Effects of climate and land management changes on conservation of Mediterranean Cork oak woodlands and their bird communities

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Contents

Title page photo: *Cork oak woodlands during spring in the Ribatejo region, Portugal*

Abstract

Cork oak woodlands are a keystone habitat for Mediterranean biodiversity but are currently undergoing a global decline and widespread management changes driven by social, economic and climatic factors. I examine the effects of both climate and land management changes on cork oak woodlands and their bird communities across the western Mediterranean Basin. Future climatic scenarios indicate that up to 60% of current cork oak woodlands may become unsuitable by 2080, especially in southern areas where they will be restricted to microclimatic refugia sites. Increasing aridity, particularly in drier microclimates, will potentiate a decline of cork oak tree condition resulting in impacts across the food web that ultimately have a negative effect on breeding bird abundance and diversity, particularly for tree-dependent forest species. Farmland and shrubland birds respond mainly to habitat features modified by land management and their abundances increase in areas with open and heterogeneous ground cover. Current abandonment, intensification and overexploitation trends are likely to have negative effects on their populations but climate change can also play an important role if it provides an additional stimulus for land management changes. The unique bird assemblages of North African cork oak woodlands seem particularly vulnerable to both factors and should therefore be considered a conservation priority. Nonetheless, climate change may benefit species of Mediterranean origin and seems to have enabled the establishment of resident populations of traditionally migratory bird species in the Iberian Peninsula. This may provide new conservation opportunities for declining migratory species as long as adequate winter habitat areas are available. Adaptation strategies should aim to incorporate biodiversity-friendly management practices, promote cork oak afforestation in areas that will become climatically suitable and evaluate alternatives to provide similar economic and environmental services in the regions where cork oak woodlands are likely to disappear.

Resumo

Os montados de sobro (*Quercus suber*), também conhecidos como dehesas em Espanha, são um sistema agro-silvo-pastoril tradicional que tem origem na gestão humana das florestas Mediterrânicas originais. Distribuído sobretudo na região oeste da bacia Mediterrânica, este tipo de gestão multifuncional foi mantido durante vários séculos devido aos valores económicos, sociais, culturais e ecológicos que providencia às populações que dele dependem. Do ponto de vista ecológico, os montados de sobro são particularmente importantes devido à capacidade de conciliar a gestão e sustentabilidade económica com a manutenção de altos níveis de biodiversidade. Os montados de sobro apresentam comunidades bastante diversas de plantas e borboletas por exemplo, mas são particularmente importantes para as aves uma vez que para além de suportarem comunidades bastante diversas, albergam também espécies endémicas ou protegidas (e.g. Águia-imperial *Aquila adalberti*, Abutre-negro *Aegypius monachus* e Cegonha-negra *Ciconia nigra*) e milhões de aves provenientes do norte da Europa que invernam na bacia do Mediterrâneo todos os anos. Por todas estas razões, os montados de sobro são protegidos a nível europeu pela Diretiva Habitats (92/43/CEE).

Apesar deste facto, os montados de sobro têm sofrido uma regressão na sua área de distribuição nos últimos anos devido a diferentes fatores económicos, sociais e ambientais. Por um lado, a variação no preço de mercado da cortiça e de outros produtos tem levado ao abandono ou intensificação do sistema de gestão mais tradicional. Por outro lado, as alterações climáticas parecem já começar a afetar o sobreiro e o aumento dos eventos de seca tem levado a uma diminuição da condição física e fitossanitária das árvores, resultando em muitos casos na sua morte. Desta forma, tanto as alterações no clima como no sistema de gestão dos montados são passíveis de resultar em efeitos importantes nos montados de sobro e na sua biodiversidade mas ainda não existe uma avaliação desta situação que abranja a distribuição Mediterrânica deste sistema. Esta tese pretendeu examinar o papel das alterações climáticas e da gestão na conservação futura dos montados de sobro e nas suas comunidades de aves na região oeste da bacia do Mediterrâneo. Mais especificamente, esta tese abordou cinco questões principais: i) como irão as alterações climáticas afetar a futura distribuição dos montados de sobro, ii) como diferem as

comunidades de aves nidificantes dos montados de sobro do Norte de África das comunidades presentes nos montados de sobro da Europa e como é que isso afeta a relevância da sua conservação, iii) qual é a importância relativa de alterações climáticas e de gestão na conservação dos diferentes grupos de aves nidificantes dos montados de sobro, iv) como irão as características microclimáticas e topográficas de pequena escala influenciar a resposta da comunidade de aves nidificantes às alterações climáticas e v) qual é a influência das alterações climáticas no recente estabelecimento de populações invernantes de aves tradicionalmente migradoras na região da bacia Mediterrânica.

As previsões obtidas no Capítulo 2 desta tese indicam que as alterações climáticas irão provocar um declínio de aproximadamente 40 a 60% da área atualmente ocupada pelos montados de sobro até 2080, sobretudo nas regiões mais a sul da sua distribuição como Marrocos, Tunísia, Argélia e o sul da Península Ibérica. Nestas regiões apenas deverão permanecer pequenos refúgios de clima adequado se os cenários de alteração climática mais drásticos se verificarem. A restante área de distribuição dos montados de sobro na zona central da Península Ibérica, em Itália e em muitas das ilhas Mediterrânicas deverá manter condições climáticas adequadas à sua manutenção. Novas áreas de clima adequado deverão a norte da distribuição atual no norte da Península Ibérica, ao longo da costa oeste de França e no sul do Reino Unido que poderão se considerada para ações de reflorestação se estas forem consideradas viáveis. Este trabalho foi o primeiro a avaliar os potenciais efeitos das alterações climáticas ao longo de toda a distribuição Mediterrânica dos montados de sobro e, desta forma, a incluir informação da sua distribuição no Norte de África. A importância de incluir esta informação foi também avaliada e os resultados confirmaram estudos anteriores que identificaram potenciais erro nas previsões futuras quando é omissa informação no processo de calibração de modelos correlativos de distribuição de espécies.

No Capítulo 3 foram analisadas as diferenças entre as comunidades de aves nidificantes dos montados de sobro no Norte de África e no Sul da Península Ibérica uma vez que a existência de diferenças significativas poderia inviabilizar a generalização para ambas as regiões das respostas observadas nesta comunidade a fatores ambientais e humanos. Os resultados indicam que os padrões de diversidade e abundância de aves são semelhantes entre as duas regiões e que a maioria das espécies registadas está presente nos montados de sobro de ambas as regiões. Este facto corrobora estudos anteriores que evidenciam a semelhança entre as comunidades de aves florestais da Europa e do Norte de África. Ainda assim, a composição da comunidade de aves em termos de espécies e guildas é diferente entre regiões. A presença do Mar Mediterrânico como barreira à dispersão impediu algumas espécies de colonizarem ambas as regiões e permitiu que outras evoluíssem de forma distinta entre elas, explicando parte das diferenças observadas. As restantes diferenças entre as comunidades de aves dos montados de sobro da Europa e do Norte de África deve-se ao aumento de espécies generalistas e à diminuição de espécies florestais no Norte de África, o que pode ser explicado com base nos padrões locais de sobre-exploração dos recursos deste sistema. Estes resultados permitem considerar que a composição da comunidade de aves dos montados de sobro do Norte de África é sobretudo fruto da resposta às condições ambientais e de intervenção humana observadas na região, que representam apenas um extremo do gradiente observado ao longo da distribuição Mediterrânica deste sistema.

Esta ideia é explorada de forma mais detalhada no Capítulo 4 que analisa a resposta da comunidade de aves nidificante aos gradientes climáticos e de estrutura de habitat observados nos montados de sobro da Península Ibérica e do Norte de África. Tanto fatores climáticos como a estrutura do habitat são importantes na composição da comunidade de aves nidificante dos montados de sobro e em conjunto explicaram mais de um terço da variabilidade total observada nas áreas amostradas. A abundância de aves associadas a ambientes agrícolas e matos como o Trigueirão (*Emberiza calandra*), o Estorninho-preto (*Sturnus unicolor*) e a Cotovia-dos-bosques (*Lullula arborea*) responde sobretudo a alterações na estrutura do habitat ao passo que a abundância de aves florestais e generalistas como o Rouxinol (*Luscinia megarhynchos*), o Rabirruivo-de-testa-branca (*Phoenicurus phoenicurus*) e a Carriça (*Troglodytes troglodytes*) está sobretudo associada a fatores climáticos. Apesar desta observação, a análise individual a cada uma das espécies registadas indica que a abundância da maioria destas espécies aumenta em áreas com uma estrutura mais aberta e heterogénea do sub-coberto e diminui em áreas onde se verificam temperaturas mais elevadas e maior sazonalidade climática. Finalmente, a análise dos padrões espaciais de fatores climáticos e da estrutura do habitat permite concluir que as comunidades de aves do Norte de África devem ser uma prioridade para medidas de conservação devido às alterações climáticas e sobre-exploração do habitat ao passo que no sul da Península Ibérica a principal ameaça são fatores climáticos.

O Capítulo 5 explora de forma mais detalhada como a comunidade de aves nidificante dos montados de sobro responde a condições microclimáticas ao longo de um gradiente de aridez no sul da Península Ibérica. Os dados obtidos com este trabalho evidenciam uma diminuição significativa da abundância e diversidade de aves em zonas mais áridas. Esta observação resulta de alterações na abundância de aves florestais em resposta às condições microclimáticas locais, particularmente evidente em encostas mais secas com orientadas a sul, e confirma o efeito das condições climáticas no na abundância de aves florestais. Em condições mais áridas, os sobreiros apresentam copas menos desenvolvidas pelo que, apesar de apresentarem densidades semelhantes, os montados de sobro nestas condições apresentam uma menor cobertura de copa total. Esta situação resulta numa diminuição dos recursos alimentares disponíveis para as aves florestais, indicando que os efeitos climáticos nas aves florestais se propagam através da cadeia trófica. Desta forma, o aumento das temperaturas e da aridez na região Mediterrânica previsto para as próximas décadas poderá representar um desafio para a manutenção das populações de aves florestais nos montados de sobro do sul da Europa.

Contudo, o aumento da temperatura poderá também proporcionar novas oportunidades para a conservação de aves na Península Ibérica. O Capítulo 6 explora o papel das alterações climáticas no aumento do número de aves invernantes de espécies tradicionalmente migradores observado nos últimos anos na Península Ibérica. Os resultados demonstram que o aumento das temperaturas durante o inverno nas últimas três décadas é uma das potenciais causas para estas alterações do comportamento migratório de várias espécies de aves. Esta hipótese é suportada pelo aumento das temperaturas na Península Ibérica durante o Inverno que se têm tornado mais semelhantes às temperaturas encontradas por estas aves nas suas áreas tradicionais de invernada em África. De facto, a semelhança climática entre estas regiões tem aumentado nas últimas décadas, apesar da diminuição da precipitação observada na Península Ibérica. Adicionalmente, as aves que invernam na Península Ibérica parecem selecionar ativamente áreas que são climaticamente mais semelhantes às suas áreas de tradicionais de invernada em África em relação ao que seria esperado ao acaso. Este comportamento tem sido observado sobretudo em espécies mais generalistas como a Cegonha-branca (*Ciconia ciconia*), a Codorniz (*Coturnix coturnix*) e a Poupa (*Upupa epops*), o que se pode dever ao facto de estas espécies apresentarem requisitos ambientais mais alargados.

Tendo em conta os resultados obtidos no âmbito desta tese, é sugerido um conjunto de medidas de adaptação que possam favorecer a manutenção dos montados de sobro e da sua diversidade em face das alterações climáticas e de gestão que estão a decorrer. Nas áreas onde as alterações climáticas deverão tornar difícil a manutenção de áreas de montado de sobro, será importante proteger potenciais refúgios microclimáticos de forma a manter a conectividade da paisagem e investigar quais as melhores opções do ponto de vista económico e ambiental para a substituição deste sistema de exploração. Em áreas onde a manutenção de áreas extensas de montado de sobro será possível, a prioridade deverá ser a manutenção de medidas de gestão e exploração que possam aumentar a resiliência económica e ecológica deste sistema. Neste sentido, será importante explorar as vantagens de um sistema de gestão e exploração económica multifacetada, que permita a manutenção da heterogeneidade característica deste sistema e que possa promover a robustez económica deste sistema às variações de mercado através da exploração de diferentes recursos. Finalmente, novas áreas de clima adequado para o sobreiro devem surgir a norte da sua distribuição atual e nestas áreas poderá ser ponderada a plantação ativa de novos montados de sobro que possam minimizar as perdas de área previstas em outras regiões.

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Chapter 1

Introduction

Photo: *Cork oak woodlands in the Alentejo region, Portugal*

The remarkable biodiversity found across the Mediterranean Basin today has led to the classification of this region as a biodiversity hotspot (Myers et al. 2000). The complex biogeography of the Mediterranean region, characterized by a particular set of geophysical, climatic and ecological pressures and long-term history of human intervention, has helped to shape the biodiversity patterns that we observe nowadays (Blondel et al. 2010). In fact, it has been argued that moderate disturbance regimes promoted by some traditional management systems are nowadays a key factor in the preservation of biological diversity (Blondel et al. 2010 and references therein).

1.1. Mediterranean cork oak woodlands

Examples of current traditional Mediterranean management systems include cereal pseudo-steppes, North African argan forests, and cork oak woodlands (e.g. Benchekroun and Buttoud 1989, Suárez et al. 1997, Blondel et al. 2010). The latter system is particularly important across much of the western Mediterranean Basin where it is still relatively widespread; it covers more than 1.5 million hectares in southern Europe and nearly 1 million hectares in North Africa (Pausas et al. 2009). Cork oak woodlands are known to support Mediterranean endemic and endangered species (e.g. Cabrera's Vole *Microtus cabrerae*, Spanish Imperial Eagle *Aquila adalberti*, Iberian Lynx *Lynx pardinus* and Cinereous Vulture *Aegypius monachus*) and host diverse communities of plants (rivalled only by the diversity found in tropical forests), butterflies and birds (Pineda and Montalvo 1995, Diáz et al. 1997). The importance of managed cork oak woodlands for biodiversity can only be understood in the light of the complex habitat structure that results from the mosaic of land uses characteristic of traditional management systems.

Cork oak woodlands are a traditional agro-silvo-pastoral system common throughout the western Mediterranean Basin (Pinto-Correia and Mascarenhas 1999). The core area of distribution nowadays is located in the south-western corner of the Iberian Peninsula, but it is also present in other countries along the northern (France and Italy) and southern (Morocco, Algeria and Tunisia) margins of the Mediterranean Sea and even in some Mediterranean islands (Pausas et al. 2009). This type of land use system, generally known as *montado* in Portugal and *dehesa* in Spain, results from a gradual human intervention on the original Mediterranean forests dominated by cork oak (*Quercus suber*) and holm oak (*Quercus rotundifolia*) trees (Joffre et al. 1999). Cork oak woodlands are generally characterized by a savannah-like physiognomy that mimics natural systems and is shaped by local management actions and environmental conditions (Marañón 1988, Joffre et al. 1999, Pereira and Tomé 2004). For this reason, several forms of cork oak woodland management can be found throughout their range (Fig. 1.1). In areas where the landscape in relatively flat, tree density is usually relatively low allowing a better use of the ground layer for agricultural crops (usually in more productive soils) or pastures for cattle grazing (Marañón 1988, Diáz et al. 1997). Land managers in areas with a more complex topography usually favour denser stands for silvicultural practices and avoid more intensive agricultural uses (Pereira and Tomé 2004). Other regular uses include hunting, mushroom collection and bee-keeping (Pereira and Tomé 2004, Bugalho et al. 2009). Common to all the different forms of Cork oak woodland uses is the importance of cork exploitation (Fig. 1.2), which represents in many cases the main source of revenue (Coelho and Campos 2009, Campos et al. 2009) and therefore guarantees the economic viability of this management system.

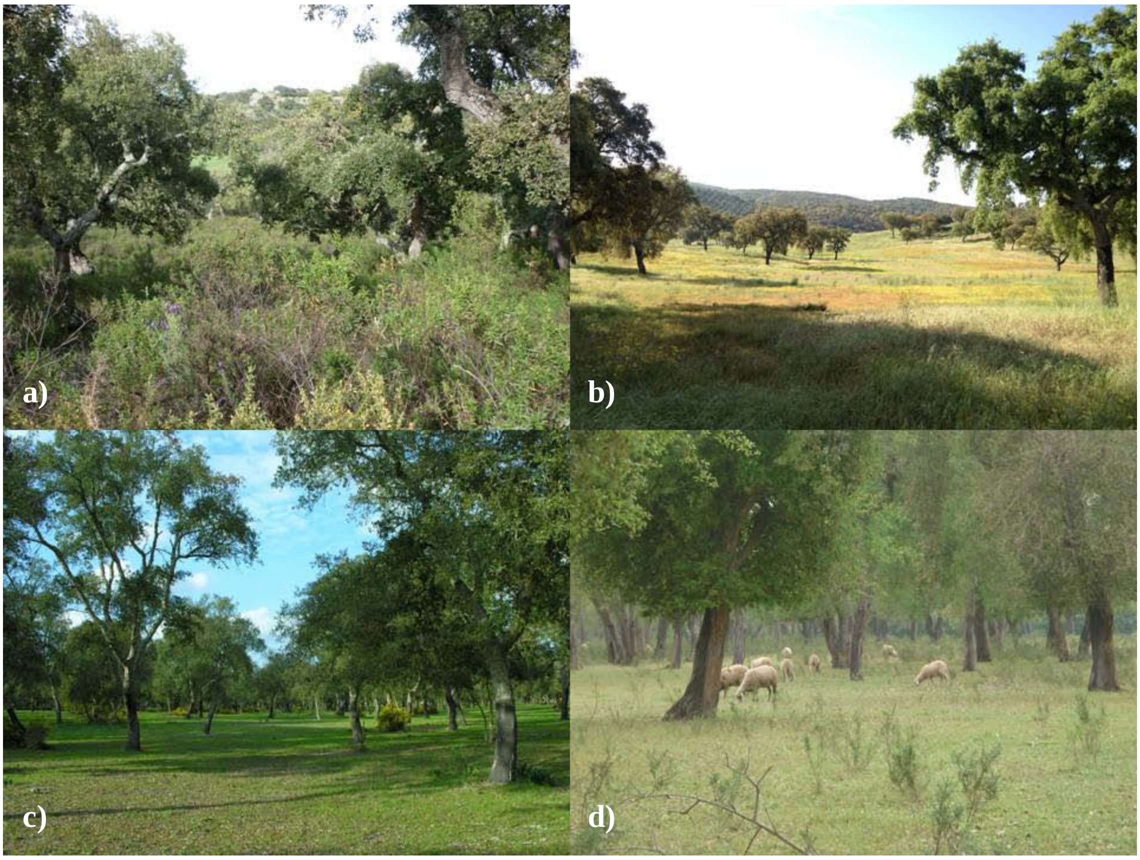

Figure 1.1. *Different cork oak woodland management forms found throughout the Mediterranean Basin. Examples include (a) shrub-dominated woodland, b) open-canopy woodland, (c) closed-canopy woodland and (d) grazed woodland.*

This diversity of uses and management activities has evolved over centuries, resulting in a complex mosaic of cork oak woodland structural and functional forms that favoured the maintenance of high biodiversity levels (Diáz et al. 1997, Telleria 2001). In fact, human intervention is actually required for cork oak woodlands to maintain part of their biodiversity and ecosystem services (Bugalho et al. 2011). This balance between human exploitation and biodiversity conservation has granted cork oak woodlands the status of High Nature Value Farmlands (Hoogeveen et al. 2004) and promoted their inclusion in the Habitats Directive (92/43/CEE). Still, the area of cork oak woodlands that is currently protected has been unable to maintain a favourable conservation status (Berrahmouni et al. 2009, Underwood et al. 2009, Santos and Thorne 2010). In most regions, the area occupied by Cork oak woodlands has decreased in recent years, mostly due to the interrelated effects of land use and climate changes, and fighting this trend will require a better knowledge of potential impacts in order to elaborate adequate conservation efforts (Berrahmouni et al. 2009).

Figure 1.2. *Cork oak planks after extraction from the tree.*

1.2. Major threats to cork oak woodlands

The last decades have seen an increase in cork oak woodland abandonment, intensification and overexploitation due to economic and socio-cultural pressures (Bugalho et al. 2009). Overexploitation occurs throughout the range of the cork oak but is more common in northern Africa, where cork oak woodlands are state-owned and have an open access. Together with a low economic condition of rural population this open access leads to overgrazing, excessive crop cultivation and over-collection of acorns and firewood (Bugalho et al. 2009, Berrahmouni et al. 2009). Abandonment and intensification trends are more common in European areas as a result of changes in market prices (particularly the devaluation of cork), rural exodus and European agricultural policies (Bugalho et al. 2009, Berrahmouni et al. 2009, Bugalho et al. 2011). Land abandonment promotes shrub encroachment, which increases fire hazard and contributes to the lack of regeneration observed in this system (Acácio et al. 2007, Bugalho et al. 2009). The intensification of management activities has been mostly associated with the increase in grazing pressure, which affects oak regeneration, and the introduction of heavy machinery for ploughing, which can destroy young trees and damage superficial roots, essential for cork oaks to survive under drier conditions (Joffre et al. 1999, Bugalho et al. 2009).

Figure 1.3. *Dead cork oak tree.*

In parallel with human-induced impacts, climate change has also increased the pressure on cork oak woodlands, mainly due to the higher frequency of extreme heat and drought events observed in the Mediterranean region over the last decades (Diffenbaugh et al. 2007, Hoerling et al. 2012). Recent research shows that, during these periods of water stress, cork oak trees show higher leaf loss (Carnicer et al. 2011) and reduced tree growth (Besson et al. 2014). These responses to drought lead to an overall decline in tree crown condition and a higher susceptibility to diseases and pests (e.g. *Phytophthora cinnamomi*), which can ultimately result in tree mortality (Fig. 1.3; Brasier and Scott 1994, Allen et al. 2010, Carnicer et al. 2011). This process, potentiated by recurring wildfire events, also made more frequent by climate change, is slowly promoting the conversion of more open cork oak woodlands into persistent shrublands (Acácio et al. 2009) and their decline in many areas (Brasier and Scott 1994, Regato-Pajares et al. 2004, Costa et al. 2011). In summary, both human and climate-induced effects are endangering the long term sustainability of cork oak woodlands and are, therefore, also likely to affect the future of the important biological diversity they support.

1.3. Birds as biodiversity indicators in cork oak woodlands

Cork oak woodlands are important for many biological groups but the abundance and diversity of birds they support is particularly remarkable (Diáz et al. 1997). The relatively open physiognomy of most cork oak woodlands allows the presence of species associated with both forest and open agricultural landscapes (Pulido and Diáz 1992, Diáz et al. 1997, Telleria 2001). Furthermore, the moderate disturbance regime promoted by traditional land management techniques supports the maintenance of endangered species such as the Black Stork (*Ciconia nigra*), Common Crane (*Grus grus*) and Spanish Imperial Eagle (*Aquila adalberti*). The abundance of winter resources also allows millions of Wood Pigeons (*Columba palumbus*), Robins (*Erithacus rubecula*) and Mistle Thrushes (*Turdus viscivorus*) from northern Europe to overwinter in these woodlands. This situation is only possible in cork oak woodlands due to the delicate balance between human intervention and environmental conditions that maintain a heterogeneous habitat structure that favours diverse and abundant bird assemblages (Diáz et al 1997, Telleria 2001). At the same time, birds are generally very responsive to any change that affects this balance and are often used as biodiversity indicators for this reason (Hutto 1998, Gregory et al. 2003).

Land use changes are currently a major threat to biodiversity across the Mediterranean Basin (Cuttelod et al. 2008) and severe impacts from climate change should also be expected (Alcamo et al. 2007). Several studies have highlighted the effects of land use change on birds (Donald et al. 2006, Sirami et al. 2008, Gil-Tena et al. 2009) and the loss of habitat heterogeneity seems particularly important (Atauri and de Lucio 2001, Benton et al. 2003). Birds have also been shown to be responding to climate change (Crick 2004, Devictor et al. 2012), inclusively in the Mediterranean region (Sanz 2002). However, much remains to be explored regarding the effects of changes in land use and climate on cork oak woodlands bird assemblages across the Mediterranean region. For example, the potential effects of different management activities have been highlighted (e.g. Camprodon and Brotons 2006, Godinho and Rabaça 2011, Santana et al. 2012, Leal et al. 2013) but the majority of studies that have addressed these issues were done in southwestern Europe, and their conclusions may not be applicable in regions with different ecological and sociological realities. The knowledge basis on the effects of climate change is even scarcer. The lack of long-term biodiversity monitoring, particularly in northern Africa, makes it difficult to evaluate the impacts of climate change on biodiversity and to disentangle them from those of other drivers of change. In order to promote the long term maintenance of the cork oak woodlands and their biodiversity across the Mediterranean region, it is important to understand the impacts of potential threats across different spatial scales and temporal periods.

1.4. Thesis structure and objectives

The main aim of this thesis was to provide an insight on the potential effects of climate and land management changes on Mediterranean cork oak woodlands and their associated biological diversity. Specifically, I aimed to answer five main questions: i) how may the predicted changes in climate affect the future distribution of cork oak woodlands; ii) how do breeding bird assemblages in North African cork oak woodlands differ from those in Europe and how does this affect their conservation relevance; iii) what is the relative importance of climate and land use change effects for the conservation of different breeding bird groups of cork oak woodlands; iv) how will small-scale topographic and micro-climatic features influence breeding bird assemblage responses to climate change; and v) what is the influence of climate change on the recent establishment of wintering populations of traditionally migratory bird species in the Mediterranean region.

This thesis contains five data chapters (Chapters 2 to 6), each aimed to answer one of the above main questions. These chapters are written in manuscript format with the objective to publish each one as individual papers in peer-reviewed journals. Because of this, each chapter includes a reference list which may facilitate the individual access to each chapter and relevant references. One chapter is currently under editorial consideration for publishing (Chapter 3) and the remaining chapters will all be submitted in due course to relevant journals.

Concerning the overall thesis structure, Chapter 1 provides a general introduction and context to this thesis. Chapter 2 evaluates the future of cork oak woodlands under different climate change scenarios. In addition, it assesses the potential problems resulting from the use of predictive models trained with geographically incomplete data, particularly in the Mediterranean region. Chapter 3 compares the breeding bird assemblages of European and North African cork oak woodlands and assesses the relative importance of a geographical barrier and of local management factors in the structuring of those assemblages. Chapter 4 assesses the response of breeding bird assemblages to climatic and habitat structure gradients across European and North

African cork oak woodlands and their role for bird conservation. Chapter 5 analyses the response of cork oak trees and breeding bird assemblages to local topographic and micro-climatic features across an aridity gradient. Chapter 6 tests the hypothesis that climate change might be linked to the increase of wintering bird populations of traditionally migratory species, using a niche-based approach. Finally, Chapter 7 compiles the key-findings of the thesis in a conservation perspective and provides suggestions for further research.

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Chapter 2

Managing the future of Mediterranean cork oak woodlands: pitfalls of using incomplete species range models for climate change adaptation planning

To be submitted as:

Correia, R. A., Palmeirim, J. M., Franco, A. M. A., Managing the future of Mediterranean cork oak woodlands: pitfalls of using incomplete species range models for climate change adaptation planning.

Abstract

The cork oak (*Quercus suber*) is a keystone species across the Western Mediterranean region and protected at the European level that is predicted to decline due to climate change. To elaborate conservation and adaptation plans for this species, it is essential to spatially forecast how it may be affected by climate change across its range. SDMs (species distribution models) are an adequate tool for this purpose but are potentially constrained by the availability of suitable data for calibration of models. In this study I assessed the consequences of using European only and full Mediterranean range data to predict climatically suitable areas for the cork oak and the implications of using restricted range models for climate change adaptation planning in the Mediterranean Basin. I used maximum entropy modelling to identify present and future climatically suitable areas for the cork oak under the A2 and B2 emissions scenarios, using both restricted and full range models. The European only model predicted significantly greater range reductions than the full Mediterranean model. The best models indicated that about 40 to 60% of the current cork oak range will decline in climatic suitability, particularly in large areas of northern Africa and southern Iberian Peninsula. In these areas, cork oaks and their associated biodiversity will only persist in refugia sites. The areas that will remain suitable by 2080 are located in central Iberian Peninsula, Italy and the Mediterranean isles. To compensate losses in southern areas and maintain the economic and ecologic value of cork oak woodlands across the Mediterranean Basin afforestation efforts are urgently needed and should focus in the new climatic suitable areas along the Atlantic coasts of northern Iberia, France and southern United Kingdom.

2.1. Introduction

The cork oak (*Quercus suber*) is a keystone species throughout much of the Western Mediterranean basin, which is part of a very important biodiversity hotspot (Myers et al. 2000). This species forms the basis of cork oak woodlands, usually known as *montados* or *dehesas* in Portugal and Spain respectively. Cork oak woodlands are a traditional agro-silvo-pastoral system of high economical and ecological value resulting from the original Mediterranean forests (Diáz et al. 1997). Most of its economic value usually comes from cork production (e.g. cork generates approximately 900M€ per year just in Portugal and represents approximately 2.5% of all Portuguese exports) and this activity that is generally compatible with high biodiversity levels (Leal et al. 2011). This allows cork oak woodlands to sustain high numbers of species endemic of the Mediterranean Basin and also regionally and globally endangered species among the diverse communities it supports (Diáz et al. 1997). For this reason, cork oak woodlands are recognized as a High Nature Value Farmland (Hoogeveen et al. 2004) and their ecological value has been recognized even at the European level, with its inclusion on the Habitats Directive (92/43/CEE). Nonetheless, this system is under several threats. Increasing trends of abandonment and over-exploitation in traditionally managed areas are affecting tree health and regeneration (Acácio et al. 2007, Bugalho et al. 2009). Climate change is an important factor promoting cork oak defoliation and mortality through increasing drought events (Allen et al. 2010, Carnicer et al. 2011). Given that the Mediterranean basin is considered a hotspot for climate change (Giorgi 2006) and the generally low adaptive capacity of Mediterranean forests (Lindner et al. 2010), it is essential to predict changes in cork oak ranges and future climatic suitability areas to develop effective conservation strategies.

Species Distribution Models (SDMs) are one of the few available tools to spatially predict the impacts of future climate change. This makes them potentially useful for the planning of conservation (Rodriguez et al. 2007) and afforestation (Hidalgo et al. 2008, Vessella and Schirone 2013), both important components of a strategy for adaptation to the consequences of climate change. Still, the application of SDMs is not without challenges as their predictions are subject to uncertainty (Diniz-Filho et al. 2009, Buisson et al. 2010). While the inherent uncertainty in predictions associated with future climatic scenarios is inevitable, other important sources of uncertainty related to the modelling framework should be minimized. The importance of the extent of the distribution data used to train models has been suggested (Thuiller et al. 2004), as not covering the full range of a species may result in erroneous assessments of suitable areas (Barbet-Massin et al. 2010, Sánchez-Fernández et al. 2011). Despite this fact, many large scale studies have failed to incorporate data from the full range of species (Huntley et al. 2008, Setelle et al. 2008), presumably because of the difficulty to obtain detailed data from some parts of the species ranges. This difficulty may explain why previous estimates of climate change impacts on many species, including the cork oak (Benito Garzón et al. 2008, Atorre et al. 2011), did not include data from their whole distribution. There is a need to understand how the usage of restricted range data may affect model predictions and, therefore, future conservation and adaptation decisions in a climate change context. This may be particularly important in the Mediterranean region as it spans an important north-south gradient in climatic conditions, which encompasses both Europe and North Africa. Due to the severity of climatic changes predicted for this region (Giorgi 2006), many projects use SDMs to forecast the future suitable range for animal and plant species of conservation concern. However, data on the distribution of some species in North Africa is much scarcer than in Europe, and thus researchers are often forced to train SDMs solely using data from their European range. This practice assumes that the range of the species in Europe is sufficiently representative of the climatic niche occupied by species to model current and future ranges.

In this manuscript I aim to (i) quantify differences in cork oak range change as predicted by European and full Mediterranean data models (ii) assess the consequences of using these two models for climate change adaptation planning in the Mediterranean Basin using the cork oak as a study species, and (iii) assess the potential of current afforestation efforts to compensate climate change impacts on the distribution of cork oak woodlands, using Portugal as a case study.

2.2. Material and methods

2.2.1. Distribution data

I obtained cork oak distribution data by geo-referencing or collecting geo-referenced distribution data resulting from national Forestry or Biodiversity Inventories for the Mediterranean countries where the species is present (Portugal – Autoridade Florestal Nacional 2009; Spain – Dirección General de Medio Natural y Política Forestal 2009; France – Institut National de l'Information Géographique et Forestière 2010, Italy – Atorre et al. 2011; Morocco – Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification 2005; Algeria – Barry et al. 1974; Tunisia – Khaldi 2004). The spatial resolution of the data differed between countries, so the complete distribution data set was upscaled to a 10 arc-minutes resolution grid. This homogenised the spatial resolution of the distribution data and matched it to the resolution of the climate data used (Fig. 2.1). The location of recent cork oak plantations in Portugal was obtained from the same source as the distribution data (Autoridade Florestal Nacional 2009).

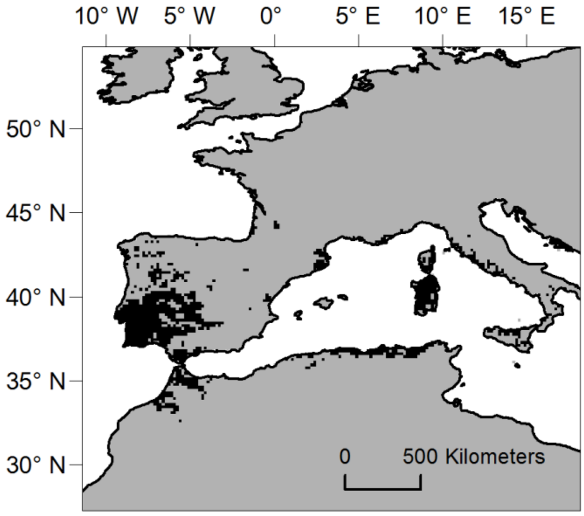

Figure 2.1. *Cork oak distribution (in black). Over 60% of the current distribution is in the Iberian Peninsula (Pausas et al. 2009).*

2.2.2. Environmental data

I obtained present climate data from the WorldClim database (http://www.worldclim.org/) at 10 arc-minutes resolution, for the time-period between 1950 and 2000. Future climate predictions for 2080 (2070-2099) were obtained from the Consultative Group on International Agricultural Research (CGIAR)'s Research Program on Climate Change, Agriculture and Food Security (CCAFS) climate data archive (http://ccafs-climate.org), at the same resolution as the present climate data, for three Global Circulation Models (GCMs – CGCM2, CSIRO MK2 and HadCM3) and two Global Emission Scenarios (GESs – IPCC SRES A2 and SRES B2). These scenarios were chosen as they represent moderate (B2 scenario, average increase of 2.4ºC by 2100) and high (A2 scenario, average increase of 3.4ºC by 2100) world-wide climate warming trends.

The full climate dataset included 19 bioclimatic variables (Hutchinson et al. 2009) for both present and future scenarios. I assessed pairwise variable correlation using Pearson's r, and only variables with r<|0.8| were retained for modelling purposes (Désamoré et al. 2012, Telleria et al. 2012). The final variables included in the models were Mean Annual Temperature, Isothermality, Temperature Seasonality, Precipitation of the Wettest Month and Precipitation Seasonality (Table 2.1).

Table 2.1. *List and description of the bioclimatic variables used for modelling purposes.*

Variable	Description
Mean Annual Temperature	Mean of weekly mean temperatures
Isothermality	Ratio of mean diurnal temperature range and annual temperature range
Temperature Seasonality	Coefficient of variation of mean weekly temperatures
Precipitation of the Wettest Month	Precipitation occurred during the wettest month of the year
Precipitation Seasonality	Coefficient of variation of weekly precipitation estimates

2.2.3. Modelling framework

In order to evaluate the consequences of using only part of the range of species in model calibration, I modelled suitable areas for the cork oak using its European only (restricted) range and Mediterranean (full) range. A maximum entropy modelling method (Phillips et al. 2004, Elith et al. 2011) was used to obtain predictions of present and future suitable areas for the cork oak. This modelling technique is known to perform well in comparison with other modelling algorithms (Elith et al. 2006), even with restricted data (Wisz et al. 2008), and is thus suitable for this study.

Maximum entropy models were run in R software package v2.15 (R Development Core Team 2011) with package *dismo*. Models were fitted using only Linear and Quadratic features in order to make results more interpretable biologically (Syfert et al. 2013) and to obtain better estimates of current and future potential distributions, which are important for conservation purposes (Thuiller at al. 2004, Jiménez-Valverde et al. 2008). Background points were selected from the whole study region, but excluded areas where the cork oak is known to be present. For each range extent, models were replicated 100 times by selecting 75% of data records for calibration and 25% for validation, using a sub-sampling approach. I obtained presence-absence maps of suitable areas for cork oak using a metohod that minimizes the absolute difference between model sensitivity and specificity (“Equal training sensitivity and specificity” threshold in MaxEnt), which has been recommended as a good threshold selection approach (Liu et al. 2005, Jiménez-Valverde and Lobo 2007). Consensus maps were calculated for the present and future climate scenarios analysed using an unweighted average of the predictions obtained from model replicates. These maps were ultimately used to identify intervention areas for conservation and adaptation measures based on the impacts predicted by the A2 scenario. Consensus and intervention maps were edited using the ‘raster’ package for R software package v2.15 (R Development Core Team 2011) and map visualization and plotting was done using ArcGIS v10.0 (ESRI, 2010).

2.2.4. Model assessment and statistical analysis

Model predictive performance was assessed using AUC test scores. I obtained predictions of present and future suitable areas for two climate change scenarios in order to quantify climate change effects on cork oak. These predictions were then used to obtain estimates of range change and range maintained for future scenarios. Range change was defined as the difference between the number of suitable pixels predicted in present and future scenarios; range maintained was the percentage of the pixels currently occupied that is likely to remain suitable in the future. The role of recent afforestations to compensate potential cork oak losses in Portugal was assessed by calculating the area of current cork oak range and new plantations likely to remain suitable in the future. Finally, I evaluated the consequences of using incomplete species ranges in model calibration by comparing predictions obtained with restricted and full distribution datasets using pairwise t-tests. All the calculations were computed with R software package v2.15 (R Core Team 2011).

2.3. Results

Average AUC test scores of both restricted and full range models were 0.97 and did not differ significantly (Table 2.2). Predictions of present suitable range were also similar between models, averaging 2419 suitable pixels for the restricted model and 2402 for the full model. However, I did find significant differences between future suitable range predictions, for both the A2 (pairwise *t*-test, t=17.64, df=299, P<0.001) and B2 scenarios (pairwise *t*-test: t=18.59, df=299, P<0.001). The full range model always predicted a larger suitable area, averaging 2423 suitable pixels in the B2 scenario and 2237 suitable pixels in the A2 scenario (Table 2.2).

All models predict a major shift in the future range of the cork oak (Fig. 2.2), with a marked reduction of suitable areas in North Africa and southern Iberia, and a major increase in suitability to the north of the current core distribution (e.g. Atlantic Iberia, France and even England). However, the extent and geographic location of the predicted changes were quite different between the models trained with the restricted and full ranges (Fig. 2.2). For example, the restricted models predict substantially greater declines in the southern part of the current range. The full range models predict an area of the current range that will remain suitable in the future to be approximately 15% larger than what is estimated by the restricted range models in both scenarios (Fig. 2.3A). Therefore, predictions are significantly different between the restricted and full range models for both the B2 (pairwise *t*-test, t=30.30, df=299, P<0.001) and A2 scenarios (pairwise *t*-test, *t*=30.30, df=299, *P*<0.001). As a result, and in spite of the predicted increase in the area suitable for cork oaks in Atlantic Europe, most models still predicted a global loss of suitable area. Estimates of range change obtained with restricted range models are approximately 10% higher than the figures predicted by the full range models. This difference was statistically significant for both the B2 (pairwise *t*-test, *t*=24.10, df=299, *P*<0.001) and A2 (pairwise *t*-test, *t*=26.74, df=299, *P*<0.001) emissions scenarios (Fig. 2.3B).

Table 2.2. *Summary of AUC scores and predicted number of suitable pixels for present and future scenarios obtained with the restricted and full range models. Indicated P-values obtained with pairwise t-test.*

Descriptor	Model		*P*-value
	Restricted range	Full range	
AUC test scores (mean ± SD)	0.97 ± 0.01	0.97 ± 0.01	0.97
No. suitable pixels (mean ± SD)			
Present	2419 ± 87	2402 ± 55	0.11
B2 scenario	2154 ± 147	2423 ± 195	<0.001
A2 scenario	2040 ± 224	2237 ± 232	<0.001

Differences between models were also evident at the local scale when analysing estimates of range loss for Portugal and the future suitability of cork oak plantations (Fig. 2.4). I found significant differences between models for the estimates of future range loss in Portugal for both the A2 (pairwise *t*-test, *t*=58.08, df=299, *P*<0.001) and B2 scenarios (pairwise *t*-test, *t*=23.22, df=299, *P*<0.001). Even the more conservative full range model predicts average cork oak range losses in Portugal of approximately 5% (~25000 ha) for the B2 scenario and 40% (~200000 ha) for A2 emissions scenario (Fig. 2.5A). In what concerns recent cork oak plantations, the same model predicts that approximately 98% and 66% (B2 and A2 scenarios respectively) of plantations are in areas that should remain suitable in the future (Fig. 2.5B). Again, these estimates were significantly greater than those obtained with the restricted range model for the B2 (pairwise t-test, *t*=24.02, df=299, *P*<0.001) and A2 scenarios (paired *t*-test, *t*=85.60, df=299, *P*<0.001).

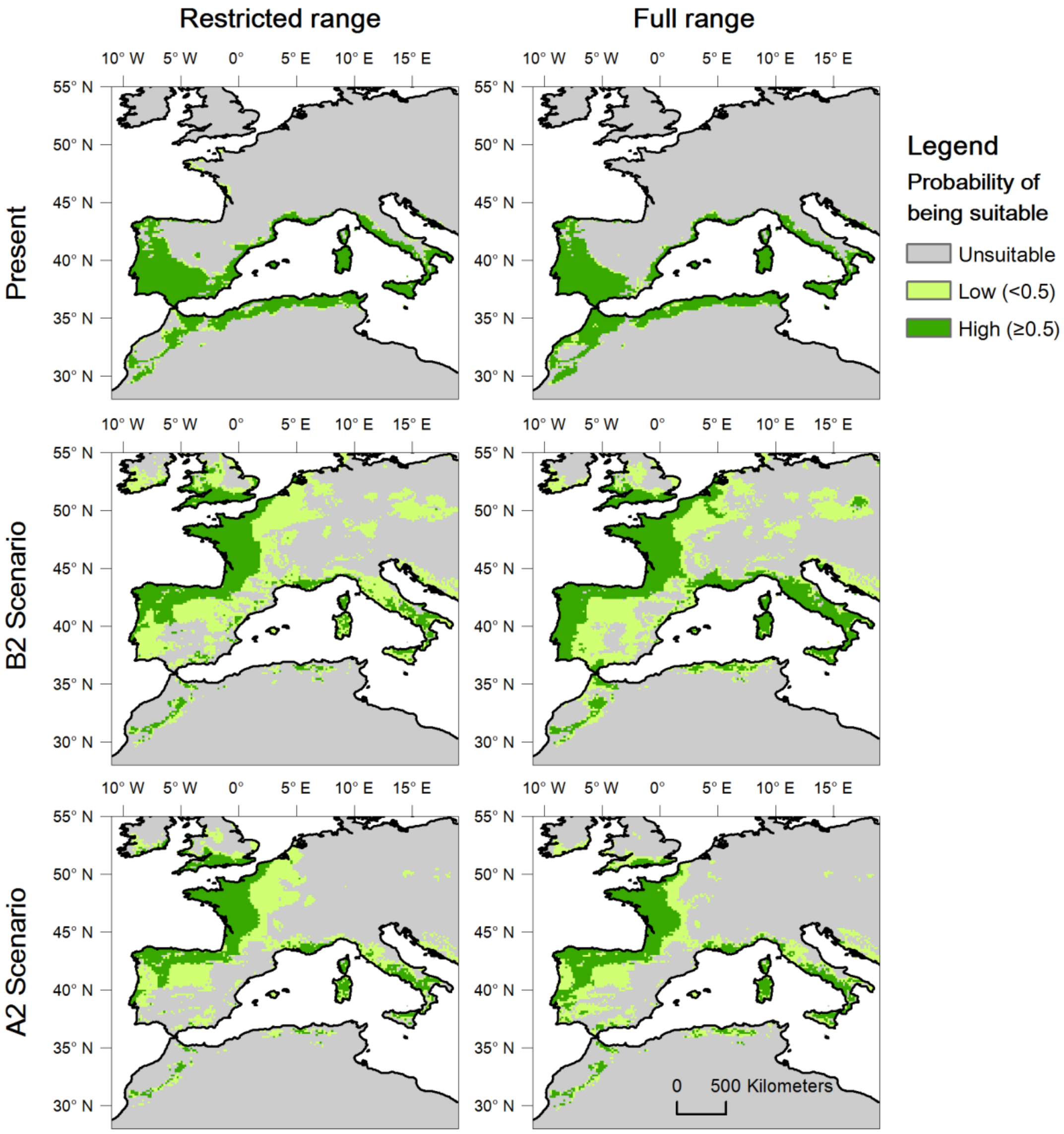

Figure 2.2. *Climatically suitable areas for the cork oak as predicted by the restricted range (left) and full range (right) models. Images represent consensus maps of predicted suitability for the present (top row) and year 2080 according to different emission scenarios (centre and bottom rows).*

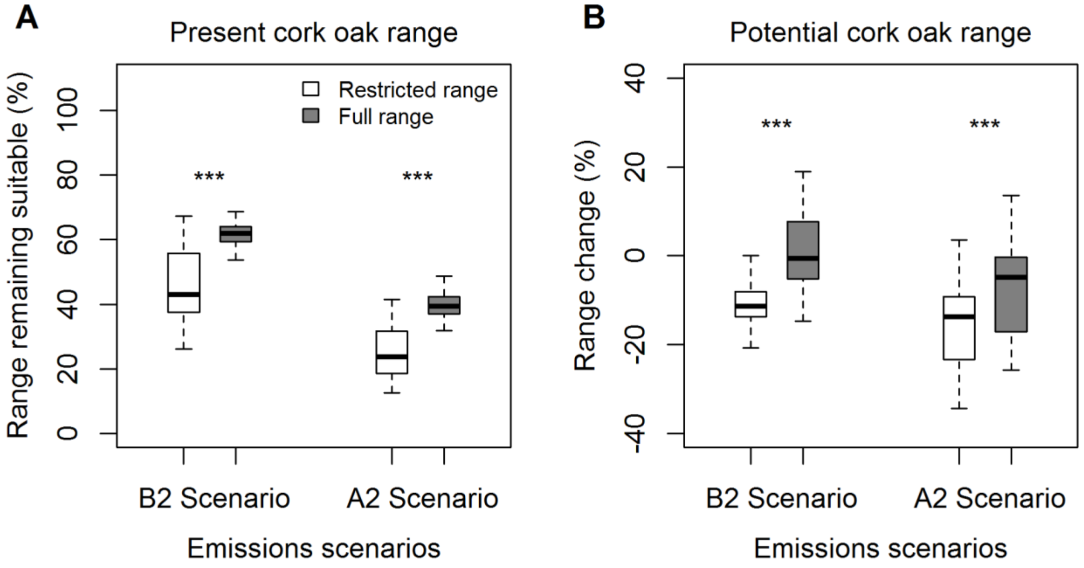

Figure 2.3. *Estimates of (A) present range likely to remain suitable in future scenarios, and (B) potential cork oak range change according to predictions made by the restricted and full range models. Significant differences between models were found for all estimates and emissions scenarios analysed (*** p<0.001, pairwise t-test).*

2.4. Discussion

2.4.1. European only vs. full Mediterranean models: implications for conservation planning

Predictions of future suitable areas obtained with the restricted range model, calibrated with the European distribution of the cork oak, differed significantly from the predictions obtained with the full range model that included both the European and North African range (Fig. 2.2). These differences can be explained by the influence of data extent on the calibration of model response curves (Thuiller et al. 2004).

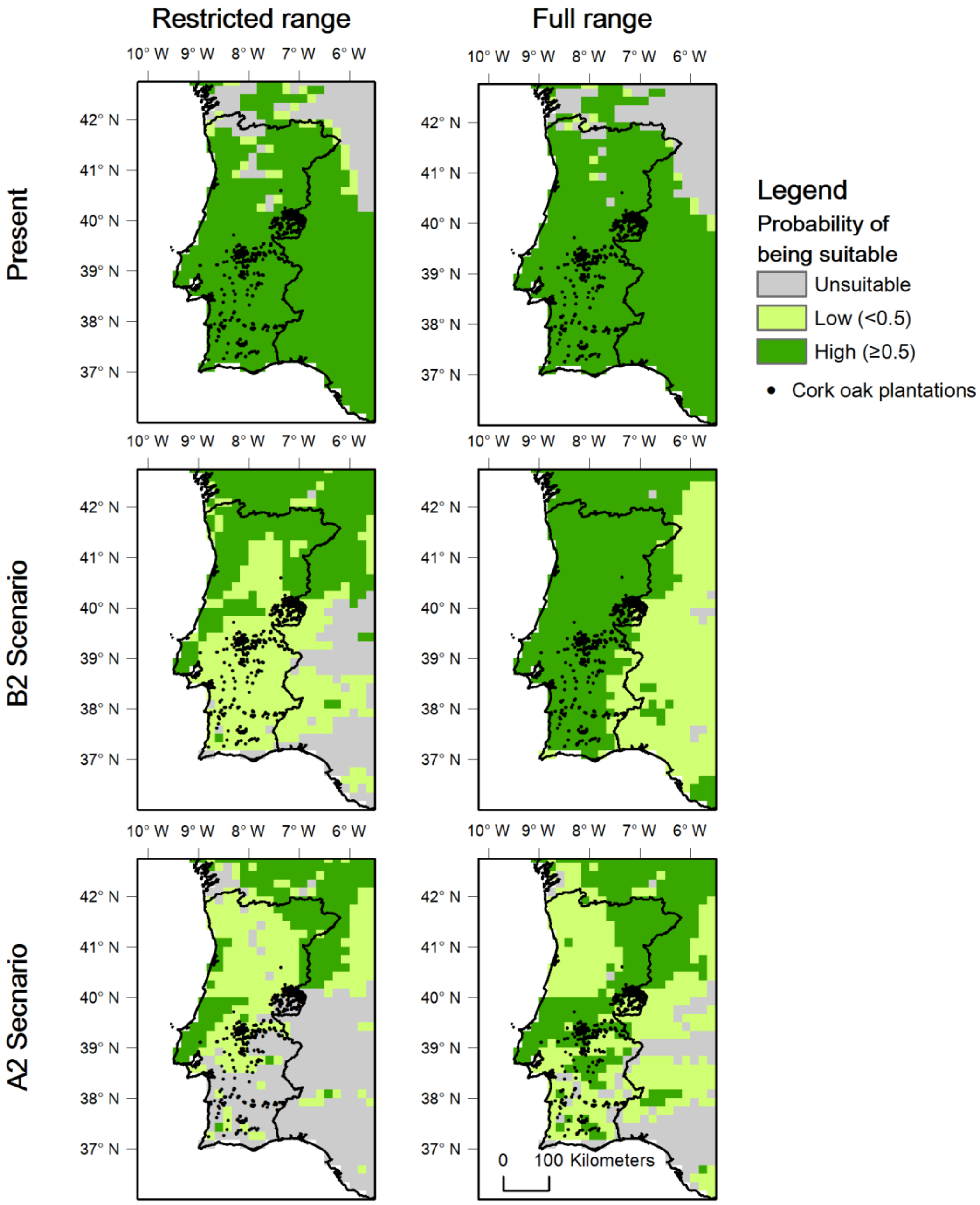

Figure 2.4. *Distribution of recent cork oak plantations in Portugal and predicted suitability for present (top row) and future emission scenarios (middle and bottom rows), as predicted by the restricted (left) and full range (right) models.*

Excluding data from regions with differing climatic conditions will likely prevent species distribution models to accurately identify all climatically suitable areas for the species. This is a particularly important drawback in a climate change context, because current climatic conditions may shift geographically or even disappear (Ohlemüller et al. 2006), which may restrict model transferability and ultimately affect predictions (Barbet-Massin et al. 2010).

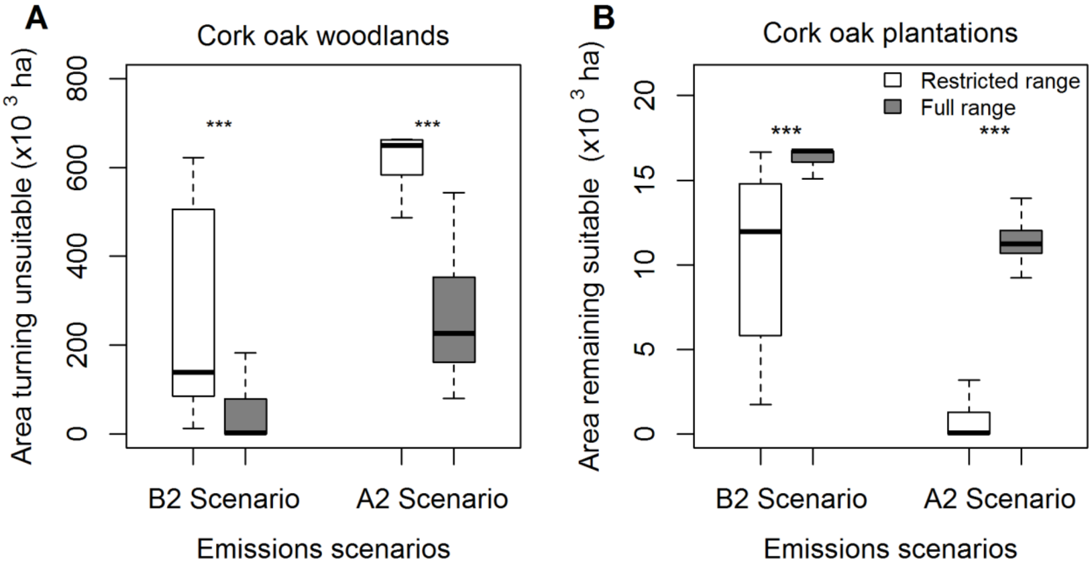

Figure 2.5. *Estimates of (A) cork oak woodland area predicted to become unsuitable and (B) area of cork oak plantations remaining suitable in Portugal, as predicted by the restricted and full range models for the B2 and A2 emissions scenarios. Significant differences were found between model predictions for each statistic and emissions scenario analyzed (*** p<0.001, pairwise t-test).*

These results have important implications for the use of SDMs for conservation planning: restricted models may fail to identify future suitable areas, hence providing inaccurate information for managers and policy-makers. Modelling techniques known to perform well with restricted data, such as maximum entropy models (Wisz et al. 2008), may result in good models of the current distributions, as results show, but are likely to be inaccurate when applied to future scenarios. Using more complete information on species distributions to calibrate models is thus important (Lobo 2008). However, data availability is still a problem in many regions, and even when available, issues with data quality may prevent their inclusion in the high-resolution models that are usually required for conservation and policy decisions. The Mediterranean Basin is an example of the difficulties of making accurate predictions for future scenarios using SDMs. For many Mediterranean species, distribution data are more easily available for southern Europe than northern Africa. In spite of the ongoing progress of Natural history research in North African countries, distribution data is still usually sparse, outdated, or of low resolution. The presence of the Mediterranean Sea separating these two regions provides additional geographical justification for excluding North Africa from modelling efforts. However, the omission of information from North Africa, where many Mediterranean species reach their warmest and driest range limits, will result in incorrect model calibration and, therefore, inaccurate future predictions. Efforts to tackle this issue should focus on increasing knowledge of species distributions through biodiversity mapping (for an example, see Jetz et al. 2012) and improving data sharing, which may also stimulate inter-regional collaborations required to tackle climate change (Brooker et al. 2010).

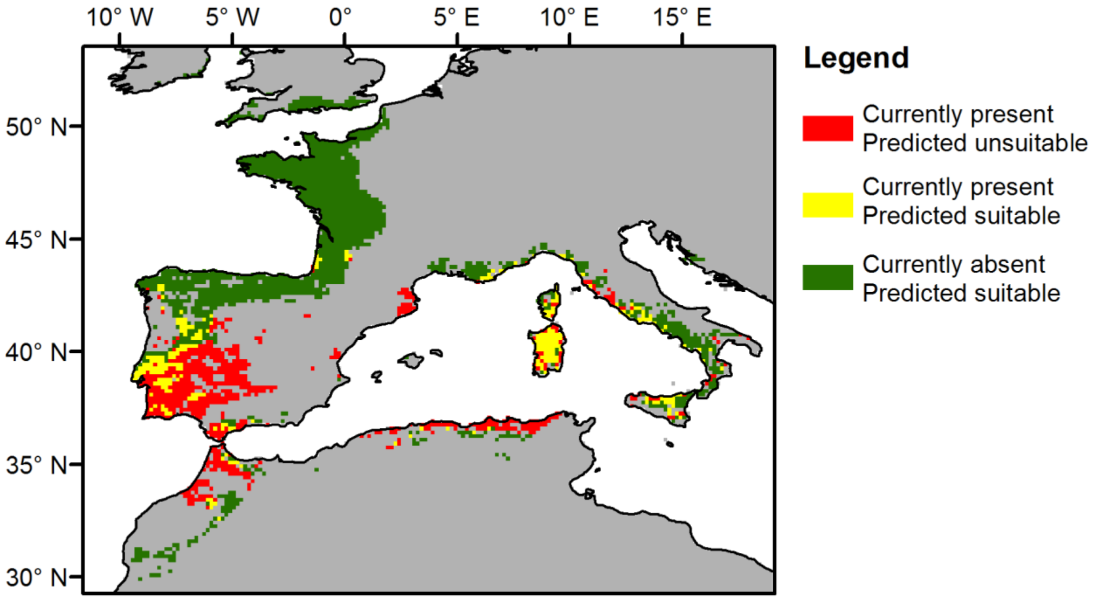

Figure 2.6. *Summary map of climate change impacts on suitable areas for the cork oak. Areas where the species is currently present but likely to become climatically unsuitable due to climate change are shown in red. In yellow are shown the areas where cork oak is currently present and climatic conditions are likely to remain suitable in the future. Green areas represent new suitable climatic space for the cork oak in areas where it is currently absent.*

2.4.2. Cork oak conservation and adaptation priorities in light of future climate change

Results show a clear message: Climate change will affect the cork oak distribution range, which will have important impacts on the future of the *Montado* system. Both its potential and occupied range are expected to decline, with predictions of only 40 to 60% of its current worldwide range likely to remain suitable in the future. Impacts will not be homogenous across its range, and will affect mostly northern Africa and the south of the Iberian Peninsula (Fig. 2.2). In the particular case of Portugal, that currently holds approximately one third of the cork oak global range (Pausas et al. 2009), between 40 to 80% of its current area may become unsuitable in higher warming scenarios (Fig. 2.5). Nonetheless, the results obtained with the full range models provide more favourable scenarios for the application of conservation and adaptation measures than previous estimates resulting from incomplete range efforts. The type intervention required varies between regions and is dependent on the presence or absence of cork oak areas and the changes in the climatic suitability predicted due to climate change (Fig. 2.6).

Conservation priorities should focus primarily in areas of the current cork oak range that are expected to remain suitable. In more extreme scenarios, extensive losses of climatically suitable areas are predicted in northern Africa and southern Iberian Peninsula and only small pockets of suitable climate are likely to maintain viable cork oak populations (red areas in Fig. 2.6). These areas of potential refugia should be primary candidates for immediate protection in order to maintain landscape connectivity and should therefore be managed to increase their resilience and long term sustainability. They would be valuable to boost the current network of European and Mediterranean protected areas, deemed necessary to face future climate change (Klausmeyer and Shaw 2009, Araújo et al. 2011).

Despite the likely reduction in suitable area for the cork oak, models still predict between 40 and 60% of the current range to remain suitable in the future. Areas likely to maintain their cork oak populations include the central Iberian Peninsula, Italy and the Mediterranean islands of Sicily, Sardinia and Corsica (yellow areas in Fig. 2.6). In these areas the conservation focus should shift to the promotion of long term sustainable management practices, required to maintain biodiversity and ecosystem services

(Bugalho et al. 2011). This should include a restriction on the usage of heavy machinery, introduced as a result of intensification trends and European policies, which usually results in root damage for the trees, management of grazing stock numbers and economic stimulus through subsidies or product certification that may buffer managers from fluctuating market prices of cork and other products thus slowing current land abandonment trends (Bugalho et al. 2009, Bugalho et al. 2011).

Adaptation efforts should take advantage of the predicted northward shift in climatically suitable areas along the Atlantic coasts of northern Iberian Peninsula, France and southern United Kingdom (green areas in Fig. 2.6) by promoting a northwards expansion of the species distribution. However, the low regenerative ability of cork oaks (Pons and Pausas 2006, Acácio et al. 2007, Caldeira et al. 2014) indicates that natural expansion is unlikely to occur at a speed compatible with the climatic changes expected for the Mediterranean region (Loarie et al. 2009). In this scenario, a proactive approach based on afforestation efforts will be required (Resco de Dios 2007). In Portugal, recent afforestation efforts may compensate potential range losses in a moderate climate change scenario, but will still fail to do so in more extreme scenarios (Fig. 2.4 and 2.5). Further afforestation efforts should be stimulated in order to compensate predicted losses in the current range and improve the long term ecologic and economic sustainability of this system. Species distribution models can contribute to identify areas climatically suitable for new plantations (Hidalgo et al. 2008, Vessella and Schirone 2013), although such models should also incorporate non-climatic factors, such as soil type and slope, which influence cork oak establishment and survival (Costa and Madeira 2011).

2.5. Conclusions

Restricted range models provide biased results of future scenarios and should be regarded with caution, as was clearly shown for the cork oak. Results illustrate how using a restricted range dataset to train models may result in predictions that exaggerate climate change impacts. In the Mediterranean region this problem is particularly serious when the driest and warmest parts of the range are excluded from the calibration. Biased models are likely to weaken the planning of minimization and adaptation measures and divert resources, so it is important to incorporate the most complete range data in models training.

Nonetheless, even when using the full cork oak distribution for calibration the models predicted a major reduction of the current cork oak distribution. Consequently, science based conservation and adaptation measures will be essential to provide a sustainable future for the species and for the agro-silvo-pastoral system that depends on it. The results point towards three major conservation and adaptation measures for the cork oak in light of climate change: protection and preservation of potential relict fragments in highly affected areas, adequate land management practices in areas of long term climatic suitability, and an active northward expansion of cork oak distribution promoted through afforestation efforts.

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Chapter 3

Role of the Mediterranean Sea differentiating European and North African woodland bird assemblages

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Abstract

The Mediterranean Sea has separated the sclerophyllous forests of southern Europe and northern Africa for millions of years, but its role structuring forest bird assemblages remains unclear. To address this issue I sampled bird assemblages in cork oak woodlands located north and south of the Strait of Gibraltar and compared abundance, diversity, and species and guild assemblage structure. Abundance and diversity patterns were remarkably similar, but dissimilarity analyses of species and guild composition revealed differences in bird assemblage structure between regions. Differences are partly attributable to the effect of the Mediterranean as barrier to the dispersal of forest birds; a few species were unable to colonize North Africa, and many that colonized it remained in sufficient isolation to evolve into distinct taxa. In addition to this divergence of biogeographic genesis, assemblages also differ because in North African cork oaks woodlands forest specialists were less abundant, and generalists more abundant. This difference is parsimoniously explained by habitat overexploitation affecting tree cover. Managed cork oak woodlands are widespread in the Western Mediterranean, and are valuable because they conciliate economic exploitation with high biodiversity, mostly of the original Mediterranean forests. Those of North Africa are of greater conservation concern because they harbour endemic bird species that give its assemblage a distinct character, cover a smaller area, and are currently under greater pressure from overexploitation. These results highlight the importance to implement management and exploitation practices that increase system resilience and maintain biodiversity value throughout the range of cork oak woodlands.

3.1. Introduction

The Mediterranean Basin is considered a hot-spot of biodiversity (Myers et al. 2000), which is to a great extent a consequence of the topo-geographical complexity of the region (Blondel et al. 2010). The Mediterranean Sea is its most evident geographic feature, physically separating the terrestrial ecosystems of southern Europe and northern Africa. The last time this separation was interrupted in the Western Mediterranean was over five million years ago, when geological forces temporarily closed the Strait of Gibraltar, causing a partial desiccation of the landlocked sea (Duggen et al. 2003).

The role of the Mediterranean Sea as a barrier to gene flow within species is relatively well studied (e.g. Broderic et al. 2003, García-Mudarra et al. 2009, Pons et al. 2011, Husemann et al. 2014), but its effects on the structure of species assemblages across the region remain somewhat unexplored. Indeed, such an extensive barrier to dispersal of biota may cause the differentiation of assemblages by limiting colonization across the barrier, and by facilitating speciation of isolated populations. Several studies confirmed speciation processes across the Strait of Gibraltar in multiple taxa, although the frequency of this phenomenon is greatly dependent on the dispersal abilities of each taxa; flying species, and those that tolerate salt water, tend to show lower levels of differentiation across the Strait (Habel et al. 2009). Existing information is still insufficient to make broad generalizations about the level of permeability of the Strait for birds, but evidence indicates that it is comparatively low for forest-adapted birds (Pons et al. 2011). In fact, a number of them have highly differentiated populations in Iberia and North Africa, whereas arid-adapted species are involved in several recent colonization events across the Strait (Pons et al. 2011).

The structure of species assemblages on the two sides of the Mediterranean may not differ solely due to its natural role as a barrier to dispersal, but also because it separates two highly contrasting socio-economic realities. These contrasts translate into different land use practices, which are known to have a marked influence on biological communities and ecological processes across the region (Blondel et al. 2010).

Large areas of the Western Mediterranean basin are dominated by cork oak (*Quercus suber*) woodlands, usually managed as an agro-silvo-pastoral system known as *montado* in Portugal and *dehesa* in Spain. This system resulted mostly from the transformation of original cork oak forests through a long history of low intensity management (Diáz et al. 1997). In spite of its semi-natural character, it harbours some of the richest bird assemblages in the Mediterranean region, both in Europe and in North Africa. The overall structure of the habitat is similar in the cork oak woodlands of the two continents, but their bird assemblages may differ not only because of the separation by the Mediterranean but also due to contrasts in their levels of exploitation (Bugalho et al. 2011). For these reasons, cork oak woodlands are particularly well suited to investigate the process of differentiation of bird assemblages, separating the role of the Mediterranean Sea as a barrier for forest birds and that of human induced factors.

The general aim of this study is to contribute to the understanding of the barrier role of the Mediterranean Sea in the structuring of biological communities, by evaluating its relevance shaping woodland birds assemblages. In addition, I quantified the relative importance of this role and that of woodland exploitation and management. To achieve these objectives I compared the bird assemblages of North African and Iberian cork oak woodlands, testing for differences in (i) assemblage structure (species richness and abundance) and (ii) assemblage composition (both species and guild-assemblages). The results of these comparisons are discussed in the light of the complex bio-geographical history of the Mediterranean Basin (Blondel et al. 2010) and of the current threats to cork oak woodlands (Berrahmouni et al. 2009).

3.2. Material and methods

3.2.1. Study area

All study sites are located within 100 km of the Strait of Gibraltar (Fig. 3.1). The region has a complex topography and a Mediterranean climate, with mild winters and dry warm summers. Annual temperatures average around 15ºC and annual precipitation is usually over 600mm (Ojeda et al. 1996). The indigenous vegetation is typically Mediterranean, and lowland woodlands are in general dominated by the evergreen cork oak (*Quercus suber*), although holm oak (*Quercus rotundifolia*), Algerian oak (*Quercus canarensis*) and Pyrenean oak (*Quercus pyrenaica*) are also locally abundant (Marañón et al. 1999; Ajbilou et al. 2006).

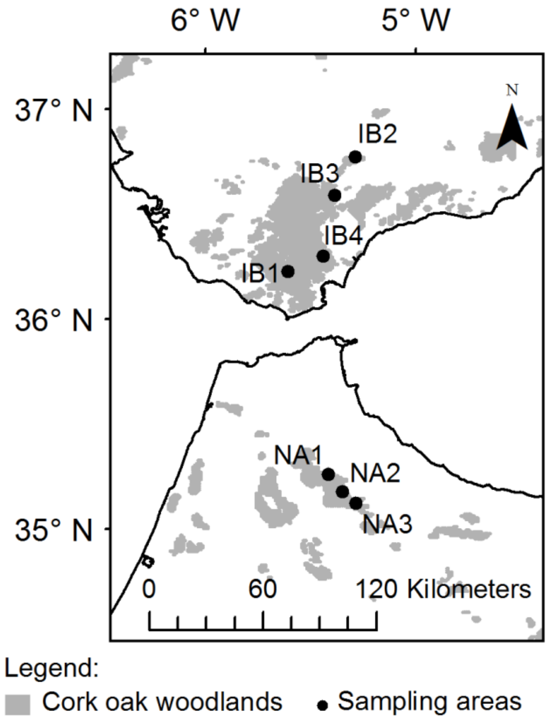

Figure 3.1. *Location of the sampled areas (dots) and regional distribution of cork oak woodland (shaded areas).*

I sampled bird assemblages in a total of seven cork oak woodlands (Fig. 3.1), four in Iberia and three in North Africa (Appendix 3.1). The main source of revenue of all these exploited forests is cork, but hunting, grazing and collection of wood products are also important in some of them. Vegetation structure was roughly similar in all areas, with tree density averaging around 60 trees/ha and shrubs covering usually more than 60% of the ground surface.

3.2.2. Bird sampling

Bird assemblages were sampled using five-minute bird point counts (Sutherland et al. 2004, Bibby et al. 2005) during the spring of 2011. The same observer sampled a total of fifteen stations in each of the seven sampled woodlands. Counting stations were separated by at least 200m and were located 100m or more from woodland edges. All stations were sampled twice, during the early and late halves of the breeding season (1 April to 15 May; 16 May to 20 June), to account for the presence of migratory species. This resulted in a total of 210 point counts, which were carried out during periods of peak activity (one visit in the morning and one visit in the late afternoon at each station) and avoiding rainy or windy days (Sutherland et al. 2004). All birds detected, visually or acoustically, within 100m from the observer were recorded and their distance was estimated. Over-flying birds and those detected more than 100m from the observer were recorded, but not included in the analysis.

3.2.3. Data analysis

Bird species were classified into four habitat specialization guilds: forest specialists, farmland specialists, shrub specialists and generalists (Godinho and Rabaça 2011). In the cases of North African endemic species, habitat specialization was considered to be the same as the phylogenetically and ecologically equivalent species found in European areas. I considered the abundance of a species in each of the seven sampling areas to be the maximum number of individuals detected in all fifteen counting stations on either of the two visits, as this represents the minimum number of birds present at the sampled location (Bibby et al. 2005). No compensation for detectability was used to estimate bird abundances as detectability biases between regions due to sampling different vegetation types are unlikely since the habitat sampled was the same and vegetation structure was generally similar between all the sampled areas.

I estimated species richness with Coleman individual-based rarefaction curves computed using EstimateS v8.2 (Colwell 2009). These curves allow for richness estimation while controlling for confounding effects of bird densities and sampling effort (Gotelli and Graves 1996). I also calculated mean bird abundance and Shannon and Equitability indexes for each region, and compared them using Student's *t*-tests.

The structure of the assemblages was compared using abundance data, to obtain more meaningful estimates of similarity; incidence-based similarity comparisons treat rare and abundant species equally and thus tend to oversimplify relationships between assemblages (Gotelli and Chao 2013). Prior to the analyses, I applied the Hellinger transformation for abundance data (standardized per site and square-root transformed), and calculated a dissimilarity matrix with distances between the seven sampling areas (Borcard et al. 2011). Analysis of similarity (ANOSIM), a nonparametric permutations test analogous to ANOVA (Legendre and Legendre 1998), was then used to test for significant differences between the assemblages of the two regions, using the package *vegan* implemented in R (R Development Core Team 2011). Due to recent criticism of distance-based multivariate analysis (Warton et al. 2012), this difference was also tested with multivariate generalized linear models (GLM), using the *mvabund* R package. This was done by fitting a multivariate GLM with negative binomial error distribution (following Warton et al. 2012) on the untransformed matrix of species abundances and by using a multivariate ANOVA with log-likelihood ratio to test for differences between the assemblages of the two regions and to assess the contribution of individual species to these differences. Finally, and based on the checklists of birds for Spain and Morocco (Lepage 2013a, 2013b), species were classified in two distribution groups: restricted (species restricted to either North Africa or Europe) or widespread (species present in both regions). I assessed the contribution of each of these groups to the total difference between assemblages (the sum of the contributions of all species in the group). Differences due to restricted species are likely to be a consequence of the barrier effect of the Mediterranean, whereas those due to widespread species are presumably the result of local factors, including human-induced factors. A list of the recorded species indicating their abundance, geographic distribution, and guild classification can be found in Appendix 3.2.

3.3. Results

3.3.1. Species richness and abundance

The 210 bird point counts resulted in the detection of a total of 1412 individuals of 46 species (Fig. 3.2). The five most abundant species (*Erithacus rubecula*, *Fringilla coelebs*, *Parus major*, *Sylvia melanocephala* and *Turdus merula*) represented approximately 45% of the individuals sampled, whereas 30% of the species sampled were represented by five or fewer birds. The majority of individuals belonged to forest specialist species (64%) followed by generalist species (23%). Species in the shrub and farmland guilds represented just eight and five percent of the total individuals, respectively.

Average bird abundance (*t*=0.94, *P*=0.41) and number of species detected per site (*t*=0.51, *P*=0.64) did not differ significantly between regions (Table 3.1). The Shannon diversity index (*t*=0.98, *P*=0.38) and the Equitability index (*t*=0.02, *P*=0.99), were also not distinct. Individual based rarefaction curves indicate that species richness is similar in both regions (Fig. 3.3).

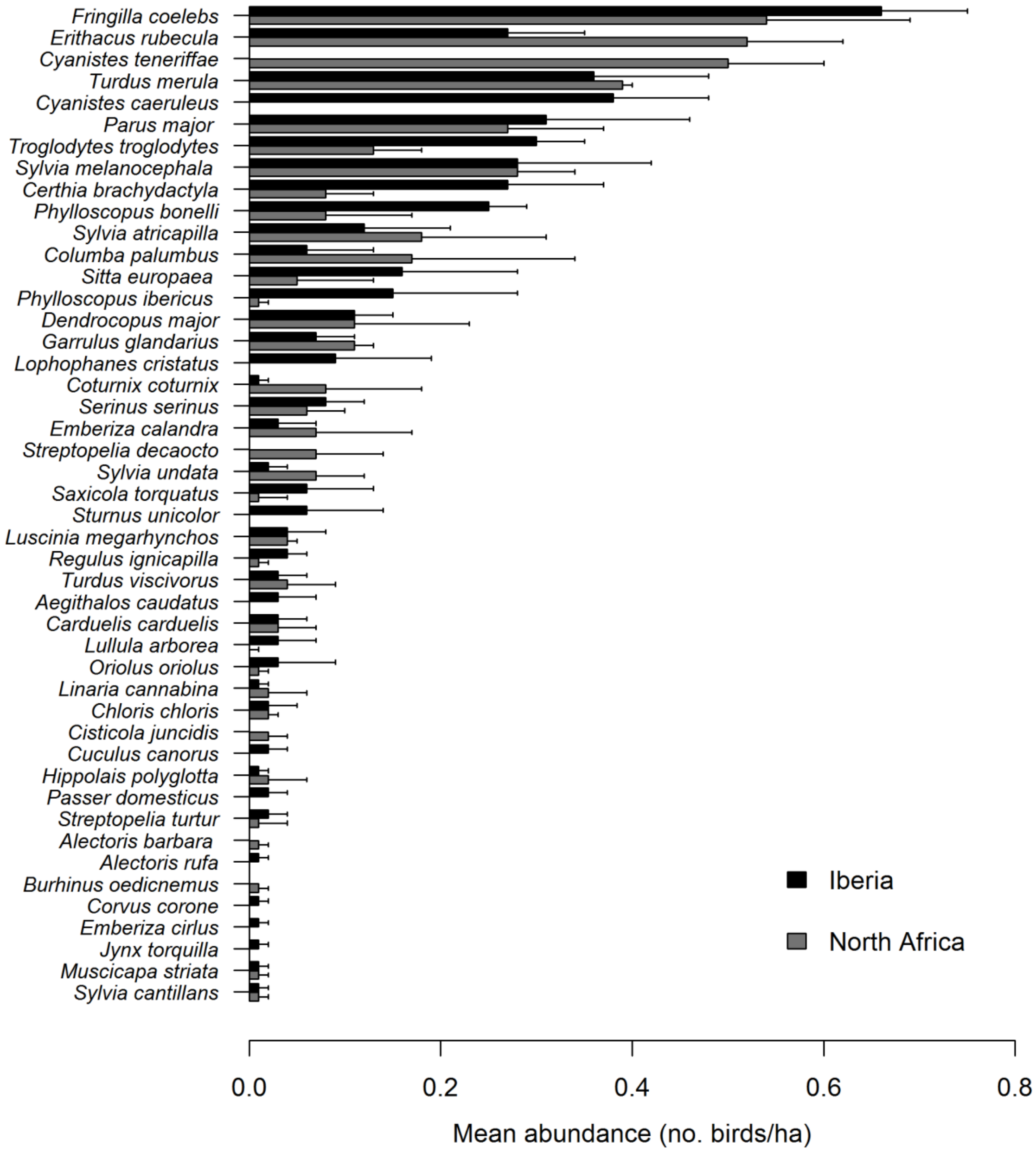

Figure 3.2. *Mean abundance and 95% confidence intervals of each species registered in North African and Iberian cork oak woodlands. Species are ordered according to their maximum abundance observed in both regions.*

3.3.2. Species composition

The results of the point counts (Fig. 3.2) show that there much in common between the species assemblages of cork oak woodlands of southern Iberia and northern Africa. This is evident both in the species present and in their abundance. However, the dissimilarity analysis of species assemblages (Table 3.2) shows that the sampling sites were more dissimilar between regions (0.74) than within them (0.51 and 0.49 for African and Iberian areas, respectively). These results suggest a difference between regions, and this was confirmed by the significant results obtained with both distance measures (ANOSIM test; R=1, P=0.03) and multivariate analysis (ANOVA Log-likelihood ratio test; Dev=145.8, P=0.03).

Table 3.1. *Key parameters (mean and 95% confidence interval) of the bird assemblages of Iberian and North African cork oak woodlands.*

Region	N[a]	Abundance[b]	Species richness[c]	Shannon index	Equitability index
Iberia	4	4.46±0.83	27.0±5.1	2.86±0.18	0.77±0.05
North Africa	3	4.03±0.24	25.3±1.5	2.76±0.08	0.77±0.02

[a] Number of sites sampled

[b] Total number of birds per hectare

[c] Number of species per sampled area

In light of these results, I assessed the contribution of individual species to the difference between the studied assemblages in Iberia and northern Africa (Fig. 3.4). Only two species made a statistically significant contribution to this difference: *Cyanistes caeruleus*, in Europe, and *Cyanistes teneriffae*, in North Africa. Two other species, although common in both regions, had a nearly significant contribution: *E. rubecula* and *Troglodytes troglodytes* (Fig. 3.4). Species restricted to either Europe or North Africa were responsible for 33% of the total difference, while those present in both regions explained the remaining 67%.

3.3.3. Guild assemblage

Dissimilarity analysis for guild assemblage also revealed that sampling sites were less dissimilar within regions (0.15 and 0.14 respectively for northern and southern areas) than between them (0.20). Differences in guild composition between regions were significant both when tested using distance based analysis (ANOSIM test; *R*=0.68, *P*=0.05) and multivariate analysis (ANOVA Log-likelihood ratio test; *Dev*=12.49, *P*=0.04).

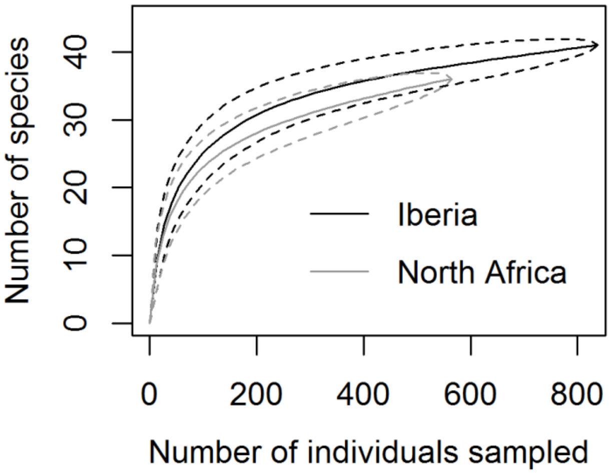

Figure 3.3. *Individual based rarefaction curves of species richness for areas north and south of the Strait of Gibraltar. Dotted lines delimit the 95% confidence envelopes.*

The combined abundance of species in forest (*t*=2.96, *P*=0.04) and generalist (*t*=2.60, *P*=0.04) guilds differed significantly between regions, with the former more abundant in Iberia and the latter in northern Africa (Fig. 3.5). The total abundance of species in the shrub (*t*=0.88, *P*=0.42) and farmland (*t*=0.25, *P*=0.81) guilds did not differ between the two regions.

3.4. Discussion

3.4.1. How different are the bird assemblages of European and African cork oak woodlands?

This study found that bird assemblages of Iberian and North African cork oak woodlands are structurally quite similar. Overall bird abundance is similar, and so is the species richness of the assemblages (Table 3.1). Values for both parameters are in line with those described for other Mediterranean oak woodlands (Telleria 2001). The total number of species observed in the counts was higher in Iberia but the rarefaction analysis (Fig. 3.3) indicates that this is due to a greater sampling effort. In fact, most species observed only at Iberian sites are also present in the North African cork oak woodlands that were sampled (Cherkaoui et al. 2004 and personal observations), but are not abundant and were not detected during the point counts for stochastic reasons.

Table 3.2. *Average dissimilarity scores based on the Hellinger dissimilarity index for species and guild assemblages, within and between regions.*

Region	Dissimilarity(%)	
	Species	Guilds
Within Iberia	0.51	0.15
Within North Africa	0.49	0.14
Between Iberia-North Africa	0.74	0.2

In spite of this similarity, the abundance-based analysis revealed a statistically significant difference between the assemblages of the two regions. However, the species that contribute most to that difference, *Cyanistes caeruleus* (Iberia) and *Cyanistes teneriffae* (North Africa) are phenotypically so similar that until recently were considered conspecific (Salzburger et al. 2002). They presumably occupy the same niche in both regions and are thus functionally equivalent. An analogous situation occurs with the pair *Alectoris rufa* (Iberia) and *Alectoris barbara* (North Africa). Differences due to such species pairs are biogeographically relevant, as discussed in the next section, but do not correspond to ecologic structural differences between the assemblages.

How can this similarity of assemblages persist, in spite of a five million year separation by the Mediterranean Sea? The bird fauna of cork oak woodlands essentially mirrors that of natural Mediterranean woodlands, which is known to harbour mostly the same species in Europe and North Africa (Blondel 1995). Palaeoecological evidence indicates that during the Pliocene and Pleistocene parts of southern Europe and North Africa had comparable climatic and ecological conditions, leading to similarities in the faunas of the two regions (Husemann et al. 2014). Comparable conditions persisted even during the Pleistocene glacial periods and in fact southern Iberia and the adjacent areas of North Africa have been classically merged in the same glacial refuge, the Atlantic-Mediterranean centre (De Lattin 1949). In the case of birds, as in that of other flying organisms (Habel et al. 2009), the Mediterranean remained a relatively permeable barrier, which partly prevented local differentiation processes and facilitated the homogenisation of the assemblages. It is thus likely that the similarity of the two assemblages is explained by a combination of analogous ecological conditions, permeability of the Mediterranean to dispersal, and a long common history.

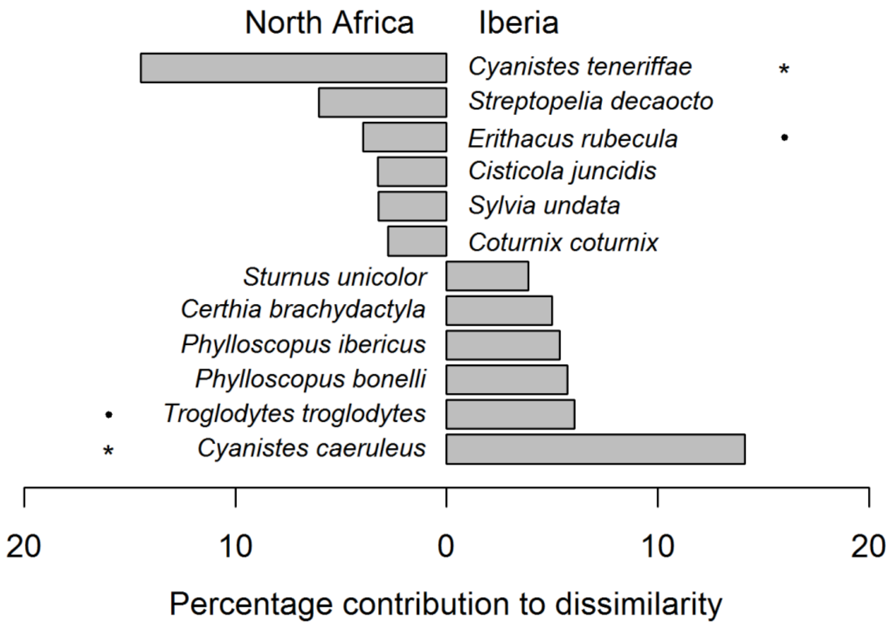

Figure 3.4. *Species making the highest contributions (>2.5%) to assemblage dissimilarities between regions. Significance level is indicated by asterisks (P<0.05) and dots (P<0.10).*

The two assemblages also differed in their guild structure, mostly as a consequence of the greater abundance of forest specialist species in Iberia, and of a greater abundance of generalist species in northern Africa (Fig. 3.5). The differences observed between regions, both in the species and guild composition of the assemblages, may be explained either by historical or current local drivers, which are discussed in the next section.

3.4.2. How important is the barrier role of the Mediterranean in the differentiation of the two assemblages?

The Mediterranean has been a barrier for dispersal of terrestrial biota for over five million years, and its narrowest point is the strait of Gibraltar, which is presently 14.5 km wide. Studies done with different animal groups found that for most of them this barrier has been of major biogeographic importance (Husemann et al. 2014). The comparison between bird assemblages of the same habitat on opposite sides of the Mediterranean contributes to the understanding of its potential role structuring forest bird communities.

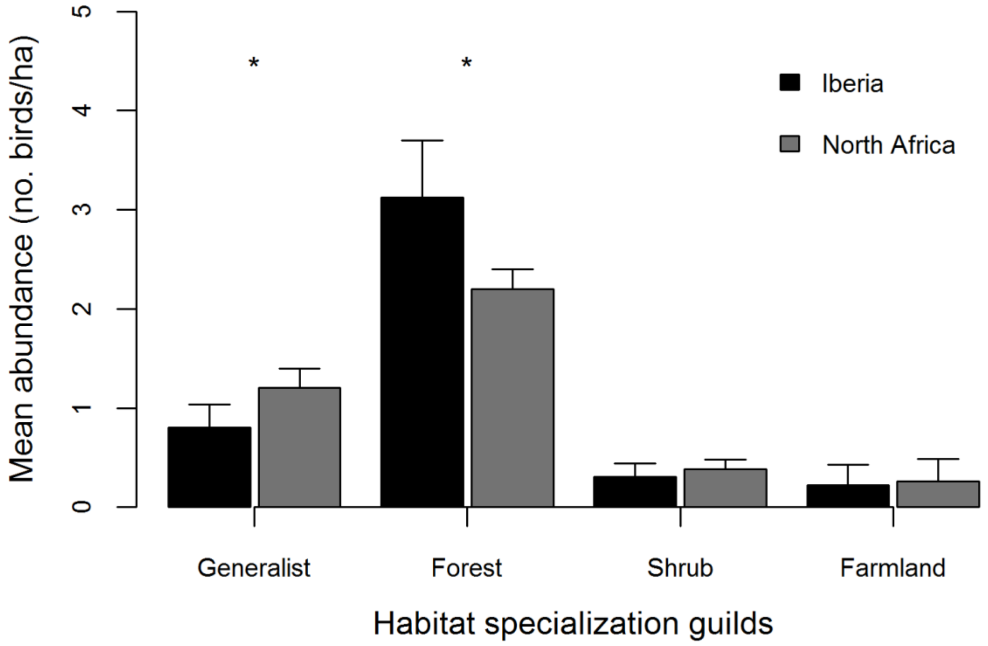

Figure 3.5. *Mean abundance and 95% confidence intervals of each habitat specialization guild for both studied regions. Asterisks indicate significant differences between regions (P<0.05).*

A major barrier to dispersal can differentiate assemblages by preventing the exchange of species through colonization, and by promoting speciation through the minimization of gene flow. There is evidence that both mechanisms contributed to some extent to the observed differentiation between North African and European cork oak woodland bird assemblages. Two of the species detected at the European study sites, *Lophophanes cristatus* and *Aegithalos caudatus*, are present all the way to the northern shores of the Strait of Gibraltar but are absent from North Africa. This indicates that the open ocean at the Strait has prevented them from colonizing suitable habitats in North Africa. However, this impediment of colonization was quite rare, and the forest breeding bird assemblages of North Africa are almost entirely dominated by species of Eurasian origin (Blondel et al. 2010).

Although virtually all forest bird species were able to cross the Mediterranean and colonize North Africa, it constitutes a sufficient barrier to minimize gene flow and allow differentiation. In some cases this differentiation has been sufficiently strong to result in full speciation, and a relevant proportion of the difference between the studied assemblages is due to such differentiation. An example of this speciation due to the barrier effect of the Mediterranean is the pair *C. caeruleus* and *C. teneriffae* (Salzburger et al. 2002), two of the species most abundant in the European and North African study sites, respectively. There are several other Mediterranean forest birds that, having colonized North Africa from Eurasia, remained in sufficient isolation to evolve into separate species. This is the case of two North African endemics that inhabit cork oak woodlands, *Picus vaillantii* that evolved from *Picus viridis* (Pons et al. 2011), and *Ficedula speculigera* that evolved from *Ficedula hypoleuca* (Saetre et al. 2001). Differentiation also occurred in several other woodland birds, which are represented in North Africa by endemic subspecies, as in the case of *Strix aluco mauritanica* (Brito 2005).

It seems clear that the Mediterranean is more permeable to birds than to most other groups of animals so far studied (Husemann et al. 2014). However, this barrier could also have an indirect impact on bird assemblages by acting on the distribution of species that are important for birds, either as resources or predators. For example, tree diversity is lower on the southern side of the Strait, and part of that difference has been attributed to historical biogeographic processes (Rodríguez-Sánchez et al. 2008). Such ecological differences between the north and south of the Strait could change the suitability of the habitat for some bird species, and thus influence their patterns of relative abundance. However, results indicate that this has not occurred, as the relative abundance of different species of birds in the studied cork oak woodlands is quite similar. This indicates that the resource base available for forest birds, as well as the predatory pressure that they suffer, is not very different in Europe and North Africa.

Although relevant for woodland birds, the barrier effect of the Mediterranean does not explain most of the observed dissimilarity in species and guild assemblage at the study sites. In fact, restricted range species, i.e. those only present in either Iberia or North Africa, account for just a third of that dissimilarity. The remaining reflects differences in the abundance of species that are present in both regions, which are more likely due to local ecological factors than to historical regional processes. Human pressure is potentially one of those factors, because it is known to vary between European and North African cork oak woodlands. For example, overgrazing and over-collection of wood are more common in North African woodlands (Marañón et al. 1999, Bugalho et al. 2009, Bugalho et al. 2011). Some exploitation and management practices, such as grazing, shrub removal and tree pruning to obtain firewood, are known to alter the habitat structure and affect bird populations in cork oak woodlands (Cherkaoui et al. 2009, Godinho and Rabaça 2011, Santana et al. 2012, Leal et al. 2013). In general they promote a more open habitat (Godinho and Rabaça 2011, Leal et al. 2011, Leal et al. 2013), that favours non-forest species (Pulido and Diáz 1992, Tellería 2001). This may explain the conclusion that North African cork oak woodlands have a lower abundance of forest birds, but a greater abundance of generalist birds, than their European counterparts (Fig. 3.5).

3.4.3. Implications for conservation

The value of managed cork oak woodlands for bird diversity is widely acknowledged, and many have been classified as Important Bird Areas in both Europe and North Africa (Heath et al. 2000, Fishpool and Evans 2001). Their overall high importance for biodiversity resulted in the classification as High Nature Value Farmland (Hoogeveen et al. 2004) and in the inclusion on the list of habitats to protect under the European Habitats Directive (92/43/CEE). These woodlands represent a particularly good habitat to protect birds and other wildlife because its economic exploitation, most often based on cork extraction and grazing, is usually compatible with the maintenance of high levels of biodiversity (Plieninger and Wildebrand 2001).

Although North African cork oak woodlands harbour a bird assemblage that is quite similar to that of the same habitat in Europe, their isolation by the Mediterranean Sea resulted in a distinct character that should be preserved. The presence in these woodlands of several North African endemics with a small global range (*Cyanistes teneriffae, Picus vaillantii, Ficedula speculigera, Sitta ledanti, Phoenicurus moussieri*) is an important part of this distinctiveness and conservation value. In addition, several of those endemic species (and subspecies) have their closest relatives across the Mediterranean, which indicates that these woodlands are hosting ongoing historical-evolutionary processes that should be maintained.

In spite of its high natural value the area covered by oak woodlands in North Africa, including that of cork oak, is much smaller than that in Europe, and is under greater human pressure (Marañón et al. 1999, Bugalho et al. 2009). It has been shown that overexploitation of this habitat has affected birds (Cherkaoui et al. 2009) and plants (Marañón et al. 1999), and other taxa, like mammals (Rosalino et al. 2011) and insects (Silva et al. 2009), are also likely to be affected. Most of the difference in the bird cork oak assemblages of Europe and North Africa reflects the lower abundance of forest specialist species in the latter, which is also likely due to overexploitation. This lower abundance of forest specialists is of particular conservation concern because it indicates a reduction of the efficiency of this economically valuable habitat as a surrogate for the conservation of natural Mediterranean forests and the species assemblages that they hold.

The range of the cork oak woodland is under increasing pressure by climate change, and there is evidence that this phenomenon is already affecting cork oaks and other Mediterranean trees (Carnicier et al 2010). While this is a major problem throughout the region, it is likely to be particularly serious in North Africa for two reasons. First, because North Africa is closer to the aridity limit of the cork oak, and woodlands in this region are thus presumably more vulnerable to further intensification of aridity. Second, because while in Europe the loss of climatically suitable range of the cork oak may be partly compensated by a northward range migration, this is not a possibility in North Africa.

In conclusion, I found that bird communities of cork oak woodlands on both sides of the Mediterranean are equally rich and share many similarities. However, there are species unique to either side, resulting in a differentiation due to natural historical processes that make the preservation of the two assemblages very important. Overexploitation, mostly due to levels of grazing that prevent tree regeneration, seems to be affecting the structure of cork oak woodland bird assemblages, especially in North Africa. In this region the situation is particularly worrisome because its cork oak woodlands are less extensive than in Europe and they harbour a bird assemblage rich in endemic species and subspecies. Throughout their range cork oak woodlands remain a valuable surrogate for the conservation of the birds and other biodiversity associated to the now very scarce natural Mediterranean woodlands, but conservation measures and better management are needed to increase resilience and maintain their value, especially in North Africa.

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Chapter 4

Major challenges for bird conservation in cork oak woodlands: climate change versus land management

To be submitted as:

Correia, R. A., Franco, A. M. A., Palmeirim, J. M., Major challenges for bird conservation in cork oak woodlands: climate change versus land management.

Abstract:

Cork oak woodlands are a keystone habitat for Mediterranean biodiversity, and to birds in particular, which led to their protection under the EU Habitats Directive (92/43/CEE). However, the area of cork oak woodlands in Europe has declined in recent decades mainly due to land use change and overexploitation and, presently, climate change also represents a threat. It is important to understand how bird communities supported by Cork oak woodlands are likely to respond to changes in land use and climate to formulate management recommendations that may minimize predicted impacts. Bird assemblages were sampled in forty sites spread across the western Mediterranean basin to explore the effect of climate and habitat management regimes on bird assemblage composition and abundance. Habitat and climatic gradients explained over a third of the overall variance in Cork oak woodland bird assemblages. Forest and generalist species responded mostly to climatic factors whereas changes in farmland and shrubland species were best explained by habitat structure. Overall, species abundance was negatively affected by higher temperatures and climatic seasonality but responded positively to heterogeneous habitat structure, the latter being particularly true for species of conservation concern. These results indicate that the current trends of increasing temperatures and decreasing precipitation leading to increased aridity, together with land use changes, are likely to cause negative impacts on the diverse and abundant bird assemblages supported by cork oak woodlands. Conservation efforts should focus primarily on promoting long-term adequate management practices, in order to minimize land use change impacts and increase the resilience of this threatened habitat to climate change impacts.

4.1. Introduction

Cork oak woodlands are an agro-silvo-pastoral system (Pinto-Correia and Mascarenhas 1999) distributed across much of the western Mediterranean Basin. Cork oak woodlands cover approximately 1.5 million hectares in Europe and 1 million hectares in Africa, but the core of its distribution is currently found in the Iberian Peninsula (Pausas et al. 2009). Resulting from the long term human intervention on original Mediterranean oak forests (Diáz et al. 1997), this system is economically sustainable mostly due to cork harvesting and is compatible with the maintenance of high biodiversity levels (Plieninger and Wildebrand 2001, Leal et al. 2011). Human intervention plays a key role in maintaining the biological communities of cork oak woodlands (Bugalho et al. 2011), characterized by some of the most diverse assemblages of birds, butterflies and plants in the western Mediterranean (Pineda and Montalvo 1995, Diáz et al. 1997). In fact, cork oak woodlands are particularly important for birds where up to 40% of the total number of bird species in the Iberian Peninsula can be found (Pineda and Montalvo 1995). Furthermore, millions of birds from northern Europe come to winter or use cork oak woodlands during migration every year (Pineda and Montalvo 1995, Diáz et al. 1997). Cork oak woodlands are managed in a variety of forms, including dense woodlands, shrub dominated areas and more open areas exploited for cattle grazing or cereal crops (Maranõn 1988, Bugalho et al. 2009), and this leads to a characteristic patchiness that is a major driver of the biodiversity levels observed in this system (Pineda and Montalvo 1995, Tellería 2001). For these reasons, Cork oak woodlands are considered High Natural Value Farmlands (Hoogeveen et al. 2004) and have been included in the Annex I of the European Union Habitats Directive (92/43/CEE).

Despite this fact, the area of cork oak woodlands is currently declining throughout its range, mainly due to land use conversion and overexploitation (Pausas et al. 2009). Changes in market prices of cork and other commodities have spurred the intensification of agriculture practices or abandonment, which has resulted in changes in the habitat structure (Eichhorn et al. 2006, Acácio et al. 2009, Costa et al. 2011). Climate change has also been identified as a major threat in recent decades, causing defoliation and reduced tree growth (Carnicer et al. 2011, Besson et al. 2014), which ultimately contribute to the ongoing decline of cork oak woodlands (Brasier and Scott 1994). Understanding how biological communities respond to changes in habitat structure and climatic conditions is important to formulate adequate management recommendations to minimize impacts on biodiversity. The diverse bird assemblages supported by Cork oak woodlands, which include many endangered and endemic species (Diáz et al. 1997), are a particularly suited study model to address this issue since birds are known to be good biodiversity indicators (e.g. Gregory et al. 2003, Hutto 1998) and are likely to respond in similar ways to bird assemblages of other biodiverse Mediterranean systems under similar pressures, such as Holm oak woodlands and Olive groves (Potter 1997, Tucker 1997).

Previous studies have addressed the response of bird assemblages along climatic and habitat gradients in the western Mediterranean Basin (e.g. Tellería and Santos 1994), and highlighted the importance of both factors for Mediterranean bird communities. This approach remains to be adopted for cork oak woodlands as, even though previous studies have addressed the role of management and climatic features on bird assemblages of Mediterranean cork oak woodlands (e.g. Pulido and Diaz 1992, Godinho and Rabaça 2011), most had a local or regional focus and did not address the joint effect of both climate and land management. This work pretends to fill this knowledge gap by aiming to (i) assess the relative importance of habitat and climatic gradients for birds of cork oak woodlands at the assemblage, guild and species level across the Mediterranean Basin and (ii) evaluate the role of specific habitat and climatic variables on species abundances. Hence, this study is to the first to compare the role of marked habitat and climatic gradients on Cork oak woodland bird assemblages across the Mediterranean Basin and the results obtained may provide important insights for the conservation of Cork oak woodlands and their biodiversity in the Mediterranean region.

4.2. Material and methods

4.2.1 Bird sampling

Bird assemblages were sampled in 40 Cork oak woodlands spread across the Iberian Peninsula and northern Africa (17 in Portugal, 15 in Spain and 8 in Morocco) (Fig. 4.1 and Appendix 4.1). All the woodlands selected for sampling had a minimum size of 50ha and were at least 10 kilometres apart. Woodlands recently harvested for cork were avoided as some species are known to avoid recently debarked areas (Godinho and

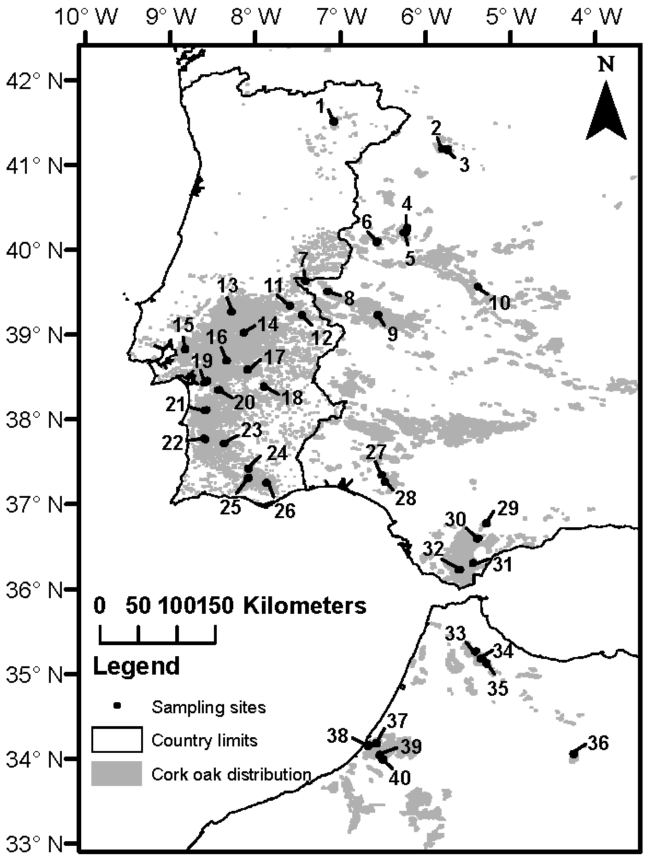

Figure 4.1. *Map of the study region. Grey areas represent the distributions of Cork oak woodlands and black dots show the location of Cork oak woodlands where bird assemblages were studied.*

Rabaça 2011, Leal et al. 2011). Birds were sampled using point counts (Sutherland et al. 2004, Bibby et al. 2005). Sampling areas were visited twice, between the 1st of April and the 20th of June 2011, and a total of fifteen five-minute point counts were carried out in each area, always by the same observer. Point counts distanced at least 100m from woodland edges and 200m from each other. Counts were done during periods of peak bird activity (one visit in the morning and one visit in the late afternoon for each area) always in suitable weather conditions, avoiding rainy or windy days (Sutherland et al. 2004). All birds detected, either visually or acoustically, were recorded and their distance to the observer was estimated. Birds detected further than 100m from the observer and over-flying birds were later excluded from the analysis as they may not be associated with the forest patches being sampled. For any given species, total abundance in a sampling area was considered to be the maximum sum of individuals detected in the fifteen counting stations for any of the two visits, as this represents the minimum number of birds present in the sampling area (Bibby et al. 2005). All species recorded were categorized into four habitat specialization guilds (generalist, forest, shrubland and farmland species) following Godinho and Rabaça (2011), and guild abundance is the total number of birds from species contained in each guild. I also categorized species according to their conservation status and highlighted results for Species of European Conservation Concern (SPEC, Burfield and van Bommel 2004).

4.2.2 Environmental variables

A range of environmental variables describing habitat structure and climatic conditions were used to characterize each sampling area. Six habitat variables were collected around a 100m radius of each of the fifteen counting stations sampled in each area and averaged between them to describe habitat structure in each sampling area. Four of these variables characterize the structure of ground cover and were visually estimated during fieldwork, always by the same observer. These include herb cover (% ground cover), herb height (in 5 cm classes), shrub cover (% ground cover) and shrub height (in 25 cm classes). Additionally, tree density (no. trees/ha) and canopy cover (% ground cover) were calculated and used to describe the arboreal vegetation structure. Both variables were estimated visually using aereal images of the study area avalibale from Google Earth v7.1. The six habitat variables were then combined using Principal Components Analysis (PCA) performed on the correlation matrix, to reduce the number of variables included in the analysis and avoid correlation between variables (Legendre and Legendre 1998). The first two components resulting from the PCA represent ground vegetation and arboreal vegetation structure gradients and were kept for further analysis (Table 4.1). These six habitat variables were also combined to describe habitat heterogeneity in each sampling area using the data obtained from each of the fifteen counting stations. A heterogeneity index (Rotenberry and Wiens 1980) was calculated for each habitat variable as the range of each variable in each sampling area (maximum minus the minimum value sampled at each of the fifteen counting stations) divided by the mean value. The heterogeneity scores of each habitat variable were then summed and used to represent habitat heterogeneity index of each sampling area.

Climatic variables included average temperature (ºC), temperature seasonality (coefficient of variation) and an aridity index (Zomer et al. 2008). Inclusion of the aridity index in the analysis was preferred to precipitation variables since it provides a better representation of water availability in a given area and avoids multi-collinearity between precipitation and temperature variables. Temperature variables were obtained from the Worldclim database (http://www.worldclim.org/) and the aridity index from the Consultative Group on International Agricultural Research (CGIAR) spatial data base (http://www.cgiar-csi.org/) at a spatial resolution of 30 arc-seconds.

Table 4.1. *Principal components analysis (PCA) loadings of habitat variables representing habitat structure. Both axes were used for bird assemblage analysis, with the first axis describing ground cover structure and the second axis characterizing tree cover structure.*

Habitat variable	Axis1 (Grd)	Axis2 (Tree)
Tree density	-0.295	0.613
Tree cover	-0.239	0.645
Herb cover	0.554	0.191
Herb height	0.403	-0.012
Shrub cover	-0.544	-0.244
Shrub height	-0.302	-0.336
Variance explained	48.3%	23.2%

I analysed the correlation between environmental variables selected for analysis and all individual correlations between variables showed Spreaman's r coefficients $\leq |0.6|$. A table describing maximum, mean and minimum values of all the variables sampled can be found in Appendix 4.2.

4.2.3 Data analysis

All environmental variables were centred and standardized for analyses in order to improve the interpretability of results (Schielzeth 2010). Also, five very rare species (<5 individuals) were excluded from the bird assemblage data as they can often have a disproportionate effect on the analysis (Legendre and Legendre 1998). A Hellinger transformation was applied to the remaining data prior to analysis (Borcard et al. 2011). I assessed the relative importance of habitat and climatic variables structuring bird assemblages by partitioning the variance explained by each environmental factor using redundancy analysis (Borcard et al. 2011), calculated on the species by site matrix. The variation explained by each component was summarized using adjusted R^2, which provides unbiased estimates of the variation in the response data that is explained by the environmental variables (Peres-Neto et al. 2006).

I also modelled species abundance responses to each environmental variable using generalized linear models (GLMs) with negative binomial error distribution on the untransformed abundance data. Species abundances were originally modelled with the full environmental dataset and I used a model selection procedure to identify the most parsimonious model using the AICc (Burnham and Anderson 2002). Spatial autocorrelation in species data was tested using Moran's I and accounted for in the models using spatial eigenvector mapping (Dormann et al. 2007). A table with the resulting models is presented in Table 4.2.

All analysis were carried out using R software v2.15 (R Development Core 2011) and the spatial plot of environmental variables across the study area was done using ArcGIS v10 (ESRI, 2011).

4.3. Results

The environmental variables considered for this study explain over one third (35%) of the total variance found in the structure of cork oak bird assemblages. Habitat structure accounts for 20% and climate 15% of the total variation explained, while the shared portion of variation explained was negligible (under 1%). The overall abundance of species of generalist and forest guilds is mostly explained by climatic factors (approximately 20% of variance explained for both groups). In contrast, for shrubland and farmland species abundance is mostly determined by habitat structure, which accounts for 25 and 70% of total variance of each guild respectively (Fig. 4.2). The species analysis shows that *Luscinia megarhynchos*, *Troglodytes troglodytes* and *Passer hispaniolensis* are the species that vary the most in response to climatic factors (approximately 40% of variance explained for each species), whereas habitat structure explains over 40% of variance in abundance for *Emberiza calandra*, *Lullula arborea* and *Sturnus unicolor* (Fig. 4.2).

Table 4.2. *Parameter estimates of generalized linear models (GLMs) relating bird species abundance to environmental variables in model with lowest AICc. Variables with a significant effect are signalled (* - P<0.05, ** - P<0.01, *** - P<0.001). Species of European Conservation Concern are represented in bold.*

Species			Environmental variable					
Common name	Scientific name	Code	Ground Cover	Tree Cover	Habitat Heterogeneity	Average Temperature	Temperature Seasonality	Aridity
Generalist birds (11 species)								
Eurasian skylark	***Alauda arvensis***	**Aa**	1.58*	-1.04***	0.95*			
European Greenfinch	*Chloris chloris*	Ch	0.69***					-0.47*
Common cuckoo	*Cuculus canorus*	Ca	0.50**		0.34*	-0.41**		
Azure-winged Magpie	*Cyanopica cyanus*	Cy	3.26***		0.95*			-1.76**
Common Wood Pigeon	*Columba palumbus*	Cp					0.62**	
European Robin	*Erithacus rubecula*	Er	-2.17***	-0.69*				0.84***
Woodlark	***Lullula arborea***	**La**	0.90***		0.38***	-0.53***		
House Sparrow	***Passer domesticus***	**Pd**	0.88**		0.43			
Eurasian Collared Dove	*Streptopelia decaocto*	Sd						-0.49*
Common Blackbird	*Turdus merula*	Tm	-0.21***				0.18**	0.18**
Mistle Thrush	*Turdus viscivorus*	Tv		0.27			0.42**	
Farmland birds (15 species)								
Red-legged Partridge	***Alectoris rufa***	**Ar**	0.98***		0.51*	-0.60*	-1.06***	
Eurasian Stone-curlew	***Burhinus oedicnemus***	**Bo**				2.48***		
European Goldfinch	*Carduelis carduelis*	Cr	0.33*	-0.21				-0.28*
Common Quail	***Coturnix coturnix***	**Co**						0.40*
Zitting Cisticola	*Cisticola juncidis*	Cj	1.10**		-0.85*		-0.91*	
Corn Bunting	***Emberiza calandra***	**Ec**	1.06***		0.39			
Cirl Bunting	*Emberiza cirlus*	Ei		0.81*		-0.69*	-0.72*	
Crested Lark	***Galerida cristata***	**Gc**	1.75**		0.97*			
Woodchat Shrike	***Lanius senator***	**Ls**	1.09***				0.76***	-0.71*
Common Linnet	***Linaria cannabina***	**Cn**			1.04*			

Table 4.2. *cont.*

Species			Environmental variable					
Common name	Scientific name	Code	Ground Cover	Tree Cover	Habitat Heterogeneity	Average Temperature	Temperature Seasonality	Aridity
Spanish Sparrow	*Passer hispaniolensis*	Ph	3.10***	-1.46**	-1.06*	-1.62**	5.49***	
European Stonechat	*Saxicola rubicola*	Sr				-0.87***	-1.20***	
European Turtle Dove	***Streptopelia turtur***	**St**						
Spotless Starling	*Sturnus unicolor*	Su	0.88***		0.25*	-0.32**		
Eurasian Hoopoe	***Upupa epops***	**Ue**	1.08**				0.77**	
Forest birds (24 species)								
Long-tailed Tit	*Aegithalos caudatus*	Ac						
Short-toed Treecreeper	*Certhia brachydactyla*	Cb	0.18	0.18*	0.26**	-0.39***		
Eurasian Blue Tit	*Cyanistes caeruleus*	Ce						
Carrion Crow	*Corvus corone*	Cc	0.94***	0.59**		-0.76**	-0.53	
African Blue Tit	*Cyanistes teneriffae*	Ct	-3.82***					
Great Spotted Woodpecker	*Dendrocopos major*	Dm			-0.30***		-0.50***	
Common Chaffinch	*Fringilla coelebs*	Fc						
Eurasian Jay	*Garrulus glandarius*	Gg	-0.47**					
Eurasian Wryneck	***Jynx torquilla***	**Jt**		-1.04*				
European Crested Tit	***Lophophanes cristatus***	**Lc**	-0.46					
Common Nightingale	*Luscinia megarhynchos*	Lm	0.31*			-0.99***	-0.69***	
Spotted Flycatcher	***Muscicapa striata***	**Ms**						-0.90
Eurasian Golden Oriole	*Oriolus oriolus*	Oo				-0.42*		
Rock Sparrow	*Petronia petronia*	Pe	2.35*					
Western Bonelli's Warbler	***Phylloscopus bonelli***	**Pb**	-0.98***	0.73***		-0.74***	-0.74***	
Iberian Chiffchaff	*Phylloscopus ibericus*	Pi					-0.99**	0.69*
Great Tit	*Parus major*	Pm		0.17**				
Common Redstart	***Phoenicurus phoenicurus***	**Pp**		0.68*		-1.31***	-1.44***	-0.53*
Common Firecrest	*Regulus ignicapilla*	Ri		1.45*				2.47**
European Serin	*Serinus serinus*	Ss						-0.34**

Table 4.2. *cont.*

Species			Environmental variable					
Common name	Scientific name	Code	Ground Cover	Tree Cover	Habitat Heterogeneity	Average Temperature	Temperature Seasonality	Aridity
Eurasian Nuthatch	*Sitta europaea*	Se	0.33**	0.43***		-0.70***	-0.35*	
Eurasian Blackcap	*Sylvia atricapilla*	Sa	-0.80**	-0.46				1.16***
Eurasian Wren	*Troglodytes troglodytes*	Tt	-0.60**		-0.32*	-1.10***	-1.49***	0.48**
Shrubland birds (5 species)								
Melodious Warbler	*Hippolais polyglotta*	Hp				-0.70*	-0.65	
Northern Wheatear	***Oenanthe oenanthe***	**Oe**						
Subalpine Warbler	*Sylvia cantillans*	Sc		-0.57**	-0.78**	-1.00***		
Sardinian Warbler	*Sylvia melanocéfala*	Sm	-0.76***			0.31**		
Dartford Warbler	***Sylvia undata***	**Sn**	-1.58***			-0.46		

The results of the multivariate analysis of species abundance show that over 50% of all the species, and over 40% of species of conservation concern, are significantly affected by the structure of ground cover, the majority of species preferring herb over shrub dominated areas (Fig. 4.3). Roughly 30% of species are significantly affected by habitat heterogeneity, generally preferring more heterogeneous habitat structures. Tree abundance and cover were statistically important for approximately 20% of the species analysed but no clear directional preference was detected since a similar number of species either decrease or increase in abundance in response to tree abundance and cover. The results of the climatic analyses indicate that approximately30% of the species show a significant negative relationships with increasing temperature and

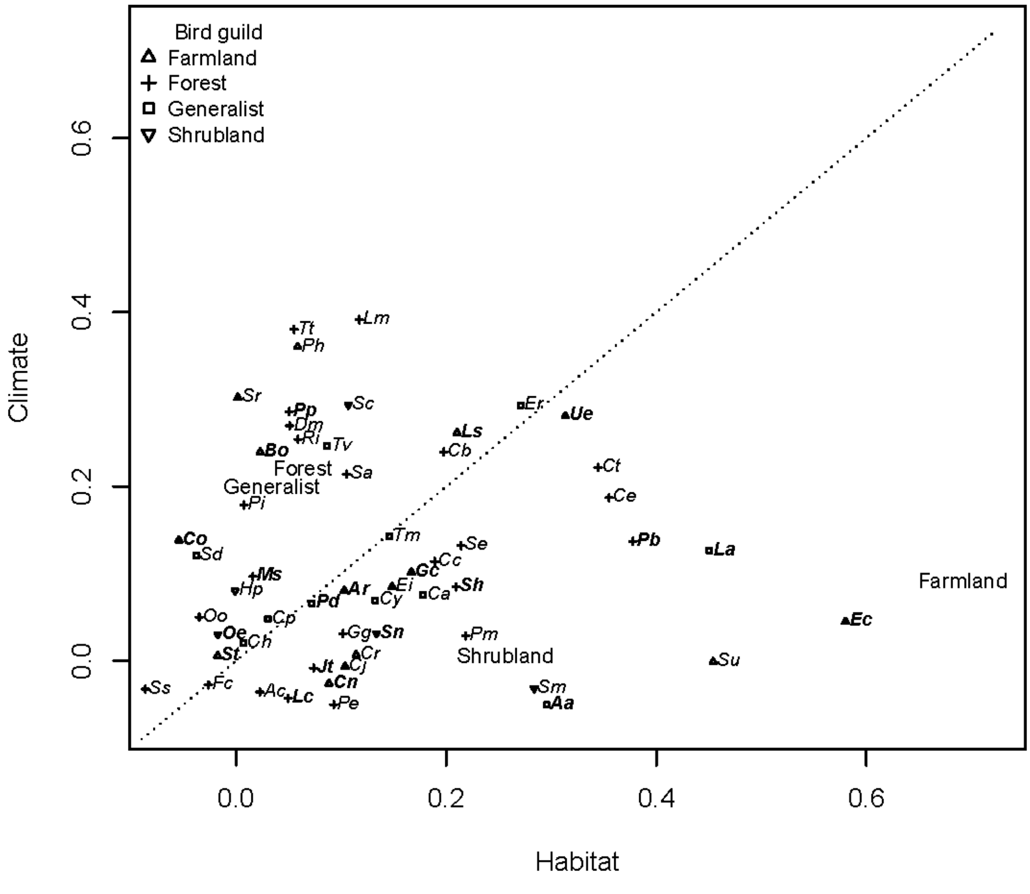

Figure 4.2. *Variance partitioning of Cork oak woodland bird species and guild responses to habitat and climatic factors. Axes represent the proportion of variance in species and guild abundance explained by climatic (vertical axis) and habitat variables (horizontal axis). Species and guilds to the left of the dashed line show a higher response to climatic variables and those to the right to habitat variables. Species abbreviations as in Table 4.2.*

seasonality (Fig. 4.3). A high proportion of species of conservation concern also show significant responses to these variables, and the majority of these species increase their abundances in areas with lower temperatures and seasonality. Nearly 20% of total species, and a similar number of species of conservation concern, respond significantly to aridity but no clear trend towards a positive or negative response was observed. Only five of the studied species did not show a significant response to any of the climatic or habitat variables analysed: *Aegithalos caudatus*, *Cyanistes caeruleus*, *Muscicapa striata*, *Oenanthe oenanthe* and *Streptopelia turtur* (Table 4.2). This fact indicates that they are not limited by these factors in the areas sampled.

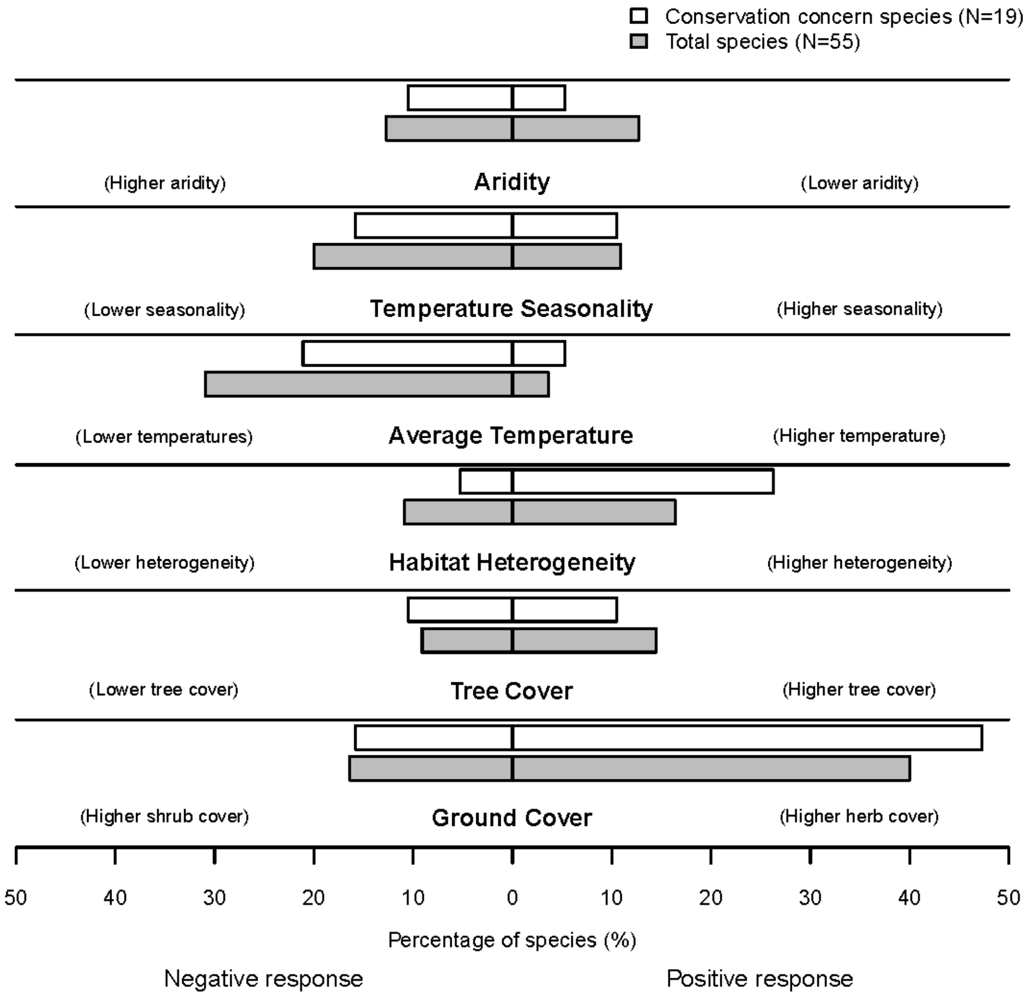

Figure 4.3. *Percentage of total species (grey bars) and of species of conservation concern (white bars) that responded significantly to each environmental variable. Bars on the right and left respectively represent the percentage of species with a positive and negative response.*

4.4. Discussion

The environmental variables included in this study were able to explain over one third of the overall variability observed in the bird assemblages of cork oak woodlands. This figure is in line with other studies that have aimed to assess the role of habitat and climatic factors on changes in bird assemblages (e.g. Suárez-Seoane et al. 2002, Archaux and Bakkaus 2007, Nikolov 2010) and likely to reflect the different, and sometimes opposing, requirements of the species that depend on this system (Tellería 2001). The absence of an important component of variation explained jointly by climatic and environmental variables is a result of the low correlation between the environmental variables of the two groups (Borcard et al. 2011). Therefore, in order to better understand this complex balance, the effects of climate and habitat structure need to be evaluated in detail for the different species and guilds that compose the bird assemblages of cork oak woodlands.

4.4.1 The role of habitat structure for Cork oak woodland bird assemblages

Results indicate that habitat structure is indeed an important factor structuring bird assemblages of Cork oak woodlands as found in previous studies done at smaller spatial scales (e.g. Pulido and Diaz 1992, Cherkaoui et al. 2009, Godinho and Rabaça 2011). The majority of species responded significantly to at least one of the habitat variables analysed but they were particularly important for shrubland and farmland guilds (Fig. 4.2). Habitat features associated with vegetation structure and heterogeneity are known to affect farmland species such as *Emberiza calandra*, *Lullula arborea* and *Sturnus unicolor* (e.g. Donald and Aebischer 1997, Cramp and Simmons 2006, Sirami et al. 2011) and in this study explained over 40% of the variability in their abundance. In addition, a large proportion of species responded positively to habitat heterogeneity and avoided shrub dominated areas (Fig. 4.3), including many species with declining populations such as *Alauda arvensis*, *Alectoris rufa* and *Galerida cristata* (Table 4.2). The main exception to this type of response was observed in Sylvia warblers, which are usually associated with taller and denser shrub vegetation (Cody 1985, Cramp and Simmons 2006). As expected, forest and non-forest guilds show opposite responses to tree cover, with the former benefiting from higher tree density and cover and the latter from more open areas. Indeed, it has been suggested that the great spatial variation in tree density of Cork oak woodlands partly explains the remarkable bird diversity that they support (Tellería 2001) and the results corroborate this hypothesis. However, the majority of changes in the bird abundance of the different guilds were associated with habitat structure variables associated with local management. High shrub cover is usually associated with land abandonment (Bugalho et al. 2009), which may benefit most shrubland species (e.g. *Sylvia cantillans, Sylvia melanocephala*, *Sylvia undata*) but will likely have a negative effect on the abundance of many generalist and farmland species (e.g. *Carduelis carduelis, Cisticola juncidis, Cyanopica cyanus, Passer domesticus*). Habitat heterogeneity is a common feature of more traditionally managed woodlands but is usually absent in intensively managed or overexploited woodlands (Bugalho et al. 2009, Vickery and Arlettaz 2012). Examples of species likely to be affected by ongoing intensification and overexploitation trends include *Galerida cristata*, *Linaria cannabina, Phylloscopus bonelli* and *Regulus ignicapilla*.

4.4.2 Bird assemblage responses to climatic conditions

The climatic influence on bird populations is mostly indirect, by affecting resources and habitat structure (Newton 1998), although extreme events can also affect bird survival. This study shows that bird assemblages of Cork oak woodlands, and particularly forest specialist and generalist species, are significantly affected by climatic conditions (Fig. 4.2). In particular, increasing temperatures and seasonality have important negative effects on Mediterranean birds (Fig. 4.3). Other studies have shown that observed increasing temperatures and seasonality promote phenological mismatches and decrease nestling and adult fitness (e.g. Thomas et al. 2001, Sanz et al. 2003, Greño et al. 2008, Catry et al. 2011). Many of the species analysed showed a negative response to these climatic factors (Fig. 4.3) and forest insectivorous cavity nesting birds, such as *Certhia brachydactyla*, *Phoenicurus phoenicurus* and *Troglodytes troglodytes*, seem particularly sensitive (Table 4.2). These species seem to benefit from warmer conditions in northern latitudes (Forsman and Mönkkönen 2003, Robinson et al. 2007), which may justify the observed northwards shift in populations of species associated with colder climates in recent decades (Devictor et al. 2008, Devictor et al. 2012). However, a few species do seem to benefit from warmer temperatures and increased seasonality, such as *Burhinus oedicnemus*, *Sylvia melanocephala* and *Upupa epops*. In contrast, no clear trend was observed in species responses to aridity (Fig. 4.3), which is likely a result from the functional diversity and different geographical origins of species that compose Cork oak woodland bird assemblages. Increasing aridity result in sparser ground vegetation (Peñuelas et al. 2004, Gouveia et al. 2009, Prieto et al. 2009) and lower tree density and cover (Carnicer et al. 2011) which may benefit generalist species with southern distributions, such as *Cyanopica cyanus*, *Serinus serinus* and *Streptopelia decaocto*, but will have the opposite effect on northern forest species that prefer denser vegetation, like *Regulus ignicapilla*, *Troglodytes troglodytes* and *Erithacus rubecula* (Tellería and Santos 1994).

4.4.3 Relevance for bird conservation in managed Cork oak woodlands

The results provide important insights for the conservation of bird assemblages in Cork oak woodlands facing climate and land use change. Many species respond significantly to changes in ground cover structure, habitat heterogeneity and temperature. For most species, abundance increased in woodlands dominated by herbaceous vegetation with heterogeneous structure and decreased in warmer and more seasonal areas (Fig. 4.3).

The results suggest that temperature conditions are important for forest species such as *Certhia brachydactyla*, *Luscinia megarhynchos* and *Trglodytes troglodytes* (Fig. 4.2) and many species of conservation concern, such as *Alectoris rufa*, *Lullula arborea*, *Phoenicurus phoenicurus* and *Phylloscopus bonelli* (Fig. 4.3). These species are less abundant under warmer and more seasonal conditions (Table 4.2) and their population numbers are likely to decline as a result of additional temperature increases (Stocker et al. 2013). Current trends of land use change resulting from both climatic and economic factors (Acácio et al. 2009, Bugalho et al. 2009, Costa et al. 2011) are likely to be negative for many species due to changes in habitat structure. Farmland and shrubland bird populations are particularly associated with habitat characteristics (Fig. 4.2) but species from all guilds showed significant responses to habitat features depending on their requirements (e.g. *Emberiza calandra*, *Lullula arborea*, *Phylloscopus bonneli* and *Sylvia melanochephala*), particularly in terms of ground cover structure and habitat heterogeneity (Fig. 4.3). The majority of species responded positively to heterogeneous areas dominated by herb ground cover (Table 4.2), corroborating the idea that habitat heterogeneity is a key feature for biodiversity (e.g. Donald et al. 2001, Benton et al. 2003, Kleijn et al. 2009). As the abandonment or intensification of farmland practices usually results in lower habitat heterogeneity (Benton et al. 2003, Vickery and Arlettaz 2012), Cork oak woodlands require a traditional management approach to maintain current biodiversity levels (Bugalho et al. 2011). Species with declining populations such as *Alauda arvensis*, *Lullula arborea*, *Alectoris rufa*, *Galerida cristata* and *Sylvia hortensis* may be particularly affected by the loss of more traditional management practices. Conservation efforts should aim to promote the long-term maintenance of sustainable management practices that focus on promoting woodland patchiness rather than fragmentation and take into account potential impacts of management practices when not properly considered and executed (e.g. Camprodon and Brotons 2006, Godinho and Rabaça 2011, Santana et al. 2012, Leal et al. 2013).

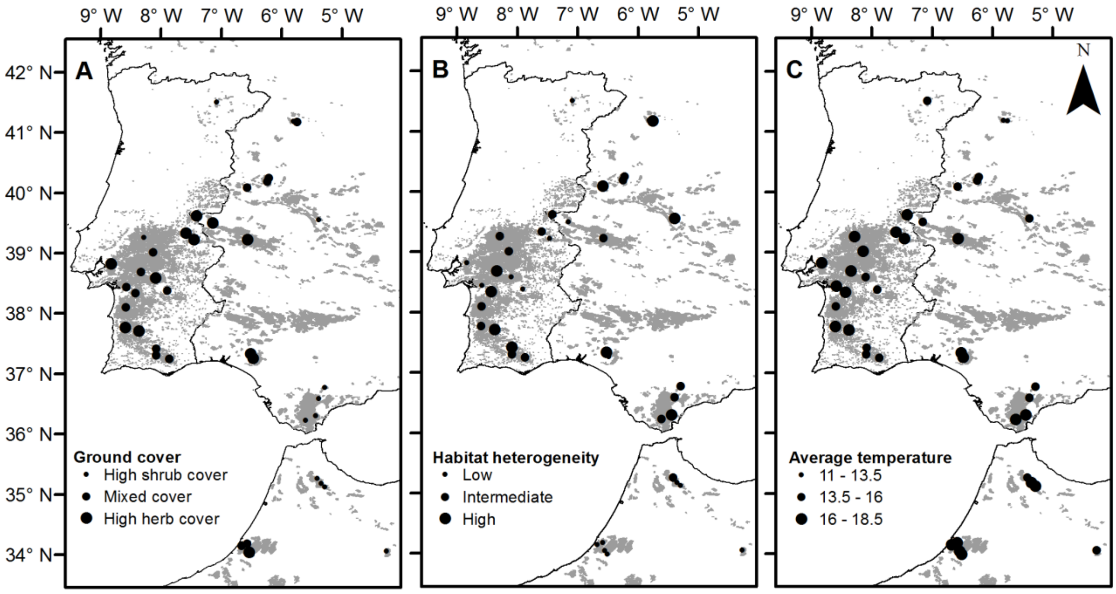

Figure 4.4. *Distribution across the study area of the three variables that proved most important to explain variations in bird abundance: (A) ground cover, (B) habitat heterogeneity and (C) average temperature. Size of dots is based on the measurements made at each sampling site*

Overall, results indicate that adaptation and conservation efforts aiming to increase the resilience of Cork oak woodland biodiversity to both climate change and land use change should focus on maintaining adequate habitat management. This will be particularly important to maintain population numbers of many species showing declining trends across Europe, as these species seem particularly sensitive to threats from climate change and land use change (Julliard et al. 2003, Crick 2004, Jiguet et al. 2007). According to the observed species responses, the spatial distribution of environmental conditions across the study area indicates that areas with more adequate habitat structure are generally located in south-western Iberian Peninsula (Fig. 4.4). Areas in northern Africa and in the northern half of the Iberian Peninsula tend to have lower habitat heterogeneity and show higher shrub dominance. In contrast, average temperatures tend to be higher across northern Africa and southern Iberian Peninsula restricting the areas likely to remain climatically suitable under future climate change to the central and northern areas of the Iberian Peninsula. Under this scenario, I propose that adaptation strategies should focus on two key actions: (i) promoting the maintenance of adequate land management practices on the southern half of the Iberian Peninsula and (ii) stimulating an expansion of Cork oak woodlands and their traditional management practices to northern areas of the Iberian Peninsula. These actions will increase the resilience of southern areas and provide new suitable habitat patches further north to facilitate ongoing species responses to climate change (Devictor et al. 2008, Devictor et al. 2012). The results presented in this manuscript can potentially be extrapolated to other similar Mediterranean traditional systems, such as Holm oak woodlands and traditional Olive groves; their biodiverse communities are currently undergoing similar pressures from land use and climate change (Potter 1997, Tucker 1997) and the two-fold adaptation strategy is suggest for Cork oak woodlands should also be considered for these systems.

4.5. Conclusions

Habitat structure and climate are both important factors determining the structure of bird assemblages in Mediterranean Cork oak woodlands. These results show that climatic and habitat variables together were able to explain over one third of the overall variability found in Cork oak woodland bird assemblages. Forest and generalist guilds generally show a higher response to climatic variables whereas farmland and shrubland species abundance was determined mainly by habitat structure. Despite species specific responses, the abundance of the majority of species increases in areas with open and heterogeneous vegetation structure and decreases in areas with higher temperatures and seasonality.

In light of these results, changes to the composition and abundance of cork oak woodlands should be expected. On one hand, ongoing land abandonment trends are likely to benefit shrubland species but will result in a lower abundance of many species belonging to generalist, forest and farmland guilds. On the other hand, intensification and overexploitation trends are likely to also have negative effects on the abundance of many farmland and generalist species that depend on a more heterogeneous habitat structure. On top of this, increasing temperatures and climatic extremes are likely to promote a negative response on many species associated with colder environments, particularly forest birds. Still, a few farmland and generalist species of Mediterranean origin may benefit from this situation. Bird assemblages of cork oak woodlands in northern Africa and southern Iberian Peninsula may be particularly affected by land management and climate change whereas in northern Iberia, bird assemblages could potentially benefit from the expansion of woodland area and management activities that promote a more adequate habitat structure.

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Chapter 5

Bird richness and abundance on cork oak woodlands decreases in drier microclimates

To be submitted as:

Correia, R. A., Haskell, W., Gill, J. A., Palmeirim, J. M., Franco, A. M. A., Bird richness and abundance on cork woodlands decreases in the drier microclimates.

Abstract

The increasing number of drought spells in southern Europe in recent decades is having negative impacts on tree species (e.g. increased defoliation, reduced growth, tree mortality), which may have consequences for other components of the trophic chain. However, local topographic features may buffer or intensify these effects through their influence on micro-climatic conditions. Existing evidence indicates that cork oak trees are already being affected by drought impacts and I aimed to understand the influence of micro-climatic conditions resulting from local topographic features on woodland structure, bird assemblages and their food resources. I characterized cork oak woodland structure and bird assemblages in three areas along an aridity gradient in Iberia, and compared caterpillar availability between north and south facing slopes in order to understand the influence of micro-climatic conditions on food resources for birds. Results show that canopy cover, bird richness and abundance can decrease by more than a third in response to arid local micro-climatic conditions when compared to more suitable areas. Predictions of future climate change indicate that southern slopes in more arid areas may be particularly under threat from increasingly arid conditions. Therefore, the characteristic topographic complexity of the Mediterranean Basin may shape woodland structure and bird communities by buffering or potentiating responses to climate change at local scales and conservation efforts should primarily be aimed at areas with potential to act as refugia in order to improve the long term maintenance of the high biodiversity levels characteristic of cork oak woodlands.

5.1. Introduction

Climate change is already having widespread impacts on natural systems across the globe (Parmesan and Yohe 2003, Root et al. 2003, Parmesan 2006). However, these impacts are not distributed homogeneously in space. At large spatial scales, some regions of the globe are expected to show faster and more pronounced changes in climate (Giorgi 2006, Loarie et al. 2009). Furthermore, at smaller spatial scales, topo-geographical features can have a very important role in determining micro-climatic conditions. For example, due to certain habitat and landscape features, local climatic conditions can change in relation to regional conditions, at similar levels to those expected from climate change (Suggitt et al. 2011). There is already ample evidence that the distribution of many species have shifted in response to climatic changes, either as a consequence of colonization of new areas (e.g. Thomas and Lennon 1999, Parmesan et al. 1999, Delzon et al. 2013) or local extinction in previously occupied areas (e.g. Lesica and McCune 2004, Wilson et al. 2005, Franco et al. 2006, Comte and Grenouillet 2013). There are also examples of species that have responded at a more local scale and have either shifted their habitat and resource use (Thomas et al. 2001), or their use of particular landscape features (Davies et al. 2006), but research on the influence of micro-climatic conditions on species responses to climate change is still rather scarce. In fact, the majority of predictions regarding climate change effects on biodiversity are usually obtained by modelling species distributions using large scale bioclimatic associations between species ranges and the climatic conditions therein observed (Elith and Leathwick 2009). These methods usually fail to incorporate more detailed spatial, ecological and physiological processes (Guisan and Thuiller 2005) that may buffer or even drive unexpected responses to climate change (e.g. Jiang and Morin 2004, Kearney et al. 2009, Lenoir et al. 2010, Scherrer and Körner 2011).

The Mediterranean Basin is considered both a biodiversity hotspot (Myers et al. 2010) and a climate change hotspot (Giorgi 2006), leading to predictions of severe biodiversity impacts across the region (Alcamo et al. 2007). The topo-geographic complexity of the Mediterranean Basin has had a defining role in current biodiversity patterns (Blondel et al. 2010) and is also likely to affect species responses to climate change. For example, there is evidence that Mediterranean tree species are increasingly being affected by frequent drought events resulting from recent climate change

(Carnicer et al. 2011), but the magnitude of such impacts is tempered by local topographic features (e.g. Lloret et al. 2004, Peñuelas et al. 2007). This also seems to be the case for the cork oak (*Quercus suber*), a keystone species in the western Mediterranean Basin. This is the key species in cork oak woodlands (locally known as *montados* or *dehesas* in Portugal and Spain respectively), a traditional agro-silvo-pastoral system in which woodland exploitation and high biodiversity levels can be maintained (Diáz et al. 1997). Cork oak woodlands are relatively widespread in the western half of the Mediterranean Basin and occur in a variety of management forms and across different landscape features (Pereira and Tomé 2004). However, during recent decades, a declining trend in cork oak woodland areas has been observed in many regions of the Mediterranean Basin (e.g. Brasier and Scott 1994, Regato-Pajares et al. 2004, Costa et al. 2011). This trend has been partly attributed to impacts from recent climate change (Brasier and Scott 1994, Carnicer et al. 2011) and has been shown in some regions to vary spatially according to local topographic and micro-climatic conditions (Costa et al. 2010). By affecting the trees that support the biological communities of this system, climate change impacts can potentially cause important disruptive effects on local biological communities due to bottom-up effects across the trophic chain, but these effects are still poorly explored (Carnicer et al. 2011), particularly at smaller spatial scales.

Here, I aimed to understand the influence of micro-climatic conditions resulting from local topographic features on woodland structure, bird assemblages and their food resources. Specifically, I aim to (i) evaluate how woodland structure and bird assemblages change along an aridity gradient, (ii) assess the influence of small scale topographic features on local differences in woodland structure and bird assemblages and (iii) explore the role of local resource availability as a driver of observed bird community changes in cork oak woodlands.

5.2. Material and methods

5.2.1. Study area

The Iberian Peninsula holds about 60% of the worldwide distribution of cork oak woodlands (Pausas et al. 2009). The study area, located in the south-western corner of the Iberian Peninsula (Fig. 5.1), represents the current core area of distribution of this system. I aimed to sample a climatic gradient representative of high (Caldeirão), intermediate (Grândola) and low (Monfurado) aridity levels within the dry sub-humid conditions of this region (UNEP 1997). Current rainfall availability values used to characterize sampling areas were collected from a global aridity database available from the Consultative Group on International Agricultural Research (CGIAR) spatial data base (http://www.cgiar-csi.org/), at a spatial resolution of 30 arc-seconds. Future rainfall availability was calculated for the year 2050 using climate predictions from the HadCM3 climate model for the A2 emissions scenario, according to the methodology described by Zomer et al. (2008).

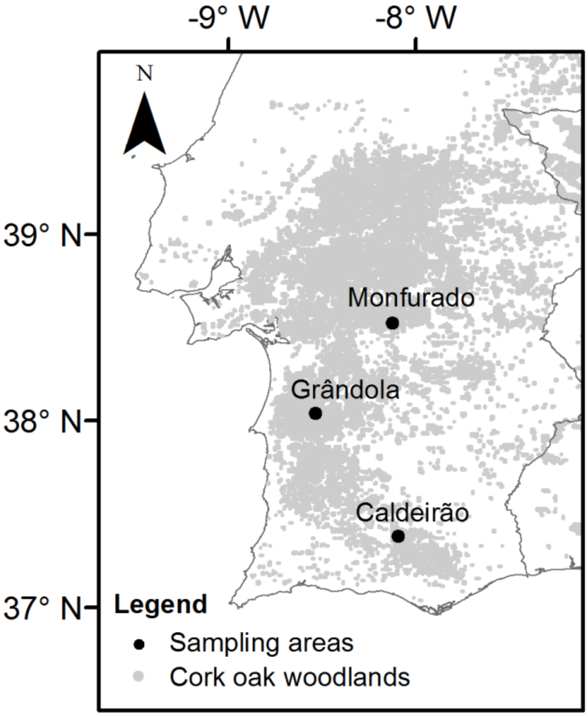

Figure 5.1. *Geographic distribution of the three sampling areas, located in the south-west corner of the Iberian Peninsula.*

5.2.2. Bird sampling

Breeding bird assemblages were studied in the three sampling areas by means of point counts (Sutherland et al. 2004, Bibby et al. 2005). Within each sampling area, forty sampling points were defined: twenty in north facing slopes and twenty in south facing slopes. Sampling points were selected in areas with a minimum inclination of 2.5° with the help of a Digital Elevation Model (DEM), at a 90m spatial resolution, obtained from the Consultative Group on International Agricultural Research (CGIAR) spatial data base (http://www.cgiar-csi.org/).

All bird counts were carried out between the 1st of April and the 31st of May 2012 and, at each sampling point, the number and species of all birds were recorded during five-minute periods always by the same observer. Counts were undertaken during the early morning, a period of peak bird activity, always in suitable weather conditions and avoiding rainy or windy days (Sutherland et al. 2004). All birds detected, either visually or acoustically, were recorded and their distance to the observer was estimated. Birds detected further than 50 m from the observer and over-flying birds were excluded from the analysis as they may not be associated with the areas being sampled. Prior to analysis, all bird species recorded were categorized into forest or non-forest guilds following Godinho and Rabaça (2011), and guild abundance was considered as the total number of birds from species belonging to each guild. A list of species belonging to forest and non-forest guilds in presented in Appendix 5.1.

5.2.3. Woodland structure

Woodland structure was characterized for each bird sampling point in all three sampling areas. Variables used to characterize woodland structure included tree density, tree cover and mean tree canopy area and were estimated with the help of aerial images obtained from Google Earth v7.1. For each sampling point, I counted the number of trees and measured the percentage of canopy cover present in the aerial photograph in the area within a 50 m radius from the bird sampling point. Tree density represents the number of trees observed within the area of each sampling point extrapolated to the number of trees present per hectare, and all cork oak trees identifiable from the aerial photograph were considered. Tree cover corresponds to the percentage of total area of ground within each sampling point that is covered by tree canopy. Mean tree canopy area was considered as a measure of the average area of canopy displayed by each individual tree and was calculated as the ratio between the area of each sampling point covered by tree canopy and the number of trees recorded in each sampling point.

5.2.4. Caterpillar frass collection

Caterpillars represent a prime food resource during the breeding season for many forest bird species (Cramp and Simmons 2006). A non-intrusive way to evaluate the abundance of caterpillars during this period can be achieved by sampling caterpillar frass droppings, which provides a measure of the caterpillar biomass present in a given area (Tinbergen and Dietz 1994, Visser et al. 2006, Burger et al. 2013). This methodology was used to characterize food resource availability for forest breeding birds at the Grândola sampling area only, due to logistical constraints.

Seventy-six sampling plastic trays (0.25 m^2) were equally deployed in the north and south facing slopes where bird counts were carried out, under trees of varying canopy size (canopy area ranged from 7 to 88 m^2). Sampling trays were visited at approximately three day intervals during the same period considered for bird sampling purposes and all the material they contained was collected. Samples were inspected with the help of a magnifying glass (10x) and frass droppings were sorted from the remaining material. Frass droppings are easily identifiable as small, cylindrical pellets that are dark brown to grey in colour (Fischbacher et al. 1998), and verified by field observations. Caterpillar frass dry weight was measured to the nearest milligram using a digital scale after samples were dried at a minimum temperature of 70°C for at least 12 hours.

5.2.5. Data analysis

Analysis of variance (ANOVA) was used to compare woodland structure variables and bird assemblages between the three sampling areas, different slopes and the interaction of these two factors. Where significant differences were found, multiple comparisons were carried out using Tukey HSD test (Zar 1999). Generalized linear mixed models (GLMMs) were used to test hypotheses regarding the role of woodland structure variables on the observed patterns of forest bird richness and abundance. These models considered tree density, tree cover and mean canopy size as fixed effects, sampling area as random effects and a Gaussian error distribution (after testing for normality and homogeneity of variance). The same modelling method was also used to test different hypothesis regarding the interaction between tree cover and topography (north versus south facing slopes) in shaping forest bird responses. In this case, tree cover and aspect were used as covariates, sampling area was included as a random effect and the error structure followed a Gaussian distribution. All the models were evaluated according to the Akaike Information Criterion corrected for sample size (AICc), Akaike weights and overall deviance explained (Burnham and Anderson 2002). All statistical calculations and analyses were carried out using R software v2.15 (R Development Core 2011).

Table 5.1. *Mean and confidence intervals (95%) of woodland structure variables and bird species richness and abundance for each of the three areas. Significant differences (Tukey HSD test, P<0.05) between sampling areas are highlighted by different characters (a, b and c).*

Descriptor	Sampling Area		
	Caldeirão	Grândola	Monfurado
Aridity level	High	Intermediate	Low
Mean rainfall availability (mm/day)	0.53	0.55	0.59
Woodland structure			
Tree density (No. trees/ha)	57.1 (±6.6)^{a}	69.9 (±8.4)^{b}	61.6 (±4.1)^{ab}
Tree cover (% ground cover/ha)	30.4 (±5.3)^{a}	41.1 (±6.7)^{b}	48.3 (±4.8)^{b}
Mean tree canopy area (m^2/tree)	50.3 (±4.8)^{a}	56.8 (±6.1)^{a}	77.2 (±5.0)^{b}
Species richness (No. species/ha)			
Total species	5.51 (±0.7)^{a}	6.50 (±0.5)^{b}	7.87 (±0.5)^{c}
Forest species	3.76 (±0.5)^{a}	4.49 (±0.6)^{a}	5.80 (±0.5)^{b}
Non-forest species	1.75 (±0.4)^{a}	2.01 (±0.4)^{a}	2.07 (±0.4)^{a}
Bird abundance (No. birds/ha)			
Total species	5.76 (±0.7)^{a}	7.07 (±0.6)^{b}	8.69 (±0.5)^{c}
Forest species	3.98 (±0.6)^{a}	4.93 (±0.7)^{b}	6.46 (±0.5)^{c}
Non-forest species	1.82 (±0.5)^{a}	2.20 (±0.5)^{a}	2.23 (±0.4)^{a}

5.3. Results

Woodland structure differed significantly between the Caldeirão, Grândola and Monfurado areas for the descriptors analysed: tree density (ANOVA, $F(2,117)=3.7$, $P<0.05$), tree cover (ANOVA, $F(2,117)=9.7$, $P<0.001$) and tree canopy area (ANOVA, $F(2,117)=26.8$, $P<0.001$). The most arid study area, Caldeirão, had the lowest mean values of tree density, tree cover and tree canopy area, whereas the area with least arid conditions, Monfurado, had significantly higher mean values of tree cover and tree canopy area than the remaining areas (Table 5.1). Grândola showed the highest mean tree density of the three study areas but this value was only significantly higher than tree density observed in the driest area (Table 5.1). Bird assemblage analysis shows that total bird species richness (ANOVA, $F(2,117)=17.4$, $P<0.001$) and abundance (ANOVA, $F(2,117)=23.0$, $P<0.001$) also differ significantly between areas. These differences are mainly driven by changes in forest bird richness (ANOVA, $F(2,117)=13.6$, $P<0.001$) and abundance (ANOVA, $F(2,117)=16.0$, $P<0.001$) as there were no significant differences in non-forest species richness (ANOVA, $F(2,117)=0.68$, $P=0.51$) and abundance (ANOVA, $F(2,117)=1.00$, $P=0.37$) between study areas. Overall, the least arid study area (Monfurado) had significantly higher mean total species richness, forest species richness, total bird abundance and forest bird abundance than the remaining two study areas (Table 5.1). While all woodland variables showed significant positive relationships with forest bird richness and abundance (model estimates ranged from 0.029 to 0.078), the analyses show that total tree cover was the variable that was most strongly associated with observed changes in both forest bird richness and abundance observed in the study areas, followed by mean tree canopy size and, to a lesser extent, tree density (Table 5.2).

Table 5.2. *Comparison of generalized linear mixed models (GLMM) assessing the relationships between each individual woodland structure variable and forest bird species richness and abundance. All models included sampling area as a random effect.*

Model	Estimate	*P*-value	AIC_c	ω_i	Deviance
Forest species richness					
Tree density	0.029	<0.001	475.4	0	467.1
Tree cover	0.057	<0.001	450.8	0.93	442.4
Mean tree canopy area	0.076	<0.001	456.1	0.07	447.7
Forest bird abundance					
Tree density	0.031	<0.001	503.8	0	495.5
Tree cover	0.060	<0.001	484.3	0.96	476.0
Mean tree canopy area	0.078	<0.001	490.5	0.04	482.2

Table 5.3. *Comparison of generalized linear mixed models (GLMM) assessing the relationships between forest bird abundance, tree cover and aspect at sites across three sampling areas (see Fig. 5.1). All models included sampling area as a random effect.*

Model	AIC_c	ω_i	Deviance
Null model	534.89	0	585.70
Tree cover	483.90	0.03	475.55
Aspect	488.77	0	480.43
Tree cover + Aspect	477.08	0.83	466.56
Tree cover + Tree cover * Aspect	490.15	0	479.63
Tree cover + Aspect + Tree cover * Aspect	480.74	0.13	467.99

Testing the response of tree cover in response to the interaction between sampling area and aspect showed that the existence of significant differences in tree cover between north and south facing slopes is not common to all areas (ANOVA, $F(2,114)=4.33$, $P<0.02$) and a post-hoc test revealed that this difference is only present in the two driest study areas, Caldeirão and Grândola (Fig. 5.2A). The same interaction was observed for forest bird abundance (ANOVA, $F(2,114)=9.07$, $P<0.001$), where a significant reduction in the abundance of forest bird species was only observed in the south-facing slopes of the Caldeirão and Grândola sampling areas. No significant difference was found in the abundance of non-forest bird species, either within (ANOVA, $F(1,114)=0.42$, $P=0.52$) or between (ANOVA, $F(2,114)=1.02$, $P=0.36$) areas (Fig. 5.2B). The changes observed in forest bird abundance between and within areas are best explained by a model that includes total tree cover and aspect as independent predictors (Table 5.3). The hypothesis for the relationship between forest bird abundance, tree cover and aspect that is best supported by the data is that forest bird abundance responds positively to an increase in total tree cover within an area but the total forest bird abundance is on average 1.07 birds/ha lower in drier south facing slopes (Fig. 5.3A). These differences may be partly explained by the significantly lower caterpillar frass fall (*t-test*, $t=2.66$, d.f.=74, $P<0.01$), in south facing than north facing slopes (Fig. 5.3B). Daily caterpillar frass fall in the Grândola sampling area averaged 29.0 $mg/m^2\ day^{-1}$ in north facing slopes, whereas the average observed value for south facing slopes was 22.0 $mg/m^2\ day^{-1}$.

Future climatic predictions indicate that all three study areas will become increasingly arid and, by the year 2050, south facing slopes in the two driest areas, Caldeirão and Grândola, are likely to drop to aridity levels of semi-arid regions (Fig. 5.4). Furthermore, only north facing slopes in the least arid study area (Monfurado) are likely to maintain significantly higher moisture levels than those observed at present in the driest area.

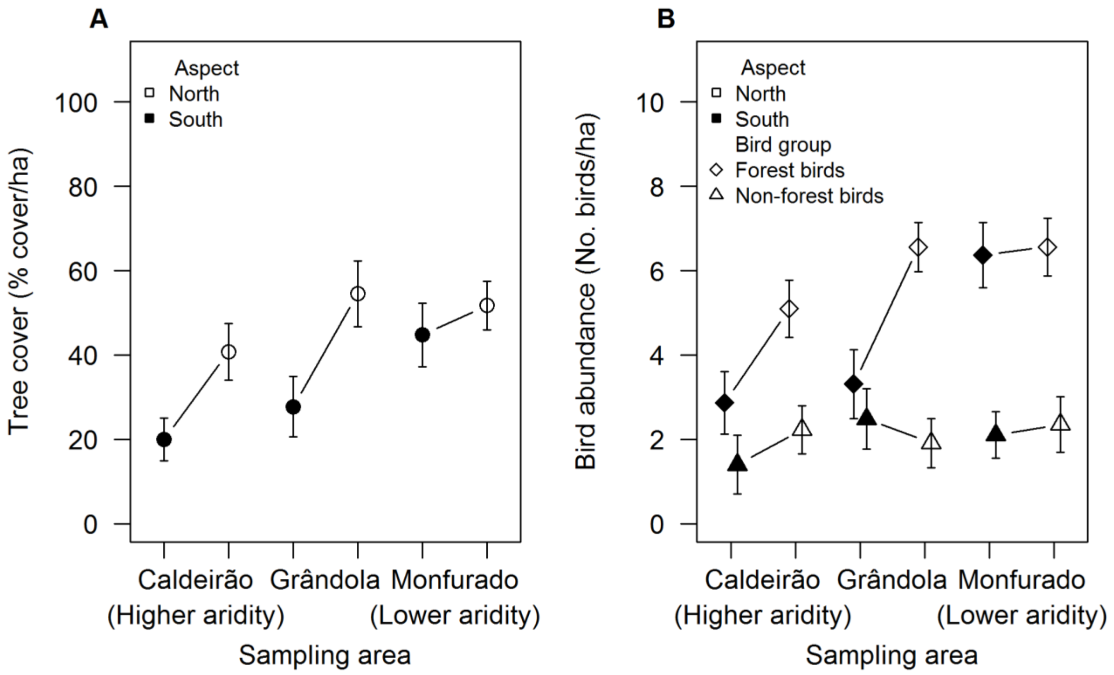

Figure 5.2. *Comparison between north and south facing slopes in the three sampling areas in terms of tree cover (A), forest and non-forest bird abundance (B). Points represent mean values and 95% confidence intervals for each sampled region and aspect.*

5.4. Discussion

5.4.1. Woodland structure and bird assemblage changes along an aridity gradient

Results indicate a significant response of woodland structure and bird assemblages to aridity. Both tree cover and mean tree canopy size decrease by over a third in more arid areas, even though there is no clear trend in tree density response to aridity (Table 5.1). Climate change has caused a significant increase in extreme heat and drought events during the last decades in the Mediterranean region (Diffenbaugh et al. 2007, Hoerling et al. 2012), resulting in higher leaf loss, reduced radial growth and increased mortality trends (e.g. Andreu et al. 2007, Allen et al. 2010, Carnicer et al. 2011, Besson et al. 2014). In drier areas, cork oak trees are likely to be more susceptible to such events and recovery periods may be longer, potentially justifying the observed differences in woodland structure between sampling areas. The lack of a significant tree density trend along this aridity gradient is somewhat surprising but is likely to change in the future considering the current mortality (Besson et al. 2014) and low regeneration trends currently observed in cork oak woodlands (Acácio et al. 2007), and the beneficial influence of nursing tree canopy protection on seedling recruitment success (Caldeira et al. 2014).

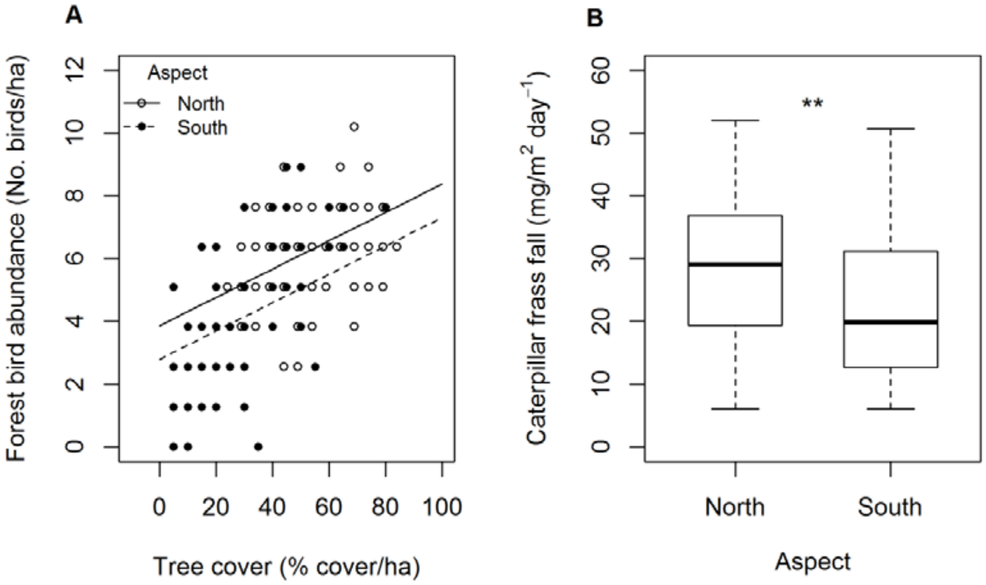

Figure 5.3. *Predicted relationship between forest bird abundance in relation to tree cover and aspect (A) and comparison of daily frass fall between north and south facing slopes. In A, lines represent predictions from the generalized linear mixed model providing the best hypothesis to explain the addressed relationships (see Table 5.3). In B, boxes represent median caterpillar daily frass fall in north and south facing slopes respectively. Significant differences for daily frass fall were found between north and south facing aspects (t-test, P<0.01).*

Bird assemblages respond in a similar fashion to woodland structure along the aridity gradient. I observed an average loss of over one species and two birds per hectare in drier areas, but this trend is mainly driven by forest bird species, as no significant differences were found between the study areas for non-forest birds (Table 5.1). In areas of rugged topography, the management of cork oak woodlands tends to favour the silvicultural component of this system, usually promoting higher tree densities (Pereira and Tomé 2004). This situation does not favour the presence of non-forest bird species (Telleria 2001) and may explain the low overall abundance of this group and the absence of a clear trend in non-forest bird abundance along the aridity gradient. On the other hand, higher tree densities generally increase the probability of presence of forest bird populations, but their local abundance is still highly dependent on local woodland structure (Telleria 2001, Godinho and Rabaça 2011).

At smaller spatial scales, the analyses revealed south facing slopes show nearly half the tree cover and forest bird abundance that was registered in north facing slopes, but only within the two driest areas sampled. Tree cover patterns between and within areas (Fig. 5.2A) agree with previous studies showing that patterns of cork oak growth and mortality are negatively affected by drier landscape and microclimatic features (Costa et al. 2008, Costa et al. 2010). The observed decrease in the abundance of local forest bird assemblages within drier areas (Fig. 5.2B) is most likely a response to both microclimatic and woodland features (Table 5.3). Forest birds were less abundant in areas with reduced tree cover, usually observed in drier south facing slopes. However, even when south-facing slopes showed similar tree cover conditions to north-facing slopes, forest birds were generally more abundant in the latter (Fig. 5.3A). This response is probably related to the lower resource abundance present in south facing slopes (Fig. 5.3B). Caterpillars are less abundant in lower quality canopies (Hunter 1987, Murakami et al. 2005) and higher temperatures may lead to changes in phenology (Stefanescu et al. 2003) and increased temperature related diapause (Held and Spieth 1999), reducing the time-frame when they are available for birds during the breeding season and potentially resulting in resource mismatches (Kerby et al. 2012). Other arthropod groups may also be negatively affected by these factors (e.g. Trotter et al. 2008, Stone et al. 2010), which could result in a significant reduction of food resources in warmer south-facing slopes for birds. Overall, results indicate that local woodland structure responses to microclimatic conditions can potentially translate into bottom-up up effects across the food-web that ultimately affect forest bird populations as well. Many bird species are already shifting their distributions in response to climate change (Thomas and Lennon 1999, Devictor et al. 2008, Devictor et al. 2012) and local processes like the one here describe may be the driving force behind such changes.

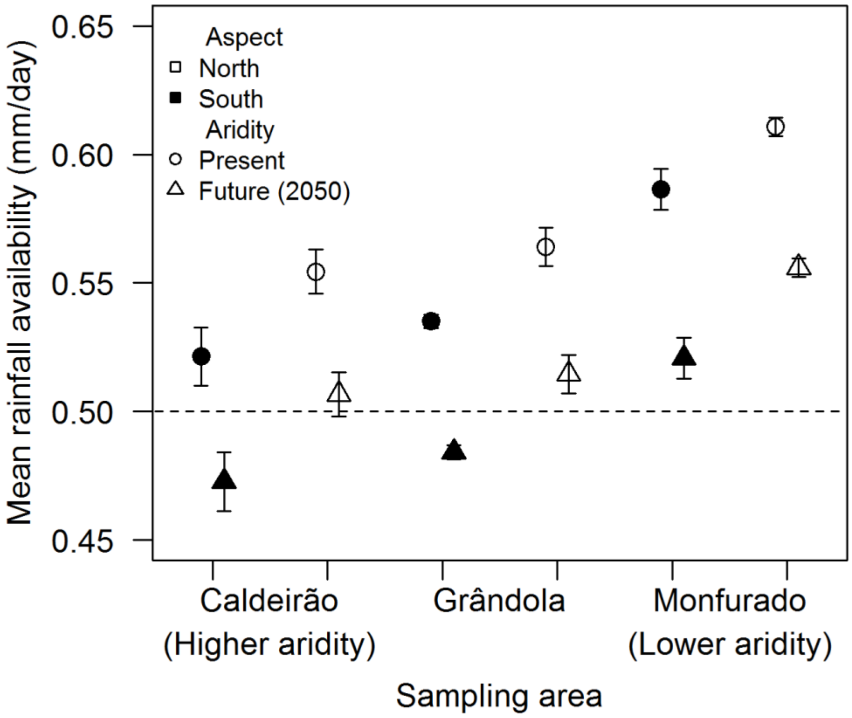

Figure 5.4. *Mean (± 95% confidence intervals) values of rainfall availability for present (circles) and predicted future (triangles) conditions at the three sampling areas. Future rainfall availability represents predictions for the year 2050 according to the HadCM3 climate model and A2 emissions scenario. The dashed line represents the transition between semi-arid and dry sub-humid conditions according to global aridity values (UNEP 1997).*

5.4.2. Implications for conservation in the face of climate change

Results indicate that future climate change is likely to have important consequences for cork oak woodlands and their biodiversity. According to future predictions, cork oak woodlands will be under higher pressure from increasing aridity, and south facing slopes in southern and drier areas seem particularly at risk (Fig. 5.4). The majority of forest bird species in the Mediterranean Basin have their southern distribution limits in the region (Cramp and Simmons 2006) and further climate change may drive the local extinction of these species. In managed systems like cork oak woodlands, adequate consideration of potential human impacts on biodiversity from activities such as cork removal, tree pruning and shrub removal (e.g. Leal et al. 2011, Santana et al. 2012, Leal et al. 2013) will be important to increase the resilience of these systems to climate change impacts. Still, the conservation of forest bird populations in this region, that for many species represents the rear edge of their distributions, is no simple task under climate change and requires innovative and more specific efforts (Hampe and Petit 2005).

For example, focusing on preserving different key landscape features may promote the maintenance of ecosystem functionality which may be more effective in a climate change scenario than just the protection of individual species (Beier and Brost 2010). The fact is that local climatic refugia have been important for many groups in past periods of global environmental change (e.g. Médail and Diadema 2009, Stewart et al. 2010) and can also play an important role under the current scenario of change. In this respect, maintaining cork oak woodlands on north facing slopes may be particularly important to buffer the effects of climate change in drier areas. While the ability of these areas to maintain the high biodiversity levels that usually characterize more open and extensive cork oak woodlands (Diáz et al. 1997) remains uncertain, results indicate that north facing slopes may have an important role in conserving local cork oak populations and their associated forest bird species. However, in order for this to be possible, current trends of land abandonment, management intensification and the lack of tree recruitment (Acácio et al. 2007, Bugalho et al. 2009) need to be tackled in order to facilitate the long term maintenance of cork oak woodlands in these areas.

5.5. Conclusions

Results show that forest bird communities of cork oak woodlands in drier conditions are already being impacted by climate change, losing about one species and two birds per hectare when compared with less arid areas. Cork oak woodlands in drier microclimates generally comprised trees with narrower canopies and a lower overall canopy cover, which is likely to be a result of increased defoliation and tree mortality trends due to recent climate change. This, in turn, seems to affect resource availability for bird species that depend on this tree species, which may ultimately drive the observed patterns of forest bird abundance.

In this scenario, the characteristic topographic complexity of the Mediterranean Basin, with the presence of diverse microclimatic conditions, seems to play an important role in shaping woodland and bird community responses to climate change. Cork oak woodlands located in drier climatic conditions, and their biodiversity, seem particularly under threat from future climate change but the presence of microclimatic refuges may provide a spatial and temporal buffer to climate change impacts. Conservation efforts should primarily be aimed at areas with potential to act as refugia and future research should focus on understanding the potential ability of these areas to conserve the high biodiversity levels characteristic of cork oak woodlands and how to maximize this potential in the long term.

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Chapter 6

Can climate change provide the opportunity for trans-Saharan migrants to overwinter in Europe?

To be submitted as:

Correia, R. A., Gill, J. A., Palmeirim, J. M., Franco, A. M. A., Can climate change provide the opportunity for trans-Saharan migrants to overwinter in Europe?

Abstract

There is increasing evidence that climate change is associated to changes in bird migratory behaviour. In recent decades several wholly migratory trans-Saharan migrant species have established overwintering populations in southern Europe. This is the first study to assess if changes in migratory behaviour of birds are linked to climate change, by comparing the European and the African climatic niche of species with overwintering populations in Iberia. Our results indicate that rising winter temperatures have increased the similarity between the climatic conditions in Iberia and the African wintering grounds, in spite of decreasing precipitation trends. This was observed for all partially migratory species that were previously wholly migratory. Birds overwintering in the Iberian Peninsula select areas that are more similar in temperature to their African wintering grounds than expected by chance, indicating that temperature is the limiting factor. Species that established overwintering populations in southern Europe in recent decades have higher climatic overlap between Iberian and African wintering grounds than similar (control) species that have not changed their migratory behaviour. These results suggest that climate change may have provided the opportunity for wholly migratory species to establish regular overwintering populations in southern Europe.

6.1. Introduction

Migratory behaviour is common in birds as a response to seasonality (Newton 2008), and is an extremely adaptable behaviour (Fiedler 2003). Recent changes in climate are causing adaptation responses across natural systems (Parmesan & Yohe 2003, Root et al. 2003), including birds (Crick 2004). For migratory birds, the most commonly observed responses have been adaptations to migratory phenology (e.g. Cotton 2003, Jenni and Kéry 2003, Saino et al. 2011) and migratory distances (e.g. La Sorte and Thompson 2007, Visser et al. 2009, Heath et al. 2012).

In the last few decades there have been more radical changes in bird migratory behaviour with individuals from migratory species completely abandoning migration (Newton 2008). In fact, particularly in southern Europe, several wholly migratory species now have overwintering populations (Berthold 2001, SEO/BirdLife 2012). This behaviour has been observed regularly in recent decades and some of these species are now considered to have established wintering populations in some regions, such as the Iberian Peninsula (SEO/BirdLife 2012). The Mediterranean Basin is considered a climate change hot-spot (Giorgi 2006) and the recent climatic changes observed the region (Peréz and Boscolo 2010) are likely associated with changes in migratory behaviour. While some authors have claimed that climate change may ultimately drive residency in bird populations (Wilcove and Wikelski 2008, Pulido and Berthold 2010), the role of climate change on the suitability of breeding sites during the winter season remains poorly explored.

Here, I explore the hypothesis that climate change may be linked to the increasing number of overwintering populations of previously wholly migratory bird species in the Iberian Peninsula, by quantifying the climatic similarity between the new (Iberian) and traditional (African) wintering grounds. I test a set of predictions linked to this hypothesis assuming that recent changes in climatic conditions during the winter in the Iberian Peninsula have provided the opportunity for the establishment of overwintering populations of previously wholly migratory species. Thus, I predict that:

(i) In recent decades the winter climatic conditions in the Iberian Peninsula became more similar to conditions in the African wintering grounds due to recent climate change;

(ii) Species that have recently started overwintering in Iberia select areas that are significantly more similar to their African wintering grounds than expected by chance;

(iii) Climatic conditions during the winter in the Iberian Peninsula have become more similar to the conditions in African wintering grounds for overwintering species than for similar species that have not yet established regular wintering populations.

Results are discussed in light of the role of climate change as a driver of migratory behaviour changes and the conservation implications of partial migration for declining long-distance migratory species (Sanderson et al. 2006).

6.2. Materials and methods

6.2.1. Distribution data

Until recently, there was a lack of organized information regarding the distribution and status of traditionally migratory species overwintering in southern Europe. I took advantage of the latest efforts to systematically map the distribution of wintering bird species in the Iberian Peninsula and collected distribution data on the wintering areas of a set of six traditionally migratory species that are now showing regular wintering populations in the Iberian Peninsula (SEO/Birdlife 2012). The selected species were: White Stork (*Ciconia ciconia* – Ccic), Common Quail (*Coturnix coturnix* – Ccot), Common House Martin (*Delichon urbicum* – Durb), Barn Swallow (*Hirundo rustica* – Hrus), Black Kite (*Milvus migrans* – Mmig) and Hoopoe (*Upupa epops* – Uepo). Iberian winter distribution records were collected from the Wintering Bird Atlas of Spain (SEO/BirdLife 2012) and Portugal (SPEA/BirdLife, *in press*). Additional observations in the Iberian Peninsula were obtained from the WorldBirds online database (www.worldbirds.org) for the wintering period considered for Wintering Bird Atlas purposes (SEO/BirdLife 2012), which spanned from the 15 of November to the 15 of February. A summary map of Iberian wintering areas used by the six species can be seen on Fig. 6.1. African wintering areas also were characterized using BirdLife distribution maps (BirdLife International and NatureServe 2014). This approach was preferred to observation or atlas data as the number of records in many countries where species potentially occur is low or inexistent. The African distribution of wintering areas only considered latitudes under 20ºN, in order to exclude zones of passage during migration. Species distribution data from both regions were then converted to a 0.5º resolution presence-absence grid in order to match the climate data used for the analysis (see below).

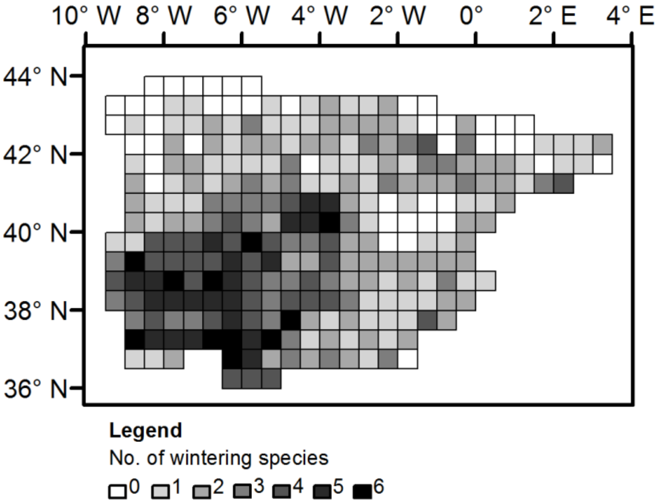

Figure 6.1. *Iberian distribution map of the six species overwintering in Iberia in recent decades. Grid squares are coloured according to the number of species registered during the winter.*

In addition, I collected distribution data for a set migratory species that show breeding distributions and requirements as similar as possible to the set of newly established wintering species but that have not yet established regular wintering populations in the Iberian Peninsula. This group included the following species: Common Swift (*Apus apus*, Aapu), Purple Heron (*Ardea purpurea*, Apur), Red-rumped Swallow (*Cecropis daurica*, Cdau), European Bee-eater (*Merops apiaster*, Mapi), European Honey Buzzard (*Pernis apivorus*, Papi) and Turtle Dove (*Streptopelia turtur*, Stur). The African wintering distributions were collected using the same procedure described for migratory species. Furthermore, I defined a set of potential wintering areas in the Iberian Peninsula for migratory species, in order to evaluate the climatic overlap between potential Iberian and African wintering grounds. Potential wintering areas for migratory species were classified as any grid cells where all recently established overwintering species were recorded (black cells in Fig. 6.1). This selection was based on the assumption that the areas occupied by all recently established wintering species in Iberia are also the areas more likely to be suitable for the establishment of overwintering populations of other migratory species.

6.2.2. Ecological trait data

I built an ecological traits dataset to compare species ability to establish wintering populations in the Iberian Peninsula between groups. The ecological traits analysed included climatic tolerance (winter climatic niche extent), habitat requirements (wintering distribution extent), winter diet (winter insectivorous diet), flight ability (wing loading), breeding strategy (clutch size) and social behaviour. Winter climatic niche extent was expressed as the percentage of available climatic niche space (see below) occupied by the species across its African wintering range. Wintering distribution extent was calculated as the area potentially occupied by each species in sub-Saharan Africa (latitudes under 20°N), measured in millions of square kilometres. Winter diet classified species as insectivorous or not according to the winter dependence on arthropods as food resource. Wing loading was calculated for each species as the ratio between mean body weight (kg) and mean wing area (m^2). Clutch size was defined as the mean number of eggs in a clutch and social behaviour classified species as social (gregarious) or non-social (solitary). BirdLife distribution data (BirdLife International and NatureServe 2014) was used to calculate winter distribution extent and mean wing area was obtained from the Bird of Switzerland database (http://www.vogelwarte.ch). The remaining information was obtained from Birds of the Western Palearctic (BWPi 2006). The complete data table can be found in Appendix 6.1.

6.2.3. Climate data

The CRU TS 3.10.01 data-set (Harris et al. 2013) was used for extracting the climate variables in the Iberian Peninsula and sub-Saharan Africa (latitudes under 20ºN). To test the first hypothesis, I determined the climate trend in the Iberian wintering areas between pre and post-residency periods, in agreement with the increasing number of wintering birds since the 1980s (e.g. *Ciconia ciconia* and *Coturnix coturnix*, BWPi

2006) . Climatic conditions in Iberia during pre and post-residency periods were compared to current conditions in the African wintering grounds. I chose to compare pre and post-residency periods in Iberia with climatic conditions that correspond to current distributions in Africa due to the fact that little distribution data is available for past African wintering areas and, therefore, could not consider potential impacts of climate change on African species distributions (Barbet-Massin et al. 2009). Iberian Peninsula climate data was collected for pre (1950-1979) and post residency (1980-2009) periods, whereas climate data for African wintering grounds was collected for the time period between 1980 and 2009. Data for both regions was collected at 0.5º resolution, for the months between November and February, period considered as the wintering season for atlas purposes (SEO/BirdLife 2012).

This data was used to calculate eight bioclimatic variables for the winter season: Mean Temperature, Total Precipitation, Maximum and Minimum Temperature, Maximum and Minimum Precipitation, Temperature Seasonality and Precipitation Seasonality. These variables were chosen for the analysis in order to represent the average winter conditions but also their variability and extremes that often condition the populations and migratory behaviour of birds (Saether et al. 2006, Newton 2008). A table defining each climatic variable considered for analysis is provided in Appendix 6.2.

6.2.4. Prediction testing

I tested the set of predictions regarding the role of climate change on the establishment of overwintering populations in Iberia by performing climatic niche overlap analysis and niche similarity tests between the wintering grounds in the Iberian Peninsula and Africa using the framework proposed by Broennimman et al. (2012). This methodology allows for niche comparisons between and within species in space and time, making it ideal for this study. Niche analyses were carried using the PCA-ENV approach, an ordination technique that uses species occurrences and climate data to characterize the species niche in a transformed two-dimensional environmental space (for further details, see Broennimann et al. 2012), and Schoener's D metric was used as the measure for niche overlap. Climatic variable loadings in relations to environmental axis can be found in Appendix 6.3. Niche overlap estimates were tested for potential biases that may arise due to records of late migrants and early arrivals being classified as overwintering birds. I tested the results by comparing niche overlap estimates obtained with the all Iberian wintering records with results from one hounded subsamples of 90% of the Iberian dataset and found no significant differences (*P*>0.05) between niche overlap estimates. Finally, I also performed a multivariate ordination analysis of migratory and overwintering species groups in relation to ecological traits to identify which factors are associated with the ability to establish regular wintering populations in the Iberian Peninsula. Species traits loadings are presented in Appendix 6.4. All calculations were computed using R software v.2.15 (R Development Core Team 2011).

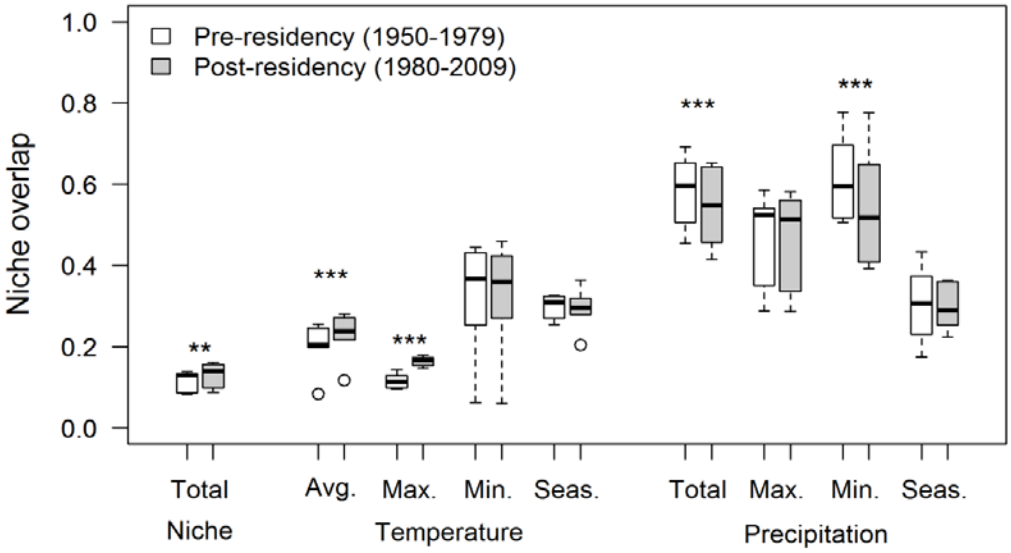

Figure 6.2. *Climatic niche overlap between Iberian and African wintering areas during pre and post-residency periods for six species with overwintering populations in Iberia. Comparisons were done for the overall climatic niche and for each climatic variable separately. Boxes represent first and third quartiles of niche overlap values, bold bar represents median value, whiskers represent the values within 1.5 times the inter quartile range and points represent values over 1.5 times the inter quartile range. Significant differences in niche overlap obtained with paired t-tests between the two time periods are identified (*, P<0.05; **, P<0.01; ***, P<0.001).*

6.3. Results

The average estimate of current climatic niche overlap between African and Iberian wintering grounds for overwintering species was 0.13, with a maximum value of 0.16 (*Ciconia ciconia*) and minimum of 0.09 (*Delichon urbicum*). There was a significant increase (*paired t-test*, t=4.01, d.f. = 5, p-value = 0.01) in the climatic niche overlap of Iberian and African wintering grounds between pre and post-residency periods (Fig. 6.2). This increase in overall climatic niche overlap between regions during the last decades is due to a significant increase in the overlap of average and maximum temperatures (*paired t-test*, d.f. =5, p<0.05) and is explained by rising winter temperatures. The overall increase in climatic niche overlap between regions was observed even when the opposite trend was found for minimum and total precipitation (*paired t-test*, d.f. = 5, p<0.05), as a result of the recent decline in winter precipitation values in the Iberian Peninsula (Fig. 6.3). All six overwintering bird species select areas in the Iberian Peninsula with temperature conditions more similar to their wintering grounds in Africa than expected by chance (Table 6.1). Four out of six species also selected areas with more seasonal precipitation conditions than expected by chance.

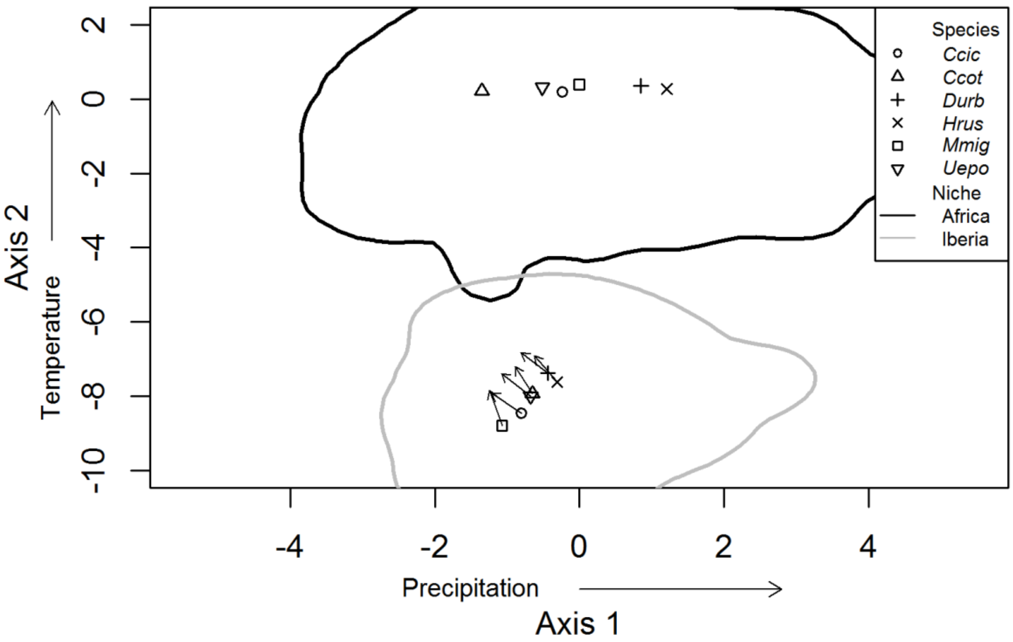

Figure 6.3. *Change in the Iberian climatic niche between pre (1950-1979) and post-residency (1980-2009) periods in relation to African overwintering climatic niche. Points represent the location of each species niche centroid in relation to both African (black line) and Iberian (grey line) available niche space. Arrows show how the climate of the Iberian range of each species changed between pre and post-residency periods. Axis loadings can be found on Appendix 6.3.*

Table 6.1. *Results of climatic niche similarity tests between Iberian overwintering areas and African wintering grounds. Comparisons for which Iberian conditions were significantly more similar to Africa than expected by chance (P<0.05) are represented by +.*

Species		Climatic niche								
Common name	Scientific name	Total niche	Avg. Temp.	Max. Temp.	Min. Temp.	Temp. Seas.	Total Prec.	Max. Prec.	Min. Prec.	Prec. Seas.
White Stork	*Ciconia ciconia*	n.s.	+	+	+	n.s.	n.s.	n.s.	n.s.	n.s.
Common Quail	*Coturnix coturnix*	+	+	+	+	+	n.s.	n.s.	n.s.	+
Common House Martin	*Delichon urbicum*	n.s.	+	+	+	n.s.	n.s.	n.s.	n.s.	+
Barn Swallow	*Hirundo rustica*	+	+	n.s.	+	n.s.	n.s.	n.s.	+	n.s.
Black Kite	*Milvus migrans*	+	+	+	+	n.s.	n.s.	n.s.	n.s.	+
Eurasian Hoopoe	*Upupa epops*	n.s.	+	n.s.	+	n.s.	n.s.	n.s.	n.s.	+

Species with overwintering populations in Iberia show significantly higher climatic niche overlap between overwintering areas in Africa and Iberia than the control group with similar migratory species (t-test, t=3.76, df=9.966, p<0.005) (Fig. 6.4). Multivariate ordination analysis of species traits showed it is possible to separate the two groups of species (Fig. 6.5). The first two axes accounted for just over 60% of the variability in traits, with overwintering and migratory species groups clearly organized along the first axis (Appendix 6.4). Overall, overwintering species show larger climatic niches, wider distribution extent insectivorous diet and larger clutch sizes than similar migratory species.

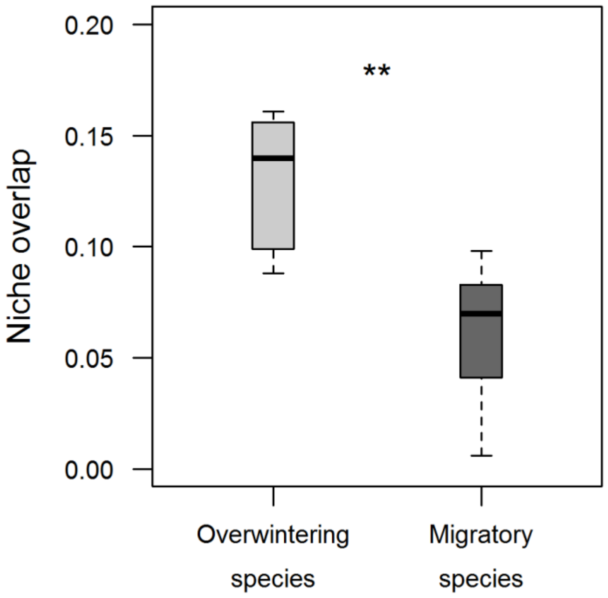

Figure 6.4. *Climatic niche overlap between the African and Iberian wintering grounds for overwintering species and a control set of similar migratory species. The climatic niche overlap for migratory species was analysed for potential wintering areas (see Methods section). There was a significant difference in average climatic niche overlap between the two groups of species (**, P<0.01).*

6.4. Discussion

6.4.1. The establishment of Iberian overwintering populations in light of climate change

Results confirmed the initial predictions that climate change is linked to the recent changes in migratory behaviour of birds. Consistently, for all species with established overwintering populations in Iberia, the climatic conditions in the Iberian Peninsula, in recent decades, have become more similar to the African wintering grounds (Fig. 6.2). Increased similarity between regions is driven by increasing temperatures, and occurred in spite of decreasing precipitation trends across the Iberian Peninsula (Fig. 6.3). The Mediterranean climate of the Iberian Peninsula is characterized by dry and warm summers and rainy winters with relatively mild temperatures (AEMET and IM 2011). Results indicate that all overwintering species selected wintering areas in Iberia that are warmer and more similar to the African wintering grounds than expected by chance (Table 6.1), supporting the idea that temperature is still likely to represent the main limiting factor during winter months, especially as rainfall is usually abundant during this period. Therefore, increasing winter temperatures in Iberia, driven by climate change (Peréz and Boscolo 2010), may have provided the opportunity for migratory species to establish wintering populations in the Iberian Peninsula, regardless of decreasing precipitation trends (Fig. 6.3). However, not all species may be able to exploit this opportunity. Climatic conditions in the Iberian Peninsula are generally more similar to conditions experienced at the African wintering grounds for species that recently established overwintering populations than for similar species that still regularly migrate to Africa (Fig. 6.4). Trait analyses also indicate that the recently established overwintering species are more generalist in their ecological requirements and have wider climatic niches and distributions (Fig. 6.5). These results help to explain why only a relatively small fraction of European migratory species now regularly overwinter in the Iberian Peninsula even though individuals of several species have been registered during the winter in the region (SEO/BirdLife 2012).

6.4.2. The role of climate change on mechanisms controlling migratory behaviour

Increasing temperatures seem to be the main ecological factor driving migrants to establish overwintering populations in the Iberian Peninsula. At low temperatures, birds show higher metabolic requirements (Anderson and Jetz 2005) but food resources tend to be a limiting factor, prompting them to migrate (Newton 2008). Recent evidence demonstrates that increasing temperatures have caused improved winter survival and earlier emergence of arthropods (e.g. Bale et al. 2002, Stefanescu et al. 2003), which is likely to result in higher food abundance for insectivorous and generalist species. Year-round food availability, as a result of increasing temperatures and other recent anthropogenic changes such as landfill sites, introduced species and supplementary feeding (Massemin-Challet et al. 2006, Robb et al. 2008, Tablado et al. 2010), is likely to provide the opportunity for the establishment of overwintering populations in the Iberian Peninsula. Still, only more generalist species exploring large climatic and ecological niches have established overwintering populations in the region, suggesting that diet is not the only determinant factor. Despite relatively mild, winter temperatures in the Iberian Peninsula may still be a limiting factor for species with higher energetic requirements or depending on more seasonal habitats.

Climate change may provide the opportunity for birds to winter in the Iberian Peninsula, but the establishment of new wintering areas will ultimately require changes in the genetic and/or phenotypic structure of migratory bird populations. It has been argued that climate change pressures may change migratory activity through microevolutionary responses (Pulido and Berthold 2010), but there is still lack of evidence in the literature that this has occurred (Gienapp et al. 2008, Charmantier and Gienapp 2013). The expression of migratory behaviour is in many cases dependent on biological constraints, such as length or timing of the breeding season (e.g. Jenny and Kéry 2003, Gill et al. 2013), and environmental cues (e.g. Studs and Marra 2011, Newton 2012), all of which potentially affected by climate change. In the Iberian Peninsula, the establishment of overwintering populations for the majority of species analysed is probably a consequence of the expected decrease in the migratory activity of northern European populations due to climate change

(Schaefer et al. 2008). Other possible justifications are the expansion of existing resident populations in North Africa or the evolution of residency in Iberian breeding populations. Regardless, these events do require either genetic or phenotypic changes that may be driven by climate change, which makes this study system an exciting prospect for the (still) poorly understood evolutionary and ecological mechanisms controlling changes in migratory behaviour as a response to climate change (Knudsen et al. 2011).

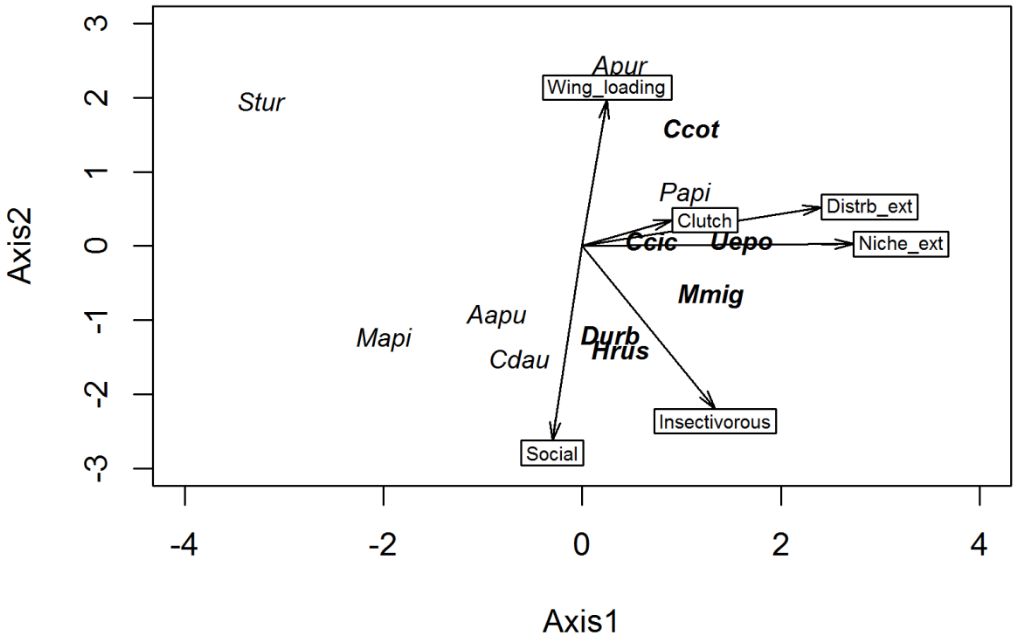

Figure 6.5. *Multivariate analysis of ecological factors differentiating overwintering and migratory species. Overwintering species are highlighted in bold font. Overwintering species are positively associated with wider wintering distributions and winter niche space occupied and, to a lesser extent larger clutches and an insectivorous diet. Axis loadings can be found in Appendix 6.4.*

6.4.3. New wintering areas provide conservation opportunities for migratory birds

The establishment of overwintering populations in Iberia may also provide new opportunities for the conservation of traditionally migratory species. It is well known that long-distance migrants are among the species showing higher population declines across Europe (Sanderson et al. 2006). This fact has been partly attributed to pressures en-route and at the wintering grounds, including effects from climate change (e.g. Sanderson et al. 2006, Barbet-Massin et al. 2009, Vickery et al. 2014). Monitoring population trends of overwintering and migratory populations will provide a better evaluation of the factors driving population declines in migratory species. Wintering populations in the Iberian Peninsula may also enable new conservation opportunities that may reduce the impacts of previously mentioned threats but this will require important wintering habitats for birds, such as cork oak woodlands (Diaz et al. 1997), to be maintained and adequately managed.

6.5. Conclusions

Recent climatic changes in the Iberian Peninsula seem to have provided the opportunity for traditionally migratory species to establish overwintering populations in the region. Rising winter temperatures have promoted an overall increase in climatic similarity between the Iberian Peninsula and Africa, in spite of declining precipitation trends. The majority of newly established overwintering species tend to show broad climatic niches but are nevertheless selecting wintering areas within the Iberian Peninsula that are warmer and thus significantly more similar to their traditional wintering grounds in Africa. This fact suggests that declining precipitation trends during the winter are not affecting the establishment of overwintering bird populations in Europe, probably due to the high rainfall during the season. Rather, low winter temperatures are likely to be the major constraint to the establishment of wintering populations. Physiological thermal limitation and resource availability are likely to be among the mechanisms limiting the establishment of overwintering populations in Europe. Future research should focus on further exploring the ecological drivers by which climate change may facilitate the establishment of wintering populations and the evolutionary mechanisms associated with these changes in migratory behaviour. Such knowledge will ultimately provide important new opportunities for the management and conservation of declining long-distance migratory bird species.

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Chapter 7

Conclusion

Photo: Extensive c*ork oak woodlands in the Alentejo region, Portugal*

Historically, the traditional multipurpose management of cork oak woodlands was greatly valued and cherished by many Mediterranean cultures for its economic, cultural, aesthetic and natural value, and provided an example of a mutually beneficial relationship between humans and the natural environment (Diáz et al. 1997, Vallejo et al. 2009). Decades of management adaptation to local and regional contexts have increased the resilience of cork oak woodlands and allowed the maintenance of a variety of management forms that are still observed nowadays (Vallejo et al. 2009). However, the remarkable balance between human activities and natural value that is characteristic of cork oak woodlands is currently under threat from the rapid ongoing global environmental, economical and societal changes (Bugalho et al. 2009). Habitat loss and degradation, due to inappropriate or absent management, and climate change effects are undoubtedly among the major threats to cork oak woodlands (Bugalho et al. 2009, Pereira et al. 2009) and Mediterranean biodiversity in general (Alcamo et al. 2007, Cuttelod et al. 2008). The rapid and global character of these changes requires a global and comprehensive assessment of their potential effects on Mediterranean cork oak woodland and its biodiversity at global, regional and local scales.

Therefore, the aim of this thesis was to contribute to this task by analysing the effects of land management changes and climatic changes on cork oak woodlands and their biodiversity, under different scenarios and at multiple spatial scales, in order to identify potential challenges and opportunities for the long term maintenance of this valuable system.

7.1. Key findings

7.1.1. Global and local climate effects on cork oak woodlands

The findings of this thesis indicate that climate change is likely to have an important role in the future global distribution of cork oak woodlands. Predictions obtained in Chapter 2 point towards a marked decline of approximately 40 and 60% of the currently occupied area up to 2080, mainly in the southern regions of its current range such as Morocco, Tunisia, Algeria and southern Iberia. In these areas, only some pockets of suitable climate are likely to remain in the more extreme scenarios of climate change. The remaining regions are likely to maintain their suitability, such as the case of Italy, many Mediterranean islands and some areas within the central Iberian Peninsula. New suitable areas are likely to emerge to the north of the current range and may provide grounds for future afforestation efforts if these are deemed economically and politically viable. This thesis includes the first attempt to predict the impacts of climate change on the distribution of suitable areas for the cork oak across their whole range. It includes information from the complete range of the species, so the results obtained are likely to be more robust than previous regional estimates (Garzón et al. 2007, Atorre et al. 2011). In fact, the role of incomplete species distribution data on model outputs was also assessed, and the results confirm previous reports of potential biases in predictions when information of the complete range of species is not included in model calibration (Thuiller et al. 2004, Barbet-Massin et al. 2010). Still, due to the large scale nature of this study, it did not address how climatic conditions at smaller spatial scales may affect the response of cork oaks to climate change. Chapter 5 aimed to fill this knowledge gap through a better understanding of how micro-climatic conditions might already be affecting cork oak trees and their associated biodiversity at local spatial scales.

The results obtained in Chapter 5 indicate that cork oak trees located in drier areas have smaller canopies than cork oaks located in areas with milder climatic conditions. Even under similar levels of tree density, total canopy cover is lower in woodlands located in drier areas as a result of individual trees having smaller canopies. Drier conditions at smaller spatial scales had a similar effect on tree canopy cover, which was observed to be significantly lower in south facing slopes when compared to north facing slopes within the same study areas. This is an indication that local microclimatic conditions may buffer or potentiate the negative effects that extreme heat and drought spells have on cork oak trees. The increasing frequency of such events around the Mediterranean Basin (Diffenbaugh et al. 2007, Hoerling et al. 2012) will promote more arid conditions across the region and a set of recommendations is suggested to manage this scenario. In regions like northern Africa and southern Iberia, where the suitability of climatic conditions for the cork oak is likely to decrease dramatically, the priority should be the protection of any areas where microclimatic conditions are likely to allow the maintenance of cork oak woodlands. These areas may have an important role in maintaining landscape connectivity in more affected regions and will be important for the conservation of the endangered species that partly depend on cork oak woodlands, particularly in northern Africa where the Mediterranean Sea may prevent these species to shift their distributions northwards. In areas where climatic conditions are likely to remain suitable and where cork oak woodlands are currently present, the conservation focus should be the promotion of sustainable management practices, in order to guarantee their long term sustainability and maintain their biodiversity and ecosystem services (Bugalho et al. 2011a). Finally, adaptation efforts can potentially take advantage of the predicted northward shift in climatically suitable areas to promote a northwards expansion of the species through a proactive approach based on new afforestations (Resco de Dios et al. 2007).

7.1.2. Bird assemblage responses to climatic and management gradients

This thesis also focused on understanding the role of ongoing climatic and management changes on the biodiversity of cork oak woodlands. By using birds as a study group, chosen for their ability to act as biodiversity indicators (e.g. Hutto 1998, Gregory et al. 2003), the results obtained are also able to shed some light on the potential responses of the biodiversity of cork oak woodlands to climate and land management changes across the Mediterranean basin.

Chapter 3 starts by analyzing the differences between the breeding bird assemblages of cork oak woodlands in northern Africa and southern Iberia. The existence of significant differences in bird assemblages between regions can potentially prevent the generalization of local bird responses observed to either human or environmental factors to both regions. Observed species diversity and abundance patterns were similar between regions and the majority of species recorded were common to both European and North African cork oak woodlands, corroborating studies that have highlighted the remarkable similarity of Mediterranean forest bird assemblages (Blondel 1995). Nonetheless, bird assemblage structure differed significantly between regions in terms of species and guild composition. The presence of a geographical barrier, the Mediterranean Sea, prevented some species of colonizing both regions and allowed other to evolve distinctly, which partly explains the differences observed. The remaining differences in bird assemblages between European and North African cork oak woodlands are explained by an increase in generalist birds and a decrease in forest specialists in northern Africa, which can be explained by a local overexploitation of woodland resources (Bugalho et al. 2009). Overall, these results indicate that the composition of North African cork oak woodland bird assemblages represents a response to regional conditions within the gradient of environmental and habitat conditions found across Mediterranean cork oak woodlands.

This idea is further explored in Chapter 4, which analyses the response of breeding bird assemblages to climatic and habitat gradients throughout Iberian and North African cork oak woodlands. Both climatic and habitat structure were important factors determining the composition of breeding bird assemblages of cork oak woodlands, and were able to explain over one third of the variability found in bird abundance among all sampled areas. Results also indicate that the relevance of habitat variables was higher for farmland and shrubland species, such as the Corn Bunting (*Emberiza calandra*), Spotless Starling (*Sturnus unicolor*) and Woodlark (*Lullula arborea*). The abundance of forest and generalist species such as the Common Nightingale (*Luscinia megarhynchos*), Common Redstart (*Phoenicurus*

phoenicurus) and Eurasian Wren (*Troglodytes troglodytes*) was generally more associated to climatic variables. Nonetheless, the analysis of individual species responses shows that the majority of species decreased their abundance in areas with higher temperatures and seasonality and increased it in areas with more open and heterogeneous ground vegetation structure. The analysis of the spatial distribution of climatic and habitat variables demonstrates that bird communities in northern Africa are of greater conservation concern due to both climatic and management factors (in agreement with the results of Chapter 3).

With these results in mind, Chapter 5 aimed to obtain a better understanding of how local microclimatic conditions along an aridity gradient in the south of the Iberian Peninsula may already be affecting local breeding bird assemblages. The data obtained with this chapter indicates a significant decrease in species diversity and abundance in drier areas. This is a result of local changes in the abundance of forest specialist species, which decreased in drier south facing slopes, and confirms the association between forest bird species and climatic conditions observed in the previous chapter. In such dry conditions, cork oak woodlands have a depleted canopy cover and a reduction in resource availability for forest birds, indicating that the relationship between forest birds and climatic conditions is most likely driven by bottom-up effects across the food-web. Furthermore, the increasing aridity expected during the coming decades is likely to provide a further challenge for the conservation of cork oak woodland bird populations, and maintaining woodlands with suitable habitat structure within adequate local microclimatic conditions may be an essential step in this task.

Still, increasing temperatures may also provide new opportunities for the conservation of bird populations within the Iberian Peninsula. Chapter 6 addressed the role of climate change on the increasing number of overwintering populations of traditionally migratory species in the Iberian Peninsula (Berthold 2001, SEO/BirdLife 2012). Results indicate that the increase in winter temperatures during the last three decades is one of the potential drivers of the observed changes in migratory behaviour. This hypothesis is supported by the fact that winter temperatures in the Iberian Peninsula are generally becoming more similar to the temperatures usually experienced by birds in their African wintering grounds. Even accounting for a decrease in precipitation, the overall winter climatic niche is becoming more similar between regions due to the increase in temperatures. This hypothesis is also supported by the fact that birds are selecting the most similar areas to Africa within the Iberian Peninsula to overwinter. While this change in migratory behaviour has so far been observed regularly in more generalist species like the White Stork (*Ciconia ciconia)*, Common Quail (*Coturnix coturnix*) and Eurasian Hoopoe (*Upupa epops*), it may nonetheless provide new opportunities for the conservation of long-distance migrants, which are among the bird with highest population declines across Europe (Sanderson et al. 2006). Overwintering species in the Iberian Peninsula have a higher overlap between the climatic conditions they experience in the wintering grounds in Africa and the Iberian Peninsula but some migratory species, like the Egyptian Vulture (*Neophron percnopterus*), Eurasian Reed Warbler (*Acrocephalus scirpaceus*), Lesser Kestrel (*Falco naumanni*) and Yellow Wagtail (*Motacilla flava*), already have individuals overwintering in the Iberian Peninsula occasionally (SEO/BirdLife 2012). Consequently, it seems likely that further climate change may drive them to establish wintering populations in Iberia as well. In this scenario, important wintering habitats for birds such as cork oak woodlands (Diaz et al. 1997) will need to be maintained and adequately managed to support the establishment and conservation of these species.

Overall, these findings highlight that if Mediterranean cork oak woodlands and their associated biodiversity are to be maintained, efforts should focus on promoting sustainable land management practices required for biodiversity and ecosystem services (Bugalho et al. 2011a). Current land abandonment and intensification trends (Bugalho et al. 2009) need to be addressed in parallel with promoting the long-term sustainability of more traditional and biodiversity friendly management practices, especially in areas under higher pressure from increasing temperatures and aridity. This should involve reducing the potential effects of management practices, such as grazing, shrub removal and tree pruning (e.g. Camprodon and Brotons 2006, Godinho and Rabaça 2011, Santana et al. 2012, Leal et al. 2013) that can have negative impacts if not properly executed. Furthermore, promoting the habitat mosaic typical of more heterogeneous traditional management practices (Diáz et al. 1997, Vickery and Arlettaz 2012) will also be important to maintain functional diversity. Finally, promoting the presence of small patches of other habitats may provide additional economic income and increase biodiversity levels within cork oak woodlands (Leal et al. 2011). These recommendations could be better implemented in the scope a multi-purpose land use system rather than in more intensive mono-exploitation systems. The former may be more resilient in the long-run to market price fluctuations and impacts from climate change on productivity, as its successful implementation in some local communities indicates (Behrramouni et al. 2007).

7.2. Future research directions

7.2.1. Climate change effects on cork oak woodlands and their biodiversity

This thesis is a contribution to the understanding of how climatic conditions influence natural systems in the Mediterranean Basin, particularly for cork oak woodlands and their biodiversity. However, many issues remain unexplored and further research should be stimulated in order to expand the knowledge required to assess the effects of climate change on this system.

In many areas the subsistence of cork oak woodlands under climate change is likely to require active human intervention (Pereira et al. 2009). This happens because natural regeneration is very low (Acácio et al. 2007), trees are already affected by extreme climatic events (Carnicer et al. 2011, Besson et al. 2014), and in fact woodland decline has started in many areas (e.g. Brasier and Scott 1994, Regato-Pajares et al. 2004, Costa et al. 2011). A better understanding of the role of microclimatic conditions (Caldeira et al. 2014), extreme events, and seed dispersers on seedling recruitment (Pons and Pausas 2007) and establishment are required. The prediction of climatically suitable areas for afforestation efforts (Hidalgo et al. 2008, Vessella and Schirone 2013) may also be important to prioritize and maximize the efficacy of these actions. Ultimately, the future of current cork oak woodlands and the decision to establish new plantations will be associated with their long-term economic sustainability. Therefore, evaluating the role of climate change and particularly of extreme events on cork growth and quality should also be a priority. Finally, it is important to understand which land uses may replace cork oak woodlands in the areas where they are likely to disappear. Holm oak (*Quercus rotundifolia*) is known to be more resistant to drought than the cork oak (Caldeira et al. 2014) and may be a suitable option to maintain a similar land use system. Olive trees (*Olea europaea*) may also be a suitable alternative given that their exploitation is likely to benefit from climate change (Ponti et al. 2014). Further efforts to predict which species and land uses may be economically and climatically suitable for these areas should be stimulated.

In respect to the potential effects of climate change on the biodiversity of cork oak woodlands, these findings may provide general insights, given that birds are generally regarded as good biodiversity indicators (Hutto 1998, Gregory et al. 2003). Still, they fail to cover in detail the possible responses of other groups with highly diverse communities in cork oak woodlands, such as plants and butterflies (Diáz et al. 1997). For example, many butterfly species have changed their distribution and phenology in the Mediterranean Basin as a response to climate change (e.g. Stefanescu et al. 2003, Wilson et al. 2005), in parallel with what has been observed in more northern latitudes (e.g. Parmesan et al. 1999, Roy and Sparks 2000), but the implications of these responses for communities in cork oak woodlands remains underexplored. Similar responses may be expected in other biological groups, such as plants, amphibians and mammals, but information on the effects of climate change for these groups is even scarcer, which makes them a research priority. Particular focus should be given to the unique biological communities of cork oak woodlands in northern Africa, where direct human impacts are also more evident (Marañon et al. 1999, Bugalho et al. 2009). The presence of the Mediterranean Sea and the Sahara desert isolate the rear edge populations of less mobile species in this region, and their future protection may require the designation of specific conservation actions (Hampe and Petit 2005).

7.2.2. Promoting nature-friendly cork oak woodland management practices

Overall information on the potential consequences of different management practices for cork oak woodlands is increasing but is still somewhat scarce for some activities (Marañón et al. 1999, Gil-Tena et al. 2007). For example, grazing pressure on cork oak woodlands has increased markedly in recent decades (Bugalho et al. 2009) which can have important consequences for woodland regeneration and biodiversity levels in this system (Plieninger 2007, Bugalho et al. 2011b). However, science based recommendations regarding the carrying capacity for different livestock types are still lacking. Pruning of cork oak trees is sometimes required for management or sanitary reasons, but this kind of intervention simplifies the canopy structure which can have negative implications for biodiversity (Leal et al. 2013, Regnery et al. 2013). Further research on the minimal adequate canopy structure necessary to sustain the requirements of the different groups that depend on this resource can provide important recommendations to minimize the effects of this practice. Deadwood can be beneficial for biodiversity (Lassauce et al. 2011) and the importance of maintaining standing dead trees in cork oak woodlands should be evaluated (Brasier and Scott 1994), as the common practice is to remove them soon after death for economic and sanitary reasons.

7.3 Final considerations about the future of cork oak woodlands

The above suggestions highlight the importance of acknowledging that cork oak woodlands are a socio-cultural system where human intervention is required to maintain natural values and services (Bugalho et al. 2011a). Therefore, the long term maintenance of cork oak woodlands and their biodiversity will only be possible as the products and services they provide remain valuable to society (Aronson et al. 2009).

Cork production and livestock rearing represent the main sources of revenue nowadays (Berrahmouni et al. 2009). The market value of cork is usually around 2€ per kilo (Coelho and Campos 2009, Cork Information Bureau 2010) in countries where the cork industry is well developed, like Portugal and Spain, but prices have dropped in recent years (Mendes and Graça 2009, Cork Information Bureau 2010). This situation is mostly due to competition from synthetic materials for the production of bottle stoppers (Vallejo et al. 2009) and can result in the replacement of cork oak woodlands by other more profitable land uses (Berrahmouni et al. 2009). In countries where the industry is not as well developed, the revenue generated by cork can be much lower (Campos et al. 2009) and may not be sufficient to guarantee by itself the economic sustainability of this system. Livestock rearing becomes more important than cork production in such countries, particularly in northern Africa, and this has resulted in an increase of overgrazing during the last decades (Bugalho et al.

2009). In Europe, direct support to farmers by means of subsidies has been attempted under the Common Agricultural Policy to counter overexploitation and abandonment trends, but such measures alone have not been enough to revert the situation (Bugalho et al. 2009).

These examples show how changes in the economic value of cork oak woodlands can affect their long-term viability and biological value, but the reverse situation is also true. Undergoing cork oak declines (Brasier and Scott 1994) will result in a reduced production of cork and other timber products as tree density and sanitary conditions decrease. Cork oak trees also provide an important barrier for desertification in more arid areas (Vallejo et al. 2009, Marinelli 2010), thus maintaining soil quality and its potential for different uses. Birds and bats (Şekercioğlu et al. 2004, Boyles et al. 2011) feed on numerous pest species and can act as important agents of biological control. Maintaining diverse and abundant communities of birds, mammals and other groups is essential to guarantee the revenue from hunting and natural recreation activities (Berrahmouni et al. 2009). Therefore, an effective approach to increase the sustainability of cork oak woodlands may be to encourage managers to diversify their income sources by recognizing the diverse range of products (e.g. mushrooms, beekeeping, timber, acorns) and services (e.g. recreation, tourism, hunting) that cork oak woodlands and their biodiversity can provide (Berrahmouni et al. 2009). In the case of cork, increasing consumer awareness of the environmental advantages of cork as a renewable and biodegradable material that is compatible with biodiversity (Leal et al. 2011), promoting product certification, and developing new applications for cork may help maintaining commercial value (Berrahmouni et al. 2009). This kind of multi-purpose approach has been implemented with economic success in some local communities (Behrramouni et al. 2007) and counters the trends of abandonment, intensification and overexploitation (Bugalho et al. 2009, Bugalho et al. 2011a).

In the end, the future of cork oak woodlands requires careful planning and the results obtained during the course of this thesis may hopefully contribute to this process from an ecological point of view. However, the complexity of this system, and the multiple stakeholders involved in management, imply that its future cannot be addressed solely from and ecological perspective. Ultimately, land owners, governments, industries, consumers and conservation scientists need to come together to develop a strategy for the future of cork oaks woodlands that makes them more resilient and capable of supporting both economic activities and natural values, across the western Mediterranean.

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Appendices

Appendix 3.1. *Central point coordinates of the seven cork oak woodlands where bird assemblages were sampled.*

Iberia			North Africa		
Area	Latitude	Longitude	Area	Latitude	Longitude
IB1	36.228ºN	5.604ºW	NA1	35.261ºN	5.412ºW
IB2	36.771ºN	5.284ºW	NA2	35.178ºN	5.345ºW
IB3	36.591ºN	5.383ºW	NA3	35.125ºN	5.283ºW
IB4	36.300ºN	5.438ºW			

Appendix 3.2. *Summary table of the species detected in each area and their abundances in Iberian and North African cork oak woodlands.*

Species		Habitat guild	Distribution
Common name	Scientific name		
Long-tailed Tit	*Aegithalos caudatus*	Forest	Restricted
Barbary Partridge	*Alectoris barbara*	Farmland	Widespread
Red-legged Partridge	*Alectoris rufa*	Farmland	Restricted
Eurasian Stone-curlew	*Burhinus oedicnemus*	Farmland	Widespread
European Goldfinch	*Carduelis carduelis*	Farmland	Widespread
Short-toed Treecreeper	*Certhia brachydactyla*	Forest	Widespread
European Greenfinch	*Chloris chloris*	Generalist	Widespread
Zitting Cisticola	*Cisticola juncidis*	Farmland	Widespread
Common Wood Pigeon	*Columba palumbus*	Generalist	Widespread
Carrion Crow	*Corvus corone*	Forest	Widespread
Common Quail	*Coturnix coturnix*	Farmland	Widespread
Common Cuckoo	*Cuculus canorus*	Generalist	Widespread
Eurasian Blue Tit	*Cyanistes caeruleus*	Forest	Restricted
African Blue Tit	*Cyanistes teneriffae*	Forest	Restricted
Greater Spotted Woodpecker	*Dendrocopus major*	Forest	Widespread
Corn Bunting	*Emberiza calandra*	Farmland	Widespread
Cirl Bunting	*Emberiza cirlus*	Farmland	Widespread
European Robin	*Erithacus rubecula*	Generalist	Widespread
Common Chaffinch	*Fringilla coelebs*	Forest	Widespread
Eurasian Jay	*Garrulus glandarius*	Forest	Widespread
Melodious Warbler	*Hippolais polyglotta*	Shrub	Widespread
Eurasian Wryneck	*Jynx torquilla*	Forest	Widespread
Eurasian Linnet	*Linaria cannabina*	Farmland	Widespread
European Crested Tit	*Lophophanes cristatus*	Forest	Restricted
Woodlark	*Lullula arborea*	Generalist	Widespread
Common Nightingale	*Luscinia megarhynchos*	Forest	Widespread
Spotted Flycatcher	*Muscicapa striata*	Forest	Widespread
Eurasian Golden Oriole	*Oriolus oriolus*	Forest	Widespread
Great Tit	*Parus major*	Forest	Widespread

Appendix 3.2. *cont.*

Species		Habitat guild	Distribution
Common name	Scientific name		
House Sparrow	*Passer domesticus*	Generalist	Widespread
Western Bonelli’s Warbler	*Phylloscopus bonelli*	Forest	Widespread
Iberian Chiffchaff	*Phylloscopus ibericus*	Forest	Widespread
Common Firecrest	*Regulus ignicapilla*	Forest	Widespread
European Stonechat	*Saxicola rubicola*	Farmland	Widespread
European Serin	*Serinus serinus*	Forest	Widespread
Eurasian Nuthatch	*Sitta europaea*	Forest	Widespread
Eurasian Collared Dove	*Streptopelia decaocto*	Generalist	Widespread
Eurasian Turtle Dove	*Streptopelia turtur*	Farmland	Widespread
Spotless Starling	*Sturnus unicolor*	Farmland	Widespread
Eurasian Blackcap	*Sylvia atricapilla*	Forest	Widespread
Subalpine Warbler	*Sylvia cantillans*	Shrub	Widespread
Sardinian Warbler	*Sylvia melanocephala*	Shrub	Widespread
Dartford Warbler	*Sylvia undata*	Shrub	Widespread
Eurasian Wren	*Troglodytes troglodytes*	Forest	Widespread
Common Blackbird	*Turdus merula*	Generalist	Widespread
Mistle Thrush	*Turdus viscivorus*	Generalist	Widespread

Appendix 4.1. *Geographical coordinates of the central point of each sampling area.*

Sampling area	Latitude	Longitude
1	41.50872	-7.07414
2	41.18415	-5.80492
3	41.17614	-5.74195
4	40.25066	-6.21399
5	40.19319	-6.24297
6	40.08948	-6.5715
7	39.622	-7.40766
8	39.50069	-7.14604
9	39.22826	-6.56217
10	39.55685	-5.38128
11	39.33717	-7.59073
12	39.22419	-7.45079
13	39.25958	-8.28124
14	39.01462	-8.13397
15	38.82376	-8.82368
16	38.68892	-8.33482
17	38.58572	-8.09225
18	38.38064	-7.8978
19	38.44052	-8.5779
20	38.34107	-8.42914
21	38.10149	-8.58572
22	37.76855	-8.59344
23	37.71144	-8.3687
24	37.41838	-8.08052
25	37.30638	-8.08284
26	37.24968	-7.86414
27	37.3366	-6.51521
28	37.26132	-6.47627
29	36.77316	-5.2837
30	36.59106	-5.3828
31	36.30048	-5.43845
32	36.22796	-5.6043
33	35.26148	-5.41232
34	35.17759	-5.34517
35	35.1247	-5.2828
36	34.05619	-4.2629
37	34.18166	-6.57416
38	34.14664	-6.66846
39	34.04243	-6.537
40	33.9868	-6.50113

Appendix 4.2. *Summary table of minimum, mean and maximum values registered for the environmental variables analysed.*

Environmental variable	Minimum	Mean	Maximum
Habitat			
Herb cover (% Ground cover)	5	49	99
Herb height (5cm Height classes)	2	4	5
Shrub cover (% Ground cover)	1	46	88
Shrub height (25cm Height classes)	1	4	5
Tree density (No. trees/ha)	19	49	68
Tree cover (% Ground cover)	11	41	68
Heterogeneity (Coef. of variation)	0.7	2.1	3.2
Climate			
Average Temperature (ºC)	11.3	15.9	18.2
Temperature Seasonality (Coef. of var./1000)	4.1	5.2	6.7
Aridity (mm)	0.4	0.6	0.9

Appendix 5.1. *List of bird species recorded in the three sampling areas and their guild classification.*

Species		Habitat specialization
Common name	Scientific name	
Long-tailed Tit	*Aegithalos caudatus*	Forest
Eurasian Skylark	*Alauda arvensis*	Non-forest
Red-legged Partridge	*Alectoris rufa*	Non-forest
European Goldfinch	*Carduelis carduelis*	Non-forest
Short-toed Treecreeper	*Certhia brachydactyla*	Forest
European Greenfinch	*Chloris chloris*	Non-forest
Zitting Cisticola	*Cisticola juncidis*	Non-forest
Common Wood Pigeon	*Columba palumbus*	Non-forest
Common Cuckoo	*Cuculus canorus*	Non-forest
Eurasian Blue Tit	*Cyanistes caeruleus*	Forest
Azure-winged Magpie	*Cyanopica cyanus*	Non-forest
Great Spotted Woodpecker	*Dendrocopus major*	Forest
Lesser Spotted Woodpecker	*Dendrocopus minor*	Forest
Corn Bunting	*Emberiza calandra*	Non-forest
Rock Bunting	*Emberiza cia*	Non-forest
Cirl Bunting	*Emberiza cirlus*	Non-forest
European Robin	*Erithacus rubecula*	Forest
Common Chaffinch	*Fringilla coelebs*	Forest
Eurasian Jay	*Garrulus glandarius*	Forest
Melodious Warbler	*Hippolais polyglotta*	Non-forest
Woodchat Shrike	*Lanius senator*	Non-forest
Common Linnet	*Linaria cannabina*	Non-forest
European Crested Tit	*Lophophanes cristatus*	Forest
Woodlark	*Lullula arborea*	Non-forest
Common Nightingale	*Luscinia megarhynchos*	Forest
Eurasian Golden Oriole	*Oriolus oriolus*	Non-forest
Great Tit	*Parus major*	Forest
Rock Sparrow	*Petronia petronia*	Forest
Common Redstart	*Phoenicurus phoenicurus*	Forest

Appendix 5.1. *cont.*

Species		Habitat specialization
Common name	Scientific name	
Western Bonelli's Warbler	*Phylloscopus bonelli*	Forest
Iberian Chiffchaff	*Phylloscopus ibericus*	Forest
Common Firecrest	*Regulus ignicapillus*	Forest
European Stonechat	*Saxicola rubicola*	Non-forest
European Serin	*Serinus serinus*	Non-forest
Eurasian Nuthatch	*Sitta europaea*	Forest
Eurasian Collared Dove	*Streptopelia decaocto*	Non-forest
Europan Turtle Dove	*Streptopelia turtur*	Non-forest
Spotless Starling	*Sturnus unicolor*	Non-forest
Eurasian Blackcap	*Sylvia atricapilla*	Forest
Subalpine Warbler	*Sylvia cantillans*	Non-forest
Sardinian Warbler	*Sylvia melanocephala*	Non-forest
Dartford Warbler	*Sylvia undata*	Non-forest
Eurasian Wren	*Troglodytes troglodytes*	Forest
Common Blackbird	*Turdus merula*	Non-forest
Mistle Thrush	*Turdus viscivorus*	Non-forest
Eurasian Hoopoe	*Upupa epops*	Non-forest

Appendix 6.1. *Summary of ecological trait data collected for overwintering and migratory species. Traits analysed included winter climatic niche extent (% of available climatic space), African winter distribution extent (10^6 km^2), Insectivorous winter diet (insectivorous or not), wing loading (kg/m^2), mean clutch size and social behaviour (solitary or gregarious).*

Species		Migratory status in Iberian Peninsula	Traits					
Common name	Scientific name		Niche extent	Distribution extent	Insectivorous winter diet	Wing loading	Clutch size	Social behaviour
White Stork	*Ciconia ciconia*	Overwintering	72.1	13.2	Yes	5.0	4	Gregarious
Common Quail	*Coturnix coturnix*	Overwintering	68.9	11.0	No	5.0	10	Solitary
Common House Martin	*Delichon urbicum*	Overwintering	61.0	16.3	Yes	1.8	4	Gregarious
Barn Swallow	*Hirundo rustica*	Overwintering	67.9	14.1	Yes	1.4	4	Gregarious
Black Kite	*Milvus migrans*	Overwintering	73.6	20.4	Yes	2.9	3	Gregarious
Eurasian Hoopoe	*Upupa epops*	Overwintering	72.9	18.9	Yes	1.6	7	Solitary
Common Swift	*Apus apus*	Migratory	52.9	9.6	Yes	2.9	3	Gregarious
Purple Heron	*Ardea purpurea*	Migratory	71.7	18.3	No	3.6	4	Gregarious
Red-rumped Swallow	*Cecropis daurica*	Migratory	67.2	4.2	Yes	1.7	4	Gregarious
European Bee-eater	*Merops apiaster*	Migratory	39.0	2.6	Yes	2.2	6	Gregarious
European Honey Buzzard	*Pernis apivorus*	Migratory	72.7	17.6	Yes	3.3	2	Solitary
European Turtle Dove	*Streptopelia turtur*	Migratory	32.4	4.5	No	3.5	2	Solitary

Appendix 6.2. *List and description of the climatic variables used to characterize winter climatic niches.*

Variable	Description
Mean Temperature	Mean temperature for the months between November and February
Minimum Temperature	Lowest minimum temperature for the months between November and February
Maximum Temperature	Highest maximum temperature for the months between November and February
Temperature Seasonality	Coefficient of variation of mean weekly temperatures for the months between November and February
Total Precipitation	Total precipitation occurred during the months between November and February
Minimum Precipitation	Precipitation of the driest month between November and February
Maximum Precipitation	Precipitation of the wettest month between November and February
Precipitation Seasonality	Coefficient of variation of weekly precipitation estimates for the months between November and February

Appendix 6.3. *Axis loadings of climate variables used to define Iberian and African niche space.*

Species trait	Axis 1	Axis 2
Average winter temperature	0.06	0.60
Maximum winter temperature	-0.20	0.52
Minimum winter temperature	0.30	0.47
Winter temperature seasonality	-0.43	-0.10
Total winter precipitation	0.48	-0.11
Maximum winter precipitation	0.48	-0.06
Minimum winter precipitation	0.45	-0.18
Winter precipitation seasonality	0.15	0.31
Variance explained	49.9%	32.0%

Appendix 6.4. *Axis loadings of species traits used to characterize overwintering and migratory species.*

Species trait	Axis 1	Axis 2
Winter niche extent	0.68	0.01
Winter distribution extent	0.62	0.13
Insectivorous diet	0.33	-0.55
Social behaviour	-0.08	-0.66
Wing loading	0.06	0.49
Clutch size	0.23	0.09
Variance explained	31.8%	29.7%