted as suitable for both groups. Because of the high number of possible combinations, this section only includes results for some species and forests, namely those with higher values in terms of conflict.

The level of spatial overlay in terms of suitable area between the alien invasive species (*Acacia mearnsii*, *A. melanoxylon*, *Pittosporum undulatum*) and the wild olive forest is predicted to increase under future climatic scenarios

Figure 61. Such result is supported mainly on the predicted upward expansion of the wild olive microforest.



Area of potential conflict

Wild olive microforest / alien invasive trees

	Community area	Island area
Current	55%	6 %
Scenario A2	50%	13%
Scenario B2	56%	9%

Figure 61 - Area of potential conflict between alien invasive trees and the wild olive microforest

The increase on the area of potential conflict is predicted to be higher in the scenario A2, reaching almost 13% of the island's area. Considering the area predicted as suitable for the native community, the results forecast a slight decrease on importance for the conflict area under the scenario A2, a fact that is supported on the decrease on suitable area for alien invasive trees at lower altitudes.

The area of potential conflict is wider if considering separately each of the species associated to the wild olive microforest. This is clear in the case of species that are shared by other vegetation series, which predicted suitable area outranges the area accepted as suitable for the community. This is the case for the endemic *Echium nervosum and*

Maytenus umbellata, which suitable area also includes lowlands on the northern face of the island Figure 62, a territory predicted as suitable for the Mediterranean laurel forest.

Comparing results from both scenarios, the area of potential conflict is higher under the scenario A2, a pattern that is common to the great majority of taxa that occurs at low altitudes, namely those associated to the wild olive microforest.

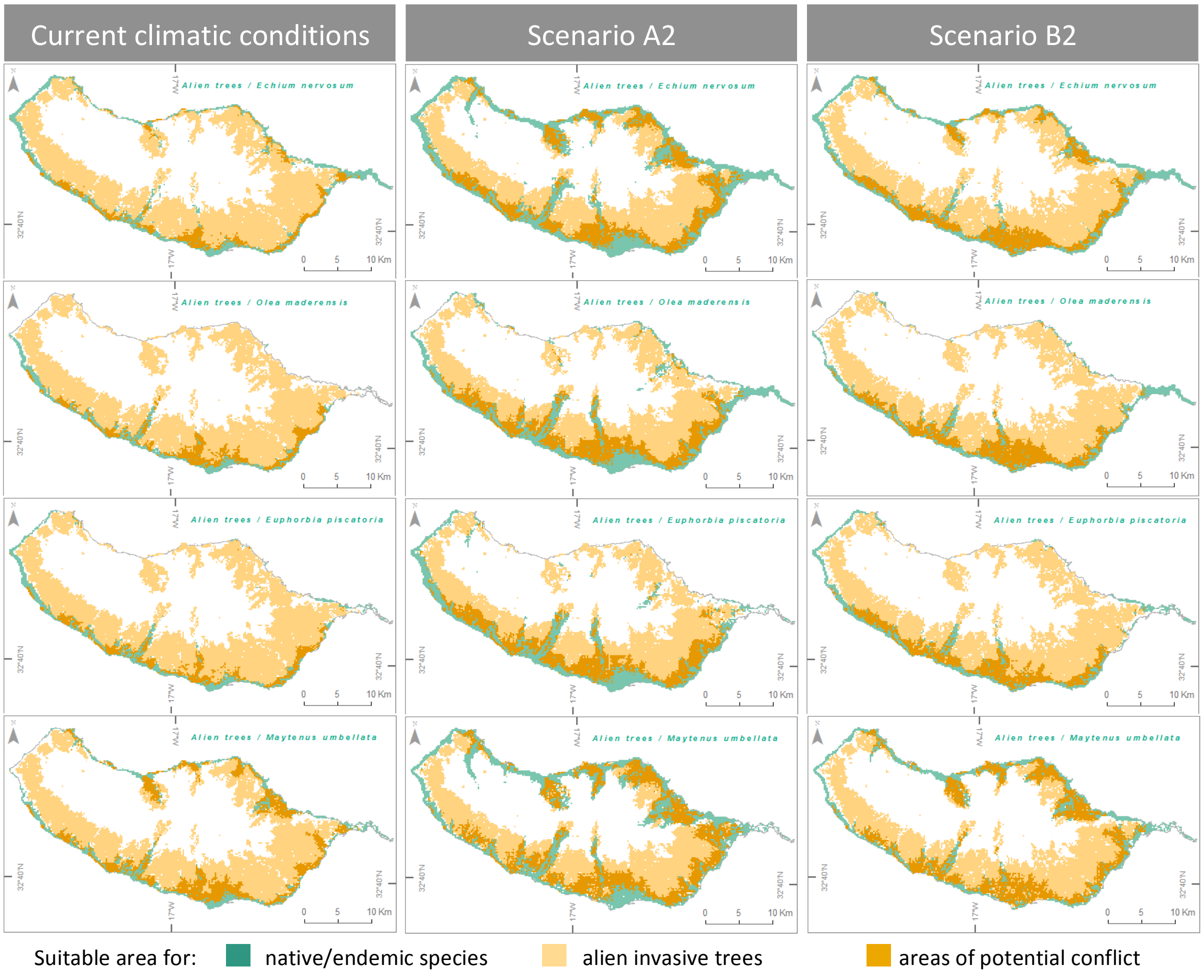


Figure 62 - Areas of potential conflict between species associated to the wild olive microforest and alien invasive trees

Among the alien invasive species considered, *Pittosporum undulatum* is the tree with higher projected overlapping suitable area in respect to the native species associated to the wild olive microforest (Figure 63), namely under the scenario A2. Such results is mostly associated to the higher predicted expansion of the native species.

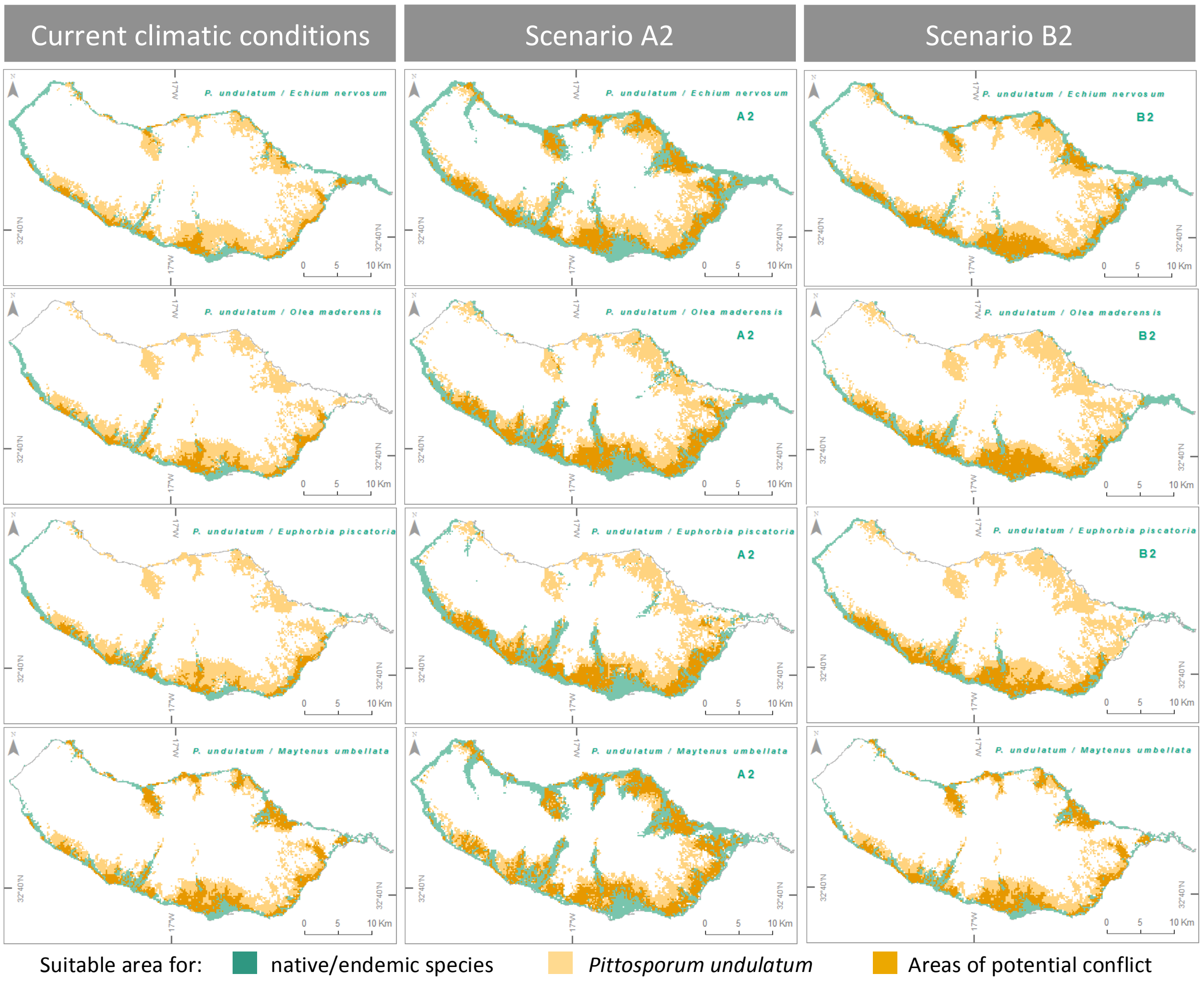
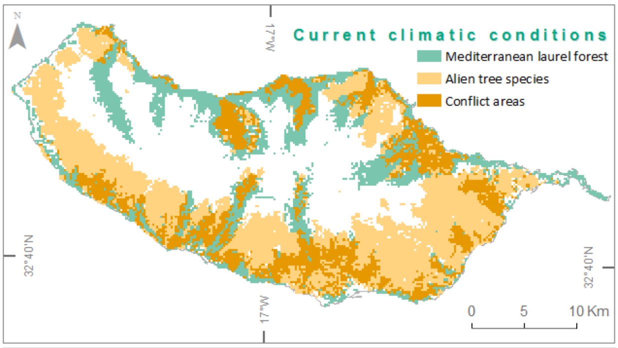


Figure 63 – Areas of potential conflict between species of the wild olive community and *Pittosporum undulatum*

4.2 CONFLICT AREAS WITH THE MEDITERRANEAN LAUREL FOREST

The area of potential conflict for the Mediterranean laurel forest is mainly structured along valleys on both faces of the island, especially on large valleys, a pattern that is more determined by the predicted patterns for the native forest.

Considering the area of the island, predictions for future climatic scenarios forecast an increase in the area of potential conflict, which is higher in the case of the scenario B2. However, the importance of the conflict in relation to the area suitable for the Mediterranean laurel forest (community) is predicted to experience a slight decrease, a result determined by the significant increase of the native forest to areas that are not predicted as suitable for the invasive trees.



Area of potential conflict

Mediterranean laurel forest / alien invasive trees

	Community area	Island area
Current	49%	14 %
Scenario A2	43%	15%
Scenario B2	42%	18%

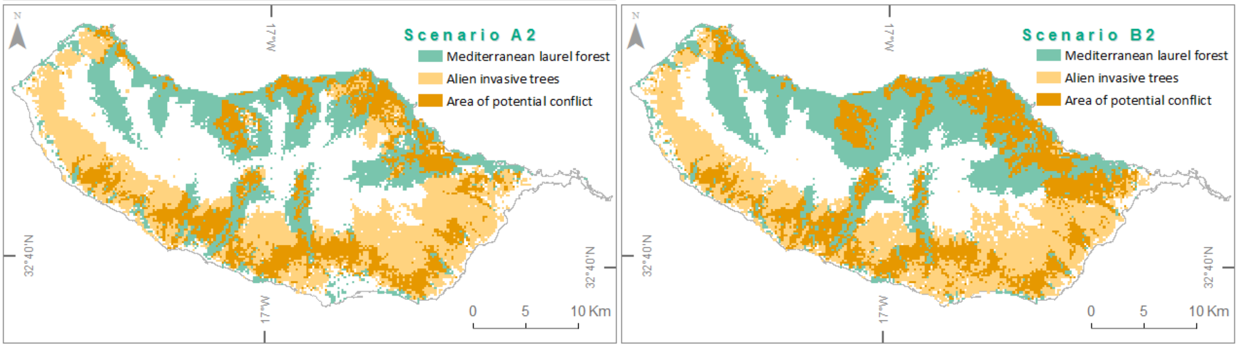


Figure 64 - Area of potential conflict between the Mediterranean laurel forest and selected invasive tree species

Considering the species associated to the potential area of the Mediterranean laurel forest, the liana type species (*Smilax pendulina* and *Semele* androgyna) exhibit the higher level of potential conflict. In fact, and despite the fact that their occurrence seems to be somehow dependent on the presence of the native forests, they were not recorded on forests dominated by exotic forests within their area of potential distribution.

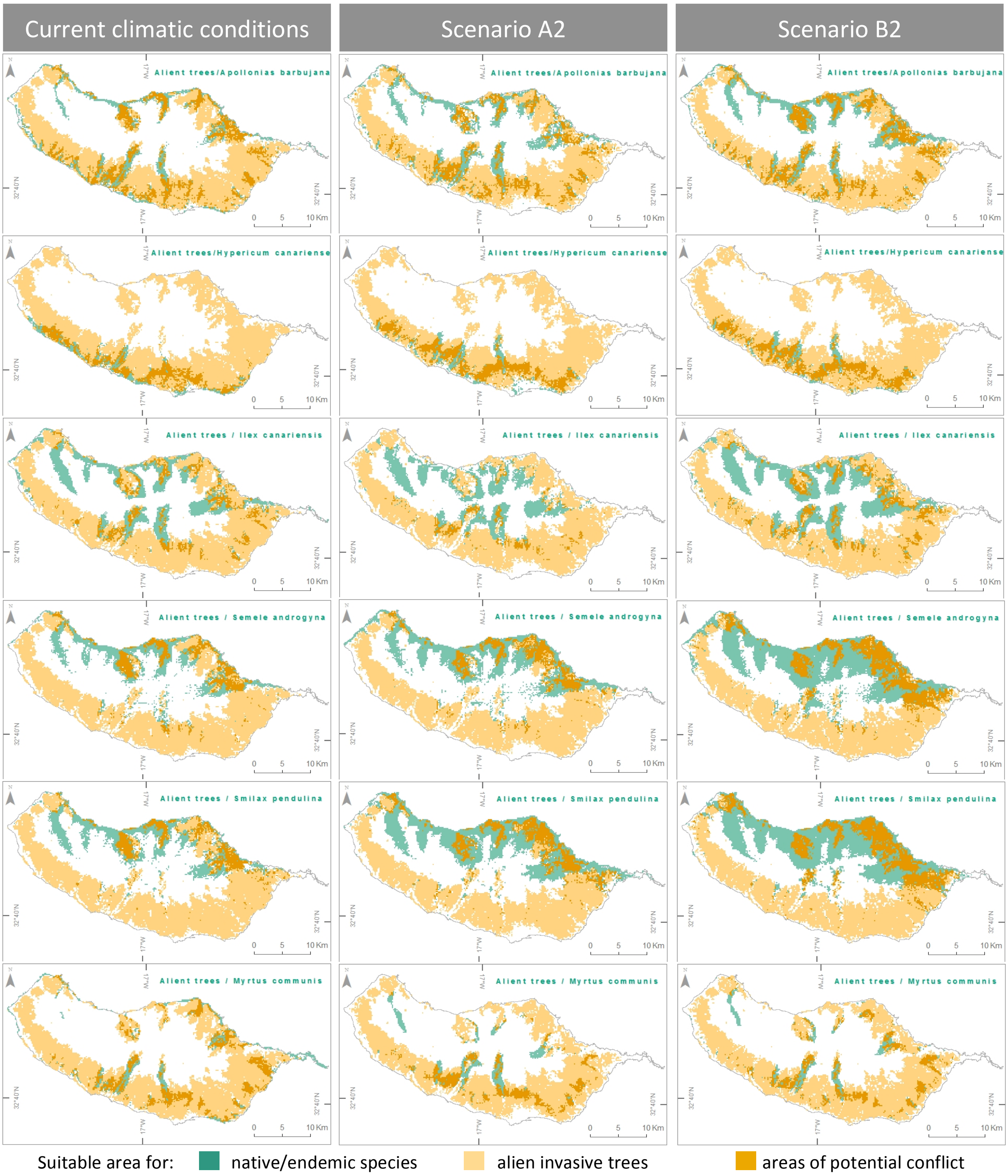
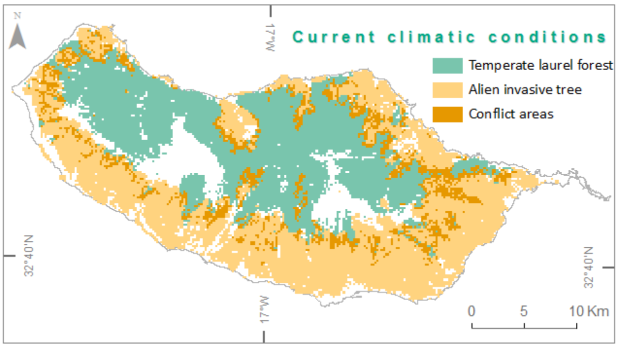


Figure 65 - Area of potential conflict between the species associated to the Mediterranean laurel forest alien invasive tree species

Considering the area of the island, the potential conflict is predicted to increase slightly under the scenario B2, and decrease under the conditions projected by the scenario A2. Such decrease in mainly associated to an upward of the area predicted as suitable for the temperate laurel forest.



Area of potential conflict
Mediterranean laurel forest / alien invasive trees

	Community area	Island area
Current	23 %	10 %
Scenario A2	12%	4%
Scenario B2	23%	12%

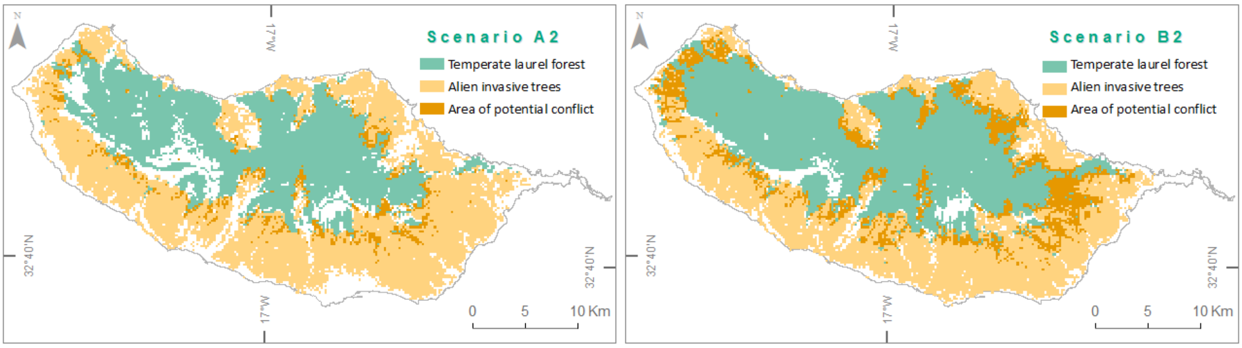


Figure 66 - Area of potential conflict between the temperate laurel forest and selected alien invasive trees

In terms of susceptibility to invasion, it is clear that the lower edge of the current range is more susceptible to invasion. That condition results from different drivers, namely the fact that those areas **i**) are also suitable for the selected alien invasive trees, **ii**) they present an important rate of abandonment by human activities, performing a critical condition for invasion, **iii**) and propagules source for the native trees are very scarce in the surrounding areas, what might support a slower than expected installation of the native community. The area of potential conflict should be likely larger on the southern face of the island than it was predicted by the models. On areas above 800 m m.s.l., expected to be suitable, only scarce occurrences were registered for characteristic taxa, a consequence from the high level of disturbance. That condition is clearly supporting the production of biased results, an assumption that can be related to the scattered pattern predicted by the models on those areas.

The analysis of conflict at the species level reveals opposite trends, depending on the scenario and species considered. While potential conflict is predicted to be higher under the scenario B2 for some of the species (*Ocotea foetens*, *Clethra arborea*), it is expected to decrease for *Laurus novocanariensis* for both scenarios (Figure 67).

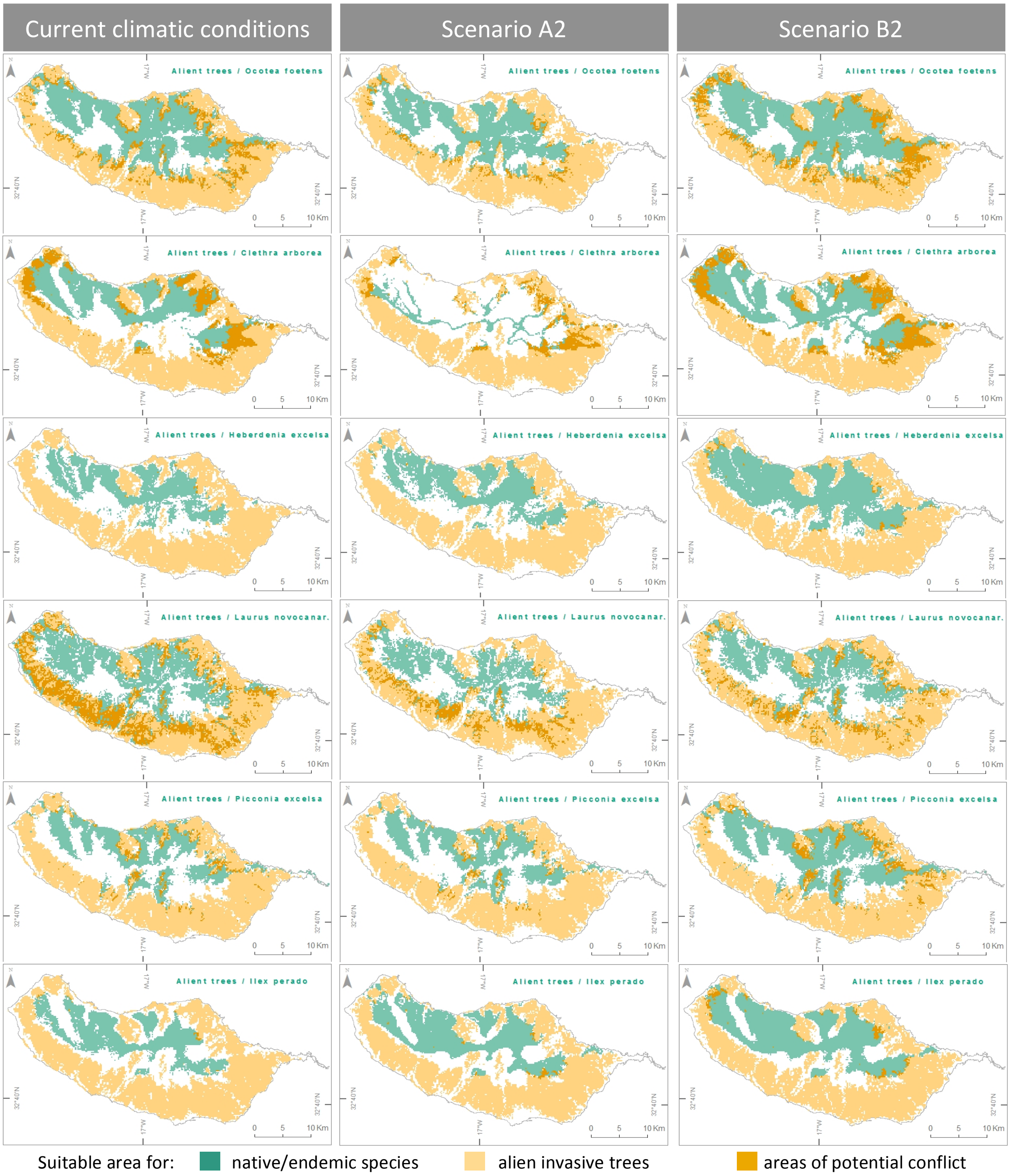
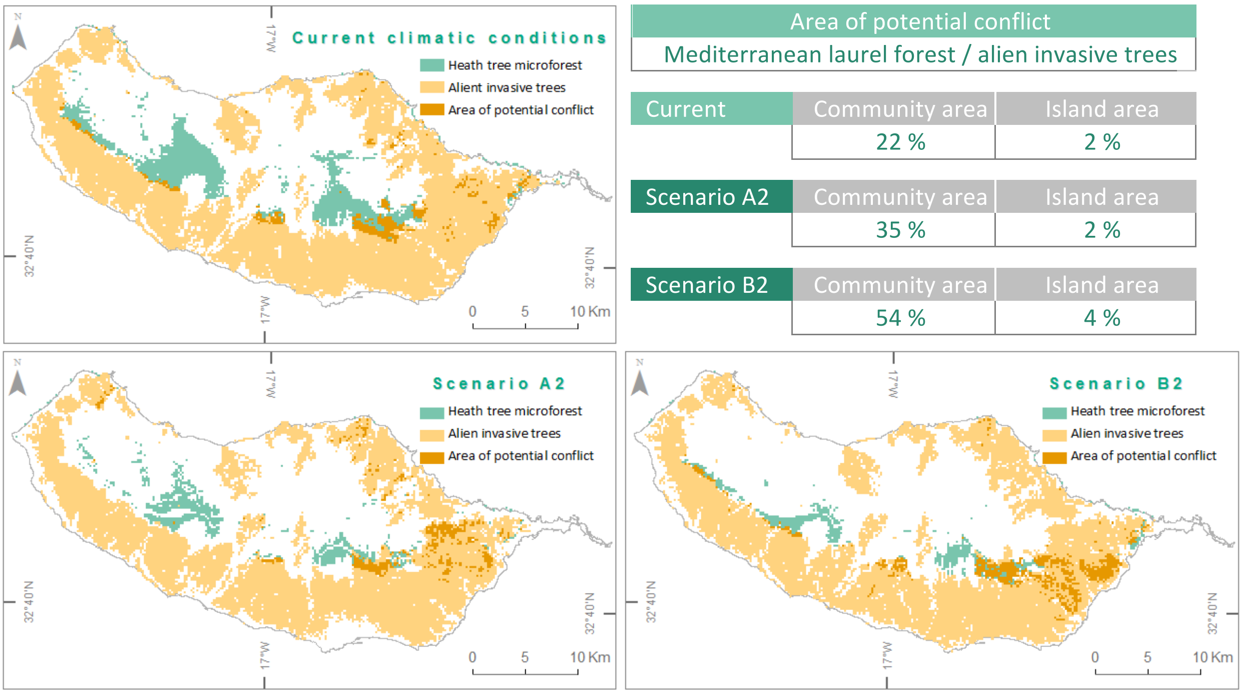


Figure 67 - Area of potential conflict between the species associated to the Mediterranean laurel forest alien invasive tree species

4.4 AREA OF POTENTIAL CONFLICT FOR THE HEATH TREE MICROFOREST

The analysis of results for the heath tree microforest must have into account that invasive trees were not detected on areas predicted as suitable for the heath tree microforest. So, bearing in mind that the alien invasive species are not in equilibrium with the environmental conditions, it is expected that predicted conflict area may change because of the arrival of the invasive species ton new areas, namely because of an upward expansion.



Area of potential conflict		
Mediterranean laurel forest / alien invasive trees		
Current	Community area	Island area
	22 %	2 %
Scenario A2	Community area	Island area
	35 %	2 %
Scenario B2	Community area	Island area
	54 %	4 %

Figure 68 - Area of potential conflict between the heath tree microforest and selected alien invasive trees

In fact, the obtained results are more influenced by the identification of conflicts at altitudes where it is expected that the community dominated by *Erica arborea* is interpreted as a subseral stage, and not the climax community.

CAP V – ANALYSIS OF RESULTS, DISCUSSION AND CONCLUSIONS

Summary

1 ANALYSIS AND DISCUSSION OF MODELS RESULTS

Results from species distribution modelling based on a correlative approach must be interpreted with caution, once a significant number of factors can have influence on them, namely spatial resolution, type of variables, sampling, modelling techniques and decisions at critical modelling stages, such as the threshold criteria used to convert continuous to binary predictions (Liu *et al.*, 2005; Araújo & Guisan, 2006). On climate change impacts assessment it is also important to consider aspects related with the territory, once the existence of physical barriers, or other types of constraints, will interfere on the capacity of the plants to colonize new territories, in the case of predicted expansion, or in the capacity of the plants to survive longer on areas predicted as unsuitable in the future (Murphy *et al*., 2010; Engler *et al*., 2011; Walther, 2004).

This chapter provides the analysis and discussion of results presented in the previous one, following two main topics:

- trends in predictions: it explores the existence of similarities in terms of shifts on distribution under projected climatic scenarios among the taxa;

- the quality and interpretation of results: it is focused on the discussion of factors that interfere in the quality and interpretation of models results, namely the robustness of the different modelling techniques in use, or the existence of factors that are very likely responsible for biasing models' results, namely those that interfere on the quality of the data used on models calibration. It is also discussed the possible interference of variables, not included in the models, that might contribute to moderate the predicted changes, such as the existence of dispersal constraints, which can limit the capacity of the species to reach areas predicted as suitable in the future, namely when significant gains on suitable area are predicted.

1.1 PREDICTED CHANGES ON MADEIRA ISLAND: THE ANALYSIS OF PATTERNS

As widely referred, plant responses to climate change depend on multiple internal organisms' traits, on habitat conditions, and external drivers of change, namely the climatic scenarios considered (Peterson *et al.*, 2008; Chen *et al.*, 2011).

The analysis of models results for Madeira Island supports the identification of different responses in terms of predicted changes among the species considered, which are different in terms of sense and magnitude. Based on predicted gain and loss for suitable area under future climatic scenarios, the taxa might be classified in one of four different categories: (Figure 68):

- **type HL:** those registering a **significant increase** on suitable area and **irrelevant loss**;
- **type HH:** species associated to profound shifts in terms of suitable area (e.g. upward shift), based on **significant gain** and **loss**;
- **type LL:** group of plant species for which modelling results forecast **small gain** and **loss** in terms of for predicted suitable area under the future climatic scenarios;
- **type LH** - species that register **significant loss** and **irrelevant gain** in terms of suitable area. This group includes some of the species that should be prioritized in terms of conservation, which are those presenting current restricted distribution and small populations.

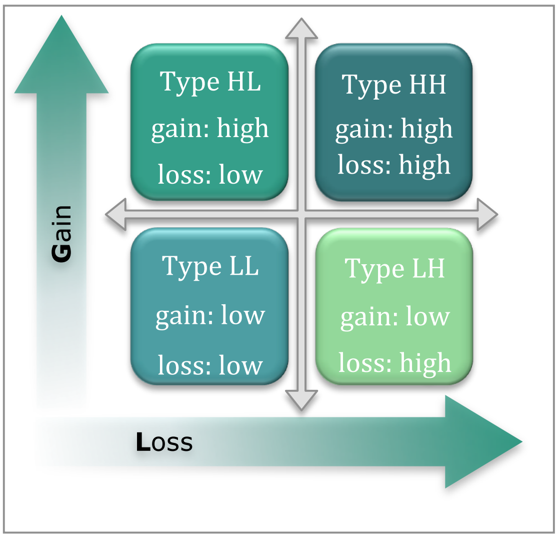


Figure 69 - Classification of species based on predicted gain and loss for suitable area

Considering the value 50% as a threshold to distinguish the types considered, it is clear that a significant number of species are associated to low gains and losses (type LL) in terms of area predicted as suitable, especially in the scenario B2 (Figure 70). It is also appreciable the number of species that present a clear gain (type HL), in opposition to those associated to significant loss and residual gain (type LH) (Figure 69).

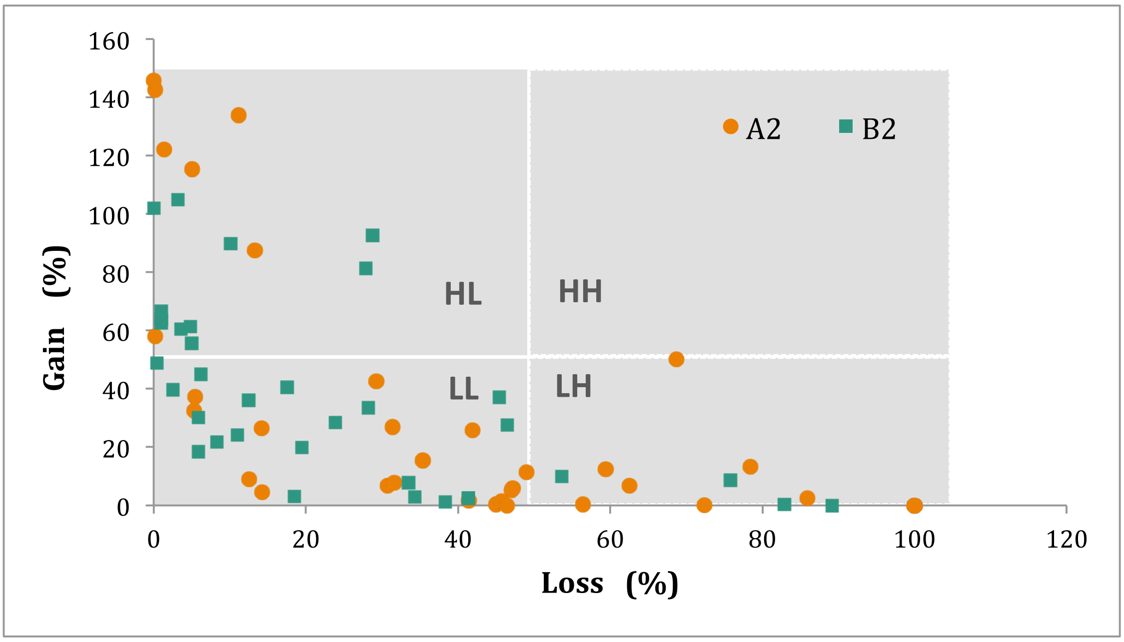


Figure 70 - Relative position of species in terms of balance gain/loss for the two scenarios

Note: Species with extreme values were not included in the chart (*Musschia aurea*, *Mathiola maderensis*, *Sonchus ustulatus*, and *Sonchus maderendis)*.

None of the species exhibits results indicating significant loss of current suitable area and expansion to new territories, a prediction that would imply a clear shift in the geographical range. The species *Myrtus communis* is the only taxon that presents the closest pattern, with a predicted gain of 50% and loss of 68%.

But the analysis of net results (gain – loss) gives a better picture about the predicted response for the species. A classification based on hierarchical clustering[1] clearly allows the identification of four groups in terms of net changes on suitable area (Figure 71):

---

[1] - Classification is based on percentage values disaggregated in gain and loss for each scenario. Distance between cases is based on the Squared Euclidean Distance, and hierarchical clustering is based on Ward's minimum variance method.

- group 1: forecasts predict a net increase for both scenarios in a range that does not exceed 150%. Detailed analysis identifies two subgroups (1.1 and 1.2);

- group 2: forecasts differ in magnitude and sense according the climatic scenario;

- group 3: forecasts predict a net decrease for both scenarios. Discussion of results considers two subgroups (3.1 and 3.2);

- group 4: predicted gain exceeds 200% in both scenarios.

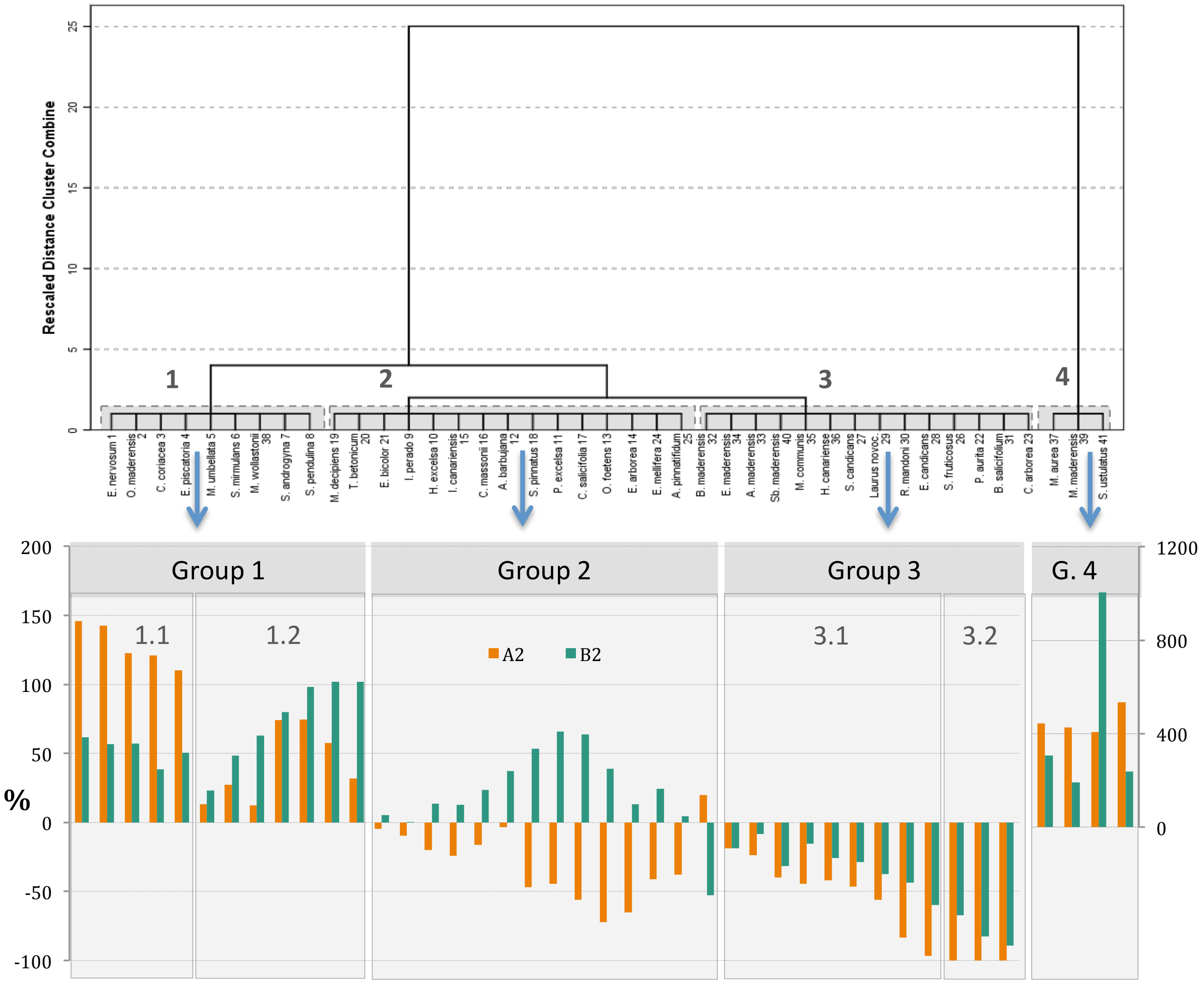


Figure 71 - Classification of results for predicted suitable area based on mean similarity (above), and associated net results for both scenarios[2]

Note: Results for cluster analysis exclude the species *Sonchus maderensis*, which predicted gain for the scenario B2 is 1006 %. The results are only included in the column chart.

---

[2] - Although assigned to the group 2 by cluster analysis, the species *Apollonias barbujana*, *Ilex perado*, and *Heberdenia* excelsa are associated to the subgroup 1.2 for discussion, once net predicted changes are positive for both scenarios.

1.1.1 GROUP 1

Predictions for taxa within this group project an increase on suitable area for both scenarios, mostly supported on an upward range shift. The group includes a significant number of characteristic species that are associated to the wild olive microforest (*Maytenum umbellatae-Oleetum maderensis*) and few taxa related to the mediterranean laurel forest (*Semele androgynae-Apollonietum barbujanae*). Despite the overall positive gain for predicted suitable area, it is possible to detect significant differences among species and between scenarios within this group. For those species that are tolerant to dryness, which currently occupy mainly areas at lower altitudes (<400m) in the southern face of the island, models predict a more significant increase for the scenario A2. This is the case for species that are interpreted as elements of the wild olive microforest (*Echium nervosum, Olea maderensis, Chamaemeles coriacea, Euphorbia piscatoria, Maytenus umbellata*), species that are aggregated in the subgroup 1.1 (Figure 72). Their distribution is deeply influenced by the minimum average temperature of the coldest month, and the projected increase in the minimum temperature seems to be the main driver for such response.

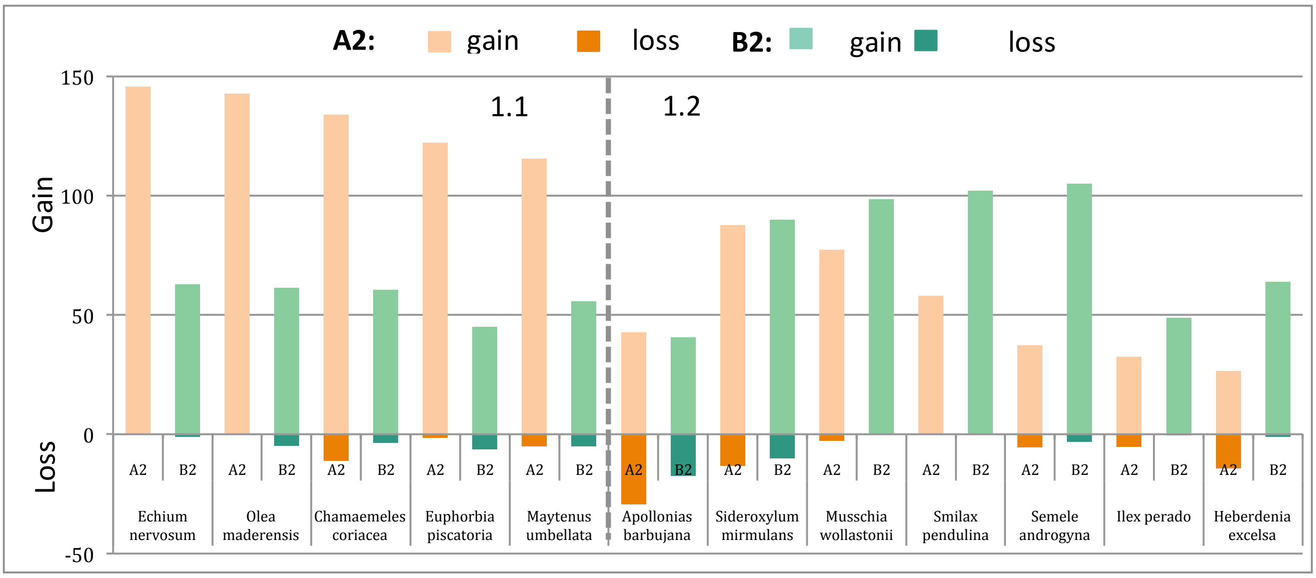


Figure 72 - Predicted gain and loss in suitable area for species of group 1

Note: Although assigned to the group 2 on cluster analysis, the species *Apollonias barbujana*, *Ilex perado*, and *Heberdenia excelsa* are associated to the subgroup 1.2 for discussion, once net predicted changes are positive for both scenarios.

The subgroup 1.2 integrates taxa with higher net increase for the scenario B2 (Figure 72). With the exception of the taxa *Apollonias barbujana*, all the other species have a current geographical range mainly associated with the northern face of the island, occurring at different altitudinal ranges - lower altitudes (<600m a.s.l.): *Sideroxylum mirmulans*, *Smilax pendulina, Semele androgyna*; medium altitudes (600m – 1200m a.s.l.): *Musschia wollastonii*; medium to high altitudes (600-1700 a.sl.): *Ilex perado*.

Predictions support a slight net increase for *Apollonias barbujana*, the Lauraceae that is dominant in the mediterranean laurel forest. But is very significant for the liana-type species related to such type of forest (*Smilax pendulina, Semele androgyna*), which might expand their area of occurrence to areas associated to the lower margin of the temperate laurel forest, a combination that is only occasional today at the lower margin.

The projected increase for suitable area is both significant if having by reference the area predicted as suitable for current climatic conditions (Figure 72), or considering the proportion in the island's area (Figure 73), a condition clearly illustrated by the taxa *Maytenus umbellata*, *Semele androgyna* and *Smilax pendulina*, since predicted values represent almost 20% of the surface of the island[3] (Figure 73).

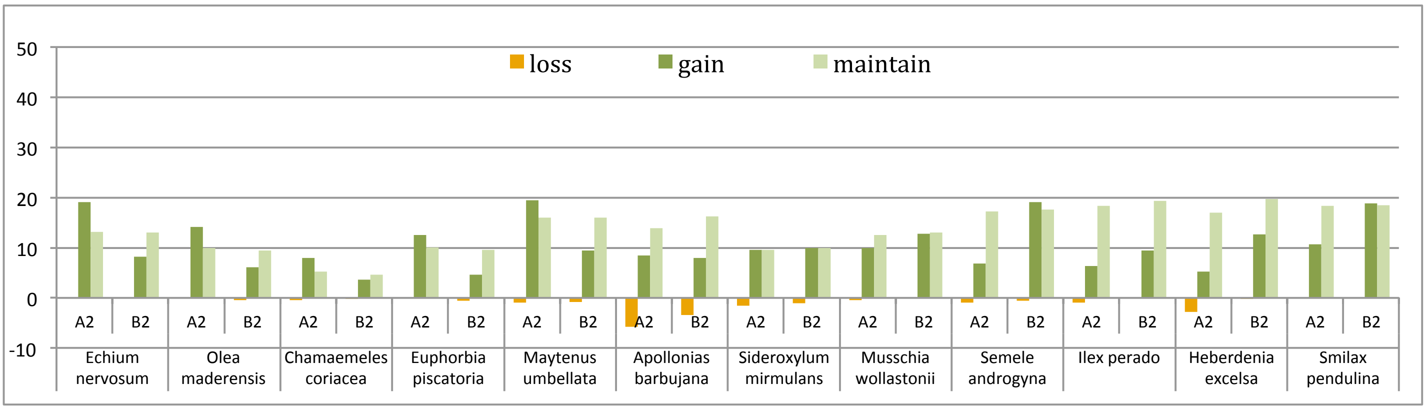


Figure 73 - Predicted changes for suitable area for both scenarios in relation to the area of the island for group 1

---

[3] - The percentage is calculated in respect to the total number of cells for the island, each cell with 200x200m size.

1.1.2 GROUP 2

Predictions for this group of species differ according to the scenario, very often exhibiting opposite directions and very different magnitudes (e.g. *Teucrium betonicum*, *Melanoselinum decipiens*). The scenario A2, more adverse, is generally associated to a net loss on suitable area, in opposition to the gains predicted for the scenario B2 (Figure 74).

The detailed analysis in terms of predicted gain and loss for each scenario shows that small-predicted net changes might be associated to significant gains and losses, determining a significant spatial shift in terms of area of distribution. This is the case of the endemic *Convolvulus massonii*, which net predicted changes are in fact determined by similar values of loss and gain in each scenario (Figure 74).

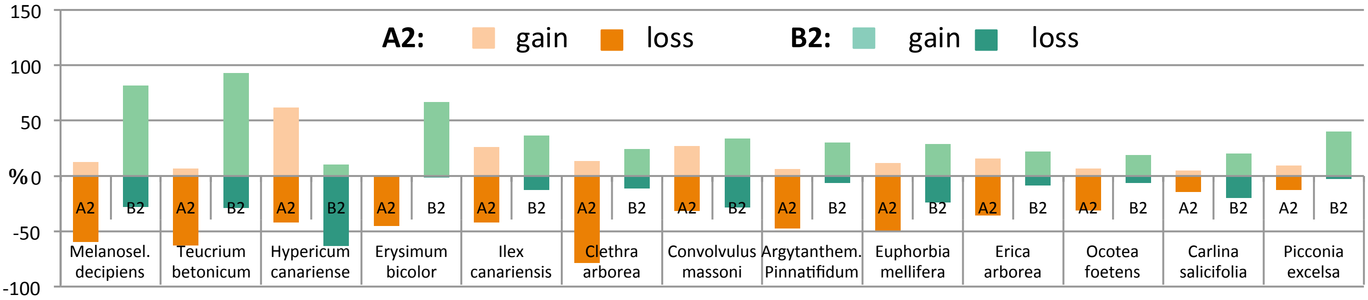


Figure 74 – Predicted gain and loss on suitable areas for species of the group 2 according the scenario

Note: Despite assigned to the group 3 in the cluster analysis, the species *Hypericum canariense* and *Clethra arborea* are included in the discussion of the group 2, a decision based on predicted net changes on suitable area.

This group includes some of the phanerophytes of the temperate laurel forest (*Ocotea foetens*, *Clethra* arborea, *Picconia excelsa*), and the dominant taxa of the tree heath community (*Erica arborea*). Considering that the taxa *Ocotea foetens* and *Erica arborea* are dominant in the structure of the respective communities, it is expected that changes on their distribution should have implications on the spatial distribution of the communities. The predicted decrease on suitable area projected for the scenario A2 for both types of vegetation reflects the predicted decrease on suitable area for the dominant taxa. Like for the dominant majority of species, the decrease on suitable area is determined by a range contraction at the rear edge of current range, corresponding to lower altitudes, and a less important upward range shift of the leading edge.

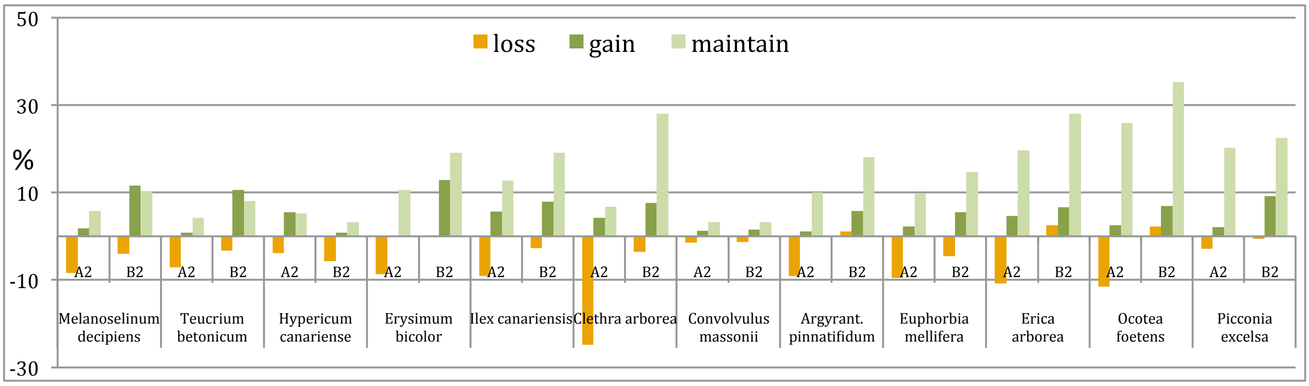


Figure 75 - Predicted changes for suitable area for the climatic scenarios in relation to the area of the island for group 2

1.1.3 GROUP 3

This group includes species which predictions are clearly associated to net losses of suitable area on both scenarios (

Figure 76). As detected for other groups, predicted changes are more significant for the scenario A2, projecting total loss of suitable area for some of the species (subgroup 3.2).

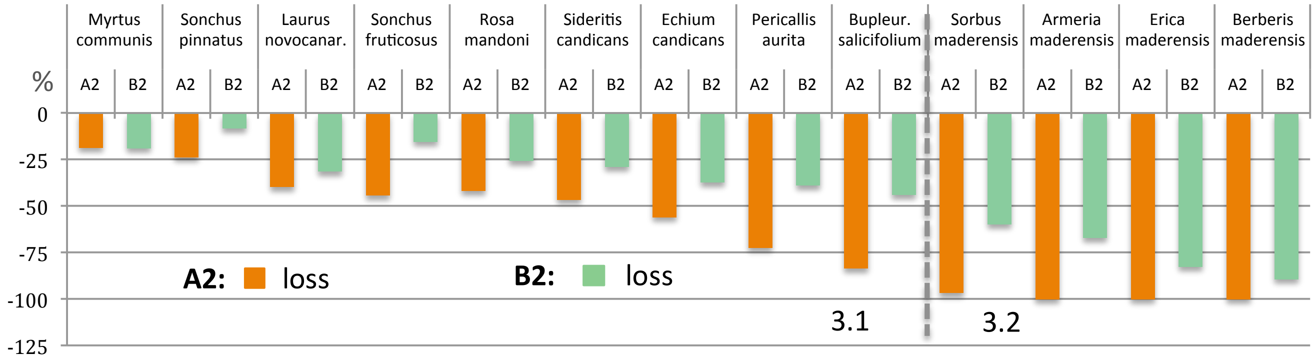


Figure 76 – Predicted response for suitable area for taxa of the group 3

Laurus novocanariensis is one of the species with wider geographical and ecological ranges, and present a very high frequency within the occupancy area. Although the lower predicted loss in terms of suitable area considering values for current climatic conditions, especially if compared with species of the subgroup 3.2, the correspondent area in the island that is predicted to become unsuitable is considerable (aprox.

20%)(Figure 77). On the oposite, although the very irrelevant loss of suitable area if having by reference the size of the island (< 1%), the predicted loss on suitable area for the species of the subgroup 3.2 is extreme when considering the restricted suitable area for current climatic conditions. In fact, models predict the absence of suitable climatic conditions under the scenario A2 for the exclusive endemics *Armeria maderensis*, *Erica maderensis*, and *Berberis maderensis*, a result that is supported by the restricted area and number of populations recorded for such species.

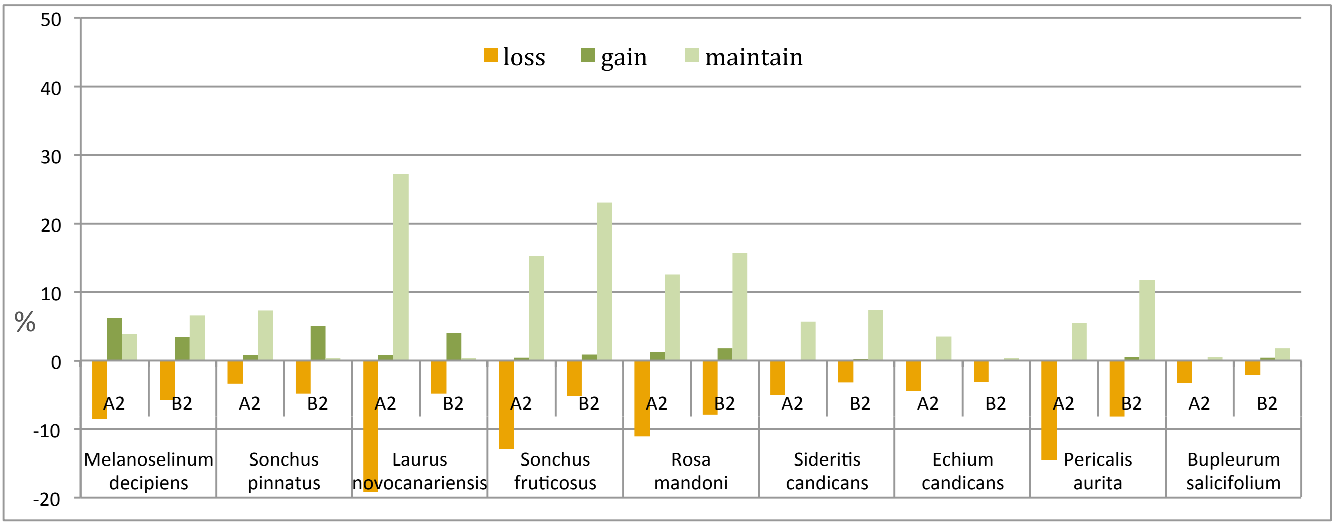


Figure 77 - Predicted changes for suitable area for the climatic scenarios in relation to the area of the island for subgroup 3.1

Despite the maintenance of suitable conditions on significant areas of the island under future climatic scenarios, the predicted loss is considerable for some of the species of the subgroup 3.1, (*Laurus novocanariensis*, *Sonchus fruticosus*, *Rosa mandonii*). But is more significant in the case of species that are rare within its potential area of occurrence (*Melanoselinum decipiens*, *Sonchus pinnatus*, *Echium candicans*, *Bupleurum salicifolium*).

1.1.4 GROUP 4

This group includes species that register a predicted increase on suitable area higher than 200% under future climatic scenarios, having by reference the area for current conditions (Figure 78).

All the species are endemics that are currently associated to a small fringe on coastal areas. With the exception of *Mathiola maderensis*, which has higher number of occurrences and seems to be less filtered by local habitat conditions, they exhibit a very low number of occurrences and are restricted to rocky walls or rocky outcrops. They are clearly specialist-habitat taxa that have rare occurrence within a narrow geographical range (NSR).

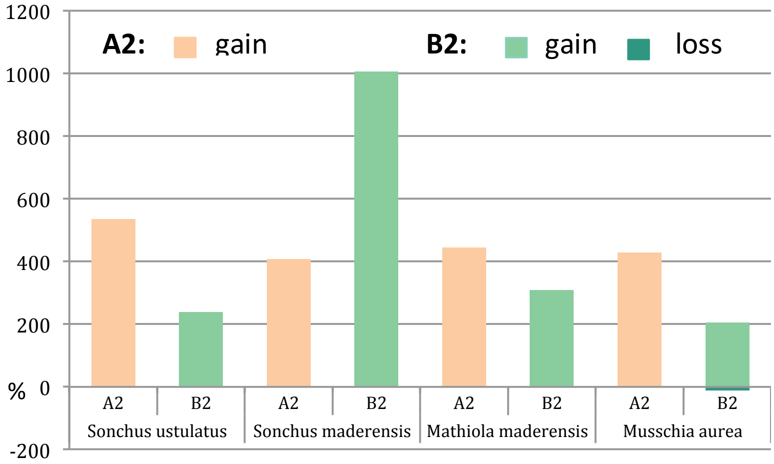


Figure 78 - Predicted changes on suitable area for taxa of the group 4 considering predicted area for current conditions

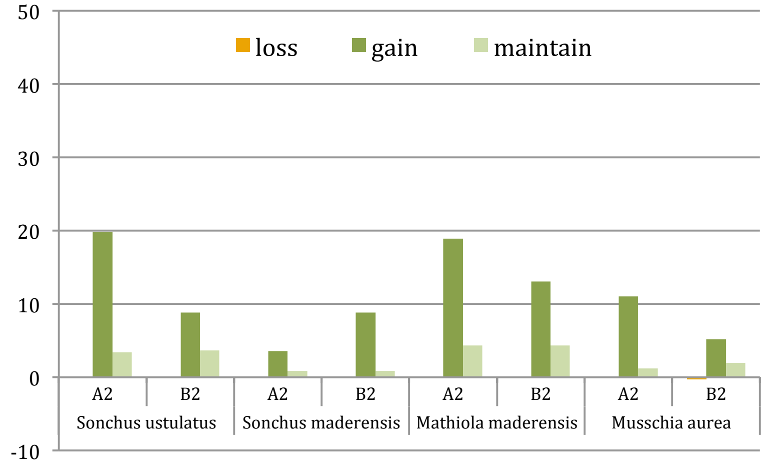


Figure 79 - Predicted changes for suitable area under future climatic scenarios in relation to the area of the island for group 4

The predicted increase on suitable area is determined by the projected rise on the mean minimum temperature of the coldest month. However, the niche of the species is also structured by specific topographic conditions, which have a low spatial representation in the area predicted as suitable in the future. Such results indicate that models were not able to capture accurately the habitat conditions, what is likely associated to the spatial resolution of the environmental variables in use (200x200m).

1.2 DISCUSSION OF RESULTS

As discussed on a previous chapter, species distribution modelling results are dependent on several factors, namely the quality of the data and type of variables used on models calibration, the modelling techniques in use, or the threshold used to convert continuous to binary outputs. Different methodologies have been implemented to measure and improve the accuracy of models results, namely the use of ensemble forecasting modelling approaches, with the aim to increase modelling robustness (Araújo & New, 2007), the use of accuracy measures that are classified as threshold-independent (Fielding & Bell, 1997), and the application of different strategies to validate models results (Araujo *et al.*, 2005).

1.2.1 THE PERFORMANCE OF MODELLING TECNHIQUES

The analysis of performance for the different modelling techniques in use, based on the accuracy measure AUC of ROC, puts in evidence which of them have higher predictive accuracy. Despite the variability of performance for the different modelling techniques in use, most of the models present good or very good performance on discriminating suitable from unsuitable conditions (AUC > 0.8). Artificial Neural Networks and Classification Tree Analysis present the average lower performance (Figure 80). In fact, models produced by such techniques were more often removed from the group of models used to project detected relationships for all the island and future climatic scenarios, a strategy focused on reducing uncertainty on results.

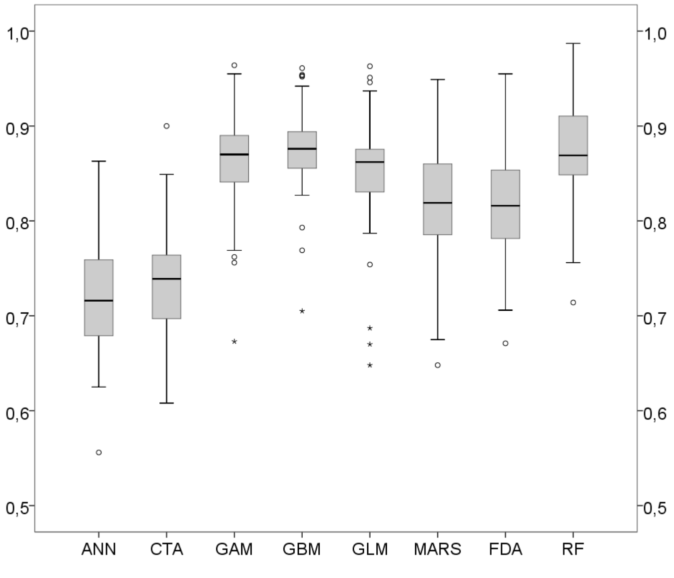


Figure 80 - Variance of performance according the modelling technique for all models produced for each species.

On the opposite, regression methods (GLM, GAM) and machine learning techniques (GBM, RF) present the higher performance. The Generalized Boosted Method (GBM) seems to be the modelling technique that is more robust, and less sensitive to species traits, a result consistent with other studies (Elith *et al.*, 2006).

Once all the models with AUC lower than 0.7 were removed, the consensus models for several species were less determined by the results produced by Artificial Neural Networks and Classification Tree Analysis, which produced significant number of models with lower predictive accuracy (Figure 80).

Although the described accuracy, the quality or usefulness of the models is dependent on other aspects, namely biasing effects associated to species spatial patterns, sampling design, or lack of information about species-specific traits, biotic interactions, or environmental variables (Hampe, 2004; Araújo & Guisan, 2006; Araújo & Luoto, 2007).

1.2.2 THE BIASING EFFECTS ON RESULTS

The analysis of results allows the identification of two principal biasing factors:

i) the effects from land-use, a factor that generally contributes to reduce species' occupancy area,

ii) the spatial resolution in use, which is critical for species with restricted distributions.

1.2.2.1 THE CONTRIBUTION OF LAND-USE

The disturbance of the natural habitats by human activities can be considered the factor with higher biasing interference on models' results. The effects are mainly negative, once most of the disturbance types are associated to a deep and long use of the territory, contributing to restrict species' occupancy areas. Therefore, absences on certain areas are very likely associated to land-use (e.g. agriculture, grazing), and do not reveal unsuitable environmental conditions (e.g. climate, topography). This is very clear on the southern face of the island, namely on areas used by agriculture, and at the highest summits, where grazing was a dominant practice during centuries (Silva & Menezes, 1946; Andrada, 1990). The existence of extensive areas afforested with exotic species at medium altitudes (*Eucaliptus* sp., *Pinus pinaster*, *Fagus sylvatica*, etc.) is also contributing to produce biased results, a conclusion that is clearly supported by the existence of empty areas when combining models results for the different vegetation types (Figure 81). The combination of models results for climax vegetation communities puts in evidence that on some areas models fail on predicting the type of vegetation. Assuming that models have good performance, once only those with better accuracy have been used on consensus forecasting (AUC > 0.7), becomes clear that results reveal the biasing effect of disturbance by human activities.

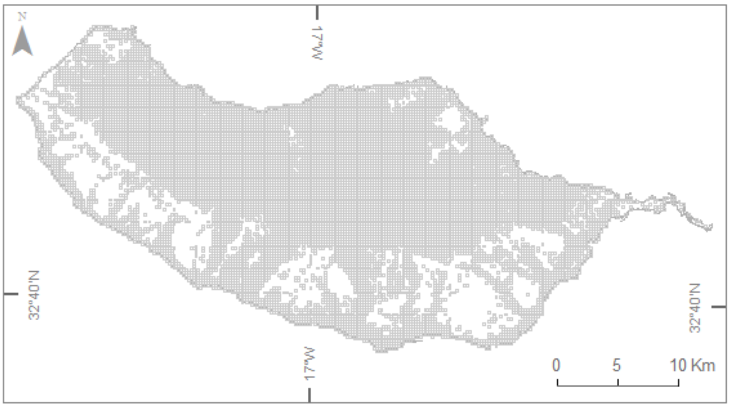


Figure 81 - Combination of predictions for the types of vegetation modelled

That relationship is more obvious on the southern face of the island, where *empty* areas are associated to the dominance of two types of land-use, agriculture and forests of exotic species. It puts on evidence the negative effects of land-use on native vegetation. Considering the model for natural potential vegetation proposed by Capelo *et al.* (2004), those areas are potentially associated to the mediterranean laurel forest on altitudes below 800m (southern face), and related to the temperate laurel forest on areas above such altitudes. Despite the fact that such results can be partially determined by the methodology used to define the area suitable for climax communities, it is clear that the current restriction of such forests on the southern face of the island, on areas expected to be suitable, and the absence of related species on vast areas, can be assumed as the main drivers for such results.

1.2.2.2 SPATIAL RESOLUTION

The opposite extreme changes on suitable area predicted for the groups 3.2 and 4, extirpation and wide expansion respectively, are likely dependent on the incapacity of the models to reproduce accurately the habitat conditions, a result that might be associated to the spatial resolution in use (200x200m). Habitats of both groups are deeply structured by specific topographic conditions, a detail that is loss when using a coarse resolution. In the case of the group 3.2, and considering the species *Armeria maderensis*, *Erica maderensis*, and *Berberis maderensis*, the resolution in use produces an overestimation in terms of loss on suitable area, once it hinders the capacity of the models to distinguish small topographic refuges, where suitable conditions might remain. In fact, it is expected that small topographic refuges will support the permanence of the species for longer periods than predicted by models based on coarser resolutions (Randin *et al.*, 2009; Engler *et al.*, 2011).

The idea that results might be overestimated because of the spatial resolution in use can be also associated to rare exclusive endemics that occupy habitats also exhibiting a strong topographic component on coastal fringes (group 4). For this group models predict a large expansion on suitable area (> 200%), despite their confined distribution. Being taxa with a distribution deeply filtered by topographic conditions, it is expected that the projected expansion will be deeply constrained by habitat availability. Thus, results reveal the incapacity of models to fully capture the habitat conditions. In fact, in these cases models attributed more weight to environmental predictors that have a better predictive at regional scales (e.g. temperature annual range, mean minimum temperature of the coldest month), and depreciated the contribution of local factors, such as topographic features. So, the extreme values in terms of predicted expansion suggests that models were not able to discriminate in detail the role of topographic features, a result that might be associated to the resolution in use (200x200m).

1.2.3 THE INTERFERENCE OF NON-CLIMATIC FACTORS

The results for changes on suitable area under future climatic conditions at Madeira Island are consistent with shifts described (Parmesan & Yohe, 2003; Chen *et al.*, 2011) and predicted (Walther *et al.*, 2002; Parmesan & Yohe, 2003) for different regions of the world. For Madeira Island, trends on predicted changes for the modelled species can be summarized by a general upward shift, which might result from an overall expansion of the predicted area, mainly supported on the expansion of the leading edge, or a retraction, mainly sustained on the erosion of the rear edge.

The upward response on mountain areas was more often described than latitudinal range shifts (Keller *et al.*, 2000; Theurillat & Guisan, 2001; Holzinger *et al.*, 2008). Despite the fact that such trend is favoured by the definition of spatially compressed climatic zones along elevation gradients on mountain areas, while slow demographic and dispersal constraints may reduce their importance in terms of latitudinal shifts (Beckage *et al.*, 2008), it supports the idea that mountain habitats are more susceptible to impacts from climate change (Thuiller *et al.*, 2005; Gottfried *et al.*, 2012). That susceptibility comes from the higher sensitivity of cold tolerant species to small changes on climatic conditions (Engler *et al.*, 2011), an attribute that contributed to the extinction of range-restricted species due to recent climate change on such environments (Parmesan, 2006).

The summits of Madeira Island do not fit on the category of high mountain, once only very limited areas on the island exceed the 1800m m.s.l. (Pico Ruivo: 1848; Pico Arieiro: 1812). However, some of the exclusive endemics restricted to the highest summits, such as *Armeria maderensis*, *Berberis maderensis*, *Erica maderensis*, and *Sorbus maderensis* can be considered as cold-tolerant species. Because of that, it is expected a decrease on suitable area under future climatic scenarios. Modelling results confirm the expectation, and project the extirpation or drastic reduction of suitable conditions under future climatic scenarios, a circumstance that creates a condition prone to extinction for such species. Such results are consistent with the assumption that the susceptibility to extinction is higher for thermally specialized species with narrow elevational ranges

(Ohlemuller *et al.*, 2008; Laurance *et al.*, 2011), especially at the summits, where the expected narrower tolerance to environmental changes (Wilson *et al.*, 2004) is reinforced by the lack of spatial contiguity (La Sorte & Jetz, 2010). Current restricted distribution to confined and fragmented habitats, low abundance, might reinforce such susceptibility (Schwartz *et al.*, 2006; Payne & Finnegan, 2007), a pattern described for habitats located at the summits of high mountains (Gottfried *et al.*, 2012). Despite the recent increase in the number of populations because of abandonment of traditional activities on such areas, the available habitat remains restricted. And the deep disturbance of the habitats during centuries, namely by grazing, combined with the likely low genetic diversity, as detected for *Armeria maderensis* (Piñeiro *et al*., 2009), are expected to be determinant factors that supports the expected high susceptibility to even soft changes on climatic conditions.

In adittion, other factors might produce synergetic effects that will promote the extirpation or reduction of suitable area for the species, such as invasion by exotic species (e.g. *Cytisus scoparius*) or disturbance by fire. A good example is performed by the species *Sorbus maderensis*. It can be considered the hypothesis that models are underpredicting suitable area for such species, assuming that its current restricted distribution is very likely determined by the effects of human activities, namely the intense and prolonged disturbance associated to firewood collection, grazing and charcoal production. Even considering a larger suitable area, and despite the uncertainty associated to its response to changes on climate, the species became more vulnerable to extirpation after the wild fires occurred in the summer of 2010, when the species almost lost all the known populations.

In fact, all the species and vegetation communities which suitable area is coincident with the summits of the island registered a significant retraction because of the negative effects of human action. The heath tree community, dominated mainly by *Erica arborea*, clearly reveals such interference, not only in terms of occupancy area, but also because of possible changes on floristic composition. The potential distribution of *Sorbus maderensis* suggests that it could integrate the species assemblage associated to the heath tree community, that should also include *Juniperus cedrus* subsp. *maderensis* (Capelo *et al.*, 2004). Past and recent disturbance, mainly by fire, may contribute to decrease the possibility of reestablishment of the community, which may take more time than expected, not only because the dominant species (*Erica* arborea) is not resprouting after fire, but also because such areas are being invaded by the alien invasive *Cytisus scoparius*. Once the invasion is occurring on significant areas, namely those used by grazing in the recent past, and taking into account the fire prone status of the species (*Cytisus scoparius*), there is a reinforcement on conditions that support a potential increase of fire frequency. In adittion to the described changes on vegetation, the possibility of increasing dryness coincident with the tradewind inversion, described for Tenerife Island (Sperling *et al.*, 2004) might emphasize the probability of increasing frequency of disturbance by fire. At the same time, such factor (increasing dryness) would obstruct the upward shift predicted for the temperate laurel forest under future climatic scenarios. According to modelling results, the projected upward of the temperate laurel forest is expected to contribute to decrease the area available for the heath tree microforest, despite the maintenance of suitable conditions for *Erica arborea*. But the predicted expansion of the temperate laurel forest to higher altitudes is dependent on the regeneration of the species accepted as characteristic, namely trees (*Clethra arborea*, *Ocotea foetens*), on areas affected by human disturbance (charcoal production grazing, firewood collection). Such shift is also dependent on other variables, which changes might cause significant impacts on the temperate laurel forest - the frequency and height of the orographic cloud banks during the dry season, climatic variables that were not considered directly on climatic models because of absence of data. It is certain that a reduction on the frequency or changes in the spatial definition of cloud banks will have deep interference in the habitats that are dependent on, a relationship already identified on tropical environments (Pounds *et al.*, 1999). But there is high uncertainty in terms of changes in the future. Though the expected upward shift of the average altitude of the base of the orographic cloud bank, in association to climate warming (Still *et al.*, 1999), a trend already confirmed for tropical mountain areas (Pounds *et al.*, 1999), the analysis of recent trends and projected changes for Tenerife Island point in a different way. Based on the analysis of relative humidity and diurnal temperature range, Sperling *et al.* (2004) report a possible increase in the frequency of low-level clouds in the last 30 years, and found partial evidences for a drying trend across the trade wind inversion, related to increased subsidence. In opposition to the projections for tropical mountain conditions (Still *et al.*, 1999), the study projects a downward shift of the area that is climatically suitable for the laurel forests. That change might occur in association to expected adjustments on global circulation patterns associated to climate warming, producing local changes that diverge from the general pattern (IPCC, 2007), what might explain the differences on projections for tropical and subtropical areas.

In the case of Madeira Island, the predicted upward shift for the temperate laurel forest, based on models that didn't include data for the frequency of the orographic cloud banks, might not happen in the case that a drying trend occurs at the upper edge of the current range. The reduction on the frequency of cloud cover will increase evapotranspiration, and will hamper the establishment of some tree species, namely because of their dependence on fog immersion or cloud cover during the dry season, which helps to reduce the demand for water due to lower losses by transpiration (Ritter *et al.*, 2009). In fact, the scenario B2 predicts an increase on the amount of precipitation, which can be significant in the case of the northern coast. Such prediction is consistent with the observed trends reported by Sperling *et al.* (2004), and support an increase on suitable area, despite small, at the rear edge of current predicted range. On the opposite, models for the scenario A2 predict a significant decrease on suitable area at the rear edge, and a more conservative increase at upper areas.

In addition to changes on the distribution, communities might suffer changes on floristic composition, a result from divergent species' responses to climate change (Wiens *et al.*, 2009; Bertrand *et al.*, 2011; Pucko *et al.*, 2011; Felde *et al.*, 2012). In the case of the temperate laurel forest, that divergence is detected for the species *Clethra arborea*, which projections predict a wide contraction, suggesting an adjustment in the floristic composition of the temperate laurel forest on significant areas, especially in the scenario A2. Another species that register a significant decrease on suitable area is the widely distributed *Laurus novocanariensis*. But the predicted erosion of the rear edge occurs mainly in the area predicted as suitable for the mediterranean laurel forest, what might lead to changes on the composition of such community. Based on predicted changes on suitable area, the taxa *Apollonias barbujana*, the most characteristic and structuring taxa, registers an upward shift on suitable area, based on the erosion of the rear edge, which is higher on the southern face under the scenario A2, and an expansion at the upper edge. Once the species plays an important role in the structure of the mediterranean laurel forest, changes on suitable area will very like dictate changes on community's spatial patterns. But such changes might not track the models predictions, namely in terms of expansion to higher altitudes, since different factors might hamper the chance to establish on all the area predicted as suitable by the models. Dispersal constraints or long-time demanding to establish might encumber the capacity of the species to colonize all the area predicted as suitable, and reduce the chance to reach areas that are predicted to be suitable in the future. In fact, the species does not presents distribution traits that are critical to the establishment on new areas in the future, namely the existence of high plant density near the range margin and high preponderance of adult species, which are expected to produce higher amounts of seeds and increase propagule pressure (Murphy *et al.*, 2010). Today the species is restricted to small areas, and its low abundance and occupancy area at the expanding edges of its current range (higher altitude) may configure a serious limitation to its capacity to migrate. That condition which might be reinforced by the higher habitat fragmentation, a factor that might explain partially the inertia of communities at lowlands in response to recent climate change (Bertrand *et al.*, 2011). In fact, the vast majority of the area predicted as suitable for the species was disturbed by agriculture, and some of the areas where the species occurs today are predicted to be unsuitable in the future. In this case, predicted climate change might be fast enough that might hinder the capacity of species to reach new suitable areas because of dispersal limitations (low number of seeds, low dispersal rate) (Corlett & Westcott, 2013). Such possibility might be attenuated by the mesophanerophytic condition of the species, which can ensure that seeds production is maintained for longer periods by old trees on areas predicted to be unsuitable in the future, because of their lower susceptibility to climatic changes, starting from the assumption that the species are in equilibrium with current climatic conditions at the lower edge of its current range. Moreover, it is expected a larger lag between the magnitude of climate warming and the response by species at lowland areas, a condition supported on the higher proportion of species that are able to cope with warmer climates (Thuiller *et al.*, 2005). But even considering the capacity of the species to install on new suitable areas, it is important the time length that it needs to start producing seeds and establish a community. Because of the slow establishment of the community, that lag should favour alien invasive fast-growing trees (Dukes & Mooney, 1999) on areas that are not occupied by the temperate laurel forest, considering the predicted upward trend predicted by the models. Not only on new areas, but also on areas currently suitable, the invasion by alien exotic species can be considered a threat that might contribute to reduce the area available for the mediterranean laurel forest. In fact, the area considered as suitable for both *Apollonias barbujana* and alien invasive trees is projected to increase under future climatic scenarios, a prediction that is shared by other species associated to the community (*Apollonias barbujana*, *Smilax* pendulina, *Semele androgyna*, *Ilex canariensis*) or associated to subseral stages (*Hypericum canariensis*, *Myrtus communis*). Because of the restricted occupancy area of the community, limited to small patches, and considering the large time-period estimated to install, it is predictable that alien invasive trees can invade areas abandoned by agriculture or exposed to episodic disturbance, as occurs today. In fact, the intensity, persistence, and ubiquity of human activities imprinted significant changes on habitat conditions, what might put native species at a competitive disadvantage with non-native species (Byers, 2002).

Despite the significant areas of potential conflict between the native forests and the alien invasive trees, it is possible that they might be underestimated, especially in the case of the laurel forests, an assumption that is based on two arguments. First, the areas predicted as suitable for both forests are very likely underestimated, a result derived from the fact that wide areas that are accepted as potentially suitable for such forests Capelo *et al.* (2004) have no occurrence records for related characteristic species, a condition derived from the high level of disturbance by human activities. Second, once the alien invasive trees did not spread throughout their potential habitat, they don’t reflect a stage of equilibrium with environment, a principle accepted as fundamental on species distribution modelling (Elith & Leathwick, 2009). Under such context, facing the fact that species have not yet occupied the full range of ecological conditions related to its fundamental niche, the potential habitat is very likely underestimated, once calibration will include occurrence data for a fraction of the fundamental niche (Phillips *et al.*, 2006). As species recently introduced/established, it is expected the existence of a discrepancy between realized and fundamental niche (Peterson *et al.*, 2007). In addition, the modelling approach is very likely producing conservative models. Despite the advisable use of a threshold that maximizes the capacity of the models to correctly predict known presences and absences (sensibility and specificity) for native species, once it reduces the importance of outliers, it seems reasonable the use of a threshold that gives more importance to the capacity of the model to predict correctly the presences in the case of invasive species, once absences are largely explained by the fact that the species had not enough time to reach such ecologies. In fact, and considering the invasive status of the species (Gleadow & Ashton, 1981; Kull *et al.*, 2011), it seems acceptable that the threshold used to produce a binary output can be based on the minimum value of suitability identified among the occurrences used on calibration. As an alternative, it can be used a combined modelling approach. Based on two different types of models (models calibrated separately by predictors that have "local" or "regional" patterns), the combined results have better performance than models calibrated by the two types of predictors together (Vicente *et al.*, 2011).

According to modelling results, on the northern face of the island the areas occupied by temperate laurel forest present a lower risk of invasion. Nevertheless, disturbance might prompt invasion on areas currently occupied by native forest, being of natural origin (Bellingham *et al.*, 2005) or induced by human activities. And at that time, bank seeds might already integrate significant quantities of seeds from alien invasive trees. This is expectable in the case of the species *Pittosporum undulatum*. Dispersal by birds increases drastically the potential of invasion by the species, reducing largely the role of the geographical constraints to dispersal. That circumstance increases largely the possibility of invasion of areas currently occupied by laurel forests, once the bird identified as vector (European blackbird) (Gleadow, 1982) is common in this type of forests. Moreover, climatic conditions on areas predicted as suitable for such forests are similar to those of its native geographical range (temperate – subtropical conditions); and it tolerates shadow, being a common sub-canopy tree in different forest types (Gleadow & Ashton, 1981; Gleadow *et al.*, 1983).

The level of conflict is considerably higher in the case of the wild olive microforest. Combining the high level of disturbance of the territory with the expected lag in the response of the species/communities at lowlands, it is predictable that invasion might obstruct the predicted expansion for this native community.

The higher predicted expansion of suitable area in the island is forecasted for species that currently occupy the lower altitudes of the island, namely those associated to the wild olive microforest. But the predicted expansion to new areas might be blocked by land use, by dispersal constraints, because of negative biotic interactions, or restrictions in terms of available habitat (Corlett & Westcott, 2013).

In terms of land-use, agriculture or urban areas occupy significant areas of the territory predicted to support the expansion of the community in the island (Figure 82).

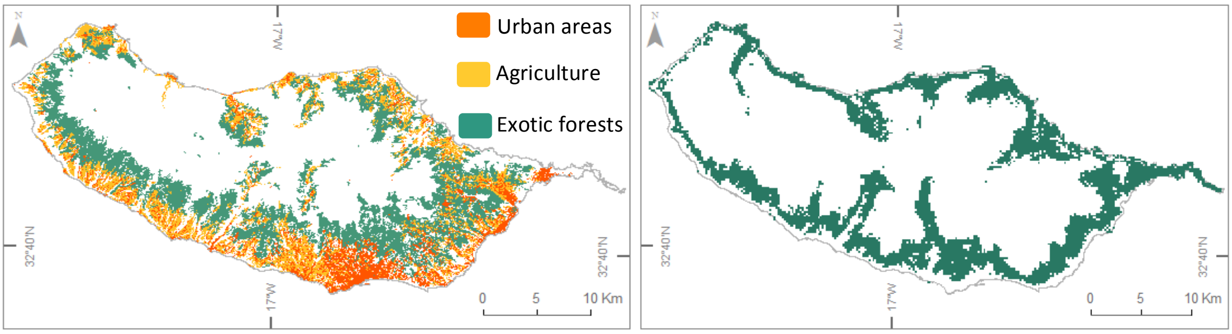


Figure 82 - Dominant land-use types (left (Source: COS, 2007)) and projected area of expansion for the scenario A2 (right) for the species of the subgroup 1.1

Even considering the high rate of abandonment by agriculture on such areas at the moment, which release area for the projected expansion, different factors might contribute to reduce the area that could be actually occupied. Some of the species are restricted to small patches isolated on steep slopes, such as *Olea maderensis* and *Chamaemeles coriacea*; a condition that imposes more limitations in terms of dispersal to the entire area projected as suitable in the future. That condition might not perform a significant barrier to dispersal for *Olea maderensis*, if we consider the fact that the wild olive is one of the most actively bird-dispersed species among fleshy fruit-producing plants in the Mediterranean region (Herrera, 1995). But might be of special significance for the taxon *Chamaemeles coriacea*. Aside from the fact that is very likely a low-seed producer that demands long time to establish, the occurrence is currently reduced to few individuals separated by significant distances. Thus, the expansion of the species to the area predicted as suitable might be deeply restrained by dispersal constraints. Moreover, predicted climate change might be fast enough to hinder the possibility of the species to reach and establish on all the predicted area, especially if considering time lags associated to plant dispersal, colonization, establishment, and maturation, which might affect both rare and abundant species (Zhu *et al.*, 2011). Aside from that, it is also necessary to bear in mind that climatic stress is expected to increase on areas where the species is currently present, which can have implications on basic functions, such as seed production. And some of the areas where the species occur today are predicted to become unsuitable. In that case, it is also possible that climate change velocity may exceed plant-movement, a situation expected for species that are restricted in number and occupy only the lower edge of current suitable area (Engler *et al.*, 2009; Murphy *et al.*, 2010; Corlett & Westcott, 2013). Moreover, significant areas are predicted to be also suitable for alien tree invasive species. As mesophanerophytes that are able to establish quickly and become dominant at the tree layer (Rejmanek & Richardson, 1996; Rejmánek *et al.*, 2005; Kull *et al.*, 2011), the alien invasive trees will certainly outcompete all the native species associated to the wild olive microforest, which have lower height or might take more time to establish. Aside from the capacity to displace native elements, because of direct and indirect impacts (see Chornesky & Randall, 2003), successful invasion may also take advantage from the expected decrease on competitive resistance from native species (Byers, 2002) and positive impacts that climate change could have on alien species (Vilà *et al.*, 2007; Hellmann *et al.*, 2008). Even in the case of species for which limitations in terms of dispersal and establishment might be less important, such as shrubs that are dominant on sub-seral stages and currently present significant rates of recovery on areas abandoned by agriculture (*Echium nervosum, Euphorbia piscatoria*), the invasion by alien species might limit the predicted expansion. In fact, processes of invasion by *Arundo donax*, *Cardiospermum grandiflorum* or *Brachiaria mutica* are already occurring on large areas on the island. The species *Arundo donax* has a significant presence on areas predicted as suitable for the species of this group, and is colonizing successfully areas abandoned by agriculture on significant areas of the island, where it was introduced (Pupo-Correia *et al.*, unpublished data) (Figure 83)[4].

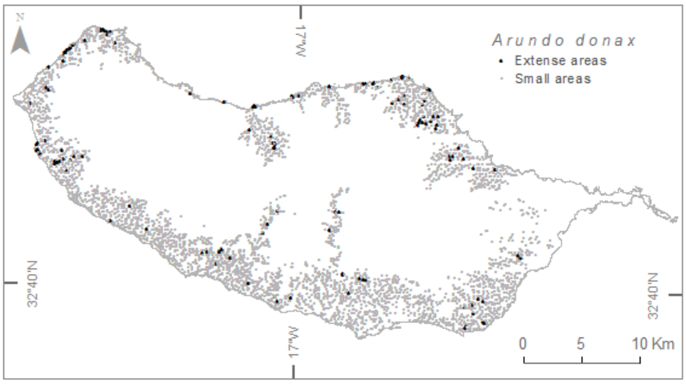


Figure 83 - Current distribution of *Arundo donax*.

The predicted loss on plant diversity in the area associated to the wild olive microforest can be also associated to other factors.

---

[4] Area for current distribution of *Arundo donax* based on interpretation of aerial-photography.

Despite the predicted maintenance and expansion of suitable areas, it is possible that predicted increasing on dryness on coastal areas might lead to loss of local diversity, the so-called biotic attrition (Colwell *et al.*, 2008). Predicted to occur on areas where the number of species that get locally extinct exceeds the number of arrivals, it might occur on coastal areas on the southern face of Madeira Island, where it is expected that dryness may surpass the tolerances of extant species. Such situation is suggested by the results obtained for *Chamaemeles coriacea* under the scenario A2, and for *Musschia aurea* for both scenarios. For such species, mainly associated to coastal areas, the models are unable to produce results for some areas that are currently suitable for the species. Such results are supported on the fact that those areas will be associated to novel climates under the future climatic scenarios. That condition is very likely supporting the definition of conditions prone to local extinction, performing a situation of loss on plant diversity. Such fact is especially concerning in the case of the exclusive endemic *Muschia aurea*, which expansion will be deeply dependent on the existence of suitable habitat. And, as explained before, the available habitat should be more restricted than predicted by the models. Another example that supports the idea that models are overestimating the expansion of habitat specialists is performed by the exclusive endemic *Musschia wollastoni*. Restricted to gaps in the temperate laurel forest, usually associated to landslides or margins of small streams, the species is currently restricted to few individuals, on areas where the laurel forest is well preserved (Jardim & Sequeira, 2008). Because of the absence of variables that introduce in the models information about the specificity of the habitat, the results are based on the relationship found with the climatic variables. Despite the use of variables related to the presence of the forest (percentage of area covered by native forest), the models didn't find a significant relationship. So, despite the considerable increase on suitable area in the future, required habitat is expected to maintain low representation. In fact, it might also decrease, based on the predicted decrease of suitable area for the temperate laurel forest. But results are surrounded by great uncertainty, once the occurrence of the species is more dependent on factors that are unpredictable.

Other examples of species which expansion is likely dependent on the presence of native forest are performed by the liana species *Semele androgyna* and *Smilax pendulina*, which occurrence is associated to the presence of the Mediterranean laurel forest. The incapacity of the forest to reach new areas, because of the mentioned factors, might also limit the expansion of such species. Considering its absence on areas occupied by exotic forests in the area predicted as suitable for the species and the native community, such as pine and eucalyptus forests, it is probable that a process of specific facilitation might occur after the installation of the native forest.

While most of the endemic and native taxa are affected negatively by the disturbance by human activities, species such as *Teucrium betonicum* and *Melanoselinum decipiens* have very likely been benefited by human activities, namely because of the creation of open habitats with low disturbance. The occurrences were very frequently associated to areas affected by disturbance in the recent past, namely agriculture and grazing respectively. Thus, because of the high abandonment of traditional activities, it is expected that the installation of shrubby formations first, and forests later, will reduce the number of populations and individuals, despite the predicted increase in terms of suitable area in the scenario B2.

Several other factors, might contribute to moderate or switch changes predicted by climatic models, namely biotic interactions between species (Davis *et al.*, 1998), which might contribute to reduce range gains (Araújo & Luoto, 2007; Jaeschke *et al.*, 2012); species dispersal traits, considered as critical to deal with environmental changes (Gaston, 2009); the capacity of species to support propagule pressure at the leading edge of the geographic range, once it controls the capacity for range expansion (Murphy et al., 2010); the role of source-sink dynamics (Berry et al., 2008); the capacity of species to adapt or tolerate the predicted unprecedented rates of climate change, coupled with land use changes (Davis & Shaw, 2001); the effects of early onset on disrupting plant-pollinators interactions (Parmesan, 2006; Kudo & Ida, 2013); or the role of time-lag response (Bertrand et al., 2011), once range expansion or contraction may still take decades or centuries to manifest or be measurable for long-lived organisms, namely for trees (Murphy et al., 2010).

1.1 MAIN CONCLUSIONS

The high plant diversity associated to the Macaronesian archipelagos is highly dependent on geographical features, namely past and present climatic conditions. One of the traits that best support the idea of high plant diversity is the high proportion of endemic taxa, which is considerable in the case of Madeira Island (Jardim & Sequeira, 2008). Because of historical land-use on the island, which imprinted deep changes on natural habitats, endemic plants become very often restricted to hilly slopes and rocky outcrops, or become extinct as consequence of deep changes on the habitats (Menezes de Sequeira *et al.*, 2007). Combined with traditional sources of threat, new factors might produce impacts that contribute to reduce plant diversity. As suggested for other regions of the world, projected climate changes and invasion by alien species are considered two factors that might have such impacts.

In the case of potential impacts from projected climatic changes, it is clear from predictions that response type is dependent on the ecological tolerance of the organisms. In fact, projections of suitable area present non-linear and contrasting predictions. In terms of response two opposite groups can be clearly identified: a group for which predictions forecast a significant increase on suitable area, and another one associated to a projected decrease. The first group integrates taxa accepted as tolerant to dryness, namely those associated to the potential territory of the wild olive microforest (*Mayteno umbellatae-Oleetum maderensis*), which are mainly related to inframediterranean areas of the southern face of the island. Such results confirm one of the hypotheses enounced at the start of this work. Notwithstanding the predicted increase in terms of suitable area in the future, the expansion of the species to such areas might be blocked by different factors. A significant percentage of the territory is occupied by urban areas or areas dedicated to agriculture. And despite the high rate of abandonment by agriculture, dispersal conditions might reduce the possibilities of the species to reach all the area predicted as suitable. In addition, a significant area predicted to support such expansion is also suitable for alien invasive species. Under these circumstances, competition with alien invasive species might also reduce the capacity of such species to resist to the direct effects from projected climatic changes (Pounds *et al.*, 1999; Peñuelas & Boada, 2003).

The opposite response is predicted for species mainly associated to the highest summits of the island, namely those currently presenting a very restricted distribution. Such conclusion is consistent with the idea that species exhibiting low frequency and restricted distribution on mountain' summits might present higher susceptibility to impacts from climate change (Theurillat & Guisan, 2001). On Madeira Island, other factors should reduce the resistance of such species to climate change, namely because of the extreme level of habitat-fragmentation associated to the high level of human-induced disturbance. Such conditions support the idea that such areas should be regarded with high priority in terms of conservation. Notwithstanding the high interest for conservation, our capacity to produce accurate models for all species exhibiting such attributes is hampered by the low number of known occurrences and the resolution in use (200x200m), a condition that very often determined their exclusion during the modelling stage. A possible strategy to overcome such limitation might be the use of higher spatial. Despite higher demanding in terms of sampling effort, such strategy seems to be appropriate for species with restricted distribution. Models should also integrate data about population dynamics, ecosystem processes and climate trends at landscape and regional scales in order to obtain more realistic predictions (Hannah *et al.*, 2002). In fact, models would be more robust if data about dispersal, number and size of populations were included on calibration.

In terms of climatic scenarios, projections based on A2 emissions scenario are more drastic than those based on B2 scenario, predicting more drastic expansions or contractions, a trend also detected on other studies (Peterson *et al.*, 2008). Because of differences in terms of predicted range shifts, plant communities might experience important reorganizations, what might support the definition of new types.

Although the uncertainty associated to the course and magnitude of climate change, the loss of suitable area might occur even in case of small changes on climate, caused by the combination of effects.

In terms of impacts from invasion by alien species, areas of potential conflict between native species/communities and alien invasive trees are very likely underestimated. It results from the correlative nature of the models, which is especially constraining in the case of alien species that are not in equilibrium with the environment, but also from the conservative methodological approach in use. Both factors are very likely contributing to the small increase in the area of potential conflict between native and alien invasive species, a result that doesn't confirm the related hypothesis set at the beginning of this work.

The level of bias on predictions due to interference of human disturbance on species occurrence is significant on areas deeply used in the past, namely on the southern face of the island and at the highest summits. Thus, potential distribution for species/communities might be underestimated. A possible strategy to overcome such weakness might be through a mechanistic approach, instead of the correlative one used to produce such results. But its application demands data that it is not available at the moment.

The spatial resolution in use was not effective on producing accurate results for exclusive endemic species restricted to low number of populations, especially those associated to habitats with a strong topographic component. For such species it is necessary to use higher spatial resolution. The increase on resolution for the environmental predictors should be accompanied by higher sampling effort on areas predicted as suitable for current conditions.

Despite the uncertainties surrounding projections for changes on suitable areas, it is widely accepted that climate change can is already causing impacts on vegetation, and such impacts can be reinforced because of the synergic contribution from other factors, namely habitat fragmentation and increasing fire frequency, which might reduce the tolerance of plant species to small environmental changes (Brook *et al*., 2008).

According to the obtained results, it is advisable that predictions of species response to climate change and invasion by alien species should integrate policies of conservation, once it could improve the relevance of decisions (Hannah *et al.*, 2002; Hannah *et al.*, 2007).

1.2 FUTURE RESEARCH PERSPECTIVES

The main aims proposed at the beginning of this work were achieved. But new questions and issues emerged during its development. Among such questions, some of them perform challenges for the near future:

- how much accuracy will increase using mechanistic approaches on species distribution modelling,
- how much will differ results for communities using other modelling approaches,
- how far from here can we go when using data for dispersal scenarios,
- how important are refugia on shaping colonization patterns,
- how well higher resolution will work for assessing the impact on distribution for species with high interest for conservation,
- how expressive could be suitable areas for other alien invasive plants.

In fact, the results of this study, more than confirming hypotheses, they open new research perspectives.

- REFERENCES -

ACIA (2004). *Impacts of a warming Arctic: Arctic Climate Impact Assessment*. Cambridge University Press, New York. 139 pp.

Adair, R. (2002). Black Wattle: South Africa Manages Conflict of Interest. *CABI Biocontrol News and Information* 23 (1): 5-7.

Aguirre, E. (2003). Messiniense: compleja y grave crisis ecologica. *Estudios Geol.* 59: 205-212.

Aigoin, D.A., Devos, N., Huttunen, S., Ignatov, M.S., Gonzalez-Mancebo, J.M., Vanderpoorten, A. (2009). And if Engler was not completely wrong? Evidence for multiple evolutionary origins in the moss flora of Macaronesia. *Evolution* 63 (12): 3248-3257.

Akçakaya, H.R., Butchart, S.H.M., Mace, G.M., Stuart, S.N., Hilton-Taylor, C. (2006). Use and misuse of the IUCN Red List Criteria in projecting climate change impacts on biodiversity. *Global Change Biology* 12 (11): 2037-2043.

Allen, M.R., Stott, P.A., Mitchell, J.F.B., Schnur, R., Delwort, D.L. (2000). Quantifying the uncertainty in forecasts of anthropogenic climate change. *Nature* 407: 617-620.

Allouche, O., Tsoar, A., Kadmon, R. (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* 43 (6): 1223-1232.

Amaro, A., Reed, D., Soares, P. (2003). *Modelling Forest Systems*. CABI publishing, Walling Ford, UK. 401 pp.

Anderson, B.J., Akçakaya, H.R., Araújo, M.B., Fordham, D.A., Martinez-Meyer, E., Thuiller, W., Brook, B.W. (2009). Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B: Biological Sciences* 276 (1661): 1415-1420.

Andrada, E.C. (1990). *Repovoamento florestal no arquipélago da Madeira (1952-1975)*. Direcção Geral de Florestas, Secretaria de Estado da Agricultura, Ministério da Agricultura, Pescas e Alimentação, Lisboa.

Anisimov, O.A., Vaughan, D.G., Callaghan, T.V., Furgal, C., Marchant, H., Prowse, T.D., Vilhjálmsson, H., Walsh, J.E. (2007). Polar Regions (Artic and Antartic). In: Parry, M.L., Canziani, O.F., Palutikof, J.P., Linden, P.J.v.d., Hanson, C.E. (eds.), *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of the Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, pp. 653-685.

Araujo, M.B., Pearson, R.G., Thuiller, W., Erhard, M. (2005). Validation of species-climate impact models under climate change. *Global Change Biology* 11 (9): 1504-1513.

Araújo, M.B., Williams, P.H. (2000). Selecting areas for species persistence using occurrence data. *Biological Conservation* 96 (3): 331-345.

Araújo, M.B., Cabeza, M., Thuiller, W., Hannah, L., Williams, P.H. (2004). Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology* 10 (9): 1618-1626.

Araújo, M.B., Pearson, R.G. (2005). Equilibrium of species' distributions with climate. *Ecography* 28 (5): 693-695.

Araújo, M.B., Thuiller, W., Williams, P.H., Reginster, I. (2005a). Downscaling European species atlas distributions to a finer resolution: implications for conservation planning. *Global Ecology and Biogeography* 14 (1): 17-30.

Araújo, M.B., Whittaker, R.J., Ladle, R.J., Erhard, M. (2005b). Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography* 14 (6): 529-538.

Araújo, M.B., Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography* 33 (10): 1677-1688.

Araújo, M.B., Thuiller, W., Pearson, R.G. (2006). Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* 33 (10): 1712-1728.

Araújo, M.B., Luoto, M. (2007). The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography* 16 (6): 743-753.

Araújo, M.B., New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution* 22 (1): 42-47.

Arques, S. (2005). *Géodynamique, colonisation végétale et phytodiversité des talus d'éboulis dans le massif de la Grande Chartreuse (Préalpes françaises du Nord). Caractéristiques géo-écologiques et sensibilité aux changements environnementaux.* Ph.D. thesis, Grenoble, France, 432 pp.

Arroyo-García, R., Martínez-Zapater, J.M., Fernández Prieto, J.A., Álvarez-Arbesú, R. (2001). AFLP evaluation of genetic similarity among laurel populations (Laurus L.). *Euphytica* 122 (1): 155-164.

Austin, M. (2007). Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling* 200 (1-2): 1-19.

Austin, M.P. (2002). Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* 157 (2-3): 101-118.

Austin, M.P., Belbin, L., Meyers, J.A., Doherty, M.D., Luoto, M. (2006). Evaluation of statistical models used for predicting plant species distributions: Role of artificial data and theory. *Ecological Modelling* 199 (2): 197-216.

Ávila, S.P., Madeira, P., da Silva, C.M., Cachão, M., Landau, B., Quartau, R., Martins, A.M.d.F. (2008). Local disappearance of bivalves in the Azores during the last glaciation. *Journal of Quaternary Science* 23 (8): 777-785.

Ávila, S.P., Madeira, P., Zazo, C., Kroh, A., Kirby, M., da Silva, C.M., Cachão, M., de Frias Martins, A.M. (2009). Palaeoecology of the Pleistocene (MIS 5.5) outcrops of Santa Maria Island (Azores) in a complex oceanic tectonic setting. *Palaeogeography, Palaeoclimatology, Palaeoecology* 274 (1–2): 18-31.

Axelrod, D.I. (1975). Evolution and Biogeography of Madrean-Tethyan Sclerophyll Vegetation. *Annals of the Missouri Botanical Garden* 62 (2): 280-334.

Azevedo, E.B., Pereira, L.S., Itier, B. (1999). Modeling the local climate in island environments: water balance applications. *Agricultural Water Management* 40: 393-403.

Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R., Latour, J.B. (2002). Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology* 8 (4): 390-407.

Barber, J.C., Francisco-Ortega, J., Santos-Guerra, A., Turner, K.G., Jansen, R.K. (2002). Origin of Macaronesian Sideritis L. (Lamioideae: Lamiaceae) inferred from nuclear and chloroplast sequence datasets. *Molecular Phylogenetics and Evolution* 23 (3): 293-306.

Barbet-Massin, M., Thuiller, W., Jiguet, F. (2012). The fate of European breeding birds under climate, land-use and dispersal scenarios. *Global Change Biology* 18 (3): 881-890.

Barrón, E., Peyrot, D. (2006). La vegetación forestal en el Terciario. In: Carrión, J.S., Fernández, S., Fuentes, N. (eds.), *Paleoambientes y cambio climático*. Fundación Séneca, Murcia, pp. 55-76.

Barry, S., Elith, J. (2006). Error and uncertainty in habitat models. *Journal of Applied Ecology* 43 (3): 413-423.

Baselga, A., Araújo, M.B. (2009). Individualistic vs community modelling of species distributions under climate change. *Ecography* 32 (1): 55-65.

Battaglia, M., Sands, P.J. (1998). Process-based forest productivity models and their application in forest management. *Forest Ecology and Management* 102 (1): 13-32.

Beaumont, L.J., Hughes, L., Poulsen, M. (2005). Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecological Modelling* 186 (2): 251-270.

Beaumont, L.J., Gallagher, R.V., Thuiller, W., Downey, P.O., Leishman, M.R., Hughes, L. (2009). Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Diversity and Distributions* 15 (3): 409-420.

Beckage, B., Osborne, B., Gavin, D.G., Pucko, C., Siccama, T., Perkins, T. (2008). A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences* 105 (11): 4197-4202.

Bellingham, P.J., Tanner, E.V.J., Healey, J.R. (2005). Hurricane disturbance accelerates invasion by the alien tree Pittosporum undulatum in Jamaican montane rain forests. *Journal of Vegetation Science* 16 (6): 675-684.

Beniston, M., Rebetez, M., Giorgi, F., Marinucci, M.R. (1994). An analysis of regional climate change in Switzerland. *Theoretical and Applied Climatology* 49 (3): 135-159.

Beniston, M., Fox, D.G., Adhikary, S., Andressen, R., Guisan, A., Holten, J., Innes, J., Maitima, J., Price, M., Tessier, L. (1996). The Impacts of Climate Change on Mountain Regions., *Second Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)*. Cambridge University Press, pp. 191-213.

Beniston, M., Haeberli, W. (2001). Sensitivity of mountain regions to climatic change. In: Losan, J.L., Grabl, H., Hupfer, P. (eds.), *Climate of the 21st Century: Changes and Risks*. GEO Publications, Hamburg, pp. 237-244.

Beniston, M., Keller, F., Koffi, B., Goyette, S. (2003). Estimates of snow accumulation and volume in the Swiss Alps under changing climate conditions. *Theoretical and Applied Climatology* 76: 125-140.

Beniston, M., Stephenson, D.B. (2004). Extreme climatic events and their evolution under changing climatic conditions. *Global and Planetary Change* 44 (1–4): 1-9.

Benito-Garzón, M. (2002). *Potencialidad y conservacion del elemento paleotropoical lauroide en la Peninsula Iberica. Predicción mediante Redes Neuronales Artificiales en el entorno de un Sistema de Información Geográfica*. MSc Thesis, Universidad Autonoma de Madrid, Madrid, 78 pp.

Benito-Garzón, M., Blazek, R., Neteler, M., Dios, R.S.d., Ollero, H.S., Furlanello, C. (2006). Predicting habitat suitability with machine learning models: The potential area of Pinus sylvestris L. in the Iberian Peninsula. *Ecological Modelling* 197 (3–4): 383-393.

Benning, T.L., LaPointe, D., Atkinson, C.T., Vitousek, P.M. (2002). Interactions of climate change with biological invasions and land use in the Hawaiian Islands: Modeling the fate of endemic birds using a geographic information system. *Proceedings of the National Academy of Sciences* 99 (22): 14246-14249.

Berry, E., Gorchov, D., Endress, B., Stevens, M. (2008). Source-sink dynamics within a plant population: the impact of substrate and herbivory on palm demography. *Population Ecology* 50 (1): 63-77.

Bertrand, R., Lenoir, J., Piedallu, C., Riofrio-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.C., Gegout, J.C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature* 479 (7374): 517-520.

Bio, A.M.F., De Becker, P., De Bie, E., Huybrechts, W., Wassen, M. (2002). Prediction of plant species distribution in lowland river valleys in Belgium: modelling species response to site conditions. *Biodiversity and Conservation* 11 (12): 2189-2216.

Böhle, U.R., Hilger, H.H., Martin, W.F. (1996). Island colonization and evolution of the insular woody habit in Echium L. (Boraginaceae). *Proceedings of the National Academy of Sciences of the United States of America* 93 (21): 11740-11745.

Bond, G.C., Lotti, R. (1995). Iceberg Discharges into the North Atlantic on Millennial Time Scales During the Last Glaciation. *Science* 267 (5200): 1005-1010.

Borges, P.A.V., Brown, V.K. (1999). Effect of island geological age on the arthropod species richness of Azorean pastures. *Biological Journal of the Linnean Society* 66 (3): 373-410.

Borges, P.A.V., Abreu, C., Aguiar, A.M.F., Carvalho, P., Fontinha, S., Jardim, R., Melo, I., Oliveira, P., Sequeira, M.M.d., Sérgio, C., Serrano, A.R.M., Sim-Sim, M., Vieira, P. (2008). Terrestrial and freshwater biodiversity of the Madeira and Selvagens archipelagos. In: Borges, P.A.V., Abreu, C., Aguiar, A.M.F., Carvalho, P., Jardim, R., Melo, I., Oliveira, P., Sérgio, C., Serrano, A.R.M., Vieira, P. (eds.), *A list of the terrestrial fungi, flora and fauna of Madeira and Selvagens archipelagos*. Direcção Regional do Ambiente da Madeira and Universidade dos Açores, Funchal and Angra do Heroismo, pp. 13-25.

Botkin, D.B., Saxe, H., Araujo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., Chesson, P., Dawson, T.P., Etterson, J.R., Faith, D.P., Ferrier, S., Guisan, A., Hansen, A.S., Hilbert, D.W., Loehle, C., Margules, C., New, M., Sobel, M.J., Stockwell, D.R.B. (2007). Forecasting the effects of global warming on biodiversity. *BioScience* 57 (3): 227-236.

Bradley, R.S. (ed.) (1999). *Paleoclimatology. Reconstructing climates of the Quaternary*. 2nd ed, Academic Press, San Diego, USA, 614 pp.

Bramwell, D. (1972). Endemism in the flora of the Canary Islands. In: Valentine, D.H. (ed.), *Taxonomy, Phytogeography and Evolution*. Academic Press, London, New york, pp. 141 - 159.

Bramwell, D. (1985). Contribuición a la biogeografia de las Islas Canarias. *Botanica Macaronesica* 14: 3-34.

Bramwell, D. (1990). Conserving Biodiversity in the Canary Islands. *Annals of the Missouri Botanical Garden* 77 (1): 28-37.

Braunisch, V., Bollmann, K., Graf, R.F., Hirzel, A.H. (2008). Living on the edge--Modelling habitat suitability for species at the edge of their fundamental niche. *Ecological Modelling* 214 (2-4): 153-167.

Breiman, L. (2001). Random Forests. *Machine Learning* 45 (1): 5-32.

Breiman, L., Cutler, A., 2005. Random Forests. *Available from* http://www.stat.berkeley.edu/~breiman/RandomForests/cc_home.htm; accessed on 10/01/2011.

Brewer, A.M., Gaston, K.J. (2003). The geographical range structure of the holly leaf-miner. II. Demographic rates. *Journal of Animal Ecology* 72 (1): 82-93.

Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A.T., Guisan, A. (2007). Evidence of climatic niche shift during biological invasion. *Ecology Letters* 10 (8): 701-709.

Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A. (2008). Synergies among extinction drivers under global change. *Trends in ecology & evolution (Personal edition)* 23 (8): 453-460.

Brotons, L., Thuiller, W., Araújo, M.B., Hirzel, A.H. (2004). Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography* 27 (4): 437-448.

Brotons, L., Herrando, S., Pla, M. (2007). Updating bird species distribution at large spatial scales: applications of habitat modelling to data from long-term monitoring programs. *Diversity and Distributions* 13 (3): 276-288.

Buisson, L., Thuiller, W., Lek, S., Lim, P.U.Y., Grenouillet, G. (2008). Climate change hastens the turnover of stream fish assemblages. *Global Change Biology* 14 (10): 2232-2248.

Bullock, J.M., Edwards, R.J., Carey, P.D., Rose, R.J. (2000). Geographical separation of two Ulex species at three spatial scales: does competition limit species' ranges? *Ecography* 23 (2): 257-271.

Busby, J.R. (1991). BIOCLIM - a bioclimatic analysis and prediction system. *Nature Conservation: cost effective biological surveys and data analysis*, pp. 64-68.

Byers, J.E. (2002). Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos* 97 (3): 449-458.

Callapez, P., Soares, A.F. (2000). Late Quaternary warm marine mollusks from Santa Maria (Azores). Paleoecologic and paleobiogeographic considerations. *Ciências da Terra (UNL)* 14: 313-322.

Capelo, J., Sequeira, M., Jardim, R., Costa, J.C. (2004). Guia da excursão geobotânica dos V Encontros ALFA 2004 à Ilha da Madeira. *Quercetea* 6: 5-46.

Capelo, J., Sequeira, M.M.d., Jardim, R., Mesquita, S. (2007). Madeira. In: Silva, J.S. (ed.), *Açores e Madeira. A Floresta das Ilhas*, vol. 6. Fundação Luso-Americana para o Desenvolvimento, Público e Liga para a Proteção da Natureza, Lisboa, pp. 81-134.

Carine, M.A., Russell, S.J., Santos-Guerra, A., Francisco-Ortega, J. (2004). Relationships of the Macaronesian and Mediterranean floras: molecular evidence for multiple colonizations into Macaronesia and back-colonization of the continent in Convolvulus (Convolvulaceae). *Am. J. Bot.* 91 (7): 1070-1085.

Carine, M.A. (2005). Spatio-temporal relationships of the Macaronesian endemic flora: a relictual series or window of opportunity? *Taxon* 54 (4): 895-903.

Carine, M.A., Schaefer, H. (2010). The Azores diversity enigma: why are there so few Azorean endemic flowering plants and why are they so widespread? *Journal of Biogeography* 37 (1): 77-89.

Carlquist, S. (1974). *Island Biology*. Columbia University Press, New York, USA.

Carpenter, G., Gillison, A.N., Winter, J. (1993). DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity and Conservation* 2 (6): 667-680.

Carrión, J.S., Fernández, S., Jiménez-Moreno, G., Fauquette, S., Gil-Romera, G., González-Sampériz, P., Finlayson, C. (2010). The historical origins of aridity and vegetation degradation in southeastern Spain. *Journal of Arid Environments* 74 (7): 731-736.

Carvalho, A.M.G.d., Brandão, J.M. (1991). *Geologia do arquipélago da Madeira*. Museu Nacional de História Natural, Lisboa. 170 pp.

Castro, E.B., González, M.A.C., Tenorio, M.C., Bombin, R.E., Antón, M.G., Fuster, M.G., Manzaneque, Á.G., Manzaneque, F.G., Sainz, J.C.M., Juaristi, C.M., Pajares, P.R., Ollero, H.S. (2005). *Los Bosques Ibéricos. Una Interpretación Geobotánica*, 4 ed. Editorial Planeta, Barcelona. 597 pp.

Castro, M., Martín-Vide, S., Alonso, S. (2004). El clima de España: pasado, presente y escenarios de clima para el siglo XXI. In: Moreno, J.M. (ed.), *Evaluación de los impactos del cambio climatico en España*. Ministerio de Medio Ambiente, Madrid, pp. 1-64.

Castroviejo, S., Laínz, M., González, G.L., Montserrat, P., Garmendia, F.M., Paiva, J., Villar, L. (eds.) (1986-2012). *Flora Iberica. Plantas vasculares de la Península Iberica e Islas Baleares*, Real Jardín Botánico, C.S.I.C., Madrid.

Catalán, A.S.d.S. (1996). La evolución de las paleofloras en las cuencas cenozoicas catalanas. *Acta Geologica Hispanica* 29 (2-4): 169-189.

Caujapé-Castells, J. (2004). Boomerangs of biodiversity?: the interchange of biodiversity between mainland North Africa and the Canary Islands as inferred from CPDNA RFLPS in genus Androcymbium. *Botanica Macaronesica* 25: 53-69.

Cermak, J., Kucera, J., Nadezhdina, N. (2004). Sap flow measurements with some thermodynamic methods, flow integration within trees and scaling up from sample trees to entire forest stands. *Trees* 18 (5): 529-546.

Chambers, J.C., Wisdom, M.J. (2009). Priority Research and Management Issues for the Imperiled Great Basin of the Western United States. *Restoration Ecology* 17 (5): 707-714.

Chapman, A.R., Conn, B.J., Court, A.B., Cowan, R.S., George, A.S., Keith, D.A., Kodela, P.G., Leach, G.J., Lewington, M.A., McDonald, M.W., Maslin, B.R., Pedley, L., Ross, J.H., Tame, T.M., Tindale, M.D., 2001. Acacia, Flora of Australia, CSIRO PUBLISHING.

Chase, J.M., Leibold, M.A. (2003). *Ecological Niches: Linking Classical and Contemporary Approaches*. The University of Chicago Press, Chicago and London. 212 pp.

Cheaib, A., Badeau, V., Boe, J., Chuine, I., Delire, C., Dufrêne, E., François, C., Gritti, E.S., Legay, M., Pagé, C., Thuiller, W., Viovy, N., Leadley, P. (2012). Climate change impacts on tree ranges: model intercomparison facilitates understanding and quantification of uncertainty. *Ecology Letters* 15 (6): 533-544.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D. (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science* 333 (6045): 1024-1026.

Chornesky, E.A., Randall, J.M. (2003). The Threat of Invasive Alien Species to Biological Diversity: Setting a Future Course. *Annals of the Missouri Botanical Garden* 90 (1): 67-76.

Clements, F.E. (1916). *Plant Sucession. An Analysis of the Development of Vegetation*. Carnegie Institution of Washington, Washington. 512 pp.

Coetzee, B.W.T., Robertson, M.P., Erasmus, B.F.N., Van Rensburg, B.J., Thuiller, W. (2009). Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. *Global Ecology and Biogeography* 18 (6): 701-710.

Colwell, R.K., Brehm, G., Cardelús, C.L., Gilman, A.C., Longino, J.T. (2008). Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics. *Science* 322 (5899): 258-261.

Connor, S.E., van Leeuwen, J.F.N., Rittenour, T.M., van der Knaap, W.O., Ammann, B., Björck, S. (2012). The ecological impact of oceanic island colonization – a palaeoecological perspective from the Azores. *Journal of Biogeography* 39 (6): 1007-1023.

Coops, N.C., Waring, R.H., Schroeder, T.A. (2009). Combining a generic process-based productivity model and a statistical classification method to predict the presence and absence of tree species in the Pacific Northwest, U.S.A. *Ecological Modelling* 220 (15): 1787-1796.

Corlett, R.T., Westcott, D.A. (2013). Will plant movements keep up with climate change? *Trends in Ecology & Evolution* In press:

Costa, J.C., Aguiar, C., Capelo, J., Lousa, M., Neto, C. (1998). Biogeografia de Portugal Continental. *Querceta* 0: 5-56.

Costa, J.C., Capelo, J., Jardim, R., Sequeira, M., Espirito-Santo, D., Lousã, M., Fontinha, S., Aguiar, C., Rivas-Martinez, S., 2004. Catálogo sintaxonómico e floristico das comunidades vegetais da Madeira e Porto Santo, in: Capelo, J. (Ed.), A paisagem vegetal da Ilha da Madeira. Quercetea, pp. 61 - 185.

Cronk, Q.C.B. (1992). Relict floras of Atlantic islands: patterns assessed. *Biological Journal of the Linnean Society* 46 (1-2): 91-103.

Cronk, Q.C.B. (1997). Islands: stability, diversity, conservation. *Biodiversity and Conservation* 6 (3): 477-493.

Dansereau, P. (1961). Études Macaronésiennes. I: Géographie des cryptogrammes vasculaires. *Agronomia Lusitana* 23: 151-181.

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B., Wood, S. (1998). Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391 (6669): 783-786.

Davis, M.B., Shaw, R.G. (2001). Range shifts and adaptive responses to quaternary climate change. *Science* 292: 673-679.

De Nascimento, L., Willis, K.J., Fernández-Palacios, J.M., Criado, C., Whittaker, R.J. (2009). The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). *Journal of Biogeography* 36 (3): 499-514.

Demangeot, J. (2000). *Os meios naturais do Globo*. Fundação Calouste Gulbenkian. 482 pp.

Désamoré, A., Laenen, B., Devos, N., Popp, M., González-Mancebo, J.M., Carine, M.A., Vanderpoorten, A. (2011). Out of Africa: north-westwards Pleistocene expansions of the heather Erica arborea. *Journal of Biogeography* 38 (1): 164-176.

Desprez-Loustau, M.-L., Robin, C., Reynaud, G., Déqué, M., Badeau, V., Piou, D., Husson, C., Marçais, B. (2007). Simulating the effects of a climate-change scenario on the geographical range and activity of forest-pathogenic fungi. *Canadian Journal of Plant Pathology* 29 (2): 101-120.

Dias, E. (2007). A Chegada dos portugueses às ilhas – o antes e o depois. Açores. In: Silva, J.S. (ed.), *Árvores e Florestas de Portugal*, vol. 6 - Açores e Madeira - A Floresta das Ilhas. Público, Fundação Luso-Americana e Liga para a Proteção da Natureza, Lisboa, pp. 137 - 164.

Dias, E., Araújo, C., Mendes, J.F., Elias, R.B., Mendes, C., Melo, C. (2007a). Espécies florestais das ilhas. Açores. In: Silva, J.S. (ed.), *Árvores e Florestas de Portugal*, vol. 6 - Açores e Madeira - A Floresta das Ilhas. Público, Fundação Luso-Americana e Liga para a Proteção da Natureza, Lisboa, pp. 199 - 254.

Dias, E., Elias, R.B., Melo, C., Mendes, C. (2007b). Açores. In: Silva, J.S. (ed.), *Açores e Madeira. A Floresta das Ilhas*, vol. 6. Fundação Luso-Americana para o Desenvolvimento, Público e Liga para a Proteção da Natureza, Lisboa, pp. 51-80.

Dias, E., Elias, R.B., Melo, C., Mendes, C. (2007c). O elemento insular na estruturação das florestas da Macaronésia. In: Silva, J.S. (ed.), *Açores e Madeira. A Floresta das Ilhas*, vol. 6. Fundação Luso-Americana para o Desenvolvimento, Público e Liga para a Proteção da Natureza, Lisboa, pp. 15-48.

Díaz-Pérez, A., Sequeira, M., Santos-Guerra, A., Catalán, P. (2008). Multiple Colonizations, In Situ Speciation, and Volcanism-Associated Stepping-Stone Dispersals Shaped the Phylogeography of the Macaronesian Red Fescues (Festuca L., Gramineae). *Systematic Biology* 57 (5): 732-749.

Dormann, C.F. (2007). Promising the future? Global change projections of species distributions. *Basic and Applied Ecology* 8 (5): 387-397.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30 (5): 609-628.

Duarte, M., Rego, F., Romeiras, M., Moreira, I. (2008). Plant species richness in the Cape Verde Islands—eco-geographical determinants. *Biodiversity and Conservation* 17 (3): 453-466.

Dukes, J.S., Mooney, H.A. (1999). Does global change increase the success of biological invaders? *Trends in Ecology & Evolution* 14 (4): 135-139.

Dullinger, S., Kleinbauer, I., Peterseil, J., Smolik, M., Essl, F. (2009). Niche based distribution modelling of an invasive alien plant: effects of population status, propagule pressure and invasion history. *Biological Invasions* 11 (10): 2401-2414.

Dupont, L. (2011). Orbital scale vegetation change in Africa. *Quaternary Science Reviews* 30 (25–26): 3589-3602.

Dye, Peter, Jarmain, Caren, G. (2004). Water use by black wattle (Acacia mearnsii): Implications for the link between removal of invading trees and catchment streamflow response. *South African Journal of Science* 100 (1-2): 40-44.

EEA, European Environmental Agency (2008). *Impacts of Europe's Changing Climate*. Report nr 4, Kopenhagen, 242 pp. Available at http://www.eea.europa.eu/publications/eea_report_2008_4 on 5/7/2010.

Ehrenfeld, J.G. (2003). Effects of Exotic Plant Invasions on Soil Nutrient Cycling Processes. *Ecosystems* 6 (6): 503-523.

Elith, J., Graham, C.H., Anderson, R.P., Dudık, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. McC., Peterson, A. T., Phillips, S. J., Richardson, K. S., Scachetti-Pereira, R., Schapire, R. E., Soberon, J., Williams, S., Wisz, M. S. and Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29 (2): 129-151.

Elith, J., Graham, C.H. (2009). Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. *Ecography* 32 (1): 66-77.

Elith, J., Leathwick, J.R. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics* 40 (1): 677-697.

Elton, C. (1927). *Animal Ecology*. Macmillan Co., New York. 207 pp.

Emerson, B.C. (2002). Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. *Molecular Ecology* 11 (6): 951-966.

Emerson, B.C., kolm, N. (2005). Species diversity can drive speciation. *Nature* 434: 1015-1017.

Engler, R., Guisan, A., Rechsteiner, L. (2004). An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data : Modelling species distribution. *Journal of Applied Ecology* 41 (2): 263-274.

Engler, R., Randin, C.F., Vittoz, P., Czáka, T., Beniston, M., Zimmermann, N.E., Guisan, A. (2009). Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? *Ecography* 32 (1): 34-45.

Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N.E., Araújo, M.B., Pearman, P.B., Le Lay, G., Piedallu, C., Albert, C.H., Choler, P., Coldea, G., De Lamo, X., Dirnbock, T., Gégout, J.-C., Gómez-García, D., Grytnes, J.-A., Heegaard, E., HØlstad, F., Nogués-Bravo, D., Normand, S., Puscas, M., Sebastiá, M.-T., Stanisci, A., Theurillat, J.-P., Trivedi, M.R., Vittoz, P., Guisan, A. (2011). 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology* 17 (7): 2330-2341.

EPICA (2004). Eight glacial cycles from an Antarctic ice core. *Nature* 429 (6992): 623-628.

Erasmus, B.F.N., Van Jaarsveld, A.S., Chown, S.L., Kshatriya, M., Wessels, K.J. (2002). Vulnerability of South African animal taxa to climate change. *Global Change Biology* 8: 679-693.

Espeland, E., Emam, T. (2011). The value of structuring rarity: the seven types and links to reproductive ecology. *Biodiversity and Conservation* 20 (5): 963-985.

Eynaud, F., de Abreu, L., Voelker, A., Schönfeld, J., Salgueiro, E., Turon, J.-L., Penaud, A., Toucanne, S., Naughton, F., Sánchez Goñi, M.F., Malaizé, B., Cacho, I. (2009). Position of the Polar Front along the western Iberian margin during key cold episodes of the last 45 ka. *Geochem. Geophys. Geosyst.* 10 (7): Q07U05.

Eynaud, F. (2010). *Long term and recent climate changes recorded in North Atlantic oceanic archives around Iceland.* Available at http://hal.inria.fr/docs/00/48/07/07/PDF/Frederique_Eynaud.pdf on 10/05/2011.

Farrell, T., Ashton, D. (1978). Population Studies on Acacia melanoxylon R. Br. I. Variation in Seed and Vegetative Characteristics. *Australian Journal of Botany* 26 (3): 365-379.

Fatunbi, A.O., Dube, S., Yakubu, M.T., Tshabalala, T. (2009). Allelopathic Potential of Acacia mearnsii De Wild. *World Applied Sciences Journal* 7 (12): 1488.

Fauquette, S., Suc, J.-P., Guiot, J., Diniz, F., Feddi, N., Zheng, Z., Bessais, E., Drivaliari, A. (1999). Climate and biomes in the West Mediterranean area during the Pliocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 152 (1–2): 15-36.

Felde, V.A., Kapfer, J., Grytnes, J.-A. (2012). Upward shift in elevational plant species ranges in Sikkilsdalen, central Norway. *Ecography* 35 (10): 922-932.

Felicisimo, A.M., Muñoz, J., Mateo, R.G., Villalba, C.J. (2012). Vulnerabilidade de la flora y vegetación españolas ante el cambio climatico. *Ecosistemas* 21 (3): 1-6.

Feria, T.P., Peterson, A.T. (2002). Prediction of bird community composition based on point-occurrence data and inferential algorithms: a valuable tool in biodiversity assessments. *Diversity and Distributions* 8 (2): 49-56.

Fernández-García, F. (1995). *Manual de climatología aplicada : clima, medio ambiente y planificación*. Sintesis, Madrid. 285 pp.

Fernández-Palacios, J.M. (1992). Climatic responses of plant species on Tenerife, The Canary Islands. *Journal of Vegetation Science* 3 (5): 595-603.

Fernández-Palacios, J.M., Andersson, C. (2000). Geographical determinants of the biological richness in the Macaronesian region. *Acta Phytogeographica Suecica* 85: 41-50.

Fernández-Palacios, J.M., Otto, R., Delgado, J.D., Arévalo, J.R., Naranjo, A., Artiles, F.G., Morici, C., Barone, R. (2008). *Los bosques termófilos de Canárias*. Excmo. Cabildo Insular de Tenerife, Santa Cruz de Tenerife. 192 pp.

Fernández-Palacios, J.M., de Nascimento, L., Otto, R., Delgado, J.D., García-del-Rey, E., Arévalo, J.R., Whittaker, R.J. (2011). A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. *Journal of Biogeography* 38 (2): 226-246.

Ferreira, D.d.B. (1989). *Le climat de l'Atlantique oriental, des Açores ausx îles du Cap Vert. Contribution à l'étude du sistéme ócean-atmosphère.* PhD Université de Paris - Sorbonne, Paris, 1657 pp.

Ferreira, D.d.B. (2005). O espaço Atlântico Oriental. In: Medeiros, C.A. (ed.), *Geografia de Portugal: O Ambiente Físico*, vol. I. Círculo de Leitores, Mem Martins, pp. 258-303.

Ferrier, S., Drielsma, M., Manion, G., Watson, G. (2002a). Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. II. Community-level modelling. *Biodiversity and Conservation* 11 (12): 2309-2338.

Ferrier, S., Watson, G., Pearce, J., Drielsma, M. (2002b). Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling. *Biodiversity and Conservation* 11 (12): 2275-2307.

Ferrier, S., Guisan, A. (2006). Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology* 43 (3): 393-404.

Fielding, A.H., Bell, J.F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24 (1): 38-49.

Figueiredo, A. (2008). Desempenho de um modelo de máxima entropia na previsão da distribuição do endemismo Euphorbia piscatoria na Ilha da Madeira. *Cadernos de Geografia* 26/27:

Figueiredo, A., Pupo-Correia, A., Almeida, A.C.d., Sequeira, M.M.d. (unpublished data). Distribuição actual e potencial de espécies do género Acacia Mill. (Fabaceae) na Ilha da Madeira e implicações para a diversidade florística em contexto de invasão. *Quercetea* accepted:

Foden, Wendy, Midgley, Guy, F., Hughes, Greg, Bond, William, J., Thuiller, Wilfried, Hoffman, Timm, M., Kaleme, Prince, Underhill, Les, G., Rebelo, Anthony, Hannah, Lee (2007). A changing climate is eroding the geographical range of the Namib Desert tree Aloe through population declines and dispersal lags. *Diversity & Distributions* 13 (5): 645-653.

Francisco-Ortega, J., Jansen, R., Santos-Guerra, A. (1996). Chloroplast DNA evidence of colonization, adaptive radiation, and hybridization in the evolution of the Macaronesian flora. *PNAS* 93 (9): 4085-4090.

Francisco-Ortega, J., Santos-Guerra, A., Hines, A., Jansen, R. (1997). Molecular evidence for a Mediterranean origin of the Macaronesian endemic genus Argyranthemum (Asteraceae). *Am. J. Bot.* 84 (11): 1595-.

Francisco-Ortega, J., Santos-Guerra, A., Kim, S.-C., Crawford, D.J. (2000). Plant genetic diversity in the Canary Islands: a conservation perspective. *Am. J. Bot.* 87 (7): 909-919.

Freeman, E.A., Moisen, G.G. (2008). A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecological Modelling* 217 (1-2): 48-58.

Friedman, J., Hastie, T., Tibshirani, R. (2000). Additive logistic regression: a statistical view of boosting. *The Annals of Statistics* 28 (2): 337-407.

Friedman, J.H. (1991). Multivariate adaptive regression splines. *The Annals of Statistics* 19 (1): 1-67.

Fronzek, S., Carter, T.R., Luoto, M. (2011). Evaluating sources of uncertainty in modelling the impact of probabilistic climate change on sub-arctic palsa mires. *Nat. Hazards Earth Syst. Sci.* 11 (11): 2981-2995.

Gaertner, M., Richardson, D., Privett, S.J. (2011). Effects of Alien Plants on Ecosystem Structure and Functioning and Implications for Restoration: Insights from Three Degraded Sites in South African Fynbos. *Environmental management* 48 (1): 57-69.

Garcia-Talavera, F. (1999). La Macaronesia. Consideraciones geologicas, biogeográficas y paleoecológicas. In: FERNÁNDEZ-PALACIOS, J.M., BACALLADO, J.J., BELMONTE, J.A. (eds.), *Ecologia y cultura en Canárias*. Organismo Autónomo de Museos y Centros, Cabildo Insular de Tenerife., Santa Cruz deTenerife, Tenerife, pp. 39-63.

Garske, S. (2010). *GLIFWC Invasive Plant Risk Assessment/Prioritization Models for Ashland, Douglas, Bayfield, and Iron Counties of Nosthern Wiscosin.* Available at http://www.glifwc.org/Reports/reports.html on 23 November 2010.

Gaston, K.J. (2009). Geographic range limits of species. *Proceedings of the Royal Society B: Biological Sciences* 276 (1661): 1391-1393.

Gaubert, P., Papes, M., Peterson, A.T. (2006). Natural history collections and the conservation of poorly known taxa: Ecological niche modeling in central African rainforest genets (Genetta spp.). *Biological Conservation* 130 (1): 106-117.

Gehrig-Fasel, J., Guisan, A., Zimmermann, N.E. (2007). Tree line shifts in the Swiss Alps: Climate change or land abandonment? *Journal of Vegetation Science* 18 (4): 571-582.

Géhu, J.M., Rivas-Martínez, S. (1981). Notions fondamentales de phytosociologie. In: Dierschke, H. (ed.), *Syntaxonomie. Berichte der Internationalen Symposien der Internationalen Vereinigung Vegetationskunde.*, Vaduz, pp. 5-33.

Gil, A., Lobo, A., Abadi, M., Silva, L., Calado, H. (2013). Mapping invasive woody plants in Azores Protected Areas by using high-resolution multiespectral imagery. *European Journal of Remote Sensing* 46: 289-304.

Givnish, T.J. (1998). Adaptive plant evolution on islands: classical patterns, molecular data, new insights. In: Grant, P.R. (ed.), *Evolution os Islands*. Oxford University Press, New York, USA, pp. 281-304.

Gleadow, R., Ashton, D. (1981). Invasion by *Pittosporum undulatum* of the Forests of Central Victoria. I. Invasion Patterns and Plant Morphology. *Australian Journal of Botany* 29 (6): 705-720.

Gleadow, R. (1982). Invasion by *Pittosporum undulatum* of the Forests of Central Victoria. II. Dispersal, Germination and Establishment. *Australian Journal of Botany* 30 (2): 185-198.

Gleadow, R.M., Rowan, K.S., Ashton, D.H. (1983). Invasion by *Pittosporum undulatum* of the Forests of Central Victoria. IV - Shade Tolerance. *Australian Journal of Botany* 31: 151-160.

Gleason, H.A. (1926). The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53 (1): 7-26.

González, S.d.R. (2005). El cambio climático y su influencia en la vegetación de Castilla y Léon (España). *Itinera Geobotanica* 16: 5-533.

González-Rodríguez, A.M., Morales, D., Jiménez, M.S. (2001). Gas exchange characteristics of a Canary laurel forest tree species (*Laurus azorica*) in relation to environmental conditions and leaf canopy position. *Tree Physiology* 21 (14): 1039-1045.

González-Rodríguez, A.M., Morales, D., Jiménez, M.S. (2002). Leaf gas exchange characteristics of a Canarian laurel forest tree species [Persea indica (L.) K. Spreng.] under natural conditions. *Journal of Plant Physiology* 159 (7): 695-704.

González-Rodríguez, Á.M., Jiménez, M.S., Morales, D. (2005). Seasonal and intraspecific variation of frost tolerance in leaves of three Canarian laurel forest tree species. *Ann. For. Sci.* 62 (5): 423-428.

Goodfriend, G.A., Cameron, R.A.D., Cook, L.M., Courty, M.-A., Federoff, N., Kaufman, A., Livett, E., Tallis, J. (1996). Quaternary eolianite sequence of Madeira: stratigraphy, chronology and paleoenvironmental interpretation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 120: 195-234.

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barancok, P., Benito Alonso, J.L., Coldea, G., Dick, J., Erschbamer, B., Fernandez Calzado, M.R., Kazakis, G., Krajci, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., Nagy, L., Nakhutsrishvili, G., Pedersen, B., Pelino, G., Puscas, M., Rossi, G., Stanisci, A., Theurillat, J.-P., Tomaselli, M., Villar, L., Vittoz, P., Vogiatzakis, I., Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Clim. Change* 2: 111-115.

Grabherr, G., Gottfried, M., Pauli, H. (1994). Climate effects on mountain plants. *Nature* 369 (6480): 448-448.

Grace, J., Berninger, F., Nagy, L. (2002). Impacts of climate change on the tree line. *Annals of Botany* 90 (4): 537-544.

Graham, C.H., Elith, J., Hijmans, R.J., Guisan, A., Townsend Peterson, A., Loiselle, B.A., The Nceas Predicting Species Distributions Working, G. (2008). The influence of spatial errors in species occurrence data used in distribution models. *Journal of Applied Ecology* 45 (1): 239-247.

Graham, M.H. (2003). Confronting multicollinearity in ecological multiple regression. *Ecology* 84 (11): 2809-2815.

Grinnell, J. (1914). Barriers to Distribution as Regards Birds and Mammals. 48 (568): 248-254.

Grinnell, J. (1917). The Niche-Relationships of the California Thrasher. *The Auk* 34 (4): 427-433.

Guimarães, A., Olmeda, C., European Comission (2008). *Management of Natura 2000 habitat. 9360 *Macaronesian laurel forests (Laurus, Ocotea)*. TR 23/24, 26 pp. Available at http://ec.europa.eu/environment/nature/natura2000/management/habitats/pdf/9360_Macaronesian_laurel_forests.pdf on 25/10/2009.

Guisan, A., Zimmermann, N.E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling* 135 (2-3): 147-186.

Guisan, A., Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8 (9): 993-1009.

Habel, J.C., Assmann, T. (eds.) (2010). *Relict Species. Phylogeography and conservation biology.*, Springer Verlag, Berlin, 449 pp.

Håkanson, L. (1995). Optimal size of predictive models. *Ecological Modelling* 78 (3): 195-204.

Hampe, A. (2004). Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography* 13 (5): 469-471.

Hampe, A., Petit, R. (2005). Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters* 8 (5): 461-467.

Hannah, L., Midgley, G.F., Millar, D. (2002). Climate change-integrated conservation strategies. *Global Ecology and Biogeography* 11 (6): 485-495.

Hannah, L., Midgley, G., Andelman, S., Araujo, M., Hughes, G., Martinez-Meyer, E., Pearson, R., Williams, P. (2007). Protected area needs in a changing climate. *Frontiers in Ecology and the Environment* 5 (3): 131-138.

Harper, K.A., Danby, R.K., De Fields, D.L., Lewis, K.P., Trant, A.J., Starzomski, B.M., Savidge, R., Hermanutz, L. (2011). Tree spatial pattern within the forest tundra ecotone: a comparison of sites across Canada. *Canadian Journal of Forest Research* 41 (3): 479-489.

Harrell, F.E., Lee, K.L., Mark, D.B. (1996). MULTIVARIABLE PROGNOSTIC MODELS: ISSUES IN DEVELOPING MODELS, EVALUATING ASSUMPTIONS AND ADEQUACY, AND MEASURING AND REDUCING ERRORS. *Statistics in Medicine* 15 (4): 361-387.

Heikkinen, R., Luoto, M., Leikola, N., Pöyry, J., Settele, J., Kudrna, O., Marmion, M., Fronzek, S., Thuiller, W. (2010). Assessing the vulnerability of European butterflies to climate change using multiple criteria. *Biodiversity and Conservation* 19 (3): 695-723.

Heikkinen, R.K., Luoto, M., Araujo, M.B., Virkkala, R., Thuiller, W., Sykes, M.T. (2006). Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography* 30 (6): 751-777.

Heikkinen, R.K., Luoto, M., Virkkala, R., Pearson, R.G., Körber, J.-H. (2007). Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecology and Biogeography* 16 (6): 754-763.

Hellmann, J.J., Byers, J.E., Bierwagen, B.G., Dukes, J.S. (2008). Five potential consequences of climate change for invasive species. *Conserv Biol* 22 (3): 534-543.

Henderson, S., Dawson, T.P., Whittaker, R.J. (2006). Progress in invasive plants research. *Progress in Physical Geography*: 25-46.

Herrera, C. (1995). Plant-Vertebrate Seed Dispersal Systems in the Mediterranean: Ecological, Evolutionary, and Historical Determinants. Annual Review of Ecology ans Systematics 26: 705-727.

Hess, J., Kadereit, J.W., Vargas, P. (2000). The colonization history of *Olea europaea* L. in Macaronesia based on internal transcribed spacer 1 (ITS-1) sequences, randomly amplified polymorphic DNAs (RAPD), and intersimple sequence repeats (ISSR). *Molecular Ecology* 9 (7): 857-868.

Hewitt, G. (2000). The genetic legacy of the Quaternary ice ages. *Nature* 405 (6789): 907-913.

Hilbert, D.W., Ostendorf, B. (2001). The utility of artificial neural networks for modelling the distribution of vegetation in past, present and future climates. *Ecological Modelling* 146 (1–3): 311-327.

Hill, M.O. (1991). Patterns of species distribution in Britain elucidated by canonical correspondence analysis. *Journal of Biogeography* 18 (3): 247-255.

Hirzel, A., Guisan, A. (2002). Which is the optimal sampling strategy for habitat suitability modelling. *Ecological Modelling* 157 (2-3): 331-341.

Hirzel, A.H., Le Lay, G. (2008). Habitat suitability modelling and niche theory. *Journal of Applied Ecology* 45 (5): 1372-1381.

Hobohm, C. (2000). Plant species diversity and endemism on islands and archipelagos, with special reference to the Macaronesian Islands. *Flora; Morphologie, Geobotanik, Oekophysiologie* 195 (1): 9-24.

Holle, B.V., Simberloff, D. (2005). Ecological Resistance to Biological Invasion Overwhelmed by Propagule Pressure. *Ecology* 86 (12): 3212-3218.

Holzinger, B., Hülber, K., Camenisch, M., Grabherr, G. (2008). Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates. *Plant Ecology* 195 (2): 179-196.

Hooghiemstra, H., Lézine, A.-M., Leroy, S.A.G., Dupont, L., Marret, F. (2006). Late Quaternary palynology in marine sediments: A synthesis of the understanding of pollen distribution patterns in the NW African setting. *Quaternary International* 148 (1): 29-44.

Hortal, J., Borges, P.A.V., Jiménez-Valverde, A., de Azevedo, E.B., Silva, L. (2010). Assessing the areas under risk of invasion within islands through potential distribution modelling: The case of Pittosporum undulatum in São Miguel, Azores. *Journal for Nature Conservation* 18 (4): 247-257.

Hou, J.-h., Mi, X.-c., Liu, C.-r., Ma, K.-p. (2006). Tree competition and species coexistence in a Quercus–Betula forest in the Dongling Mountains in northern China. *Acta Oecologica* 30 (2): 117-125.

Howell, C. (2008). Consolidated list of environmental weeds in New Zealand. *DOC Research & Development Series* 292: 42 pp.

Hughes, L. (2000). Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution* 15 (2): 56-61.

Hughes, L. (2003). Climate change and Australia: Trends, projections and impacts. *Austral Ecology* 28 (4): 423-443.

Hutchinson, G.E. (1957). Concluding Remarks. *Cold Sping Harb. Symp. Quant. Biol.* 22: 415-427.

Hutchinson, G.E. (1978). *An Introduction to Population Ecology*. Yale University Press, New Haven.

IPCC, IPCC (2007a). *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom and New York, NY,USA, 996 pp. Available at http://www.ipcc.ch/publications_and_data/ar4/wg1/en/contents.html on 10/05/2009.

IPCC, IPCC (2007b). *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom and New York, NY,USA, 996 pp. Available at http://www.ipcc.ch/publications_and_data/ar4/wg2/en/contents.html on 10/05/2009.

Iverson, L.R., Prasad, A.M. (1998). Predicting abundance of 80 tree species following climate change in eastern United States. *Ecological Monographs* 68 (4): 465-485.

Iverson, L.R., Prasad, A.M. (2002). Potential redistribution of tree species habitat under five climate change scenarios in the eastern US. *Forest Ecology and Management* 155 (1–3): 205-222.

Iverson, L.R., Schwartz, M.W., Prasad, A.M. (2004). How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography* 13 (3): 209-219.

Jackson, S.T., Overpeck, J.T. (2000). Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* 26 (sp4): 194-220.

Jaeschke, A., Bittner, T., Jentsch, A., Reineking, B., Schlumprecht, H., Beierkunlein, C. (2012). Biotic Interactions in the Face of Climate Change: A Comparison of Three Modelling Approaches. *PLos ONE* 7 (12): e51472.

Jardim, R., Sequeira, M.M., Capelo, J. (2007). Espécies florestais das ilhas. 2 - Madeira. In: Silva, J.S. (ed.), *Açores e Madeira. A floresta das ilhas*, vol. 6. Fundação Luso-Americana para o Desenvolvimento, Público e Liga para a Proteção da Natureza, Lisboa, pp. 255 - 296.

Jardim, R., Sequeira, M.M.d. (2008a). The vascular plants (Pteridophyta and Spermatophyta) of Madeira and Selvagens archipelagos. In: Borges, P.A.V., Abreu, C., Aguiar, A.M.F., Carvalho, P., Jardim, R., Melo, I., Oliveira, P., Sérgio, C., Serrano, A.R.M., Vieira, P. (eds.), *A list of the terrestrial fungi, flora and fauna of Madeira and Selvagens archipelagos*. Direcção Regional do Ambiente da Madeira e Universidade dos Açores, Funchal e Angra do Heroísmo, pp. 157-208.

Jardim, R., Sequeira, M.M.d. (2008b). List of vascular plants (Pteridophyta and Spermatophyta). In: Borges, P.A.V., Abreu, C., Aguiar, A.M.F., Carvalho, P., Jardim, R., Melo, I., Oliveira, P., Sérgio, C., Serrano, A.R.M., Vieira, P. (eds.), *A list of the terrestrial fungi, flora and fauna of Madeira and Selvagens archipelagos*. Direcção Regional do Ambiente da Madeira e Universidade dos Açores, Funchal e Angra do Heroísmo, pp. 157-208.

Jewell, K.J., Arcese, P., Gergel, S.E. (2007). Robust predictions of species distribution: Spatial habitat models for a brood parasite. *Biological Conservation* 140 (3-4): 259-272.

Jiménez, M.S., Cermák, J., Kucera, J., Morales, D. (1996). Laurel forests in Tenerife, Canary Islands: the annual course of sap flow in Laurus trees and stand. *Journal of Hydrology* 183 (3–4): 307-321.

Jimenez-Moreno, G., Popescu, S.-M., Ivanov, D., SUC, J.-P. (2007). Neogene flora, vegetation and climate dynamics in southeastern Europe and the northeastern Mediterranean. In: Williams, M., Haywood, A.M., Gregory, F.J., Schmidt, D.N. (eds.), *Deep-time perspectives on climate change: marrying the signal from computer models and biological proxies.* The Micropaleontological Society, Special Publications. The Geological Society, London, pp. 503-516.

Jiménez-Moreno, G., Suc, J.-P. (2007). Middle Miocene latitudinal climatic gradient in Western Europe: Evidence from pollen records. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253 (1–2): 208-225.

Jiménez-Moreno, G., Fauquette, S., Suc, J.-P. (2010). Miocene to Pliocene vegetation reconstruction and climate estimates in the Iberian Peninsula from pollen data. *Review of Palaeobotany and Palynology* 162 (3): 403-415.

Jiménez-Valverde, A., Lobo, J.M. (2006). The ghost of unbalanced species distribution data in geographical model predictions. *Diversity and Distributions* 12 (5): 521-524.

Jones, C.C., Reichard, S. (2009). Current and Potential Distributions of Three Non-Native Invasive Plants in the Contiguous USA. *Natural Areas Journal* 29 (4): 332-343.

Jurasinski, G., Kreyling, J. (2007). Upward shift of alpine plants increases floristic similarity of mountain summits. *Journal of Vegetation Science* 18 (5): 711-718.

Kadmon, R., Farber, O., Danin, A. (2003). A Systematic Analysis of Factors Affecting the Performance of Climatic Envelope Models. *Ecological Applications* 13 (3): 853-867.

Kadmon, R., Farber, O., Danin, A. (2004). Effect of Roadside Bias on the Accuracy of Predictive Maps Produced by Bioclimatic Models. *Ecological Applications* 14 (2): 401-413.

Kearney, M. (2006). Habitat, environment and niche: what are we modelling? *Oikos* 115 (1): 186-191.

Kearney, M., Porter, W. (2009). Mechanistic niche modelling : combining physiological and spatial data to predict species ranges. *Ecology Letters* 12 (4): 334-350.

Keitt, T.H., Lewis, M.A., Holt, R.D. (2001). Allee effects, invasion pinning, and species' borders. *American Naturalist* 157 (2): 203-216.

Keller, F., Kienast, F., Beniston, M. (2000). Evidence of response of vegetation to environmental change on high-elevation sites in the Swiss Alps. *Regional Environmental Change* 1 (2): 70-77.

Keller, F., Goyette, S., Beniston, M. (2005). Sensitivity Analysis of Snow Cover to Climate Change Scenarios and Their Impact on Plant Habitats in Alpine Terrain. *Climatic Change* 72 (3): 299-319.

Kim, S.-C., Crawford, D.J., Francisco-Ortega, J., Santos-Guerra, A. (1999). Adaptive radiation and genetic differentiation in the woodySonchus alliance (Asteraceae:Sonchinae) in the Canary Islands. *Plant Systematics and Evolution* 215 (1): 101-118.

Kim, S.-C., McGowen, M.R., Lubinsky, P., Barber, J.C., Mort, M.E., Santos-Guerra, A. (2008). Timing and Tempo of Early and Successive Adaptive Radiations in Macaronesia. *PLoS ONE* 3 (5): e2139.

Kim, S.C., Crawford, D.J., Francisco-Ortega, J., Santos-Guerra, A. (1996). A common origin for woody Sonchus and five related genera in the Macaronesian islands: molecular evidence for extensive radiation. *Proceedings of the National Academy of Sciences of the United States of America* 93 (15): 7743-7748.

Kirschbaum, M.U.F., Fischlin, A., Cannell, M.G.R., Cruz, R.V.O., Galinski, W. (1996). Climate Change Impacts on Forests. In: Watson, R.T., Zinyowera, M.C., Moss, R.H. (eds.), *Working Group II Report "Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses". Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, pp. 191-213.

Korzukhin, M.D., Ter-Mikaelian, M.T., Wagner, R.G. (1996). Process versus empirical models: which approach for forest ecosystem management? *Canadian Journal of Forest Research* 26 (5): 879-887.

Kovar-Eder, J., Kvacek, Z., Martinetto, E., Roiron, P. (2006). Late Miocene to Early Pliocene vegetation of southern Europe (7-4 Ma) as reflected in megafossil plant record. *Paleoceanography* 238: 321-339.

Kriticos, D.J., Sutherst, R.W., Brown, J.R., Adkins, S.W., Maywald, G.F. (2003). Climate change and the potential distribution of an invasive alien plant: Acacia nilotica ssp. indica in Australia. *Journal of Applied Ecology* 40 (1): 111-124.

Kudo, G., Ida, T.Y. (2013). Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology*:

Kull, C.A., Shackleton, C.M., Cunningham, P.J., Ducatillon, C., Dufour-Dror, J.-M., Esler, K.J., Friday, J.B., Gouveia, A.C., Griffin, A.R., Marchante, E., Midgley, S.J., Pauchard, A., Rangan, H., Richardson, D.M., Rinaudo, T., Tassin, J., Urgenson, L.S., von Maltitz, G.P., Zenni, R.D., Zylstra, M.J. (2011). Adoption, use and perception of Australian acacias around the world. *Diversity and Distributions* 17 (5): 822-836.

Kullman, L. (2001). 20th Century Climate Warming and Tree-limit Rise in the Southern Scandes of Sweden. *AMBIO: A Journal of the Human Environment* 30 (2): 72-80.

La Sorte, F.A., Jetz, W. (2010). Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society B: Biological Sciences* 277 (1699): 3401-3410.

Lambdon, P.W., Pyšek, P., Basnou, C., Hejda, M., Arianoutsou, M., Essl, F., Jarošík, V., Pergl, J., Winter, M., Anastasiu, P., Andriopoulos, P., Bazos, I., Brundu, G., Celesti-Grapow, L., Chassot, P., Delipetrou, P., Josefsson, M., Kark, S., Klotz, S., Kokkoris, Y., Kühn, I., Marchante, H., Perglová, I., Pino, J., Vila, M., Zikos, A., Roy, D., Hulme, P.E. (2008). Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia* 80 (2): 101-149.

Lancaster, N., Kocurek, G., Singhvi, A., Pandey, V., Deynoux, M., Ghienne, J.-F., Lô, K. (2002). Late Pleistocene and Holocene dune activity and wind regimes in the western Sahara Desert of Mauritania. *Geology* 30 (11): 991-994.

Landsberg, J. (2003). Modelling forest ecosystems: state of the art, challenges, and future directions. *Canadian Journal of Forest Research* 33 (3): 385-397.

Lasram, F.B.R., Guilhaumon, F., Albouy, C., Somot, S., Thuiller, W., Mouillot, D. (2010). The Mediterranean Sea as a 'cul-de-sac' for endemic fishes facing climate change. *Global Change Biology* 16 (12): 3233-3245.

Laternser, M., Schneebeli, M. (2003). Long-term snow climate trends of the Swiss Alps (1931–99). *International Journal of Climatology* 23 (7): 733-750.

Laurance, W.F., Carolina Useche, D., Shoo, L.P., Herzog, S.K., Kessler, M., Escobar, F., Brehm, G., Axmacher, J.C., Chen, I.C., Gámez, L.A., Hietz, P., Fiedler, K., Pyrcz, T., Wolf, J., Merkord, C.L., Cardelus, C., Marshall, A.R., Ah-Peng, C., Aplet, G.H., del Coro Arizmendi, M., Baker, W.J., Barone, J., Brühl, C.A., Bussmann, R.W., Cicuzza, D., Eilu, G., Favila, M.E., Hemp, A., Hemp, C., Homeier, J., Hurtado, J., Jankowski, J., Kattán, G., Kluge, J., Krömer, T., Lees, D.C., Lehnert, M., Longino, J.T., Lovett, J., Martin, P.H., Patterson, B.D., Pearson, R.G., Peh, K.S.H., Richardson, B., Richardson, M., Samways, M.J., Senbeta, F., Smith, T.B., Utteridge, T.M.A., Watkins, J.E., Wilson, R., Williams, S.E., Thomas, C.D. (2011). Global warming, elevational ranges and the vulnerability of tropical biota. *Biological Conservation* 144 (1): 548-557.

Lavorel, S., Díaz, S., Cornelissen, J., Garnier, E., Harrison, S., McIntyre, S., Pausas, J., Pérez-Harguindeguy, N., Roumet, C., Urcelay, C. (2007). Plant Functional Types: Are We Getting Any Closer to the Holy Grail? , pp. 149-164.

Le Maitre, D.C., Gaertner, M., Marchante, E., Ens, E.-J., Holmes, P.M., Pauchard, A., O'Farrell, P.J., Rogers, A.M., Blanchard, R., Blignaut, J., Richardson, D.M. (2011). Impacts of invasive Australian acacias: implications for management and restoration. *Diversity and Distributions* 17 (5): 1015-1029.

Leathwick, J.R., Whitehead, D., McLeod, M. (1996). Predicting changes in the composition of New Zealand's indigenous forests in response to global warming: a modelling approach. *Environmental Software* 11 (1–3): 81-90.

Leathwick, J.R. (1998). Are New Zealand's *Nothofagus* species in equilibrium with their environment? *Journal of Vegetation Science* 9 (5): 719-732.

Leathwick, J.R., Austin, M.P. (2001). Competitive interactions between tree species in New Zealand's old-growth indigenous forests. *Ecology* 82 (9): 2560-2573.

Lehman, S.J., Keigwin, L.D. (1992). Sudden changes in North Atlantic circulation during the last deglaciation. *Nature* 356 (6372): 757-762.

Lek, S., Delacoste, M., Baran, P., Dimopoulos, I., Lauga, J., Aulagnier, S. (1996). Application of neural networks to modelling nonlinear relationships in ecology. *Ecological Modelling* 90 (1): 39-52.

Leonelli, G., Pelfini, M., Morra di Cella, U., Garavaglia, V. (2011). Climate Warming and the Recent Treeline Shift in the European Alps: The Role of Geomorphological Factors in High-Altitude Sites. *Ambio* 40 (3): 264-273.

Levine, J.M., Vilà, M., Antonio, C.M.D., Dukes, J.S., Grigulis, K., Lavorel, S. (2003). Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270 (1517): 775-781.

Li, H., Wu, J. (2007). Landscape pattern analysis: key issues and challenges. In: Wu, J., Hobbs, R. (eds.), *Key topics in Landscape Ecology*. Cambridge University Press, pp. 39-61.

Lischke, H., Guisan, A., Fischlin, A., Williams, J., Bugmann, H. (1998). Vegetation responses to climate change in the Alps: Modeling studies. In: Cebon, P., Dahinden, U., Davies, H., Imbonden, D., Jaeger, C. (eds.), *A View from the Alps: Regional Perspectives on Climate Change*. MIT Press, Boston, pp. 309-350.

Lisiecki, L.E., Raymo, M.E. (2005). A Pliocene-Pleistocene stack of 57 globally distributed benthic ^{18}O records. *Paleoceanography* 20 (1): PA1003.

Liu, C.R., Berry, P.M., Dawson, T.P., Pearson, R.G. (2005). Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28 (3): 385-393.

Lloyd, A., Fastie, C. (2003). Recent changes in treeline forest distribution and structure in interior Alaska. *Écoscience* 10 (1): 176 - 185.

Lloyd, A.H. (2005). Ecological Histories from Alaskan Tree Lines Provide Insight into Future Change. *Ecology* 86 (7): 1687-1695.

Lobo, J.M., Jimenez-Valverde, A., Real, R. (2008). AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* 17 (2): 145-151.

Loiselle, B.A., Howell, C.A., Graham, C.H., Goerck, J.M., Brooks, T., Smith, K.G., Williams, P.H. (2003). Avoiding Pitfalls of Using Species Distribution Models in Conservation Planning

Evitando Dificultades Resultantes del Uso de Modelos de Distribución de Especies en Planeación de Conservación. *Conservation Biology* 17 (6): 1591-1600.

López-Gómez, J., López-Gómez, A. (1979). El clima de Canarias según la clasificación de Koppen. *Estudios Geograficos* 40 (156-157): 321-340.

López-Merino, L., López-Sáez, J.A., Alba-Sánchez, F., Pérez-Díaz, S., Carrión, J.S. (2009). 2000 years of pastoralism and fire shaping high-altitude vegetation of Sierra de Gredos in central Spain. *Review of Palaeobotany and Palynology* 158 (1–2): 42-51.

Loustau, D., Bosc, A., Colin, A., Ogee, J., Davi, H., Francois, C., Dufrene, E., Deque, M., Cloppet, E., Arrouays, D., Le Bas, C., Saby, N., Pignard, G., Hamza, N., Granier, A., Breda, N., Ciais, P., Viovy, N., Delage, F. (2005). Modeling climate change effects on the potential production of French plains forests at the sub-regional level. *Tree Physiol* 25 (7): 813-823.

Luis, V.C., Jiménez, M.S., Morales, D., Kucera, J., Wieser, G. (2005). Canopy transpiration of a Canary Islands pine forest. *Agricultural and Forest Meteorology* 135 (1–4): 117-123.

Lütolf, M., Kienast, F., Guisan, A. (2006). The ghost of past species occurrence: improving species distribution models for presence-only data. *Journal of Applied Ecology* 43 (4): 802-815.

MacArthur, R.R., Wilson, E.O. (1967). *The theory of island biogeography*. Princeton University Press, Princeton.

Maciel, O.M.G. (2005). *Precipitações intensas na Ilha da Madeira : incidência, contrastes espaciais e causas sinópticas*. M.Sc. Thesis, Faculdade de Letras, Universidade de Coimbra, Coimbra, 171 pp.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A. (2000). Biotic Invasions: Causes, Epidemiology, Global Consequences, and Control. *Ecological Applications* 10 (3): 689-710.

Madeira, J., Mata, J., Mourão, C., Silveira, A.B.d., Martins, S., Ramalho, R., Hoffmann, D.L. (2010). Volcano-stratigraphic and structural evolution of Brava Island (Cape Verde) based on ^{40}AR/^{39}AR, U-Th and field constraints. *Journal of Volcanology and Geothermal Research* 196: 219-235.

Maggini, R., Lehmann, A., Kéry, M., Schmid, H., Beniston, M., Jenni, L., Zbinden, N. (2011). Are Swiss birds tracking climate change?: Detecting elevational shifts using response curve shapes. *Ecological Modelling* 222 (1): 21-32.

Mai, D.H. (1989). Development and regional differentiation of the European vegetation during the Tertiary. *Plant Systematics and Evolution* 162 (1): 79-91.

Mäkelä, A., Landsberg, J., Ek, A.R., Burk, T.E., Ter-Mikaelian, M., Ågren, G.I., Oliver, C.D., Puttonen, P. (2000). Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. *Tree Physiology* 20 (5-6): 289-298.

Manel, S., Dias, J.M., Ormerod, S.J. (1999). Comparing discriminant analysis, neural networks and logistic regression for predicting species distributions: a case study with a Himalayan river bird. *Ecological Modelling* 120 (2): 337-347.

Manel, S., Williams, H.C., Ormerod, S.J. (2001). Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* 38 (5): 921-931.

Mann, M.E. (2007). Climate Over the Past Two Millennia. *Annual Review of Earth and Planetary Sciences* 35 (1): 111-136.

Mann, M.E., Zhang, Z., Hughes, M.K., Bradley, R.S., Miller, S.K., Rutherford, S., Ni, F. (2008). Proxy-based reconstructions of hemispheric and global surface temperature variations over the past two millennia. *Proceedings of the National Academy of Sciences* 105 (36): 13252-13257.

Mansion, G., Selvi, F., Guggisberg, A., Conti, E. (2009). Origin of Mediterranean insular endemics in the Boraginales: integrative evidence from molecular dating and ancestral area reconstruction. *J Biogeogr* 36 (7): 1282-1296.

Marchante, E., Freitas, H., Marchante, H. (eds.) (2008). *Guia Prático para a Identificação de Plantas Invasoras de Portugal Continental*, Imprensa da Universidade de Coimbra, Coimbra, 183 pp pp.

Marchante, H. (2001). *Invasão dos ecossistemas dunares portugueses por Acacia: uma ameaça para a biodiversidade nativa*. Dissertação de Mestrado, Universidade de Coimbra, Coimbra, 157 pp.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K., Thuiller, W. (2009). Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions* 15 (1): 59-69.

Marques, C.A.G. (2013). *Paleobotânica da Ilha da Madeira: Inventário e Revisão da Macroflora Fóssil de São Jorge e Porto da Cruz*. MSc. thesis, Universidade de Lisboa, Lisbon, 144 pp.

Mateo, R.G., Croat, T.B., Felicísimo, Á.M., Muñoz, J. (2010). Profile or group discriminative techniques? Generating reliable species distribution models using pseudo-absences and target-group absences from natural history collections. *Diversity and Distributions* 16 (1): 84-94.

McCarty, J.P. (2001). Ecological Consequences of Recent Climate Change

Consecuencias Biológicas de Cambios Climáticos Recientes. *Conservation Biology* 15 (2): 320-331.

McKenney, D.W., Pedlar, J.H., Lawrence, K., Campbell, K., Hutchinson, M.F. (2007). Potential Impacts of Climate Change on the Distribution of North American Trees. *BioScience* 57 (11): 939-948.

MEA, Millenium Ecosystem Assessment (2005). *Ecosystems and human well-being: synthesis report*. Washington, DC, pp. Available at http://www.millenniumassessment.org/ on 7/06/2009.

Meco, J., Petit-Maire, N., Guillou, H., Carracedo, J.C., Lomoschitz, A., Ramos, A.J.G., Ballester, J. (2003). Climatic changes over the last 5,000,000 years as recorded in the Canary Islands. *Episodes* 26: 133-134.

Meco, J., Scaillet, S., Guillou, H., Lomoschitz, A., Carracedo, J.C., Ballester, J., Betancort, J.-F., Cilleros, A. (2007). Evidence for long-term upflit on the Canary Islands from emergent Mio-Pliocene littoral deposits *Global and Planetary Change* 57: 222-234.

Meco, J. (ed.) (2008). *Historia geológica del clima en Canarias*, Laboratorio de Paleontología, Departamento de Biología, Universidad de Las Palmas de Gran Canaria (ULPGC), Las Palmas de Gran Canaria, 296 pp.

Médail, F., Quézel, P. (1999a). Biodiversity Hotspots in the Mediterranean Basin: Setting Global Conservation Priorities. *Conservation Biology* 13 (6): 1510-1513.

Médail, F., Quézel, P. (1999b). The phytogeographical significance of S.W. Morocco compared to the Canary Islands. *Plant Ecology* 140 (2): 221-244.

Meier, E.S., Kienast, F., Pearman, P.B., Svenning, J.-C., Thuiller, W., Araújo, M.B., Guisan, A., Zimmermann, N.E. (2010). Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography* 33 (6): 1038-1048.

Menezes de Sequeira, M., Jardim, R., Capelo, J. (2007). A Chegada dos portugueses às ilhas – o antes e o depois - Madeira. In: Silva, J.S. (ed.), *Árvores e Florestas de Portugal*, vol. 6 - Açores e Madeira - A Floresta das Ilhas. Público, Fundação Luso-Americana e Liga para a Proteção da Natureza, Lisboa, pp. 165-196.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kubler, K., Bissolli, P., Braslavska, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, A., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Magee, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remisova, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.-E., Zach, S., Zust, A.N.A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology* 12 (10): 1969-1976.

Mesquita, S., Capelo, J., Sousa, J.d. (2004). Bioclimatologia da Ilha da Madeira. Abordagem numérica. *Quercetea* 6: 47-60.

Mesquita, S., Capelo, J., Jardim, R., Menezes de Sequeira, M. (2007). Distribuição das principais manchas florestais. Madeira. In: Silva, J.S. (ed.), *Açores e Madeira. A Floresta das Ilhas*, vol. 6. Fundação Luso-Americana para o Desenvolvimento, Público e Liga para a Proteção da Natureza, Lisboa, pp. 323 - 335.

Meynard, C.N., Quinn, J.F. (2007). Predicting species distributions: a critical comparison of the most common statistical models using artificial species. *Journal of Biogeography* 34 (8): 1455-1469.

Midgley, G.F., Thuiller, W., Higgins, S.I. (2007). Plant Species Migration as a Key Uncertainty in Predicting Future Impacts of Climate Change on Ecosystems: Progress and Challenges. In: Canadell, J.G., Pataki, D.E., Pitelka, L.F. (eds.), *Terrestrial Ecosystems in a Changing World*. Springer Berlin Heidelberg, pp. 129-137.

Miller, J., Franklin, J., Aspinall, R. (2007). Incorporating spatial dependence in predictive vegetation models. *Ecological Modelling* 202 (3-4): 225-242.

Miller, R. (1986). Predicting rare plant distribution patterns in the southern Appalachians of the southeastern U.S.A. *Journal of Biogeography* 13 (4): 293-311.

Mimura, N., Nurse, L., McLean, R.F., Agard, J., Briguglio, L., Lefale, P., Payet, R., Sem, G. (2007). Small islands. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., Linden, P.J.v.d., Hanson, C.E. (eds.), *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, UK, Cambridge, pp. 687-716.

Miranda, P.M.A., Valente, M.A., Tomé, A.R., Trigo, R., Coelho, M.F.E.S., Aguiar, A., Azevedo, E.B. (2006). O clima de Portugal nos séculos XX e XXI. In: Santos, F.D., Miranda, P. (eds.), *Alterações Climáticas em Portugal. Cenários, Impactos e Medidas de Adaptação. Projecto SIAM II*. Gradiva, Lisboa, pp. 45-113.

Morales, D., Gonzalez-Rodriguez, A.M., Cermak, J., Jiménez, M.S. (1996). Laurel forest in Tenerife, Canary Islands: the vertical profiles of the leaf characteristics. *Phyton* 36: 251-263.

Morris, T.L., Esler, K.J., Barger, N.N., Jacobs, S.M., Cramer, M.D. (2011). Ecophysiological traits associated with the competitive ability of invasive Australian acacias. *Diversity and Distributions* 17 (5): 898-910.

Mueller-Dombois, D. (1992). The formation of island ecosystems. *GeoJournal* 28 (2): 293-296.

Muñoz, J., Felicísimo, Á.M. (2004). Comparison of statistical methods commonly used in predictive modelling. *Journal of Vegetation Science* 15 (2): 285-292.

Murphy, H.T., VanDerWal, J., Lovett-Doust, J. (2010). Signatures of range expansion and erosion in eastern North American trees. *Ecology Letters* 13 (10): 1233-1244.

Murray, K., Conner, M.M. (2009). Methods to quantify variable importance: implications for the analysis of noisy ecological data. *Ecology* 90 (2): 348-355.

Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G., Nemani, R.R. (1997). Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386 (6626): 698-702.

Neter, J., Wasserman, W., Kutner, M.H. (1983). *Applied linear regression models*. Richard D. Irwin, Homewood, Illinois.

Nicolás, J.P., Fernandez-Palacios, J.M., Ferrer, F.J., Nieto, E. (1989). Inter-island floristic similarities in the Macaronesian region. *Plant Ecology* 84 (2): 117-125.

NRC (2006). *Surface temperature reconstrucions for the last 2000 years*. The National Academies Press, Washington, DC.

Oerlemans, J. (2005). Extracting a Climate Signal from 169 Glacier Records. *Science* 308 (5722): 675-677.

Ohlemuller, R., Anderson, B.J., Araujo, M.B., Butchart, S.H.M., Kudrna, O., Ridgely, R.S., Thomas, C.D. (2008). The coincidence of climatic and species rarity: high risk to small-range species from climate change. *Biology Letters* 4 (5): 568-572.

Olea, P.P., Mateo-Tomás, P., de Frutos, Á. (2010). Estimating and Modelling Bias of the Hierarchical Partitioning Public-Domain Software: Implications in Environmental Management and Conservation. *PLoS ONE* 5 (7): e11698.

Olsson, U. (2002). *Generalized Linear Models. An Applied Approach*. Studentlitteratur, Lund, Sweden. 232 pp.

Oreskes, N., Shrader-Frechette, K., Belitz, K. (1994). Verification, Validation, and Confirmation of Numerical Models in the Earth Sciences. *Science* 263 (5147): 641-646.

Oreskes, N. (2004). The scienctific consensus on climate change. *Science* 306: 1686.

Pais, J. (2010). Plantas do Neogénico e paleoclimas. Evidências em Portugal. In: Neiva, J.M.C., Ribeiro, A., Victor, L.M., Noronha, F., Ramalho, M. (eds.), *Ciências Geológicas: ensino e investigação.*, vol. I (Geologia Clássica). Associação Portuguesa de Geólogos. Sociedade Geológica de Portugal., Lisboa, pp. p. 357-363.

Paiva, J. (1997). *Pittosporum* Banks & Sol. ex Gaertn. In: Castroviejo, S., Aedo, C., Lainz, M., Muñoz-Garmendia, F., Nieto-Feliner, G., Paiva, J., Benedí, C. (eds.), *Flora Iberica*, vol. V. Real Jardín Botanico de Madrid, Madrid, pp. 70-73.

Paiva, J. (1999). *Acacia* Mill. In: Talavera, S., Aedo, C., Castroviejo, S., Zarco, C.R., Sáez, L., Salgueiro, F.J., Velayos (eds.), *Flora Iberica - Plantas Vasculares de la Peninsula Iberica e Islas Baleares*, vol. Vol. VII(I). Real Jardín Botánico, CSIS, Madrid, pp. 11-25.

Panero, J.L., Francisco-Ortega, J., Jansen, R.K., Santos-Guerra, A. (1999). Molecular evidence for multiple origins of woodiness and a New World biogeographic connection of the Macaronesian Island endemic Pericallis (Asteraceae: Senecioneae). *Proceedings of the National Academy of Sciences of the United States of America* 96 (24): 13886-13891.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A., Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399 (6736): 579-583.

Parmesan, C., Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421 (6918): 37-42.

Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics* 37 (1): 637-669.

Pauli, H., Gottfried, M., Grabherr, G. (1996). Effects of climate change on mountain ecosystems - Upward shifting of alpine plants. *World Resource Review* 8 (3): 382 - 390.

Pauli, H., Gottfried, M., Hohenwallner, D., Reiter, K., Grabherr, G. (2005). Ecological Climate Impact Research in High Mountain Environments: GLORIA (Global Observation Research Initiative in Alpine Environments) — its Roots, Purpose and Long-term Perspectives. In: Huber, U., Bugmann, H.M., Reasoner, M. (eds.), *Global Change and Mountain Regions*, vol. 23. Springer Netherlands, pp. 383-391.

Payne, J.L., Finnegan, S. (2007). The effect of geographic range on extinction risk during background and mass extinction. *Proceedings of the National Academy of Sciences* 104 (25): 10506-10511.

Pearce, J., Ferrier, S. (2000a). *An evaluation of alternative algorithms for fitting species distribution models using logistic regression*. Elsevier, Amsterdam, PAYS-BAS.

Pearce, J., Ferrier, S. (2000b). Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* 133 (3): 225-245.

Pearson, R.G., Dawson, T.P., Berry, P.M., Harrison, P.A. (2002). SPECIES: A Spatial Evaluation of Climate Impact on the Envelope of Species. *Ecological Modelling* 154 (3): 289-300.

Pearson, R.G., Dawson, T.P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12 (5): 361-371.

Pearson, R.G., Dawson, T.P. (2005). Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. *Biological Conservation* 123 (3): 389-401.

Pearson, R.G., Thuiller, W., Araujo, M.B., Martinez-Meyer, E., Brotons, L., McClean, C., Miles, L., Segurado, P., Dawson, T.P., Lees, D.C. (2006). Model-based uncertainty in species range prediction. *Journal of Biogeography* 33 (10): 1704-1711.

Peet, R., Fridley, J., Gramling, J. (2003). Variation in species richness and species pool size across a pH gradient in forests of the southern Blue Ridge Mountains. *Folia Geobotanica* 38 (4): 391-401.

Peixoto, J.P., Oort, A.H. (1992). *Physics of Climate*. Springer. ISBN 0883187124.

Peñuelas, J., Boada, M. (2003). A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biology* 9 (2): 131-140.

Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guénette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R., Walpole, M. (2010). Scenarios for Global Biodiversity in the 21st Century. *Science* 330 (6010): 1496-1501.

Peterson, A.T. (2001). Predicting species' geographic distributions based on ecological niche modeling. *The Condor* 103 (3): 599-605.

Peterson, A.T. (2003). Predicting the Geography of Species Invasions via Ecological Niche Modeling. *The Quarterly Review of Biology* 78 (4): 419-433.

Peterson, A.T. (2006). Uses and Requirements of Ecological Niche Models and Related Distributional Models. *Biodiversity Informatics* 3: 59-72.

Peterson, A.T., Papeş, M., Eaton, M. (2007). Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography* 30 (4): 550-560.

Peterson, A.T., Papes, M., Soberón, J. (2008a). Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling* 213 (1): 63-72.

Peterson, A.T., Stewart, A., Mohamed, K.I., AraÃºjo, M.B. (2008b). Shifting Global Invasive Potential of European Plants with Climate Change. *PLoS ONE* 3 (6): e2441.

Phillips, S.J., Anderson, R.P., Schapire, R.E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190 (3-4): 231-259.

Phillips, S.J., Dudik, M. (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31 (2): 161-175.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S. (2009). Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* 19 (1): 181-197.

Pickett, S.T.A., Kolasa, J., Jones, C.G. (2007). *Ecological Understanding: The Nature of Theory and the Theory of Nature*, 2nd ed. Academic Press, Amsterdam.

Pimentel, D., Zuniga, R., Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273-288.

Piñeiro, R., Fuertes Aguilar, J., Menezes de Sequeira, M., Nieto Feliner, G. (2009). Low Genetic Diversity in the Rare Madeiran Endemic <i>Armeria maderensis</i> (Plumbaginaceae). Folia Geobotanica 44 (1): 65-81.

Pliny, T.E., Rackham, H. (1938). *Natural history / with an English translation by H. Rackham*. W. Heinemann, London. http://citebank.org/uid.php?id=83091.

Postigo-Mijarra, J., Gómez Manzaneque, F., Morla, C. (2008). Survival and long-term maintenance of tertiary trees in the Iberian Peninsula during the Pleistocene: first record of Aesculus L. (Hippocastanaceae) in Spain. *Veg Hist Archaeobot* 17 (4): 351-364.

Postigo-Mijarra, J.M., Barrón, E., Gómez Manzaneque, F., Morla, C. (2009). Floristic changes in the Iberian Peninsula and Balearic Islands (south-west Europe) during the Cenozoic. *Journal of Biogeography* 36 (11): 2025-2043.

Postigo-Mijarra, J.M., Morla, C., Barrón, E., Morales-Molino, C., García, S. (2010). Patterns of extinction and persistence of Arctotertiary flora in Iberia during the Quaternary. *Review of Palaeobotany and Palynology* 162 (3): 416-426.

Pounds, J.A., Fogden, M.P.L., Campbell, J.H. (1999). Biological response to climate change on a tropical mountain. *Nature* 398 (6728): 611-615.

Prada, S., Silva, M.N. (1998). Contribuição da precipitação oculta para os recursos hídricos da Ilha da Madeira. *Comunicações do Insituto Geológico e Mineiro* 84 (2): 118-121.

Prada, S., Silva, M.N. (2001). Fog precipitation on the Island of Madeira (Portugal). *Environmental Geology* 41: 384-389.

Prada, S., Sequeira, M.M.d., Figueira, C., Silva, M.O.d. (2009). Fog precipitation and rainfall interception in the natural forests of Madeira Island (Portugal). *Agricultura and Forest Meteorology* 149: 1179-1187.

Prada, S., de Sequeira, M.M., Figueira, C., Vasconcelos, R. (2012). Cloud water interception in the high altitude tree heath forest (Erica arborea L.) of Paul da Serra Massif (Madeira, Portugal). *Hydrological Processes* 26 (2): 202-212.

Prasad, A., Iverson, L., Liaw, A. (2006). Newer Classification and Regression Tree Techniques: Bagging and Random Forests for Ecological Prediction. *Ecosystems* 9 (2): 181-199.

Pucko, C., Beckage, B., Perkins, T., Keeton, W. (2011). Species shifts in response to climate change: Individual or shared responses? *Journal of the Torrey Botanical Society* 138 (2): 156-176.

Pulliam, H.R. (2000). On the relationship between niche and distribution. *Ecology Letters* 3 (4): 349-361.

Pupo-Correia, A., Figueiredo, A., Aranha, J., Sequeira, M.M.d. (unpublished data). Evolução da invasão por Arundo donax L. (Poaceae) na Ilha da Madeira e os seus efeitos sobre a biodiversidade vegetal. *Querceta in press*:

Quante, M. (2010). The Changing Climate - Past, Present, Future. In: Habel, J.C., Assmann, T. (eds.), *Relict species. Phylogeography and conservation biology.* Springer Verlag, Berlin, pp. 9-56.

Quézel, P. (1978). Analysis of the Flora of Mediterranean and Saharan Africa. *Annals of the Missouri Botanical Garden* 65 (2): 479-534.

R Development Core Team (2011). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org/.

Rabinowitz, D. (1981). Seven forms of rarity. In: Synge, H. (ed.), *Biological aspects of rare plant conservation*. Wiley & Sons, New York, pp. 205-217.

Ramalho, R., Helffrich, G., Cosca, M., Vance, D., Hoffmann, D., Schmidt, D.N. (2010). Episodic swell growth inferred from variable upflit of the Cape Verde hotspot islands. *Nature Geoscience* 3: 774 - 777.

Rammig, A., Jonas, T., Zimmermann, N.E., Rixen, C. (2010). Changes in alpine plant growth under future climate conditions. *Biogeosciences* 7 (6): 2013-2024.

Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M., Guisan, A. (2006). Are niche-based species distribution models transferable in space? *Journal of Biogeography* 33 (10): 1689-1703.

Randin, C.F., Vuissoz, G., Liston, G.E., Vittoz, P., Guisan, A. (2009). Introduction of Snow and Geomorphic Disturbance Variables into Predictive Models of Alpine Plant Distribution in the Western Swiss Alps. *Arctic, Antarctic, and Alpine Research* 41 (3): 347-361.

Real, R., Barbosa, A., Vargas, J. (2006). Obtaining Environmental Favourability Functions from Logistic Regression. *Environmental and Ecological Statistics* 13 (2): 237-245.

Rejmanek, M., Richardson, D.M. (1996). What Attributes Make Some Plant Species More Invasive? *Ecology* 77 (6): 1655-1661.

Rejmánek, M., Richardson, D.M., Pysek, P. (2005). Plant invasions and invasibility of plant communities. In: Maarel, E.V.d. (ed.), *Vegetation Ecology*. Blackwell Publishing, Oxford, pp. 332-355.

Retuerto, R., Carballeira, A. (2004). Estimating plant responses to climate by direct gradient analysis and geographic distribution analysis. *Plant Ecology* 170 (2): 185-202.

Reyes-Betancort, J.A., Guerra, A.S., Guma, I.R., Humphries, C.J., Carine, M.a. (2008). Diversity, rarity and the evolution and conservation of the Canary Islands endemic flora. *Anales del Jardin Botânico de Madrid* 65 (1): 25-45.

Ribeiro, L., Ech-Chakroun, S., Mata, J., Boven, A., Mattielli, N., Hus, J., Maerschalk, C., 2005. Elemental and lead isotopic evidence for coeval heterogeneities at Madeira/Desertas mantle source, VIII Congresso de Geoquímica dos Países de Língua Portuguesa (Portugal), Lisbon, pp. 485-488.

Ricardo, R.P., Câmara, E.M.S., Ferreira, M.A.M. (1992). *Carta dos Solos da Ilha da Madeira*. Secretaria Regional de Economia da Região Autónoma da Madeira, CEP/ISA/CPUTL/DRAM, Lisboa. 162 pp.

Richardson, D.M. (1998). Forestry Trees as Invasive Aliens. *Conservation Biology* 12 (1): 18-26.

Richter-Menge, J., Overland, J., Hanna, E., Loonen, M.J.J., Proshutinsky, A., Romanovsky, V., Russell, D., Bogaert, R.V., Armstrong, R., Bengtsson, L., Box, J., Callaghan, T.V., Dapper, M.d., Ebbinge, B., Grau, O., Hallinger, M., Hinzman, L.D., Huybrechts, P., Jia, G.J., Jonasson, C., Morison, J., Nghiem, S., Oberman, N., Perovich, D., Przybylak, R., Rigor, I., Shiklomanov, A., Walker, D., Walsh, J., Zockler, C. (2007). Artic Report Card 2007. Tacking recent environmental changes. Available from http://www.arctic.noaa.gov/report07; accessed on 20/10/2011.

Ritter, A., Regalado, C.M., Aschan, G. (2007). *An impaction model for estimating fog water collection in a subtropical laurel cloud forest of the Garajonay National Park.* Available at http://www.icia.es/icia/download/suelosyriegos/355-358.pdf on

Ritter, A., Regalado, C.M., Aschan, G. (2008). Fog Water Collection in a Subtropical Elfin Laurel Forest of the Garajonay National Park (Canary Islands): A Combined Approach Using Artificial Fog Catchers and a Physically Based Impaction Model. *Journal of Hydrometeorology* 9 (5): 920-935.

Ritter, A., Regalado, C.M., Aschan, G. (2009). Fog reduces transpiration in tree species of the Canarian relict heath-laurel cloud forest (Garajonay National Park, Spain). *Tree Physiology* 29 (4): 517-528.

Rivas-Martinez, S. (2004). *Global Bioclimatics (Clasificación bioclimática de la Tierra).* Available at http://www.globalbioclimatics.org/book/bioc/global_bioclimatics_2.htm - 2d on 17th September 2012.

Rivas-Martínez, S., Torre, W.W.d.l., Arco-Aguilar, M.d., Rodríguez, O., Pérez-de-Paz, P.L., García-Gallo, A., Acebes, J.R., Díaz, T.E., Fernández-González, F. (1993). Las comunidades vegetales de la isla de Tenerife (Islas Canarias). *Itinera Geobotanica* 7: 169 - 374.

Rivas-Martínez, S., Sánchez-Mata, D., Costa, M. (1999). North American Boreal and Western Forest Vegetation. *Itinera Geobotanica* 12: 5-316.

Rivas-Martínez, S., Díaz, T.E., Fernández-González, F., Izco, J., Loidi, J., Lousã, M., (ed.), A.P. (2002). Vascular plant communities of Spain and Portugal. Addenda to syntaxonomical checklist of 2001. Part II. *Itinera Geobotanica* 15 (2): 433-922.

Rivas-Martínez, S. (2007). Mapa de series, geoseries y geopermaseries de vegetación de España (Memoria del mapa de vegetación potencial de España, 2005). Parte 1. *Itinera Geobotanica* 17: 5-436.

Robertson, M.P., Caithness, N., Villet, M.H. (2001). A PCA-Based Modelling Technique for Predicting Environmental Suitability for Organisms from Presence Records. *Diversity and Distributions* 7 (1/2): 15-27.

Rodríguez-Sánchez, F., Arroyo, J. (2008). Reconstructing the demise of Tethyan plants: climate-driven range dynamics of Laurus since the Pliocene. *Global Ecology and Biogeography* 17 (6): 685-695.

Rodríguez-Sánchez, F., Guzmán, B., Valido, A., Vargas, P., Arroyo, J. (2009). Late Neogene history of the laurel tree (Laurus L., Lauraceae) based on phylogeographical analyses of Mediterranean and Macaronesian populations. *Journal of Biogeography* 36 (7): 1270-1281.

Rognon, P., Coudé-Gaussen, G. (1996). Paleoclimates Off Northwest Africa (28°–35°N) about 18,000 yr B.P. Based on Continental Eolian Deposits. *Quaternary Research* 46 (2): 118-126.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A. (2003). Fingerprints of global warming on wild animals and plants. *Nature* 421 (6918): 57-60.

Rouget, M., Richardson, D.M. (2003). *Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors*. 0003-0147, http://www.biomedsearch.com/nih/Inferring-process-from-pattern-in/14737709.html, 713-724 pp.

Ruiz-Benito, P., Lines, E.R., Gómez-Aparicio, L., Zavala, M.A., Coomes, D.A. (2013). Patterns and Drivers of Tree Mortality in Iberian Forests: Climatic Effects Are Modified by Competition. *PLoS ONE* 8 (2): e56843.

Rutishauser, T., Luterbacher, J., Defila, C., Frank, D., Wanner, H. (2008). Swiss spring plant phenology 2007: Extremes, a multi-century perspective, and changes in temperature sensitivity. *Geophys. Res. Lett.* 35 (5): L05703.

Sabiiti, E.N., Wein, R.W. (1987). Fire and Acacia Seeds: A Hypothesis of Colonization Success. *Journal of Ecology* 75 (4): 937-946.

Safranyik, L., Carroll, A.L., Régnière, J., Langor, D.W., Riel, W.G., Shore, T.L., Peter, B., Cooke, B.J., Nealis, V.G., Taylor, S.W. (2010). Potential for range expansion of mountain pine beetle into the boreal forest of North America. *The Canadian Entomologist* 142 (5): 415-442.

Sala, O.E., Chapin , F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M.n., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H. (2000). Global Biodiversity Scenarios for the Year 2100. *Science* 287 (5459): 1770-1774.

Santos, F.D., Aguiar, R. (eds.) (2006). *Impactos e medidas de adaptação às alterações climáticas no arquipélago da Madeira*, Projecto CLIMAAT II e Direcção Regional do Ambiente da Madeira, Funchal, 110 pp.

Santos, F.D., Miranda, P. (eds.) (2006). *Alterações climáticas em Portugal. Cenários, impactos e medidas de adaptação*. 1st ed, Gradiva, Lisboa, 505 pp.

Sax, D.F., Brown, J.H. (2000). The paradox of invasion. *Global Ecology and Biogeography* 9: 363-371.

Sax, D.F., Gaines, S.D., 2008. Species invasions and extinction : The future of native biodiversity on islands. National Academy of Sciences of the United States of America, Washington, DC, ETATS-UNIS, p. 8.

Schaefer, H., Moura, M., Belo Maciel, M.G., Silva, L., Rumsey, F.J., Carine, M.A. (2011). The Linnean shortfall in oceanic island biogeography: a case study in the Azores. *Journal of Biogeography* 38 (7): 1345-1355.

Schaefer, H., Hechenleitner, P., Santos-Guerra, A., de Sequeira, M., Pennington, R., Kenicer, G., Carine, M. (2012). Systematics, biogeography, and character evolution of the legume tribe Fabeae with special focus on the middle-Atlantic island lineages. *BMC Evolutionary Biology* 12 (1): 1-19.

Schleip, C., Rutishauser, T., Luterbacher, J., Menzel, A. (2008). Time series modeling and central European temperature impact assessment of phenological records over the last 250 years. *J. Geophys. Res.* 113 (G4): G04026.

Schwartz, M.W., Iverson, L.R., Prasad, A.M., Matthews, S.N., O'Connor, R.J. (2006). Predicting extinctions as a result of climate change. *Ecology* 87 (7): 1611-1615.

Segurado, P., Araújo, M.B. (2004). An evaluation of methods for modelling species distributions. *Journal of Biogeography* 31 (10): 1555-1568.

Serrado, J.E.L. (1960). *Subsídios para o estudo da situação económica da Ilha da Madeira no tempo do Marquês de Pombal*. Degree thesis, Universidade de Coimbra, Coimbra, 81 + appendices pp.

Silva, A.R.P.d. (1991). Algumas caracterísitcas da flora de Portugal. *Ciência e Natureza* 1: 73-92.

Silva, F.A., Menezes, C.A. (1946). *Elucidário Madeirense. Fac-simile edition of 1998*. DRAC, Funchal.

Silva, J.M.A. (1993). *A Madeira e a construção do mundo atlântico. Séculos XV - XVIII*. Secretaria Regional de Turismo. Centro de Estudos de História do Atlântico, Coimbra. 633 pp.

Silva, L., Ojeda-Land, E., Rodríguez-Luengo, J.L. (2008). *Invasive terrestrial flora and fauna of Macaronesia. Top 100 in Azores, Madeira and Canaries*. ARENA, Ponta Delgada. 546 pp.

Silvertown, J. (2004). The ghost of competition past in the phylogeny of island endemic plants. *Journal of Ecology* 92: 168-173.

Simberloff, D. (2000). Global climate change and introduced species in United States forests. *The Science of the Total Environment* 262: 253-261.

Siqueira, M.F.d., Durigan, G., de Marco Júnior, P., Peterson, A.T. (2009). Something from nothing: Using landscape similarity and ecological niche modeling to find rare plant species. *Journal for Nature Conservation* 17 (1): 25-32.

Soares, A.F. (1973). A formação eolianítica de Porto Santo. *Memórias e Notícias (Rev. Mus. Lab. Min. Geol. Universidade de Coimbra)* 73 (1): 47-88.

Soberon, J., Peterson, A.T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics* 2: 1-10.

Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10 (12): 1115-1123.

Soberón, J., Nakamura, M. (2009). Niches and distributional areas: Concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences* 106 (Supplement 2): 19644-19650.

Sperling, F.N., Washington, R., Whittaker, R.J. (2004). Future Climate Change of the Subtropical North Atlantic: Implications for the Cloud Forests of Tenerife. *Climatic Change* 65 (1): 103-123.

Still, C.J., Foster, P.N., Schneider, S.H. (1999). Simulating the effects of climate change on tropical montane cloud forests. *Nature* 398 (6728): 608-610.

Stockwell, D.R.B., Peterson, A.T. (2002). Effects of sample size on accuracy of species distribution models. *Ecological Modelling* 148 (1): 1-13.

Stow, D.A., Hope, A., McGuire, D., Verbyla, D., Gamon, J., Huemmrich, F., Houston, S., Racine, C., Sturm, M., Tape, K., Hinzman, L., Yoshikawa, K., Tweedie, C., Noyle, B., Silapaswan, C., Douglas, D., Griffith, B., Jia, G., Epstein, H., Walker, D., Daeschner, S., Petersen, A., Zhou, L., Myneni, R.

(2004). Remote sensing of vegetation and land-cover change in Arctic Tundra Ecosystems. *Remote Sensing of Environment* 89 (3): 281-308.

Sunding, P. (1979). Origins of the Macaronesian flora. In: Bramwell, D. (ed.), *Plants and Islands*. Academic Press, London, UK, pp. 13-40.

Takhtajan, A.L. (1969). *Flowering plants: origin and dispersal.* Oliver & Boyd, Edinburgh.

Tape, K., Sturm, M., Racine, C. (2006). The Evidence for Shrub Expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology* 12:

Tenorio, M.C., Anton, M.G., Juaristi, C.M., Ollero, H.S. (1990). La evolucion de los bosques de la Peninsula Iberica: una interpretacion basada en datos paleobiogeograficos. *ECOLOGIA* 1: 31-58.

Theoharides, K.A., Dukes, J.S. (2007). Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist* 176 (2): 256-273.

Theurillat, J.-P., Felber, F., Geissler, P., Gobat, J.-M., Fierz, M., Fishlin, A., Kuffer, P., Schlussel, A., Velluti, C., Zhao, G.-F., Williams, J. (1998). Sensitivity of Plant and Soil Ecosystems of the Alps to Climate Change. In: Cebon, P., Dahinden, U., Davies, H., Imbonden, D., Jaeger, C. (eds.), *A View from the Alps: Regional Perspectives on Climate Change*. MIT Press, Boston, pp. 309-350.

Theurillat, J.P., Guisan, A. (2001). Potential Impact of Climate Change on Vegetation in the European Alps: A Review. *Climatic Change* 50: 77-109.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M., Conradt, L. (2001). Ecological and evolutionary processes at expanding range margins. *Nature* 411 (6837): 577-581.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Townsend Peterson, A., Phillips, O.L., Williams, S.E. (2004). Extinction risk from climate change. *Nature* 427 (6970): 145-148.

Thuiller, W. (2003). BIOMOD - optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology* 9 (10): 1353-1362.

Thuiller, W., Vayreda, J., Pino, J., Sabate, S., Lavorel, S., Gracia, C. (2003). Large-scale environmental correlates of forest tree distributions in Catalonia (NE Spain). *Global Ecology and Biogeography* 12 (4): 313-325.

Thuiller, W., Araújo, M.B., Lavorel, S. (2004a). Uncertainty in predictions of extinction risk. *Nature* 430: 34.

Thuiller, W., Brotons, L., Araújo, M.B., Lavorel, S. (2004b). Effects of restricting environmental range of data to project current and future species distributions. *Ecography* 27 (2): 165-172.

Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T., Prentice, I.C. (2005a). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America* 102 (23): 8245-8250.

Thuiller, W., Richardson, D.M., Pysek, P., Midgley, G.F., Hughes, G.O., Rouget, M. (2005b). Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology* 11 (12): 2234-2250.

Thuiller, W., Lavorel, S., Sykes, M.T., Araujo, M.B. (2006a). Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Diversity and Distributions* 12 (1): 49-60.

Thuiller, W., Midgley, G.F., Hughes, G.O., Bomhard, B., Drew, G., Rutherford, M.C., Woodward, F.I. (2006b). Endemic species and ecosystem sensitivity to climate change in Namibia. *Global Change Biology* 12 (5): 759-776.

Thuiller, W., Richardson, D., Midgley, G. (2007). Will Climate Change Promote Alien Plant Invasions? In: Nentwig, W. (ed.), *Biological Invasions*, vol. 193. Springer Berlin Heidelberg, pp. 197-211.

Thuiller, W., Albert, C., Araujo, M.B., Berry, P.M., Cabeza, M., Guisan, A., Hickler, T., Midgely, G.F., Paterson, J., Schurr, F.M., Sykes, M.T., Zimmermann, N.E. (2008). Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology Evolution and Systematics* 9 (3-4): 137-152.

Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B. (2009). BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography* 32 (3): 369-373.

Travis, J.M.J. (2003). Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270 (1514): 467-473.

Twitchett, R.J. (2006). The palaeoclimatology, palaeoecology and palaeoenvironmental analysis of mass extinction events. *Palaeogeography, Palaeoclimatology, Palaeoecology* 232 (2–4): 190-213.

Tzedakis, P.C., Roucoux, K.H., de Abreu, L., Shackleton, N.J. (2004). The Duration of Forest Stages in Southern Europe and Interglacial Climate Variability. *Science* 306 (5705): 2231-2235.

Tzedakis, P.C., Hooghiemstra, H., Pälike, H. (2006). The last 1.35 million years at Tenaghi Philippon: revised chronostratigraphy and long-term vegetation trends. *Quaternary Science Reviews* 25 (23–24): 3416-3430.

UNEP, 2010. Global Biodiversity Outlook 3, in: UNEP (Ed.). Secretariat of the Convention on Biological Diversity, Montréal, Canada, p. 94.

Václavík, T., Kanaskie, A., Hansen, E.M., Ohmann, J.L., Meentemeyer, R.K. (2010). Predicting potential and actual distribution of sudden oak death in Oregon: Prioritizing landscape contexts for early detection and eradication of disease outbreaks. *Forest Ecology and Management* 260 (6): 1026-1035.

Valladares, F. (2006). Certezas e incertidumbres sobre el impacto del cambio climatico en los ecosistemas terrestres. In: Carrión, J.S., Fernández, S., Fuentes, N. (eds.), *Paleoambientes y cambio climatico*. Fundación Séneca, Agencia de Ciencia y Tecnologia de la Región de Murcia, Murcia.

van der Knaap, W.O., van Leeuwen, J.F.N. (1995). Holocene vegetation succession and degradation as responses to climatic change and human activity in the Serra de Estrela, Portugal. *Review of Palaeobotany and Palynology* 89 (3–4): 153-211.

van der Knaap, W.O., van Leeuwen, J.F.N. (1997). Late Glacial and early Holocene vegetation succession, altitudinal vegetation zonation, and climatic change in the Serra da Estrela, Portugal. *Review of Palaeobotany and Palynology* 97 (3–4): 239-285.

Vanderpoorten, A., Rumsey, F.J., Carine, M.A. (2007). Does Macaronesia exist? Conflicting signal in the bryophyte and pteridophyte floras. *Am. J. Bot.* 94 (4): 625-639.

Vanderwal, J., Shoo, L., Graham, C., Williams, S. (2009). Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? *Ecological Modelling*:

Vargas, P. (2007). Are Macaronesian islands refugia of relict plant lineages?: a molecular survey. In: Weiss, S., Ferrand, N. (eds.), *Phylogeography of Southern European Refugia*. Springer, pp. 297-314.

Verdú, J.R., Galante, E. (2002). Climatic stress, food availability and human activity as determinants of endemism patterns in the Mediterranean region: the case of dung beetles (Coleoptera, Scarabaeoidea) in the Iberian Peninsula. *Diversity & Distributions* 8 (5): 259-274.

Vicente, J., Alves, P., Randin, C., Guisan, A., Honrado, J. (2010). What drives invasibility? A multi-model inference test and spatial modelling of alien plant species richness patterns in northern Portugal. *Ecography* 33 (6): 1081-1092.

Vicente, J., Randin, C., Gonçalves, J., Metzger, M., Lomba, Â., Honrado, J., Guisan, A. (2011). Where will conflicts between alien and rare species occur after climate and land-use change? A test with a novel combined modelling approach. *Biological Invasions* 13 (5): 1209-1227.

Vieira, R.S. (2002). Flora da Madeira. Plantas vasculares naturalizadas no Arquipélago da Madeira. *Boletim do Museu Municipal do Funchal* 8: 5-281.

Vilà, M., Corbin, J., Dukes, J., Pino, J., Smith, S. (2007). Linking Plant Invasions to Global Environmental Change. In: Canadell, J., Pataki, D., Pitelka, L. (eds.), *Terrestrial Ecosystems in a Changing World*. Springer Berlin Heidelberg, pp. 93-102.

Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., Hulme, P.E., DAISIE partners (Adriopoulos, P., Arianoutsou, M., Augustin, S., Baccetti, N., Bacher, S., Bacon, J., Bazos, I., Bolshagin, P., Bretagnolle, F., Chiron, F., Clergeau, P., Cochard, P.O., Cocquempot, C., Coeur d'Acier, A., Cooper, J., Daunys, D., David, M., Delipetrou, P., Didžiulis, V., Dorkeld, F., Essl, F., Galil, B., Gasquez, J., Georghiou, K., Gudžinskas, Z., Hatzofe, O., Hejda, M., Hill, M., Jarošík, V., Kark, S., Klotz, S., Kobelt, M., Kokkoris, Y., Kotarac, M., Kühn, I., Lambdon, P., Lange, E., Lopez-Vaamonde, C., Loustau, M.-L., Marcer, A., Martinez, M., McLoughlin, M., Migeon, A., Minchin, D., Navajas, M., Navajas, P., Olenina, I., Ostler, R., Ovcharenko, I., Panov, V.E., Papacharalambous, E., Pascal, M., Pergl, J., Perglová, I., Phillipov, A., Pino, J., Poboljsaj, K., Rabitsch, W., Rasplus, J.-Y., Rodionova, N., Roy, H., Sauvard, D., Scalera, R., Schwartz, A., Sedláček, O., Shirley, S., Trocchi, V., Winter, M., Yart, A., Yiannitsaros, A., Zagatti, P., Zikos, A.). (2010). How well do we understand the impacts of alien species on ecosystem services? A pan-European cross-taxa assessment. *Frontiers in Ecology and the Environment* 8: 134-144.

Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Westbrooks, R. (1996). Biological invasions as global environmental change. *American Scientist* 84: 468 - 478.

Vucetich, J., Waite, T. (2003). Spatial patterns of demography and genetic processes across the species' range: Null hypotheses for landscape conservation genetics. *Conservation Genetics* 4 (5): 639-645.

Wallace, A.R. (1878). *Tropical Nature and Other Essays*. MacMillan & Co., London.

Wallace, A.R., 1881. Island life. Or the Phenomena and Causes of Insular Faunas and Floras. Harper & Bros., New York, New York, USA.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F. (2002). Ecological responses to recent climate change. *Nature* 416 (6879): 389-395.

Walther, G.-R. (2004). Plants in a warmer world. *Perspectives in Plant Ecology, Evolution and Systematics* 6 (3): 169-185.

Walther, G.-R., Beißner, S., Burga, C.A. (2005). Trends in the upward shift of alpine plants. *Journal of Vegetation Science* 16 (5): 541-548.

Wanner, H., Beer, J., Bütikofer, J., Crowley, T.J., Cubasch, U., Flückiger, J., Goosse, H., Grosjean, M., Joos, F., Kaplan, J.O., Küttel, M., Müller, S.A., Prentice, I.C., Solomina, O., Stocker, T.F., Tarasov, P., Wagner, M., Widmann, M. (2008). Mid- to Late Holocene climate change: an overview. *Quaternary Science Reviews* 27 (19–20): 1791-1828.

Whittaker, R., Araújo, M., Jepson, P., Ladle, R., Watson, J., Willis, K. (2005). Conservation Biogeography: assessment and prospect. *Diversity & Distributions* 11 (1): 3.

Whittaker, R.H., Levin, A.A., Root, R.B. (1973). Niche, Habitat, and Ecotope. *The American Naturalist* 107 (955): 321-338.

Whittaker, R.J., Fernández-Palacios, J.M. (2007). *Island biogeography: ecology, evolution and conservation*. Oxford University Press, Oxford.

Whittaker, R.J., Ladle, R.J., Araujo, M.B., Fernandez-Palacios, J.M., Delgado, J.D., Arevalo, J.R. (2007). The island immaturity - speciation pulse model of island evolution: an alternative to the "diversity begets diversity" model. *Ecography* 30 (3): 321-327.

Whittaker, R.J., Triantis, K.A., Ladle, R.J. (2008). A general dynamic theory of oceanic island biogeography. *Journal of Biogeography* 35 (6): 977-994.

Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A., Snyder, M.A. (2009). Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences* 106 (Supplement 2): 19729-19736.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E. (1998). Quantifying Threats to Imperiled Species in the United States. *BioScience* 48 (8): 607-615.

Wilgen, B.W.v., Richardson, D.M., Le Maitre, D.C., Marais, C., Magadlela, D. (2001). The Economic Consequences of Alien Plant Invasions: Examples of Impacts and Approaches to Sustainable Management in South Africa. *Environment, Development and Sustainability* 3 (2): 145-168.

Williams, J.W., Jackson, S.T., Kutzbach, J.E. (2007). Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences* 104 (14): 5738-5742.

Williams, P., Hannah, L., Andelman, S., Midgley, G., Araujo, M., Hughes, G., Manne, L., Martinez-Meyer, E., Pearson, R. (2005). Planning for climate change: Identifying minimum-dispersal corridors for the Cape proteaceae. *Conservation Biology* 19 (4): 1063-1074.

Wilson, R.J., Thomas, C.D., Fox, R., Roy, D.B., Kunin, W.E. (2004). Spatial patterns in species distributions reveal biodiversity change. *Nature* 432 (7015): 393-396.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., Group, N.P.S.D.W. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions* 14 (5): 763-773.

Woodward, F.I. (1987). *Climate and plant distribution*. Cambridge University Press, Cambridge.

Woodward, F.I., Williams, B.G. (1987). Climate and plant distribution at global and local scales. *Plant Ecology* 69 (1): 189-197.

Woodward, F.I., Cramer, W. (1996). Plant functional types and climatic change: Introduction. *Journal of Vegetation Science* 7 (3): 306-308.

Wyputta, U., Grieger, B. (1999). Comparison of eastern Atlantic atmospheric trajectories for present day and last glacial maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* 146 (1): 53-66.

Yelenik, S., Stock, W., Richardson, D. (2007). Functional Group Identity Does not Predict Invader Impacts: Differential Effects of Nitrogen-fixing Exotic Plants on Ecosystem Function. *Biological Invasions* 9 (2): 117-125.

Zazo, C., J.L.Goy, Dabrio, C.J., Bardají, T., Hillaire-Marcel, C., Ghaleb, B., González, J.A., Soler, V. (2003). Pleistocene raised marine terraces of the Spanish Mediterranean and Atlantic coasts: records of coastal upflit, sea-level highstands and climatic changes. *Marine Geology* 194: 103-133.

Zazo, C., Goy, J.L., Dabrio, C.J., Soler, V., Hillaire-Marcel, C., Ghaleb, B., González-Delgado, J.A., Bardají, T., Cabrero, A. (2007). Quaternary marine terraces on Sal Island (Cape Verde archipelago). *Quaternary Science Reviews* 26: 876-893.

Zazo, C., Goy, J.L., Dabrio, C.J., Cabero, A., Bardaji, T., Ghaleb, B., Soler, V. (2010). Sea level changes during the last and present interglacials in Sal Island (Cape Verde archipelago). *Glob Planet Change* 72 (4): 16-16.

Zhu, K., Woodall, C.W., Clark, J.S. (2011). Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology* 18 (3): 1042-1052.

Zimmermann, N.E., Edwards, T.C., Graham, C.H., Pearman, P.B., Svenning, J.-C. (2010). New trends in species distribution modelling. *Ecography* 33 (6): 985-989.

- ANNEXES -

ANNEXE 1

CLIMAX AND SUBSERAL COMMUNITIES FOR CLIMATOPHYLLOUS VEGETATION SERIES[1] CONSIDERED ON MODELLING

WILD OLIVE MICROFOREST – *Mayteno umbellatae - Oleo maderensis sigmetum*

Climax community - microforest

***Mayteno umbellatae – Oleeteum madrensis* Capelo**, J. C. Costa, Lousã, Fontinha, Jardim, Sequeira & Rivas-Martinez 2000

Low shrubby community

Euphorbietum piscatoriae Sjogren *ex* Capelo, J. C. Costa, Lousã, Fontinha, Jardim, Sequeira & Rivas-Martinez 2000

Artemisio argenteae – Genistetum tenerae Capelo, J. C. Costa, Lousã, Fontinha, Jardim, Sequeira & Rivas-Martinez 2000

Perennial herbaceous community

Cenchro ciliaris-Hyparrhenietum sinaicae Wildpret & O. Rodríguez in Rivas Martinez, Wildpret, Del Arco, O. Rodríguez, Pérez de Paz, García Gallo, Acebes, T. E Díaz & Fernández-González 1993, Corr. Díez-Garretas & Asensi 1999

Annual herbaceous community

Galactito tometosae – Brachypodietum distachyi Rivas-Martinez, Wildpret, Del Arco, O. Rodríguez, Pérez de Paz, García Gallo, Acebes, T. E Díaz & Fernández-González 1993

---

[1] - Based on Costa, J.C., Capelo, J., Jardim, R., Sequeira, M., Espirito-Santo, D., Lousã, M., Fontinha, S., Aguiar, C., Rivas-Martinez, S., 2004. Catálogo sintaxonómico e floristico das comunidades vegetais da Madeira e Porto Santo, in: Capelo, J. (Ed.), A paisagem vegetal da Ilha da Madeira. Quercetea, pp. 61 - 185.

MEDITERREANEAN LAUREL FOREST – *Semele androgynae – Apollonio barbujanae sigmetum*

Climax community - forest

Semele androgynae-Apollonietum barbujanae Capelo, J. C. Costa, Lousã, Fontinha, Jardim, Sequeira & Rivas-Martinez 2000

Microphanerofitic community [2]

Facies A – *Myrto communities-Hypericetum canariensis* Capelo, J. C. Costa, Jardim, Sequeira & Rivas-Martinez 2004

Facies B – *Globulario salicinae-Ericetum arboreae* Capelo, J. C. Costa, Lousã, Fontinha, Jardim, Sequeira & Rivas-Martinez 2000

Low shrubby community

Euphorbietum piscatoriae Sjogren *ex* Capelo, J. C. Costa, Lousã, Fontinha, Jardim, Sequeira & Rivas-Martinez 2000

Perennial herbaceous community

Dactylo hyodis-Hyparrhenietum sinaicae Capelo, J. C. Costa, Lousã, Fontinha, Jardim, Sequeira & Rivas-Martinez 2000

Annual herbaceous community

Campanulo erini-Wahlenbergietum lobelioidis Capelo, J. C. Costa, Jardim, Sequeira & Rivas-Martinez 2004

TEMPERATE LAUREL FOREST

Climax community - forest

Clethro arboreae-Ocoteetum foetentis Capelo, J. C. Costa, Lousã, Fontinha, Jardim, Sequeira & Rivas-Martinez 2000

Microphanerofitic community

Vaccinio padifoli-Ericetum maderincolae Capelo, J. C. Costa, Lousã, Fontinha, Jardim, Sequeira & Rivas-Martinez 2000

---

[2] Facies are not distinguished for modelling.

Low shrubby community

Bystropogono punctate-Telinetum maderensis Capelo, J. C. Costa, Lousã, Fontinha, Jardim, Sequeira & Rivas-Martinez 2000

Perennial herbaceous community

Pericaulido auritae-Geranietum palmatae Capelo, J. C. Costa, Lousã, Fontinha, Jardim, Sequeira & Rivas-Martinez 2000

Annual herbaceous community

Leontodo longirostris-Ornithopetum perpusillis Capelo, J. C. Costa, Lousã, Fontinha, Jardim, Sequeira & Rivas-Martinez 2000

HEATH TREE MICROFOREST – *Ploysticho falcinelli-Erico arboreae sigmetum*

Climax community – microforest

Ploysticho falcinelli-Ericetum arboreae Capelo, J. C. Costa, Lousã, Fontinha, Jardim, Sequeira & Rivas-Martinez 2000

Microphanerofitic community

Community dominated by *Erica maderincola*

Low shrubby community

Argyranthemo montani-Ericetum maderensis Capelo, J. C. Costa, Lousã, Fontinha, Jardim, Sequeira & Rivas-Martinez 2000

Perennial herbaceous community

Vicio capreolatae-Odontidetum hollianae Capelo, J. C. Costa, Jardim, Sequeira & Rivas-Martinez 2004

Annual herbaceous community

Leontodo longirostris-Ornithopetum perpusillis Capelo, J. C. Costa, Lousã, Fontinha, Jardim, Sequeira & Rivas-Martinez 2000

- TABLES OF CONTENTS -

INDEX FOR FIGURES

INDEX FOR TABLES

CONTENTS