

**COMPARISON OF
AUTECOLOGICAL AND
SYNECOLOGICAL APPROACHES
IN MODELLING PRESENT AND
FUTURE CLIMATE DISTRIBUTION
OF RARE AND ENDEMIC ALPINE
PLANT SPECIES IN LEFKA ORI
(SAMARIA) NATIONAL PARK-
BIOSPHERE RESERVE, CRETE**

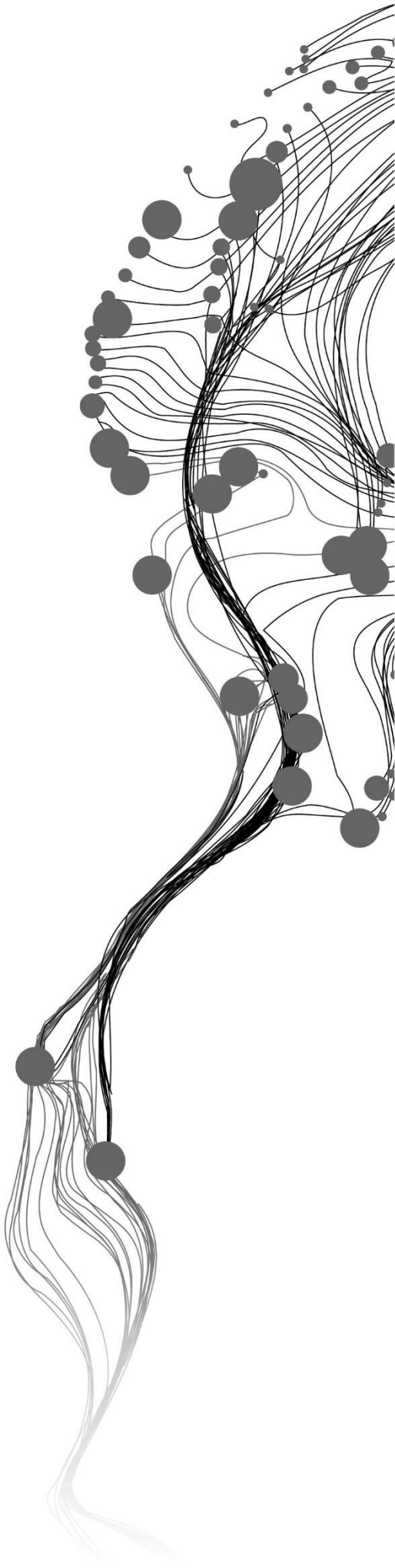
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ABSTRACT

Anthropogenic warming is anticipated to impact and change species communities globally. The Mediterranean, a hotspot of endemics, is projected by many global and regional estimates of future climate scenarios to have less precipitation and rising temperatures, thus more vulnerable to climate change. As a result, the impacts of climate change are anticipated to be immense on Mediterranean islands and mountains. Plant species within this alpine region will be vulnerable to climate change, and a potential loss of suitable habitats is expected in the future.

Several studies have extensively used species distribution models (SDM) to predict and model the impacts of climate change on species. These SDMs are commonly used to model individual species and make predictions of plant distribution in relation to the environment in an autecological way. SDMs are not built to account for species associations and communities of species in a single model. Nevertheless, species are associated, and some form of biotic interactions affects species co-occurrences within plant communities and the spatial distribution of plants. Hence, Joint Species Distribution models (JSDM), which is an improvement of the common SDMs, are structured to capture biotic interactions between species in relation to the environment and predict the distribution of plants in a Synecological way. JSDMs offers the advantage of modelling species communities in a single model and depicts species co-occurrences.

The alpine plant species on Lefka Ori Mountains in the Island of Crete, Greece, is the focus of this study. It was aimed to compare JSDMs with SDMs in predictions of alpine plant species distribution and determine whether a predicted distribution range shift resulting from climate change is different in JSDMs compared to SDMs. The alpine species dataset used in this study comprises forty-two rare and endemics, and environmental variables include altitude, curvature, distance to road, geology, snow, aspect. The Hierarchical Modelling of Species Community (HMSC) is used to model the 42 plant species in a single model (JSDM). Furthermore, five individual species were selected through a residual correlation matrix derived in JSDM and other parameters. They were modelled on their own with the same HMSC as SDMs and compared with JSDMs. Predictions from both models are extrapolated using climate proxies of snow and altitude to model the climate change scenario by a century to derive potential species range shifts and suitable habitats shifts. JSDM and SDMs were compared through prediction accuracies, regression coefficient matrix, variance proportions, range shift, and suitable habitats derived from climate change scenarios.

This study found that JSDM models the potential biotic interaction between species, resulting in identified co-occurrences within the species community. The study's statistical analysis revealed a significant difference in the mean AUC values of JSDMs and SDMs. In addition, the accuracies of co-occurring species are lower in JSDMs than SDMs, while the non-co-occurring species had lower accuracies in JSDMs. The important variables contributing to plant distribution are geology, snow, curvature, road and altitude. The proportion of variances are slightly higher in SDMs than JSDMs. The results from the future climate scenario indicate suitable areas net lost, and these losses are more pronounced in JSDM than SDM for all five species investigated. Lastly, the results of this study indicate that the potential future changes to species suitable habitat due to climate change are species-specific and not dependent on the modelling approach.

Keywords: Autecology, Climate change, HMSC, Synecology, SDM, JSDM, Range Shift

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LIST OF ACRONYMS AND GLOSSARY

AUC	Area Under Curve
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature
HMSC	Hierarchical Modelling of Species Communities
MCMC	Markov chain Monte Carlo
JSDM	Joint Species Distribution Model
RMSE	Root Mean Square Error
SDM	Species Distribution Model

Glossary

Terminology	Definition	Source
Autecology	The study of species ecology in relation to the environment.	(Evert et al., 2010a; Pianka, 2008a)
Synecology	The study of species interaction (biotic factors) within a community of species and in relation to the environment (abiotic).	(Evert et al., 2010b; Pianka, 2008b)

1. INTRODUCTION

1.1. Background

Species loss is estimated to be increasing in recent years due to climate change, fragmentation and destruction of habitats, overexploitation of natural resources, invasive species, and environmental degradation (IUCN, 2010; WWF, 2020). The International Union for Conservation of Nature (IUCN) describes species as a collection of living organisms that reproduces offspring, sharing a genetic heritage and commonly separated by geographic and genetic barriers (Anderson, 1994; IUCN, 2003). IUCN (2003) describes endemic species as natives to a region of geographic isolation and can be endemic to a continent, country or island; these species can be rare and threatened (Anderson, 1994; Foggi et al., 2015). Species are rare because of geographic isolation to a specific region or habitat with low numbers due to geographic range restriction. Rare species are not per se threatened or endangered, but the likelihood of such risk is high (Enquist et al., 2019; IUCN, 2003).

Species thrive under favourable environmental and bioclimatic conditions in a location known as a niche, which determines the occurrence, abundance, and distribution of species (Wiens et al., 2009). Similarly, species ecological niches are locations suitable for survival, often known globally and derived through different species distribution models (Franklin, 2012; Vieira et al., 2018). These ecological niches are a part of the biological diversity across continents, and the changing climate also impacts such regions.

The perceived impacts of climate change are the disruption of biological diversity and loss of plants ecological niches globally, and assumptions are human-induced factors are the significant drivers of climate change (Díaz et al., 2019; Rinawati et al., 2013). The Intergovernmental Panel on Climate Change (IPCC) 2014 report highlights human-induced anthropogenic impacts such as greenhouse gas emissions, fossil fuel combustion, urbanisation, and population growth as contributing to climate change and thus changing ecosystems (IPCC, 2014). Furthermore, climate change affects species distribution, community interactions, phenology, habitats and ecological niches across continents (Díaz et al., 2019). Presently, plant species cannot shift geographical ranges quick enough to cope with the current and projected climate change (IPCC, 2014).

1.2. Autecology and Synecology

Autecology and Synecology are two approaches in ecology for studying species coexistence patterns (Hagen, 2010). Autecology is the adaptation of plants to environmental and bioclimatic factors, while synecology is the communal plant growth which is essential in understanding the spatial distribution of plant species (Hagen, 2010; Nyktas, 2012). Synecology is a different approach in studying the interactions between species (biotic) such as competition, facilitation, mutualism, predation, neutralism; and the non-living environment (abiotic) such as rainfall or temperature within communities in defined biomes (Evert et al., 2010b; Hagen, 2010; Pringle, 2000). These biotic interactions affect resource availability within communities, which can be competition for resources (negative interactions) or species facilitating the existence of other species (positive interactions) (Boulangeat et al., 2012). Furthermore, studies on plant species involve two approaches. Firstly, the quantification of the relationship between species and their

environment without biotic interactions (Habitat modelling) using species distribution models. Secondly, the biotic interactions of species using co-occurrence patterns to identify ecological processes (Community Ecology) using Joint species distribution models (Pollock et al., 2014; Soberon and Peterson, 2005).

1.3. Rare and endemic plant species

Plant species can be common in some areas and rare within a locality or other geographic ranges; rarity results from a comparison between abundance and occurrences of species within a specific geographic range, usually derived at a global scale (Enquist et al., 2019; Stebbins, 1942). Also, rare species can arise due to competition of resources within ecological niches, depletion of genetic variability over time, reduction of species geographic distribution and occurrences due to climate and geological processes (Stebbins, 1942). Certain plant species are endemic to a region or geographic location and usually defined by the geographic scale of the location where found; it can be a local, island or continental endemics (Anderson, 1994; Işık, 2011; National Research Council, 1992). Mountainous regions and islands are biodiversity hotspots hosting rare and endemic plant species across the world. However, these mountains act as barriers, and islands' long isolation limits species migration and promotes endemism (Körner, 1999; Menteli et al., 2019). As a result, these ecosystems are endangered, making mountain ranges within islands "dual" endangered (Thuiller et al., 2005).

1.4. Plant Species Distribution

Studies of plant species distribution have been through observations, point maps, ranges maps for small areas. Large scale atlases and maps are available for continental or country levels, usually of low resolution, which does not necessarily depict what is on the ground (Franklin, 2010; Soberon and Peterson, 2005). Modelling has opened new approaches for studying plant species distribution. These models, also known as species distribution models (SDMs), ecological or environmental niche models (ENM), are used to investigate how abiotic and biotic factors influence the distribution patterns of plant species in ecological niches (Franklin, 2010).

1.4.1. Species Distribution Models

Species distribution models (SDMs) are empirical models that make predictions throughout a geographic range based on a theoretical and statistical link between the presence of a species and predictor variables. (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000). SDMs use occurrence data, abundance data, and environmental data to determine species distribution over space and time (Franklin, 2010; Naimi et al., 2011; Sofaer et al., 2019). The extrapolation of SDMs predictions to new locations to generate predictive maps gives insight into current habitat and enables the monitoring of potential habitat changes in the future (Franklin, 2010).

SDMs has extensively been used in plant species modelling. For instance, Williams et al. (2009) fitted four SDMS to compare their performances in predicting the occurrences of rare plant species. Consequently, evaluating the models with the Area Under Curve (AUC) values, the random forests (RF) and maximum entropy (ME) models outperformed the generalised linear models (GLM), artificial neural networks (ANN) in predicting species occurrences. Furthermore, the predictions from these models led to the

discovery of new species occurrences in areas of high occurrence probability from a field validation. Therefore, SDM will be explored to identify the occurrence probability of plant species in this study.

SDMs have also been used in analysing the potential impact of climate change on the alpine treeline using an ensemble model to study *Betula utilis* in the Himalayas and a projection made from the current to future scenarios. The assessment of habitat suitability and range contraction changes indicates that the prediction into the future scenario depicts a moderate shift of the climatic niche from the current range. Furthermore, the findings suggest that currently unsuitable regions are becoming suitable, whereas currently suitable locations are becoming unsuitable (Hamid et al., 2019). In this study, models will be explored to ascertain changes in species distribution by making predictions of the future climatic scenario.

Additionally, to evaluate if biotic interactions matter in modelling alpine plant distribution at the landscape scale. Meineri et al. (2012) identified that most SDMs ignore biotic interactions, therefore predicting the distribution of *Viola biflora* and *Veronica alpine*, lowland species that co-occur with these species are re-predicted on the landscape. Modelling with biotic and abiotic factors enhanced the precision of both species, although the prediction accuracy was reduced due to the collinearity of the predictor variables. The study concludes that biotic interactions enhance predictions, that neglecting these interactions leads to biased predictions of species distribution, and that adding biotic and abiotic variables strengthens SDM predictions.

Similarly, Godsoe et al. (2017) study on the effects of biotic interactions on the distribution patterns of species. Used a Lotka-Volterra model to simulate two virtual species competing and dispersing across an environmental gradient. Two GLM models are fitted with abundance data, one disregarding competition and the other including it. The inferences made are that abiotic factors are strong predictors of species even when competition influences the occurrence. The study further identifies the difficulty in making inferences from SDM whether the focal species are rare or common when there is competition due to the intertwined relationship of biotic interactions and the abiotic environment.

Also, Meier et al. (2010), using a GLM, examines how the explained variance of biotic and abiotic factors affects the distribution of eleven common tree species in Switzerland. The model performances improved with the inclusion of other species as predictor variables. Also, the variances indicate improved contributions of abiotic and biotic factors by adding species that act as facilitators as predictor variables. The effects of biotic predictors were observed in species with a large dispersion distance, frequent occurrences, and minimal abiotic stress. The author recognises that with the addition of biotic components, predicting the impacts of global warming on a small geographic scale will be more reliable than SDM predictions with just the abiotic factors.

Some challenges of SDM are related to the concept of species niches, which are determined either by the environmental requirement of species or species-specific responses to the environment. Several SDMs focus is on species environmental requirements to model the distribution of species and not the interactions between species. Also, SDMs assumptions are that the species are at equilibrium with the environment; therefore, the inclusion of the migratory process of species that often affect species distribution patterns is absent in these models (Guisan and Thuiller, 2005). Similarly, modelling patterns of species composition in relation to the environment and detecting the relationship between environmental variables are lacking in SDMs (Austin, 2002). Furthermore, the competition for resources among species is not fully integrated into SDMs; most SDMs include the competitors as predictor variables in the models, as indicated in Meier et al. (2010) studies. Also, Guisan and Thuiller (2005) view that SDMs are inadequate in modelling individual species in functional groups and communities to understudy the ecological

processes leading to species distribution patterns. SDMs assumes species are statistically independent and only related via environmental variables (Ovaskainen and Abrego, 2020).

1.4.2. Joint Species Distribution Models

The Joint Species Distribution Models (JSDMs) are extensions to SDMs. JSDMs models species shared responses to environmental variables, combines species co-occurrences patterns, and enables the prediction of the distribution of multiple species concurrently in a single model (Pollock et al., 2014) while accounting for biotic interactions within species communities (Wilkinson et al., 2019). Similarly, JSDMs assume that species within a functional group have similar responses to variations in the environment. Also, JSDM enables identifying closely related species and if these species have similar responses to the same environmental variables compared to unrelated species (Ovaskainen and Abrego, 2020). JSDM is commonly used in community ecology to estimate species associations after accounting for the effects of environmental variables, often using huge data. JSDM models species dependency independently of environmental and climatic predictors, how closely related species have similar responses to predictors, and quantifies variations in species niches or occurrences attributed to other factors (Ovaskainen and Abrego, 2020). Similarly, the predictive performances of species distribution models increase by including species association, which are often implemented in JSDMs (Tikhonov et al., 2017).

Several studies have utilised JSDMs in modelling plant species distribution. For example, Pollock et al. (2014) modelled the eucalyptus community and frogs in Grampians national park in Australia concurrently using a Probit regression model with latent variables fitted to a Markov Chain Monte Carlo (MCMC) Bayesian framework. The same study views environmental and residual correlations as indicators of co-occurrences resulting from shared environmental responses or ecological processes (biotic interactions). Also, JSDM considers that species distribution patterns are affected by the relationship between species; hence this overcomes the drawbacks of SDMs that only consider species environmental responses.

Similarly, Clark et al. (2014) research on forest climate responses in the eastern United States identifies that modelling climate change impact on species distribution is mainly with individual SDM. These results are combined to make inferences of collective species responses to climate change. The authors also identify, disregarding species responses to similar climatic variables, competition between species, which limits species abundance and growth as potential shortcomings of SDMs. Therefore, not including these relationships does not depict the forest's joint responses to the climate, which affects the trees collectively. Consequently, a JSDM is fitted with abundance, presence, and absence data to capture species joint responses and perhaps more accurate predictions. The prediction from this study into future climate scenarios identifies the geographic locations where the impacts of potential climate change will be severe on species communities. Thus, assisting in evaluating the threats of climate change to biodiversity.

Warton et al. (2015) fitted a Multivariate Generalized Linear Mixed Model (GLMM) and Latent Variable Model (LVM) to explore the correlation patterns of alpine plant species in south-eastern France and predictions of tree species richness across Europe to account for missing predictors. Similarly, Magory Cohen and Dor, (2019) studies of *Acridotheres tristis* in Israel used JSDM to detect co-occurrences patterns of species after accounting for environmental predictors. The study identified species with positive correlation respond to similar environmental variables while negatively correlated species rarely occur together and respond to different environmental variables.

Zurell et al. (2020b) also used JSDMs and stacked SDMs to test species assemblage predictions' accuracy. The models are fitted with presence-absence data of Switzerland's 56 common forest birds and 63 rare

tree species. Estimations from both models were to predict species-specific occurrence probabilities using 70% as training and 30% as test data. The comparison of model performances after cross-validation identifies that SDMs performances are higher than JSDMs. The authors also identify that JSDMs provide insights into biotic interactions within communities; however, species co-occurrences did not lead to a better community prediction than the SDM predictions. Therefore, in this study, a comparison will be made of model performances in SDMs and JSDMs.

JSDM has been used virtually everywhere to determine dependencies between tree species and identify species clusters in Mississippi (Taylor-Rodríguez et al., 2017). In estimating the influences of biotic and abiotic factors in species ranges of lagomorph species in Europe (Leach et al., 2016). To evaluate whether species association is a by environmental variables or biotic interactions in the Swiss Alps and Finland (Mod et al., 2020), and in separating biotic interactions, environmental filters, and dispersal limitation as drivers of alpine species co-occurrence across elevation gradients in the Swiss Alps (D'Amen et al., 2018). Also, the reproductive interactions between plant communities in Norway (Opedal and Hegland, 2020). Although JSDMs have been used to model plant species in Australia, United States, and Europe, they have not been used extensively in modelling Mediterranean alpine plants.

The Mediterranean alpine areas are different from other alpine regions and mountains in the world. The plant species found within the Mediterranean region are from Africa, Asia and Europe, and these plant communities are found nowhere else in the world (Médail, 2017; Médail and Quézel, 1997). Similarly, Médail (2017) states that the Mediterranean basin comprising many islands is a biodiversity hotspot, with complex biogeography, environmental and climatic heterogeneity, and diverse ecological processes that have created a unique ecosystem. The uniqueness of the Mediterranean basin makes it a suitable “experimental laboratory” (Médail, 2017); to study how plant communities and species have evolved over time in a synecological way. Also, Médail (2017) identifies that the Mediterranean islands host plant communities found nowhere else globally, with over 12,500 endemic plant species and endemism ranging from 8% to 17%; however, mountain endemics are approximately 40% of the plant species. Furthermore, the plants on these mountains often experience extreme conditions such as sudden freezing and intense summer droughts (Pescador et al., 2016). These endemics face threats from anthropogenic activities, overexploitation, grazing and tourism (Médail and Quézel, 1997).

Plant species communities on the Mediterranean islands respond collectively to these anticipated threats to their habitat. Hence, JSDM will be used to model these plant communities and identify co-occurrence patterns, species environmental responses and interspecific relationships between these alpine species. Although JSDMs produce predictions of communities of species responses as opposed to individual species and identify possible biotic interactions between species (Wilkinson et al., 2019), individual species can likewise be fitted into JSDMs. The predictive performances of these models will be compared to ascertain if there are similarities and differences in predictions of species distribution individually and within communities.

1.4.3. Plant Species and Climate

Multiple studies have shown that the general expectation is that plants will shift to higher altitudes due to anthropogenic warming. For example, Parmesan and Yohe (2003) study on a globally coherent fingerprint of climate change impacts across natural systems using 1,700 species. Found that species experience a range shift on an average by “6.1 kilometres per decade poleward or 6.1 meters per decade upwards”. Additionally, Kelly and Goulден (2008) studies on the rapid shifts in plant distribution with recent climate change used plant cover data from 1977 to 2007 across the elevation gradient of Santa Rosa Mountains in

Southern California. The study found changes in precipitation patterns, a decrease in snowfall, and an increase in temperature within thirty years. Also, the dominant plant species had an upward range shift of 65m, attributed to changes in the regional climate.

Similarly, Grabherr et al. (1994) research on the effect of climate on mountain plants in the Alps found that the mean annual temperature from 1900 to 1992 has increased by 0.7°C. Furthermore, the study theoretically assumes an “average decrease of 0.5°C per 100m of increasing altitude”, which is anticipated to “shift altitudinal vegetation belts by 8-10 m per decade”. Furthermore, the authors conclude that an increase in temperature, no matter how small, causes alpine plants to migrate to higher altitudes, signifying a threat to these plants by global warming. Finally, findings in these pieces of literature anticipate a wide range of plant responses to anthropogenic warming, ranging from shifts of 6.1 to 10 m per decade. However, all suggesting upwards shifts rather than downward shifts.

The Mediterranean, a hotspot of endemics, is projected by many global and regional estimates of future climate scenarios to have less precipitation and rising temperatures, thus vulnerable to climate change (Giorgi and Lionello, 2008). As a result, the impacts of climate change is anticipated to be immense on these islands and mountain summits (Kougioumoutzis et al., 2020; Thuiller et al., 2008). Furthermore, the island endemics are found within mountain ranges (Kougioumoutzis et al., 2020), which are barriers to species dispersal and are often referred to as “climatic traps”, so these species are constrained to shift upwards to suitable climatic gradients (Lenoir and Svenning, 2015). Similarly, Weiskopf et al. (2020) views that species responses to range shifts are immediate or long term, with long term responses arising from evolutionary changes over time.

Although SDMs have been used extensively to analyse the potential effects of climate change on species (Jeschke and Strayer, 2008; Morin and Thuiller, 2009; Niskanen et al., 2017; Yu et al., 2019), and assumes a constant relationship between species and the environment, nevertheless there are also interactions between these species within communities. Several of these SDMs are not built to model species interactions and communities of species in a single model. Also, Anderson (2013) highlights the deficiency of “abiotic interactions, genetic heterogeneity, integration of biotic variables and quantification of uncertainties in estimations of future impacts of climate change on species distribution” in niche models and identifies it is a challenge to be addressed. Subsequently, this study will use a JSMD, an improvement of the common SDMs, to examine the effect of future climate projections with abiotic and abiotic factors within species communities. Also, to examine how plant species distribution on a Mediterranean mountain will be affected by the anticipated climate change.

1.5. The study area

Crete is the fifth-largest island in the Mediterranean basin and the largest Greek island. The island has a unique Mediterranean and North African climate with three mountain massifs above 2000 m (Lefka Ori, Idi Oros and Dikti Oros) (Menteli et al., 2019). Lefka Ori or White Mountain is an 'island-within-an-island', a known hotspot of endemics in Europe (Bergmeier, 2002; Nyktas, 2012) and the focus of this study is indicated in Figure1-1. The mountain is approximately located on latitude 35° 17' 30"N & longitude 24° 1' 52"E in southwest Crete. Lefka Ori highest summit is 2,453m and is covered by snow until spring, with the sun reflecting off the limestone in the summer, hence the acronym 'White Mountain'. The Lefka Ori is within the Samaria Biosphere Reserve, which was made a National Park by the Greek Government in 1962 and recognised by UNESCO in 1981 (Spanos et al., 2008; UNESCO, 2014). The

study area is in the alpine zone above the natural treeline of 1700m above sea level and approximately 32.66 km² (3266.17 ha) in the park centre (Nyktas, 2012).

Lefka Ori Mountain has deep gorges, steep slopes with an enormous cave system; it is of tertiary sedimentary rocks of karst topography and hosts a diversity of plant species due to its geographical isolation (Bergmeier, 2002; Campaign et al., 2005; Spanos et al., 2008). The mean annual rainfall at sea level is 600mm, which increases with altitude; annual precipitation (rain and snow) in the highest peaks exceeds 2500 mm. The mean annual temperature above 2000m is below 0°C during winter (Nyktas, 2012). The rainfall and snowfall on the White Mountain sip through the porous rocks to streams, rivers, and ground aquifer, thus providing water on the island (Nyktas, 2012). Lefka Ori provides socioeconomic, political, and religious services to Cretans; through livestock grazing, beekeeping, tourism and harvesting of aromatic medicinal plants (Bergmeier, 2002; Spanos et al., 2008).

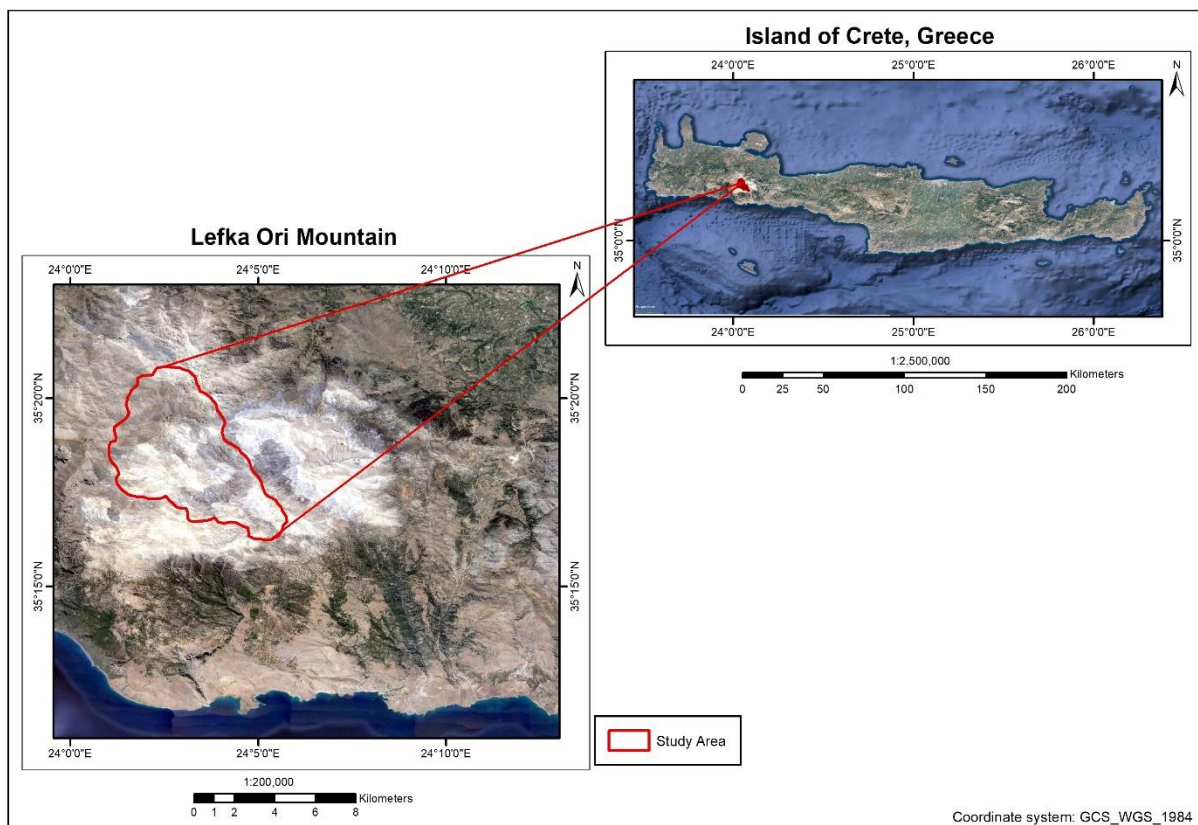


Figure 1-1: Satellite view showing the location of Lefka Ori, Crete, Greece, and study area (red polygon).Map source: (“Google Earth,” n.d.)

1.5.1. Diversity and Distribution of Plant Species in Crete

Numerous research on endemic and rare plant species is ongoing in Crete. Menteli et al. (2019) researched the current trade patterns in the endemic plants in Crete, listed 16 of the 223 Cretan endemics as priority targets for conservation. Trigas et al. (2013) study on elevation patterns of vascular plant species richness and endemics in Crete identified a decrease in species richness as elevation gradient increases, but an increase in Cretan endemics due to ecological isolation. Similarly, Kazakis et al. (2007) view that a potential range shift due to climate change would affect Cretan endemics. All the above studies do not encompass the distribution of plant species over space and time. Studies by Bergmeier (2002) on the vegetation of the high mountains of Crete identify rock and soil type, snowmelt, topography as enabling species clusters. Also, Goedecke and Bergmeier (2018) study on *Zelkova abelivea* endemic tree species in Crete identifies altitude and temperature as the main variables affecting its distribution on the island. The study on patterns and drivers of species richness in Crete used topographic and climate data to determine the hotspots and spatial patterns of neo-endemics and paleo-endemic richness and turnovers on the island (Lazarina et al., 2019).

Vogiatzakis and Griffiths (2001) researched the relationship between plant communities in Crete and the environment. The latter derived five distinctive vegetation communities with Two Way Indicator Species Analysis (TWINSPAN), and the ordination results identified specific environmental predictors to determine endemic plant distribution across Lefka Ori. Similarly, Vogiatzakis et al. (2003) studies on environmental factors and vegetation composition in Lefka Ori proposes a further analysis geared at mapping species association to the environment using geographical information systems (GIS), which was implemented in 2006 (Vogiatzakis and Griffiths, 2006). Also, Nyktas (2012) research in Lefka Ori predicted the distribution of 59 plant species with a GLM model, an SDM that focuses on the autecology of species distribution and proposes an alternative framework for modelling plant species distribution.

Theories on species coexistence patterns within communities identify various filters and assembly processes to influence species occurrences at regional or local scales (Zobel, 1997). Similarly, the identified filters (factors) influencing species communities are ecological processes such as dispersal abilities, species abiotic environment relationship, and biotic interactions of species (Ovaskainen et al., 2017). These ecological processes differ across localities; however, the identified environmental factors (abiotic filters) influencing plant species distribution (rare and endemics) in Lefka Ori include climate variability, topography, water availability, substrate and anthropogenic influences (Bergmeier, 2002; Nyktas, 2012). Likewise, these plant distributions are affected by biotic interactions that may negatively lead to the competition of resources, thereby affecting the abiotic environment or positively when species act as facilitators, thereby enabling the coexistence of species in extreme conditions (Boulangat et al., 2012).

Considering that the studies mentioned above in Lefka Ori rely on species relationship to environmental variables (Autecology) while ignoring species interspecific interactions within communities (Synecology). Additionally, this biodiversity hotspot has not been investigated using multiple species model to identify co-occurrence patterns and the biotic interactions within plant communities. Therefore, this present study will compare autecology and synecological approaches in modelling single and multiple plant species in SDMS and JSDMs. At the same time, examine the importance of species interspecific interactions in Lefka Ori as indicated in Figure 1-2.

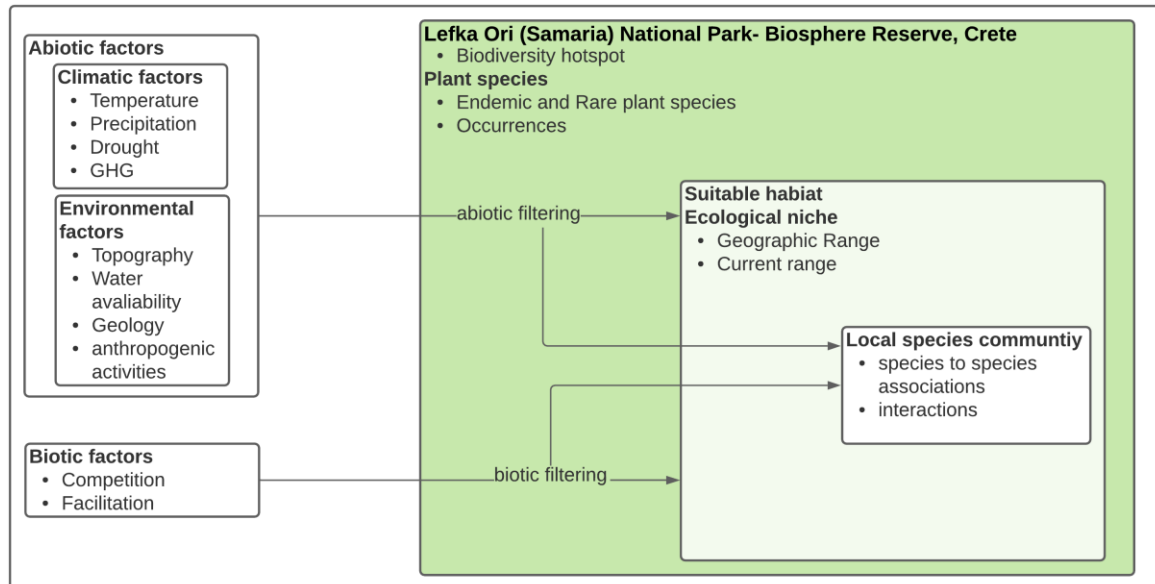


Figure 1-2: The Conceptual framework depicting the importance of abiotic and biotic factors in defining ecological niche and species communities.

1.6. Problem Statement

Anthropogenic climate change is reported to lead to a shift in species distribution. Islands and alpine regions have been reported to be among the most vulnerable environments to these changes. Following the impact of climate change on species, species communities are also expected to be altered with potential biodiversity loss. SDMs are potent tools used extensively to model current and future species distribution in an autecological way. In recent years, research is focusing on the missing link of species interactions, and JSDM is becoming a popular technique to account for species interaction in a synecological way. JSDMs have predicted interactions of a few alpine plant species on European mountains. However, the Mediterranean environment and climate are distinct from other regions globally, plant species within this unique region are yet to be studied using JSDMs. Therefore, this research aims to explore the differences between autecological and synecological approaches in this unique endemic alpine vegetation by accounting for the differences in model predictions when considering species interactions and predicting the influence of future climate change projection on species distribution.

1.7. General Objective

The general objective of this research is to compare JSDMs with SDMs in predictions of alpine plant species distribution. Furthermore, to determine whether a predicted distribution shift resulting from climate change is different in JSDMs compared to SDMs in the alpine region of Lefka Ori (Samaria) National Park- Biosphere Reserve, Crete.

Sub-objectives and Research questions

Objective 1. To account for species interaction in modelling the distribution of alpine plant species.

Research question 1. In modelling species that are dependent on other species, do they perform better in JSMD than SDMs?

Hypothesis 1. JSMD show higher accuracy as measured by AUC and RMSE than SDMs.

Objective 2. To compare autecological and synecological approaches in modelling the distribution of plant species.

Research question 2. Which variables are important for modelling plant species, and is there a difference in JSMD and SDMs?

Hypothesis 2. The variables importance of the same species in JSMD and SDM will (or will not) change between JSMD and SDM.

Objective 3. To project the impact of future climate scenarios on modelled species distribution and compare the outcomes of JSMDs and SDMs.

Research question 3. What is the effect of species community interactions in future climate projections?

Hypothesis 3. The projected range shift extent of suitable area for species distribution will differ between JSMD and SDM.

2. MATERIAL AND METHOD

2.1. Methodology

The methods used for this study is in three steps (Figure 2-1). The first step is fitting a JSJM and SDM with environmental variables influencing the spatial distribution of vascular alpine plant species. The second step is comparing predictions in SDMs (single species) and JSJM (multiple species). Finally, the last step compares species distribution projections under a future climate scenario in SDMs and JSJM.

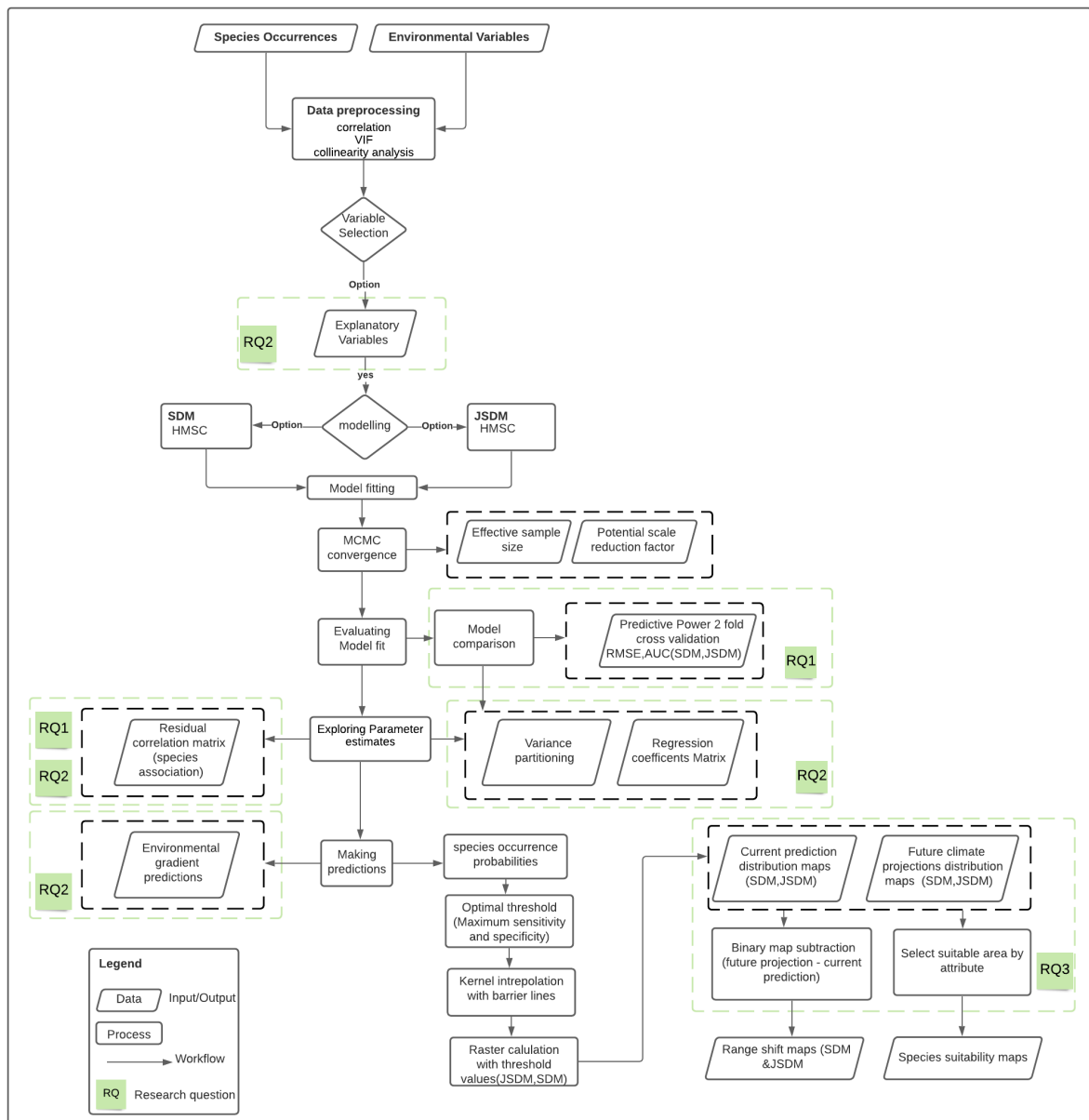


Figure 2-1: Methodology showing the general steps adopted for this study

The data provided for this research is from Nyktas (2012) PhD study on Dynamic Feedbacks Between Landform, Landscape, Processes and Vegetation Patterns. A modelling framework to predict the distribution of plant species in Lefka Ori, Crete, Greece.

2.2. Species Dataset

The species occurrences data are samples from 155 plots within Lefka Ori, with a dimension of 10m x 10m following a random stratified sampling strategy by Nyktas (2012). 80 plots were from previous studies by Vogiatzakis between summers of 1997-1998, and Nyktas between summers of 2010-2012 sampled 75 plots are merged for this study. In these plots, 42 vascular alpine plant species had a prevalence > 0.1 (10%) at plot level and are provided for this study as listed in Table 2-1. All data are explored in ArcGIS before model fitting to verify they are correctly georeferenced and within Lefka Ori, the study area.

Table 2-1: Selected 42 vascular alpine plant species on Lefka Ori by Nyktas (2012)

Plant Species	Abbreviation	Plots observed (N=155)	Status (Bergmeier, 2002; Nyktas, 2012; Vogiatzakis et al., 2003)
<i>Acantholimon androsaceum</i>	Acanan	120	Greek Endemic
<i>Alyssum fragillimum</i>	Alyfra	56	Lefka Ori Endemic
<i>Alyssum sphacioticum</i>	Alysph	17	Greek Endemic
<i>Anchusa cespitosa</i>	Anchces	82	Lefka Ori Rare\ Endemic
<i>Asperula idaea</i>	Aspeid	94	Greek Endemic
<i>Astragalus angustifolius subsp. angustifolius</i>	Astran	58	Greek Endemic
<i>Aubrieta deltoidea</i>	Aubdel	24	Greek Endemic
<i>Berberis cretica</i>	Berber	93	Greek Endemic
<i>Bufoia stricta ssp.stricta</i>	Bufost	38	Greek Endemic
<i>Carlina corymbosa subsp. Curetum</i>	Carlcu	34	East Mediterranean
<i>Centaurea idaea</i>	Centid	46	Greek Endemic
<i>Cicer incisum</i>	Cicein	56	Greek Endemic
<i>Cirsium morinifolium</i>	Cirsmo	73	Greek Endemic
<i>Crepis sibthorpiana</i>	Crepsi	54	Greek Endemic
<i>Cuscuta atrans Feinbrun</i>	Cuscat	16	Greek Endemic
<i>Daphne oleoides</i>	Daphol	25	Mediterranean
<i>Dianthus sphacioticus</i>	Diansp	19	Greek Endemic
<i>Draba cretica</i>	Drabcre	24	Greek Endemic
<i>Euphorbia berniariifolia</i>	Eupher	76	Greek Endemic

<i>Festuca sipylea</i>	Festsip	37	East Mediterranean
<i>Hypochaeris tenuiflora</i>	Hypoten	38	Greek Endemic
<i>Lactuca alpestris</i>	Lactal	61	Greek Endemic
<i>Lomelosia sphaeotica</i>	Lomesph	26	Greek Endemic
<i>Minuartia verna subsp. attica</i>	Minuver	42	Greek Endemic
<i>Muscari spreitzenhoferi</i>	Musspr	26	Greek Endemic
<i>Paracaryum lithospermifolium</i>	Parlith	45	East Mediterranean
<i>Paronychia macrosepala</i>	Parmac	29	East Mediterranean
<i>Peucedanum</i>	Peucal	36	Greek Endemic
<i>Pimpinella tragiun subsp. depressa</i>	Pimptr	73	Greek Endemic
<i>Prunus prostrata</i>	Prunpro	62	Greek Endemic
<i>Rhamnus saxatilis ssp. Prunifolia</i>	Rhamsa	61	Greek Endemic
<i>Satureja alpina</i>	Satualp	26	Greek Endemic
<i>Satureja spinosa</i>	Satusp	80	East Mediterranean
<i>Scutellaria hirta</i>	Scuthi	56	Greek Endemic
<i>Sideritis syriaca</i>	Sidersyr	38	Greek Endemic
<i>Silene variegata</i>	Sileva	58	Greek Endemic
<i>Taraxacum bithynicum</i>	Tarabith	26	East Mediterranean
<i>Telephium imperati</i>	Teleim	33	Greek Endemic
<i>Valantia aprica</i>	Valanapr	37	Balkan
<i>Veronica arvensis</i>	Verarv	29	European-SW Asian
<i>Veronica thymifolia</i>	Verothym	32	Greek Endemic
<i>Viola fragrans Sieber</i>	Violfr	53	Greek Endemic

2.3. Environmental Variables

The first step in modelling species distribution is to study species habitat requirements to determine the environmental variables contributing to their presence (Franklin, 2010). Similarly, a model's accuracy depends on good variable selection, adequately depicting species occurrences and predictions within a defined habitat (Cruse et al., 2012). The selection of environmental variables is crucial in species modelling because it restricts the distribution of species and communities (Guisan and Zimmermann, 2000). Several studies identify altitude, slope angle, aspect, rock type, temperature and landform as predictor variables for plant community distribution on Lefka Ori (Bergmeier, 2002; Goedecke and Bergmeier, 2018; Trigas et al., 2013; Vogiatzakis et al., 2003; Vogiatzakis and Griffiths, 2001). Previous modelling of the same dataset using GLMs by Nyktas (2012) identified the main predictor variables of snow, topographic variables

(altitude, aspect, slope, curvature), landforms, and geology. Further analysis of the environmental variables in ArcGIS 10.7. The variable data and maps of 30 x 30 m resolution are used for this study.

Table 2-2: Environmental layers generated by Nyktas (2012) except for Elevation that the Hellenic Cadastral acquired

Variables	Data Type	Unit
Elevation	Continuous	meters
Slope	Continuous	degree
Curvature	Continuous	degree
Aspect	Continuous	degree
Eastness (sin of aspect)	Aspect on the west-east axis	No unit, a real number between -1(west) and 1(east)
Northness (cos of aspect)	Aspect on the south-north axis	No unit, a real number between -1(south) and 1(north)
Geology	Geology groups (categorical)	-
Snow cover persistence (patterns)	Snow groups (Categorical)	-
Distance to Road	Continuous	meters

Elevation, Slope and Curvature

Elevation gradient affects plant species communities through changes in temperature, rainfall patterns and wind exposure on mountains (Huston, 1995). Studies by Treml and Chuman (2015) on the ecotonal dynamics of an altitudinal forest identify altitude and curvature as influencing timberline upward shift on concave and convex slopes. Predictions of plant species in Lefka Ori identify elevation as an essential variable for the community distribution of plants (Fernandez-Calzado et al., 2013; Vogiatzakis and Griffiths, 2006). Bergmeier (2002) further states that endemism increases with altitude on the mountain, confirmed by Trigas et al. (2013). The first derivative of elevation is slope and the second is curvature (Nyktas, 2012); these are additional land surface data that define species habitat.

Mass movement on slopes causes disturbances to vegetation and affects the spatial distribution of species. The differences in plant communities can be attributed to species adapting to instability on mountain slopes (Nagy and Grabherr, 2009). The fixed slopes of Lefka Ori host 20-36% of endemics, while the steep mobile scree slopes found below ridges and mountain peaks host 42-56% of endemics (Bergmeier, 2002). These slopes affect transportation and deposition downslope and are dispersal barriers to these alpine plants (Nyktas, 2012). Considering the variables mentioned above are topographic, Nyktas (2012) utilized several ESRI ArcGIS analyses to derive hydrologically corrected digital elevation model (DEM) from topographic maps of the study area. Further analysis on the DEM with curvature tool from 3D analyst extension in ArcGIS provided indications of convex, concave and flat surfaces.

Snow

Snow is a significant component of the alpine climate, and it affects the distribution of plant species in alpine regions (Inouye, 2020; Körner, 1999). Snowfall is the typical precipitation above 1700m in Lefka Ori (Bergmeier, 2002). The snow covers protect plants from harsh weather conditions and control the length of growing seasons, which influences the growth of dwarf shrubs and cushion plants communities (Vogiatzakis et al., 2003). Also, the melting snow water percolates through the porous rocks on the mountain, leaving little for plant growth (Bergmeier, 2002; Vogiatzakis and Griffiths, 2006). Similarly, Nyktas (2012) notes that the plants have a microclimate affected by snow duration and identify 27 plant species as significantly been affected by snow cover within the study area. Moreover, snow affects patterns of alpine plant distribution while protecting the plants from freezing (Nyktas, 2012), and changes in snow cover patterns on mountains may indicate the changing climate.

Aspect (Eastness and Northness)

Aspect is derived from topographic data. It offers insight into species distribution patterns crucial to plant species distribution; these are often accurate maps derivable for an area (Guisan et al., 1998; Guisan and Zimmermann, 2000). Aspect and altitude determine the amount of precipitation on Lefka Ori, and the windward facing northwestern slopes are more humid than southeastern slopes (Bergmeier, 2002).

The Aspect data is further explored using the Spatial analyst tool in ArcGIS 10.7.1 to derive eastness and northness variables. Extract by point function links plant species data to aspect values generated in degrees from (0 -360) and exported as database files to MsExcel. The data generated is in degrees from 0-360, representing a uniform north direction. A transformation from degree to radians is needed to get the other cardinal directions by Zar (1999) in Katsaounis (2012). These values are converted to geographic radians in MsExcel by applying the formula below.

$$\text{radians} = \pi * \text{degrees} / 180$$

A trigonometric function is applied. A cosine function is applied to the radians in deriving the northness, while the eastness is derived by applying a sine function to the radians.

$$\text{northness} = \cos(\text{aspect})$$

$$\text{eastness} = \sin(\text{aspect})$$

The data generated for northness is between 1 (due north) and -1 (due south), with zero being neither north nor south in aspect and eastness is +1 directly east and -1 directly west (Vogiatzakis et al., 2003; Wallace and Gass, 2008).

Geology

Previous studies have identified that the underlying geological composition on the mountain is a significant driver of the plant species distribution (Bergmeier, 2002; Vogiatzakis and Griffiths, 2001). Also, Nyktas (2012) updated the geological map of the study area from a scale of 1:50,000 to 1:5000 and classified lithological units associated with plant species distribution on Lefka Ori (Table 2-3). Plattenkalk series consisting of crystalline limestone and is the dominant geological unit on the mountain; the Tripali series is also composed of crystalline limestone, which was separated due to tectonic activities (Bergmeier, 2002; Krespi, 2018). Dolomites and partly dolomitic limestone rocks are a part of the karst system on the mountain. At the same time, the depositional areas and debris flow result from frost weathering and severe karst erosion on the mountains (Bergmeier, 2002). However, platy limestone, recrystalline limestones and dolomites are the three main lithological units above the tree line of Lefka Ori (Nyktas, 2012). Therefore, this study has adopted a further grouping of the geological units into plattenkalk, recrystalline, dolomites and partly dolomitized rocks.

Table 2-3: Recent geological unit classification in the study area by Nyktas (2012) and newly adopted units

Geological Units	New Geological units
Plattenkalk	Plattenkalk
Tripali series	
Recrystalline	Recrystalline
Dolomites	Dolomites
Depositional areas	
Partly dolomitized	Partly dolomitized
Debris flows	

Landform

Limestone is the main lithological unit on Lefka Ori, giving rise to a karstic landscape composed of caves, gorges, springs, plateau and aquifers. The mountain is affected by frost weathering and erosion, with no surface streams, but with an underground aquifer intensely recharged by rain and snow-melt water, which feeds springs and rivers (Bergmeier, 2002; Nyktas, 2012).

Road

Roads provide access to remote areas and increase human activities within a locality (Trombulak and Frissell, 2000). Road networks cause anthropogenic disturbances to plant distribution, alters plant communities composition and ecosystem services. Also, these road networks constitute direct or indirect threats to ecological habitats (Marcantonio et al., 2013). Ecological habitats are altered by roads through; fragmentation, barriers to species distribution, pollution, introducing alien and exotic species detrimental to the native species within a locality (Forman and Alexander, 1998; Trombulak and Frissell, 2000).

Habitat fragmentation caused by road is a threat to Mediterranean forest diversity (Marcantonio et al., 2013). For example, there is intense harvesting and trading of endemic plants in Crete, and road offers access to these remote plant locations; for instance, *Sideritis syriaca*, an aromatic tea that is heavily harvested, is found in summit areas having most presence locations far away from the road (Menteli et al., 2019). Furthermore, Katsaounis, (2012) study on the habitat use of endemic and domestic goats on Lefka Ori found domestic goats are near roads, thus a high grazing pressure on roadside plants. Roads create natural islands, and proximity to roads exposes organisms to edge effects, where biotic and abiotic changes are prominent along habitat edges (Marcantonio et al., 2013). Subsequently, data on the road is derived by calculating the Euclidean distance to the road, extracting multi-value to point and mask analysis using ArcGIS. An overlay of species locations on the road layer is performed to derive values for model input. The road layer is a new data added to this study.

2.4. Data Preprocessing

2.4.1. Environmental Variable Exploration

Uncertainty may arise from data collated for species modelling, leading to inaccuracies in estimating species-environment relationships (Naimi et al., 2011). Therefore, considering the above-mentioned environmental variables in Section 2.3 serves as model inputs, the variables are explored using R 4.0.4 software through boxplots, correlation analysis and Variance Inflation Factor (VIF) test to identify environmental variables that may lead to multicollinearity (Dormann et al., 2012).

Outlier detection

Extreme observations, occurring as outliers, can be detected through boxplots of variables (Kutner et al., 2005). Therefore, a boxplot of the environmental variables was explored to inspect the data and detect data points not within the normal distribution called outliers see Appendix 1. The Interquartile range (IQR) enables the identification of outliers, which is the distance between the first quartile and third quartile. A common rule of thumb states that a data point is an outlier when located more than $1.5 * IQR$ lower than the first quartile or higher than the third quartile (Vinutha et al., 2018).

Correlation and Collinearity analysis

Pearson correlation coefficient measures the strength and direction of the linear relationship between two variables, ranging from +1 to -1 (Kutner et al., 2005; Taylor, 1990; Yule, 1938). Correlation depicts how a change in one variable affects another variable. The correlogram function in R is used to analyze the pairwise correlation between environmental variables. Correlation identifies pairs of variables that are correlated which may cause multicollinearity in the data. Multicollinearity leads to statistical biases, excluding important variables, model uncertainty and unreliable inferences (Graham, 2003).

Therefore, to avoid the effects of multicollinearity, a Variance Inflation Factors (VIF) test is performed to estimate collinearities among the variable (Kutner et al., 2005). The VIF identifies the correlation among variables, and the values vary because the inflation factor is due to the partial relationship between variables (Marquardt, 1970). To remove correlated variables, a rule of thumb states the VIF should not be larger than 10; when the values are greater than 10, it often indicates multicollinearity, affecting model estimates (Kutner et al., 2005; Marquardt, 1970).

2.5. Joint Species Distribution Modelling

JSDM are used to predict inferences of multiple species distribution concurrently in a single model. Therefore, in this thesis, a JSDM is fitted with all species occurrence data to predict species environmental responses, species association patterns and species interspecific responses to each predictor variable (Abrego et al., 2017; Wilkinson et al., 2019). Similarly, JSDMs quantify these co-occurrence patterns as graphical plots, correlation matrices, regression coefficients and ordination plots. The JSDM fitted for this thesis is the Hierarchical Modelling of Species Communities (HMSC) 3.0 R package statistical framework (Ovaskainen and Abrego, 2020; Tikhonov et al., 2020b) see Figure 2-2, which utilizes multivariate data from species communities to make predictions and inferences (Warton et al., 2015). The advantages of HMSC are that it gives estimations of species shared responses to predictor variables and quantifies species variations after accounting for the influence of environmental variables through residuals (Opedal and Hegland, 2020).

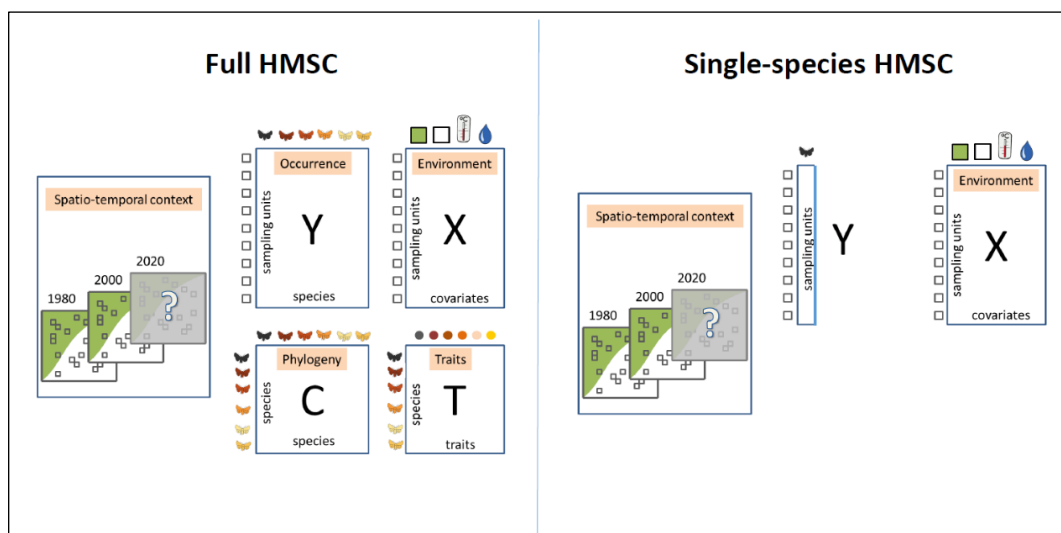


Figure 2-2: Multi-species HMSC and single-species HMSC data used for modelling. Source: Ovaskainen et al., 2017

2.5.1. Hierarchical Modelling of Species Communities (HMSC) framework

HMSC is a *multivariate hierarchical generalized linear mixed model fitted with Bayesian inference*; the novelty of HMSC arises from the combination of different data types to make inferences about interactions within species communities (Ovaskainen and Abrego, 2020,p.40). The inferences are based on the likelihood of observation over several parameters. HMSC models single species and multiple species distributions. The HMSC modelling framework incorporates community data (species occurrences or abundance) (Y matrix), environmental data (X matrix), and optional data such as traits and phylogenetic relationships to make inferences at the species and community level (Ovaskainen et al., 2017; Tikhonov et al., 2020b). The abiotic factors (environmental, climatic) are modelled at the species level to measure how each variable influences species occurrence. These factors are integrated through a hierarchical structure to determine how species shared responses are affected by the influences of factors such as species traits (T matrix) or species phylogenetics (C matrix) on species-environmental responses, when such data are available in the model. These associations can be determined at different spatial and temporal scales, as indicated in Figure 2-2 (Tikhonov et al., 2020b).

2.5.2. HMSC structure

The HMSC structure consists of fixed effects (inferences on species niches) and random effects (estimates of species association). The fixed effect part models species' relationship to the environment (abiotic factors), denoted as β (beta) matrix, which is the species niche. The species responses to specific environmental variables are filtered by traits and phylogenetic signal captured as ρ . The random effect part models how the biotic filtering of species interactions determines occurrences and co-occurrences, denoted by the Ω (omega) matrix. The species-to-species association matrix. The Ω matrix captures species occurrences after species environmental response have been determined, and it is described as the residual co-occurrences as indicated in Figure 2-3 (Ovaskainen et al., 2017; Ovaskainen and Abrego, 2020).

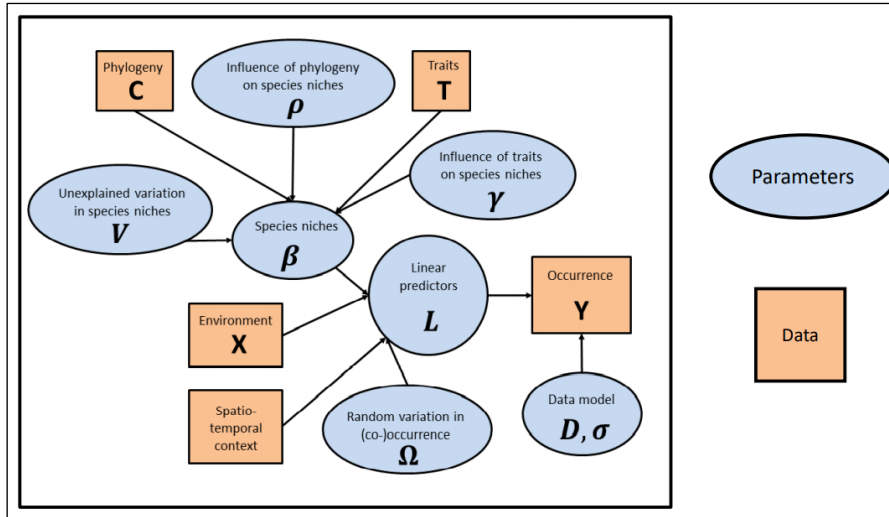


Figure 2-3: The HMSC Structure depicting the Links between fixed effect and random effects parts of the model.

Source: HMSC | Statistical Ecology | University of Helsinki, 2020; Ovaskainen and Abrego (2020, p.41)

The HMSC statistical framework incorporates the fixed and random effects of community interactions represented by Equations 1 and 2.

The linear equation of HMSC model with fixed effects depicts sampling unit n index is i , the species index is j , where nc is the number of covariates and the index is k , x_{ik} is a measured covariate $k=1$, in sampling unit i , β_{kj} is the regression coefficient of linear responses of species j to specific environmental covariate (Ovaskainen and Abrego, 2020; Tikhonov et al., 2017) as represented in Equation 1.

$$L_{ij}^F = \sum_{k=1}^{nc} x_{ik} \beta_{kj}$$

Equation 1

The random effect model utilizes latent variables. The number of latent factors in nf indexed by h , λ_{hj} is species responses to environmental covariates, η_{ih} is the latent factor loading and represents species responses to unaccounted environmental covariates (Ovaskainen and Abrego, 2020). The linear equation of the HMSC model with random effects is Equation 2.

$$L_{ij}^R = \sum_{h=1}^{nf} \eta_{ih} \lambda_{hj}$$

Equation 2

2.5.3. HMSC Workflow

The HMSC analysis is implemented through five steps: (1) Setting up the model structure and fitting the model, (2) Examining MCMC convergence, (3) Evaluating model fit, (4) Exploring parameter estimates, and (5) Making predictions (Tikhonov et al., 2020b).

Comparing predictions from the autecological approach (single species SDMs) and synecological approach (multiple species JSDMs) of plant species distribution with the HMSC is run in two batches. The first batch is fitting the HMSC model with the 42 plant species, which is the JSDM, and ten replicates are derived from the models. Subsequently, the second batch is fitting the HMSC model with selected candidate species from the JSDM residual correlation matrix, which are the SDMs, and ten replicates derived for comparison. These replicates are essential because Araújo and Guisan (2006) view that models produce different results when fitted with the same predictor and response variables. Likewise, this is the case where model replicates produce slightly different estimates of model fit parameters. Therefore, the model results are presented in two sections. Firstly, the results of the residual correlation matrix of the JSDM model fitted with the 42 plant species is presented to select candidate species. Secondly, a comparison is made of selected species in the JSDM, of which those species are modelled individually in SDMs, all with ten replicates. Therefore, in this study, **JSDMs refer to all species modelled in a single model, while SDMs refer to individual species models.**

In using presence-absence data to discriminate occurrence probabilities, HMSC uses Area Under Curve (AUC)(Pearce and Ferrier, 2000) and Root Mean Square Error (RMSE) values (Ovaskainen and Abrego, 2020). These mentioned parameters are used in comparing JSDMs and SDMs. Therefore, the prediction values (AUC, RMSE) after two-fold cross-validation will be compared to identify which model produces higher accuracies. Similarly, the variance proportions are examined to identify important variables contributing to the distribution of these plant species to identify if differences will emerge in JSDMs and SDMs. Also, a comparison will be made of JSDMs and SDMs current predictions, future climate projections to know the extent of suitable areas from both models. Finally, the potential range shift output will be examined to determine differences in species distribution projections in JSDMs and SDMs.

Step 1: Setting model structure and fitting the model

Setting up the model structure entails defining the purpose of the model, which is comparing JSDMs and SDMs in modelling plant species distribution and understanding the ecological processes within the study area. Therefore, selecting suitable predictor variables are crucial to achieving set objectives (Tikhonov et al., 2020b). In this study, the JSDM is fitted with 42 plant species occurrences (presences-absences) from 155 plots as input to the **Y** matrix of HMSC. While the SDMs are fitted with single species occurrences from 155 plots as input to the **Y** matrix. The environmental variables identified as affecting the plant species in Lefka Ori are in the **X** matrix. These are variables obtained from correlation analysis, VIF test, and previous studies in the study area by Bergmeier (2002), Nyktas (2012), Vogiatzakis et al. (2003). The variables of the **X** matrix are curvature, snow, distance to road, altitude, slope, geology, northness, eastness. The categorical variables of snow and geology made the model computationally Intensive, which takes a minimum of five days to complete a model run. In this study, the landform is excluded from the model to reduce the model computational intensity, and other topographic features give insights into the landform.

Similarly, the study design incorporates how the data is collated or designed, enabling the inclusion of random effects or processes in the model. Ovaskainen and Abrego (2020) view that random effects account for species associations and influence the data's dependency structure while averting wrong inferences. Also, the same study identifies that plot level random effects enables the identification of co-occurring species, which are often than expected by random in the same plots. In considering sample plots as random effects, it is assumed that species within these plots are naturally distributed and are considered as factors in the model because interest is in the total amount of variations caused by these factors

(Ovaskainen and Abrego, 2020). Therefore, the 155 plots sampled in two different time frames by Vogiatzakis and Nyktas, depicted as operators in the data set, are included as the random effect in the model. These are assumed as latent variables in the model that approximates the residual correlation matrix in this study.

The HMSC modelling framework is fitted with a Markov Chain Monte Carlo function (MCMC). The Markov chain function generates the random samples from a sampling distribution, and the Monte Carlo process generates a statistical summary (Hamra et al., 2013). MCMC draws samples from a target distribution to make inferences based on the convergence of the distribution of interest; continuous and categorical variables are utilized. Therefore, the HMSC model having a Bayesian inference based on the likelihood of occurrences in the data uses the `sampleMcmc` function to get posterior samples of the data (Ovaskainen and Abrego, 2020). The length of chains, number of samples per chain, thinning, length of transient or burn-in is determined through several model iterations. Ovaskainen and Abrego (2020) view that long Markov chain iterations generate samples representing the actual values of the posterior distribution. Also, transients or burn-in are set because the initial samples at the beginning of the chain do not depict the posterior distribution. Likewise, many samples are needed to get the posterior means, and a 95% credible interval is needed to analyse model results. The study by Ovaskainen and Abrego, 2020; Tikhonov et al., 2020b on Finnish birds found that 1000 samples for each Markov chain run are effective in deriving the posterior distribution.

Similarly, studies using the HMSC framework for plant species distribution sampled the posterior distribution satisfactorily using two chain replicates (Bystrova et al., 2021; Opedal and Hegland, 2020). Also, to derive independent samples from the Markov chains, the thinning intervals reduce the correlation between samples and increase the model computational time. Ovaskainen and Abrego (2020) views that when running models, the thinning should be set to the lowest value of 1 and the MCMC convergence examined until the chains have effectively converged; if the chains do not converge, the thinning should be increased. Similarly, they found that when chains do not converge, it leads to a biased posterior distribution. Subsequently, the JSMD is fitted with 155 sampling units, 42 species, 16 covariates (continuous environmental variables, each class of the categorical environmental variables) and 2 random levels, with a posterior MCMC sampling having 2 chains each with 1000 samples, thin 10 and transient 500 with ten replicates. Similarly, the SDM is fitted with the same parameters as the JSMD but with single species.

Step 2: Examining MCMC convergence

The MCMC convergence plots depict estimates of the posterior distribution of samples in the MCMC chain. (Ovaskainen and Abrego, 2020; Tikhonov et al., 2020b). Two parameters used to examine the MCMC convergence are the effective sample size (ESS) and the potential scale reduction factor (PSRF) (Ovaskainen and Abrego, 2020). The ESS is the number of independent samples needed to estimate the posterior distribution. It examines the autocorrelation structure within the MCMC chains and indicates if the chains have been run satisfactorily (Drummond et al., 2006; Lanfear et al., 2016). Also, the ESS values should be close to the actual sample size. If this is less than the actual sample size, the mixture of the chains is not satisfactory, thereby not depicting the posterior distribution (Harrington et al., 2020). The actual sample size adopted for this study is 2000 and 1000 per chain (Ovaskainen and Abrego, 2020).

Similarly, Gelman-Rubin Diagnostic criterion or PSRF compares within and between chain variation and requires a minimum of two chains for an effective diagnostic to make inferences, hence the selection of

two chains for this study (Brooks and Gelman, 1998; Gelman and Rubin, 1992). Also, Harrington et al. (2020) views that the PSRF is used to compare the ratio of variance within and among chains from the model parameters, a variance of 1.0 indicates similar variations within and between chains and above 1.0 indicates the variance among chains exceeds the variance within chains and thus different spatial parameters are being utilized. Therefore, ESS and PSRF parameters will be examined in JSDBMs and SDMs to determine the convergence of the MCMC chains. These parameters are evaluated through the coda-object function in HMSC (Ovaskainen and Abrego, 2020). See Appendix 1.

Step 3: Evaluating Model fit

Step 3 consist of evaluating how well the model fits the reality on the field. Ovaskainen and Abrego (2020) identify three methods of model evaluation. First, model fit can be measured through accuracy, discrimination power, calibration, or precision. Secondly, model fit can be evaluated for single species (SDMs) or species community (JSDBM). Thirdly, through analysing the explanatory or predictive performances of the model.

Selected parameters for evaluating model fit are the RMSE, a measure of accuracy estimating the proximity between predicted and actual data values. Also, the AUC, a measure of discrimination and an independent threshold metric for presence-absences models, is used to determine how well occurrence probabilities are discriminated at sampling units. Species with an AUC value of 0.5 imply a random discrimination, and 1 indicates perfect discrimination (Pearce and Ferrier, 2000; Wilkinson et al., 2021). These measures are returned separately for each species in JSDBMs and SDMs, and an overall assessment of model fit is derived through the means of the ten replicates. Subsequently, RMSE and AUC values derived in JSDBMs and SDMs of candidate species are compared to identify which model produces higher accuracy and determine if species co-occurrences influence model performances. Also, a Two-way ANOVA and Tukey's Honest Significant Difference (HSD) test is conducted to test if the mean differences are statistically significant at a 95% confidence level ($\alpha = 0.05$). The Two-way ANOVA is used to check how the means of the independent variable change according to two dependent variables, with the effects of the interaction indicating if there are changes based on the relationship between the independent variable (AUC) and dependent variables (species and model types)(Bevans, 2021). Tuckey HSD test compares multiple means and controls for experiment-wise error rate to reduce the chances of increasing the false positives in the test (Allen, 2017; Frost, 2019).

The predictive power of a model through validation (predictions using independent test data) is assumed preferable to explanatory powers through verification (fitting the model with training data) in examining model performances (Araújo and Guisan, 2006). Independent data are recommended to evaluate model predictions, but if training and test data are from the same dataset, a data partitioning or splitting resampling technique is recommended (Guisan and Zimmermann, 2000; Randin et al., 2006). Therefore, a partition function is used for two-fold cross-validation. The model is refitted to a subset of data and predictions made from data not included in the model fitting. Also, the partition function ensures that the posterior distribution derived from the model is based on the cross-validated dataset (Ovaskainen and Abrego, 2020). The two-fold cross-validation approach is adopted for this study. Subsequently, each replicate of the JSDBMs and SDM is fitted using a two-fold cross-validation method. The data is split in two for model fitting and predictions to evaluate the predictive performance of the models. The AUC and RMSE values from the two-fold cross-validation data are analysed to determine the predictive performance in JSDBMs and SDMs and comparison made.

Step 4: Exploring parameter estimates

Step 4 is exploring parameter estimates of which inferences are derived for several ecological processes. Such inferences include variance proportions, responses of species to environmental variables (abiotic), species-to-species association (biotic interactions) and the dependency of species niches on association with environment variables (Ovaskainen and Abrego, 2020; Tikhonov et al., 2020b). This study will examine variance partitions, regression coefficients, and residual correlation matrix in JSDMs and SDMs.

Firstly, variance partitioning is examined to compare the multiple predictors in a model and identify the contribution of each predictor variable to plant species distribution (Araújo and Guisan, 2006). Therefore the total variance in the model is determined with the `computeVariancePartitioning` function in the HMSC, which generates partitions explaining the contributions of fixed and random effects to each species distribution (Ovaskainen and Abrego, 2020; Tikhonov et al., 2020b). The variance proportions of predictor variables are examined in JSDMs and SDMs to ascertain if community interactions influence predictors' contributions to species distribution and identify important variables contributing to the distribution of these plant species.

Secondly, the species regression coefficients matrix (β matrix) explains species responses to environmental variables. It is represented with a heat map of species association to environmental variables, determined by the `plotBeta` function. The regression matrix is examined to identify environmental variables influencing the variations between species. These variations are depicted through the strength and direction of species responses to environmental variables, which are accounted for with statistical positive and negative responses to the environmental variables (Ovaskainen and Abrego, 2020). Prior to the regression plot, a credible interval is set to determine the posterior probabilities, which indicates the range of values within which the actual values belong (Ovaskainen and Abrego, 2020). Several model estimates are derived using the 95% credible interval threshold depicting the values are within 95% of the actual value, and it is implemented for this study (Opedal and Hegland, 2020; Ovaskainen and Abrego, 2020; Pollock et al., 2014; Tikhonov et al., 2020b; Wilkinson et al., 2019). Therefore, the regression coefficient matrix of candidate species in JSDMs and SDMs is compared to identify if the variable importance of the same species differs in modelling approaches.

Thirdly, the residual correlation matrix (Ω matrix) estimates species-to-species associations which may arise due to biotic interactions or unmeasured predictors, but the type of interactions are determined through field observations (Bystrova et al., 2021; Ovaskainen and Abrego, 2020). Also, Dormann et al. (2018) view that further experiments and field observation are essential to verify the model output to relate residual co-occurrences to species interactions. JSDMs assumes a constant association between species after accounting for environmental variables defining their specific niche (Tikhonov et al., 2017; Warton et al., 2015). Similarly, Dormann et al. (2018) view that factors not controlled by the model influences species associations. In HMSC models, the `omegaCor` function is used to reveal co-occurrence patterns. These co-occurrence patterns depict positive, negative, and neutral associations between species (Ovaskainen and Abrego, 2020). The result of the residual correlation matrix enhanced the selection of candidate species for model comparison. The following criteria are applied to select candidate species for comparison in SDMs and JSDMs.

- Species with a threshold of 95% credible interval of species association in the residual correlation matrix
- A further selection of species that do and do not occur with more than 50% occurrences within the study area

- Species identified to be climate-dependent or positively associated with snow and altitude in this study and other studies by Nyktas (2012); Vogiatzakis and Griffiths (2001).
- Protected species with high conservation status and neutral association with other species in the residual correlation matrix from this study and studies by Nyktas (2012)
- Finally, species with low association with climatic variables of snow and altitude in the regression coefficient matrix, variance proportions in this study and studies by Nyktas (2012)

Step 5: Making predictions

Step 5 in the HMSC workflow involves using the fitted model in making predictions to examine species community responses and dependency on changes in environmental variations and scenarios of climate change impacts on species. Predictions are made over environmental and spatial gradients in the HMSC framework in JSDM and SDMs (Ovaskainen and Abrego, 2020). Therefore, these prediction methods are adopted for this study and explained in the subsequent paragraphs.

The spatial prediction in the HMSC model is made over point locations (latitude & longitude grid), and these predictions are extrapolated using a grid that covers the entire study area. Therefore, the `prepareGradient` function in HMSC; is used to convert new environmental and spatial data into formats to be used as input to the `predict` function (Ovaskainen and Abrego, 2020) and extrapolations are made using the fitted model. The `predict` function creates new study designs and random effects needed to model a posterior predictive distribution. Subsequently, I generated new grid points over Lefka Ori using the `createFishnet` tool in ArcGIS by creating rectangular polygon cells with centroids. Also, Li et al. (2016) view the fishnet tool as commonly used in creating grid cells in recent versions of ArcGIS software and used it to create a mesh having a cell size of 0.2*0.2 square meters. Therefore, in this study, the template of the fishnet is the polygon shapefile of Lefka Ori, the dimensions of the fishnet cells are set at 100*100, and the `create label points` is selected to derive centroids of each cell. Using the points (latitude & longitude) generated by the fishnet, an overlay is made over each environmental variable layer. The `extract value to point` tool in ArcGIS is used to extract the attributes for each new location. The attributes of these new locations are exported as database files and converted to comma delimited files, and used as input for spatial predictions and projections in the HMSC.

Finally, in making spatial predictions, the summaries of the posterior predictive distribution defined by the mean value of each species are denoted by the `EpredY`. Furthermore, using the `prepareGradient` function, the posterior distribution of current predictions are derived as point values of occurrence probabilities for each candidate species in JSDMs and SDMs. Subsequently, I imported the occurrence probabilities values into ArcGIS to make spatial interpolation with the point data values in JSDMs and SDMs. Also, to create predictions over a continuous surface of the study area, I used the `Kernel Interpolation with Barriers` tool. The `Kernel Interpolation` function interpolates discrete point data to a continuous surface (Shi et al., 2019). The occurrence probability maps of species derived in JSDMs and SDMs are created through the `Kernel Interpolation` tool.

Liu et al. (2005) found that producing presence-absence predictions is the end product of species distribution models and is needed to estimate species range shift and analyse climate change impacts on species distribution. Therefore, the results of species occurrence probabilities in models need a specific threshold to depict presence-absences (1 or 0) to enable comparative analysis of model predictions. Several approaches are used in determining thresholds, such as 0.5 commonly used in ecology, 95% credible interval, kappa statistics, sensitivity, and specificity (Cantor et al., 1999; Liu et al., 2005).

Therefore, to derive binary probability maps, the optimal thresholds function of the PresenceAbsence package in R is used to derive several threshold dependent performance measures. The Maximum sensitivity and specificity threshold identified as minimizing the error rates by Liu et al. (2013) in Yu et al. (2019) is selected as the cut-off threshold for producing the binary maps (suitable and unsuitable areas). Subsequently, I used the raster calculator function in ArcGIS and the threshold values of each species derived in JSDBM and SDMs in creating the suitability maps of current predictions and future projections.

Environmental variables define species niches, but the occurrences of species may differ across environmental gradients, especially when these variables are correlated (Ovaskainen and Abrego, 2020). Therefore, species predictions are modelled over environmental gradients using the construct gradient function in HMSC. The model gives an option to use the environmental variables as focal and non-focal variables. Subsequently, using a generalised linear model, the focal variable is modelled as a function of the non-focal variable. These species occurrence probabilities are made over continuous and categorical variables with the construct gradient function. Therefore, in this study, species predictions over the environmental variables in JSDBM and SDMs are explored to examine the occurrence probabilities of species.

2.6. Future climate projection scenario

Guisan and Thuiller (2005) found that global parameters of climate change scenarios are coarse to make suitable predictions of species distribution patterns at a local scale. Studies have used proxies of climate to model changes in species distribution at a local scale. For example, Heegaard (2002) model of alpine species in relation to snowmelt time and altitude found a linear relationship between altitude and temperature. The author also found that species distribution will retreat or increase as changes occur in snowmelt patterns across the altitude gradients due to climate change. Increasing temperature will also reduce snow cover.

Randin et al. (2009) view that a model fitted with indirect predictor variables will provide accurate predictions of species distribution on a local scale such as on a mountain. For instance, altitude indirectly affects species distribution through its influence on temperature variation in mountains. Furthermore, temperature is known to have a direct effect on species physiology and thus survival and distribution. Similarly, in alpine regions, snow distribution is influenced by topography. Snow affects species distribution, plant growth, soil moisture and protects alpine plants from below zero temperatures in winter. Altitude is a proxy for temperature, and snow is not a direct proxy of a climatic variable though, it has a stochastic positive effect on species distribution. Therefore, in predicting the potential impact of climate change on species distribution in Lefka Ori, snow and altitude are used to formulate future climate scenarios for modelling.

Additionally, Parmesan and Yohe (2003) study of a globally coherent fingerprint of climate change found that species will experience a 6.1 meters per decade upwards range shift. Therefore, projecting into 100 years, the range shift estimates will be $6.1\text{m} \times 10 = 61\text{m}$ (ten decades); this will be subtracted from the current altitude gradient over Lefka Ori to illustrate species' potential upward range shift due to climate change. The current data over Lefka Ori are from 1997-1998 and 2010-2012; the reference year is 2012, and future climate projections are estimated for the year 2112 in this study.

Likewise, the potential increase in temperature will increase snowmelt and reduce snow cover across alpine mountains (Heegaard, 2002; Körner, 1999; Schöb et al., 2009). Keller et al. (2005) research on sensitivity analysis of snow cover to climate change scenarios and impacts on alpine plants found that an increase in temperature by 3^o to 5^o K reduces snow cover of plant habitat zones in the Swiss Alps, thus affecting plant growth and plant species distribution. Therefore, in Lefka Ori, the current snow persistence pattern with six categories would have a value of 1 subtracted from all the classes to capture the effect of potential climate change. Likewise, this subtraction will yield a reduction in snow persistence and an increase in snow absence, and these values are used in modelling the climate change scenario.

Finally, the climate change scenario in this study is derived by extrapolating the fitted model into a future warmer scenario where snow will persist less in the landscape. All other variables unrelated to climate variables are kept the same in future suitable habitat projections of plant species distribution in Lefka Ori. Additionally, selected candidate species modelled in JSDMs and SDMs are examined to identify changes in suitable habitat that may occur under the future climate scenario model in Lefka Ori.

2.7. Species range shift

Range shifts are changes to the geographical distribution of species over time, and these changes are often observed over decades to millennium (Lenoir and Svenning, 2013). Anticipated range shifts of species due to climate change can be poleward, upwards, eastwards or westwards across different elevation gradients. However, the common type is an upward elevational shift in the geographical distribution of species (Lenoir and Svenning, 2015). Several methods are used to derive range shift. For example, Liang et al. (2018) studied shifts in plant distribution in response to climate warming in Hengduan Mountains, using ArcGIS 10.2 tools to extract and compute species' range sizes across different elevation zones. The range size changes were derived by calculating the differences in range size of selected species between three stages of global warming (Last Glacial Maximum, current year and 2050). They found that the selected species on the mountain moved upwards due to climate change, and their ranges also expanded. Similarly, Neumann et al., (2015) research on climate change impact on *Procapra Przewalskii* on the Tibetan Plateau used the absolute difference between periods (current, 2020,2050 and 2080) to derive changes to habitat ranges and found that as the years increase, the impacts of climate change leads to a loss in range size of the species.

Therefore, in this study, the range shift is derived in ArcGIS using the raster calculator tool to subtract the binary maps (suitable and unsuitable) derived for each species, as indicated in Figure 2-4. The future climate projection (2112) binary maps are subtracted from the current predictions (2012) binary maps to get the differences in the range of selected species in JSDMs and SDMs. The product is a map having values of -1(loss), 0 (no change) and 1 (gain). A column is added to the attribute table, and the total area in hectares is derived by calculating field geometry.

In addition, I extracted from the binary maps of each species the presence (1) or suitable habitat to derive differences in the area (hectares) of each species in JSDMs and SDMs. Also, I used the Union analysis tool in ArcGIS to derive the total suitable area of species modelled in JSDMs and SDMs. In order to identify the changes in suitable habitat from current predictions to the future projection for each species. Similarly, I used the Intersect analysis tool to derive an overlap of suitable areas in JSDMs and SDMs. These are the unchanged suitable areas in JSDM, and SDM models of each species in 2012 and 2112 see Figure 2-4.

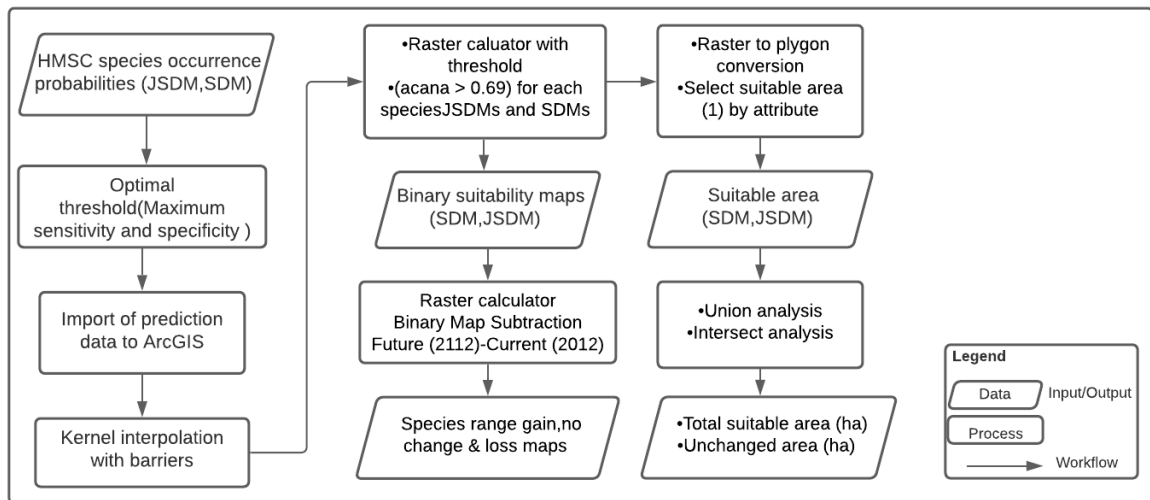


Figure 2-4: Steps followed to derive species range shift maps

3. RESULTS

3.1. Environmental Variable Correlation and Multicollinearity Test

3.1.1. Correlation Plots

The correlation plots of eleven environmental variables are presented in Appendix 2. The Pearson correlation coefficient values indicate planar surfaces (0.922) and profile surfaces (0.833) have a positive correlation trend with curvature, and these are expected because they are types of curvature. The other eight variables have a low positive or negative correlation between variables.

3.1.2. Multicollinearity Test

The VIF test of six continuous environmental variables in Table 3-1 shows the variables have values lower than 10, which is the rule of thumb that identifies collinearities. Therefore, having these low values indicate multicollinearity will not affect model estimates.

Table 3-1: Selected Environmental Variables after Multicollinearity Test

Environmental Variable	Variance Inflation Factor (VIF)
Altitude	1.21
Curvature	1.14
Slope	1.07
Northness	1.05
Eastness	1.03
Road	1.02

3.2. Species co-occurrences and residual correlation matrix

The results of the residual correlation matrix (Ω matrix) depicting species co-occurrences in JSDMs after ten replicates of the 42 plant species is presented in Figure 3-1. The residual correlation matrix indicates a relatively strong correlation (positive or negative) between fifteen species listed in Table 3-2. For instance, *Prunus prostrata* (PRUNPRO) is positively correlated with *Alyssum sphacioticum* (ALYSPPH: 0.982), *Crepis sibtborpiana* (CREPSI: 0.925), *Draba cretica* (DRABCRE: 0.986), *Festuca sipylea* (FESTIP: 0.966), *Hypochaeris tenuiflora* (HYPOTEN: 0.966), *Paronychia macrosepala* (PARMAC: 0.984), *Veronica arvensis* (VERARV: 0.890) and negatively correlated with *Acantholimon androsaceum* (ACANAN: -0.893) and *Cirsium morinifolium* (CIRSMO: -0.909) see Appendix 3. Similarly, across the 15 co-occurring species, pairs of associated species are negatively or positively correlated based on the 95% credible interval set for the residual correlation matrix.

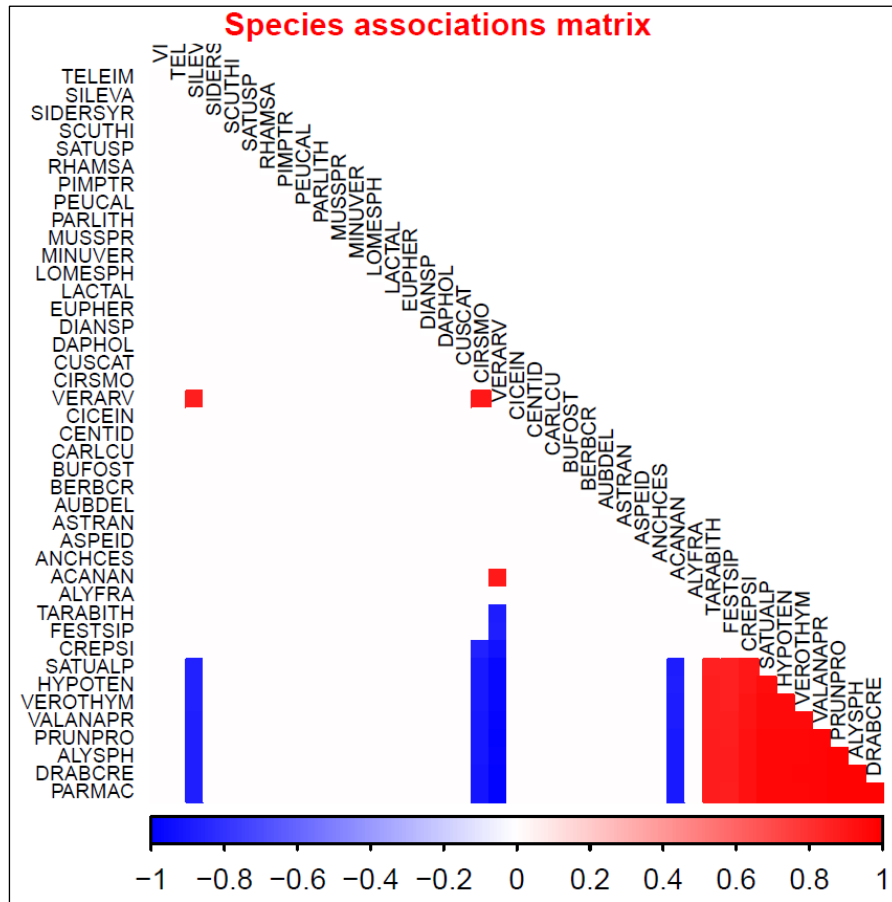


Figure 3-1: Residual species correlation matrix heat map showing associations with 95% posterior probability. The species-to-species association matrix depicts pairs of positive associations (red), negative association (blue) and species with less than 95% posterior probability are white, with the intensity of the colours depicting the strength of the associations.

Table 3-2: Co-occurring species from the residual species correlation matrix

Species	No Plots observed	Status	Climatic proxies(Nyktas, 2012)
Acanan	120	Greek endemic	snow
Alysph	17	Greek endemic	
Cirsmo	73	Greek endemic	snow
Crepsi	54	Greek endemic	elevation
Festip	37	East Mediterranean	
Drabcre	24	Greek endemic	Snow/elevation
Hypoten	38	Greek endemic	snow/elevation
Parmac	29	East Mediterranean	snow
Prunpro	62	Mediterranean	elevation
Satualp	26	Mediterranean	Snow/elevation
Sileva	58	Greek endemic	elevation

Tarabith	<i>Taraxacum bithynicum</i>	26	East Mediterranean
Valanapr	<i>Valantia aprica</i>	37	Balkan snow
Verarv	<i>Veronica arvensis</i>	29	European-SW Asian
Verothym	<i>Veronica thymifolia</i>	32	Greek endemic

Subsequently, using the criteria described in Section 2.5.3 and Figure 3-1 to select candidate species, the following species are selected for further analysis in the SDMs:

- Species with a threshold of 95% credible interval of species association: Figure 3-1.
- Co-occurring species with more than 50% occurrences within Lefka Ori: *Acantholimon androsaceum* (120 occurrences), *Prunus prostrata* (62 occurrences)
- Non-co-occurring species with more than 50% occurrences within Lefka Ori: *Berberis cretica* (93 occurrences)
- Species identified to be dependent on climate proxies: *Acantholimon androsaceum*
- Protected species with high conservation status and neutral association in Figure 3-1: *Anchusa cespitosa*
- Species with low association with climate proxies: *Alyssum sphacioticum*

In this thesis, the term **co-occurring species** refers to positively or negatively associated species in the species association matrix in Figure 3-1. At the same time, **non-co-occurring species** are not associated with other species in Figure 3-1. Therefore, the five candidate species are in Table 3-3.

Table 3-3: Selected candidate species for comparison in JSMD and SDM

Co-occurring species	Non-co-occurring species
<i>Acantholimon androsaceum</i>	<i>Anchusa cespitosa</i>
<i>Alyssum sphacioticum</i>	<i>Berberis cretica</i>
<i>Prunus prostrata</i>	

3.3. Comparison of JSMD and SDM

In order to make a comparison of the autecological (SDM) and synecological (JSMD) approaches in modelling the distribution of plant species, the results of model accuracy, variance partitioning, regression coefficients of co-occurring and non-co-occurring species are presented in this section.

3.3.1. Model evaluation JSMD and SDM

The first research question of this study is: In modelling species that are dependent on other species, do they perform better in JSMD than SDMs?

Subsequently, to answer this research question, the RMSE accuracy in JSMD and SDM of co-occurring species and non-co-occurring species are shown in Figure 3-2. The RMSE values of *Acantholimon androsaceum*, *Alyssum sphacioticum* and *Prunus prostrata* (co-occurring species) in JSMDs are between 0.259 to 0.466, while the values in SDMs are between 0.243 to 0.442. The SDMs have lower RMSE values than the

JSDMs for the co-occurring species. Similarly, the RMSE values of *Anchusa cespitosa* and *Berberis cretica* (non-co-occurring species) in JSDMs are between 0.427 and 0.477, while the SDM values are between 0.452 and 0.538. For the non-co-occurring species, the RMSE values in JSDMs are lower than the SDMs values.

The lower RMSE values indicate a better species fit in SDMs than in JSDMs of the co-occurring species. In comparison, the better fit of the non-co-occurring species is in JSDMs, which have lower values than the SDMs. However, I would expect a slight difference where the non-co-occurring species would have lower RMSE values in SDMs. Furthermore, co-occurring species should have higher values in JSDMs, which may be attributed to species interactions; however, there are slight differences in the predictions.

The AUC values of the co-occurring species in Figures 3-3 in JSDM are between 0.703 to 0.923, whereas in SDMs, the values are between 0.750 and 0.901. Also, the two co-occurring species had higher AUC values in the JSDMs than SDMs. In contrast, *Prunus prostrata* has higher values in SDM than JSDM in Figure 3-3 C. Similarly, the AUC values of the non-co-occurring species in JSDMs are between 0.680 to 0.803, whereas the SDMs values are between 0.541 to 0.760. Similarly, from the non-co-occurring species, the AUC values are higher in the JSDM than SDMs. The AUC values are greater than 0.5, indicating the predictions are better than random at explaining the discriminations of presences from absences.

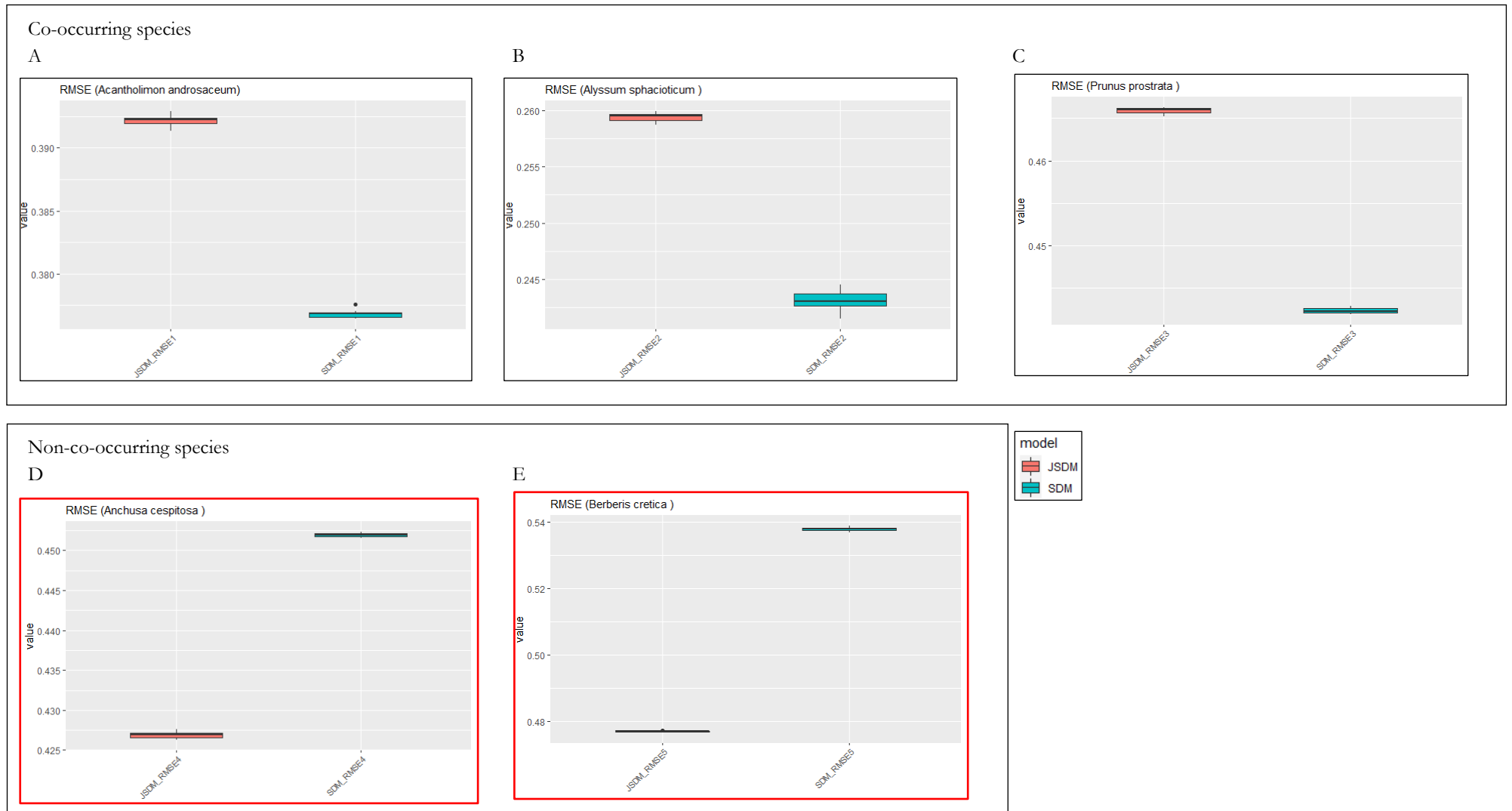


Figure 3-2: The predictive performance of fitted JSDM (orange) and SDM (blue) from 10 replicates measured by RMSE (a measure of accuracy). The red boxes indicate species with differences.

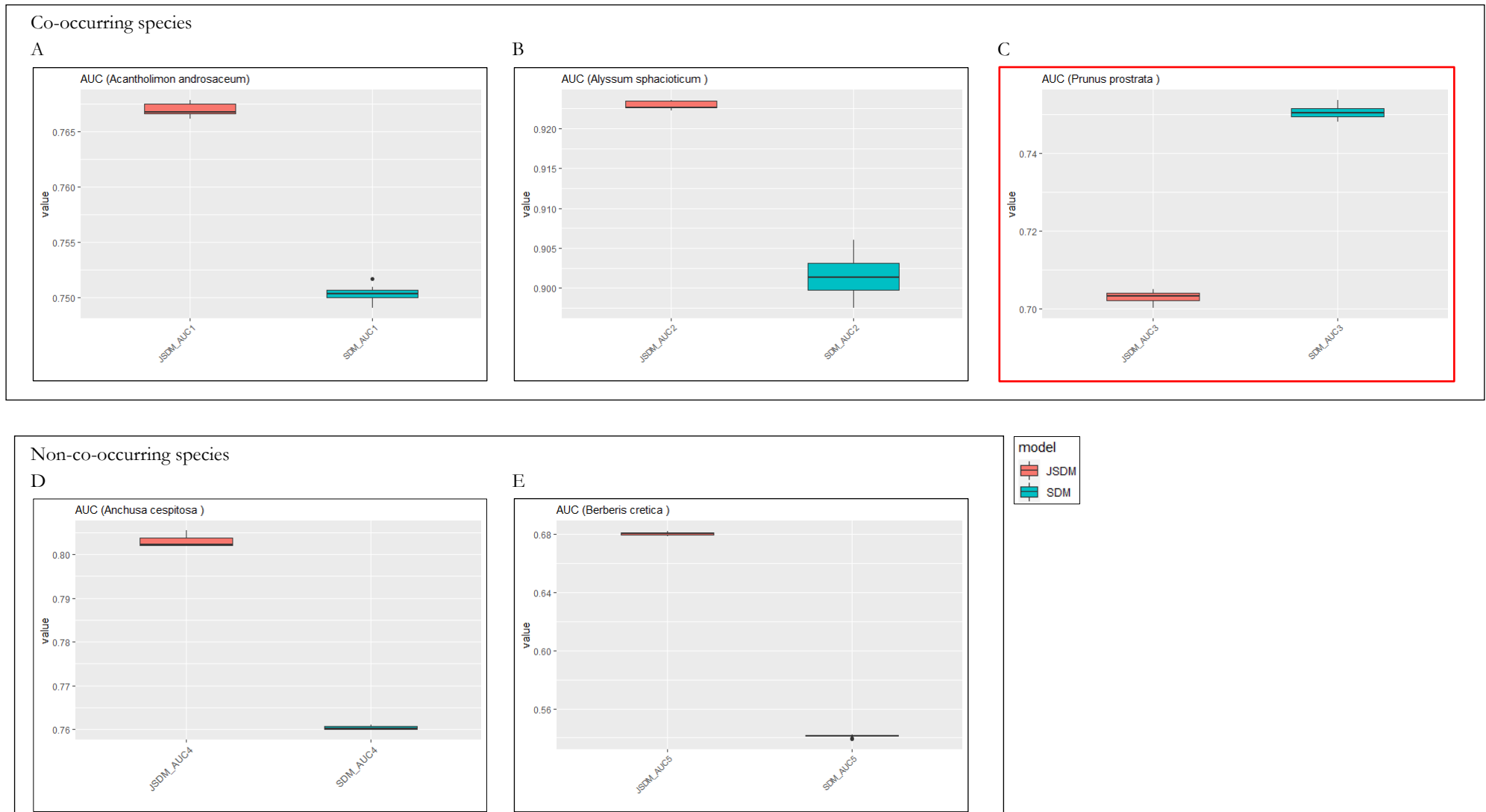


Figure 3-3: The predictive performance of fitted JSDM (orange) and SDM (blue) from 10 replicates measured by AUC (a measure of discrimination). The red box indicates species with differences.

The first research hypothesis of this study is if JSDBMs show higher accuracy as measured by AUC and RMSE than SDMs.

The result in Figures 3-2 and 3-3 show slight differences and variations in accuracies in JSDBMs and SDMs. In Table 3-4, the co-occurring species' RMSE values in JSDBMs are higher than the SDMs, indicating the SDMs have higher accuracy, whereas the AUC values in JSDBMs are higher in two species compared to the SDMs. Whereas the non-co-occurring species RMSE values of JSDBM are lower than the SDMs, indicating better accuracy, the AUC values of the JSDBM are higher than those from the SDMs, indicating it is better at discriminating presence from absence see Appendix 4.

Table 3-4: Average RMSE and AUC values from replicates in JSDBMs and SDMs

	Species	JSDBM RMSE	SDM RMSE	JSDBM AUC	SDM AUC
Co-occurring species	<i>Acantholimon androsaceum</i>	0.392	0.377	0.767	0.750
	<i>Abyssum sphacioticum</i>	0.259	0.243	0.923	0.901
	<i>Prunus prostrata</i>	0.466	0.442	0.703	0.751
Non-co-occurring species	<i>Anchusa cespitosa</i>	0.427	0.452	0.803	0.760
	<i>Berberis cretica</i>	0.477	0.538	0.680	0.541

Also, the Two-way ANOVA and Tuckey HSD test at 95% confidence interval was used to test if there is a significant difference between the mean AUC values of JSDBM and SDM and the interaction effect between species and models. The test results are in Appendix 5, and the conclusions drawn from the results are summarised in Table 3-5.

Table 3-5: Summary mean AUC statistical test

Multiple Comparisons	Result
Species	Different*
SDMs vs JSDBMs	Different*
Species vs Model	Different*

*Significantly different where $p < 0.05$

The results of Two-way ANOVA showed a statistically significant difference in the means of AUC by species ,model type, and the interaction between species and model types ($p < 0.001$). The Tuckey HSD post hoc follow-up test showed a significant pairwise difference between species, model types and interactions between species and model ($p < 0.05$).

3.3.2. Explanation of species variations in JSDBM and SDMs

The second research question of this study is: Which variables are important for modelling plant species, and is there a difference between JSDBMs and SDMs?

Consequently, the variance proportion and regression coefficient parameters are examined in this section to answer this research question. Firstly, the result of the variance proportions in Figure 3-4 showing the contribution of each predictor variable to the five species distribution shows there are variations, and there is no uniform pattern in the variance proportions in JSDBMs and SDMs. The important variables

contributing to the distribution of plant species are geology in JSDM (13-73%) and SDMs (11-69%), snow in JSDM (6-21%) and in SDMs (6-27%), distance to road in JSDM (3-14%) and SDMs (3-48%), and curvature in JSDM (2-23%) and SDMs (3-21%) see Appendix 6. The graphs show that the variance proportions of geology and snow are higher in JSDM than SDMs, whereas snow has lower variance proportions in JSDMs than SDMs. Also, the variance proportion of distance to road in co-occurring species is higher in SDMs than JSDMs; however, from the non-co-occurring species, a species has equal variances while the other has a higher contribution in JSDM. Similarly, Figure 3-4 F shows the total variance contribution of variables in JSDMs and SDMs. The fixed effects, which are the environmental variables in both models, are higher than the random effects.

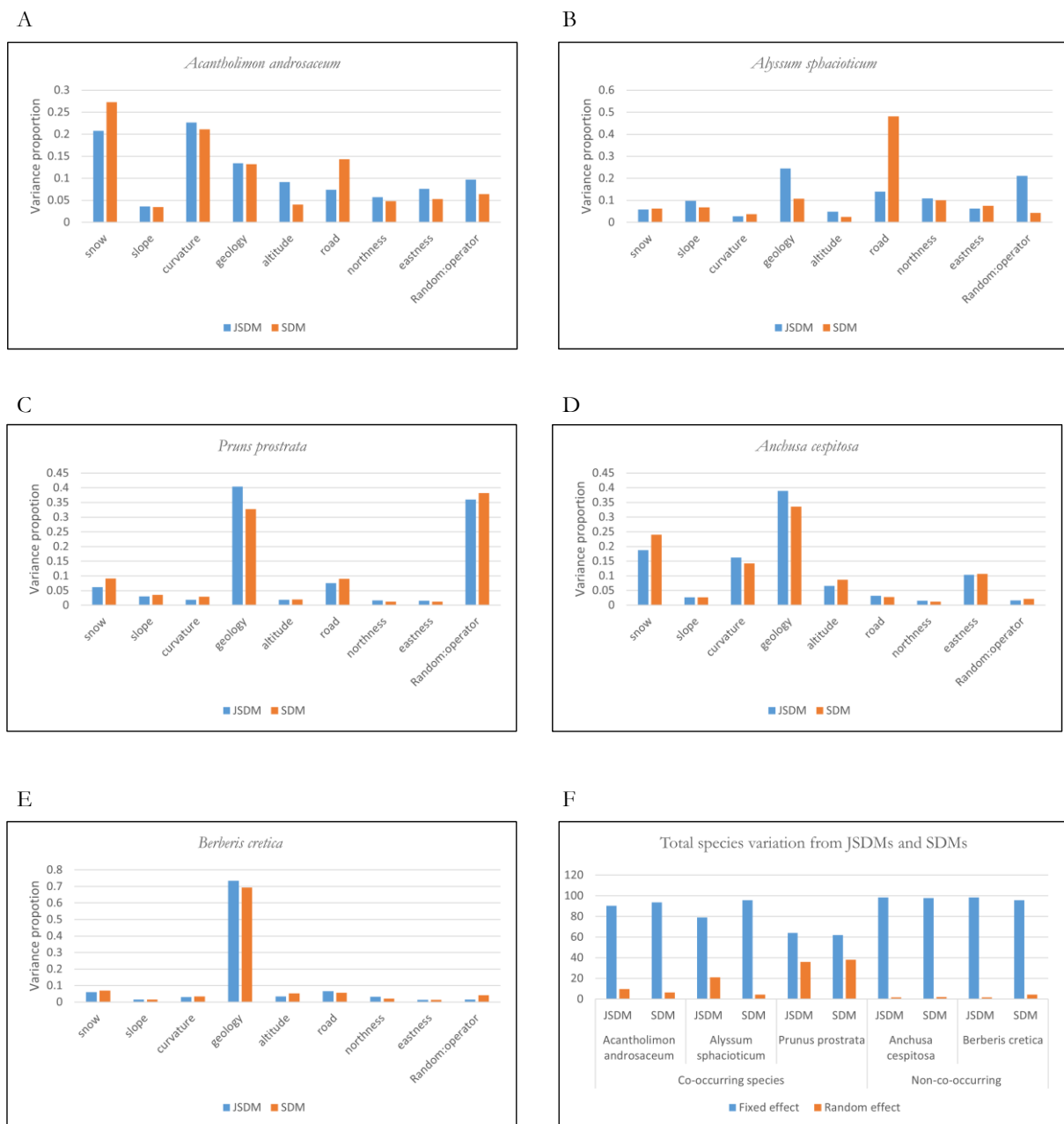


Figure 3-4: Explained variance in the distribution of co-occurring species (A, B, C), non-co-occurring species (D, E) in JSDMs(blue bars) and SDMs(orange bars), And total variance contribution from fixed effects (blue bars) and random effects (orange bars) of the species (F).

Secondly, in the results of the regression coefficient matrix (β matrix) in Figure 3-5 and Appendix 7, showing the strength and direction of species responses to environmental variables, I see from the graphs that none of the species has a statistical response to all environmental variables within a 95% credible interval threshold. However, the candidate species respond to geology and snow, which is expected from the explained variance contribution of these variables, although mostly negative and a few positive responses to the different categories. Also, I see that *Acantholimon androsaceum* (Figure 3-5A), *Anchusa cespitosa* (Figure 3-5D), *Berberis cretica* (Figure 3-5E) have positive responses to snow in the JSDMs and SDMs. However, species responses to distance to the road in both models are relatively low compared to its contribution to the explained variances of species distribution.



Figure 3-5: Strength and direction of species responses to environmental variables in the regression coefficient matrix, JSMD (blue bars) and SDM (orange bars)

The second research hypothesis of this study is to identify if variables importance of the same species in JSMD and SDM will (or will not) change between SDM and JSMD.

I can infer from the results in Figures 3-4 and 3-5 that the important environmental variables influencing the distribution of species do not differ for species with co-occurrences and non-co-occurrences in JSMDs and SDMs. The contributions of variables are similar in both models with slight variations. However, the environmental variables in the SDMs compared to the JSMDs are higher either positively or negatively except for *Berberis cretica* in Figure 3-5E, which is a non-co-occurring species as indicated in Figure 3-1.

3.4. Predictions in JSMD and SDM

The HMSC-R predict function produces predictions over the environmental gradient and spatial gradients viewed at the individual species level in JSMDs and SDMs (Tikhonov et al., 2020b).

3.4.1. JSMD and SDM predictions over environmental gradients

The occurrence probability of each species over the snow and altitude gradients (climate proxies) are presented in this section. In comparing the occurrence probability of species represented with the black dots, which is the actual data in Figure 3-6 over the snow gradient, the graphs indicate similar patterns but with slight variations in JSMDs (Figure 3-6: A, C, E, G, I) and SDMs (Figure 3-6: B, D, F, H, J) independent of occurrence status. However, *Alyssum sphaerolobum*, identified as having low snow persistence, I can see from results in Figure 3-6: C, D that the link is even less in SDM than in JSMD (Figure 3-6: C).

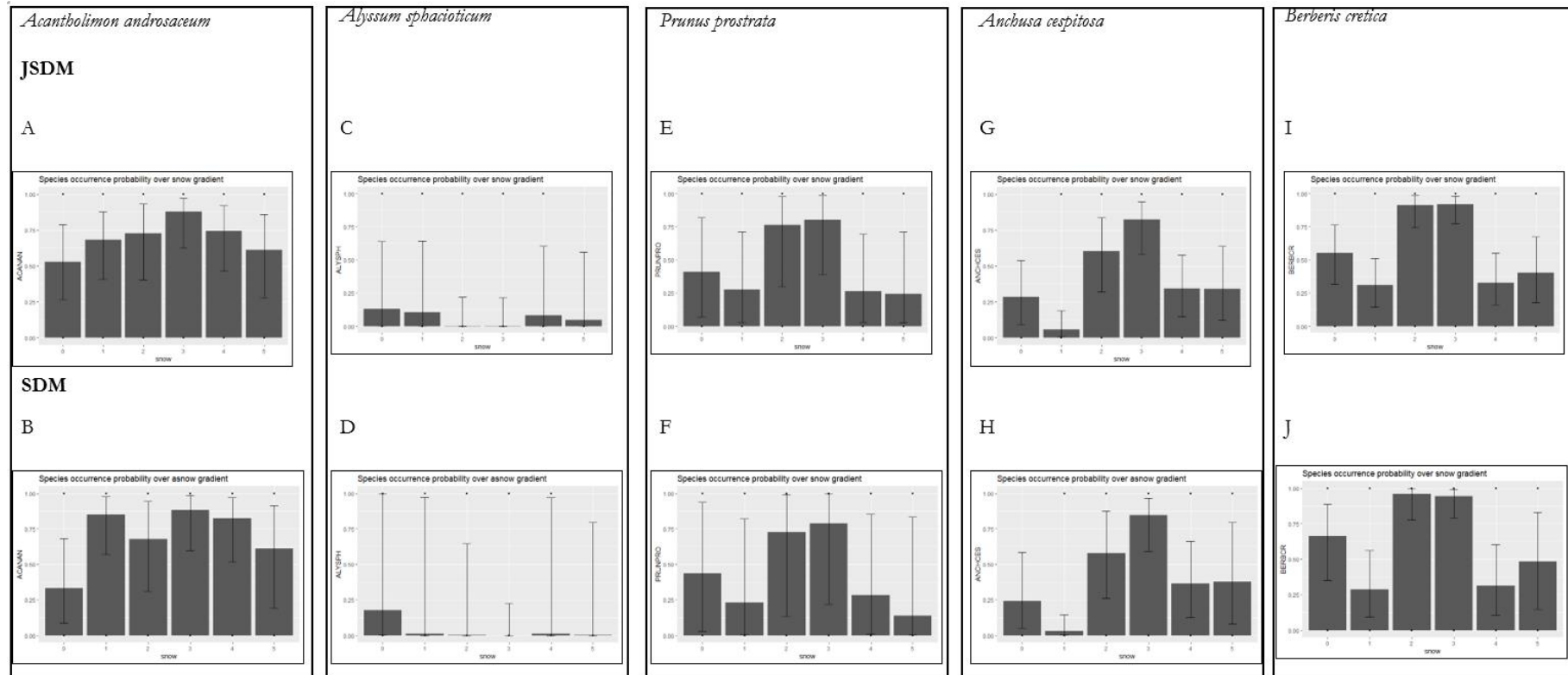


Figure 3-6: Predictions of species occurrence probability over snow gradient in JSDMs (A, C, E, G, I) and SDMs (B, D, F, H, J).

Similarly, in comparing species occurrence probability along altitude gradient in JSDMs in Figure 3-7:A, C, E, G, I and SDMs in Figure 3-7: B, D, F, H, J, the curves show there is a general trend of decrease in species occurrences with increasing altitude with high predictions ranging from 0.78 to 1.0. Also, the species responses to altitude shown in SDMs and JSDMs depict similar patterns. The plunge in the curves is because of categorical variables of geology and snow included in the models. Generally, at about 2100 meters along the altitude gradient, species presences start to decline, leading to an abrupt drop in the curve as shown in Figure 3-7: E, F, G, H, I, J. The blue area shows the 95% credible interval of the model prediction of each species. The data points are outside the 95% credible interval set for the model predictions because these intervals are not for the occurrence data. Also, for instance, *Alyssum sphacioticum* in Figure 3-7 C, D and *Prunus prostrata* in Figure 3-7 E, F have values of 1.00 and 0.99. These values are synonymous with the large blue area around the curve, indicating high predictions in the model. Whereas *Acantholimon androsaceum*, with values of 0.78 and 0.92, has a smaller blue area than the other species, indicating that the species

has a lower occurrence probability in the model predictions than the other species. Generally, these patterns identified in Figures 3-7 are independent of species co-occurrences.

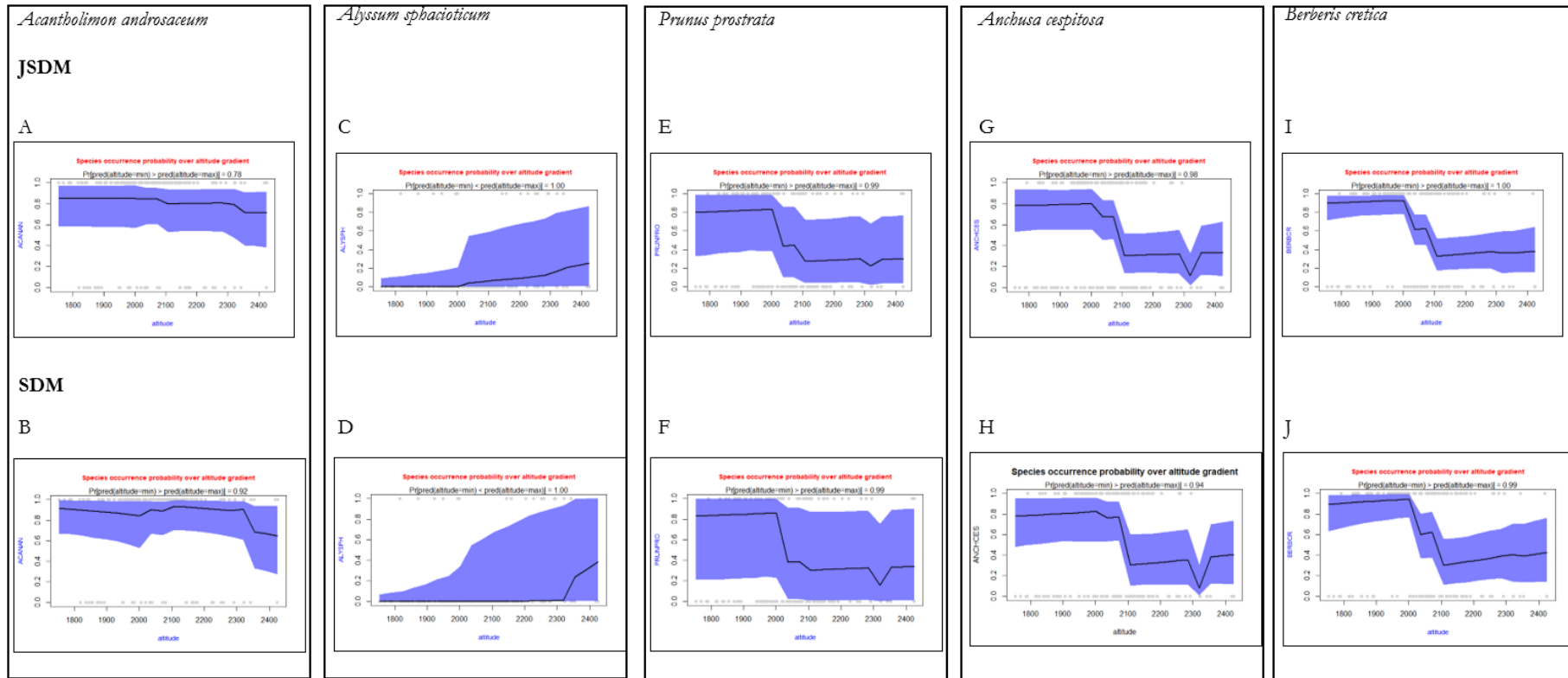


Figure 3-7: Predictions of species occurrence probability over altitude gradient in JSDM(A, C, E, G, I) and SDM (B, D, F, H, J). Black line shows the posterior mean, and the blue area is the 95% credible interval of model prediction

3.5. Species current predictions, projection of future climate scenario and range shift in JSDMs and SDMs

The third research question of this study is: What is the effect of species community interactions in future climate projections?

Subsequently, to answer this research question, current prediction, future climate projections, and range shift is derived for the five selected species in JSDMs and SDMs and are presented in this section. The current species occurrence probability is in Appendix 8. Nevertheless, Figure 3-8 shows the results of *Acantholimon androsaceum*, a co-occurring species but negatively associated with most species. The differences in the current prediction in 2012 in JSDM in Figure 3-8A and SDMs in Figure 3-8D are approximately 147.98 ha see Table 3-7. Similarly, in 2112, the projected suitable areas in JSDM in Figure 3-8B will be smaller than the SDM in Figure 3-8E; the difference is approximately 812.12 ha see Table 3-7. The smaller suitable areas in JSDM or larger areas in SDM projections are expected because extrapolations are made from the current predictions. Similarly, the results of the range shift in JSDM in Figure 3-8C and SDM in Figure 3-8F indicates approximately 14.1 - 31.6% will be lost, and 1.4 - 4% will be gained of the suitable areas within 100 years, see Table 3-6.

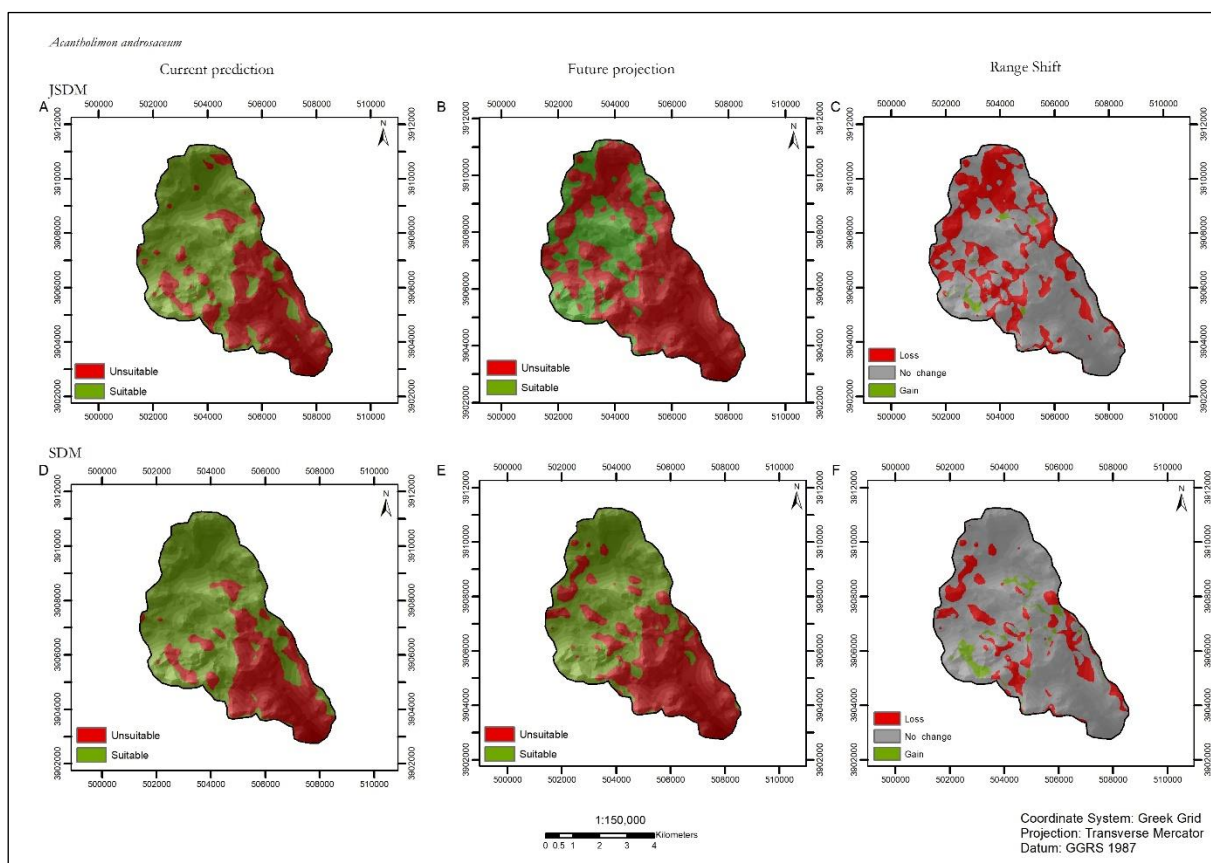


Figure 3-8: The current prediction (A and D), future-projection (B and E), and range shift (C and F) of *Acantholimon androsaceum* in JSDM (upper section) and SDM (lower section).

Prunus prostrata in Figure 3-9 which is mostly positively associated with other species in 2112, will have more suitable areas in the JSMD (1460.46 ha) as shown in the map in Figure 3-9B, compared to the SDMs (1048.91 ha) in Figure 3-9E, also see Table 3-7. The potential range shift in JSMD shown in Figure 3-9C and SDM in Figure 3-9F indicate that approximately 12.1 - 18.8% will be lost and 2.1 -7.9% will be gained in suitable areas from 2012 to 2112, see Table 3-6.

Similarly, *Alyssum sphacioticum* in Figure 3-10 with mostly positive association with other species in 2112 will have more suitable areas in JSMD (699.13 ha) as shown in Figure 3-10B than SDMs (128.52 ha) in Figure 3-10E, Table 3-7. The potential range shift in JSMD shown in Figure 3-10C and SDM in Figure 3-10F indicate that approximately 0.93 -1.4% will be lost, and 1.01 - 2.46% will be gained of the suitable area within 100 years (Table 3-6).

The results show that *Acantholimon androsaceum*, with a more negative association with other species, have more suitable areas in SDMs than JSMDs. *Prunus prostrata* and *Alyssum sphacioticum*, having a more positive association with other species, have larger suitable areas in JSMDs than SDMs in 2112. Generally, the five species' unchanged areas in JSMDs and SDMs reduced from 6340.56 ha in 2012 to 2494.28 ha in 2112 (Appendix 11). Although I expect community interaction to affect these patterns, other factors such as species prevalence, uncertainties of models, data, projections and selected threshold may also have influenced these differences.

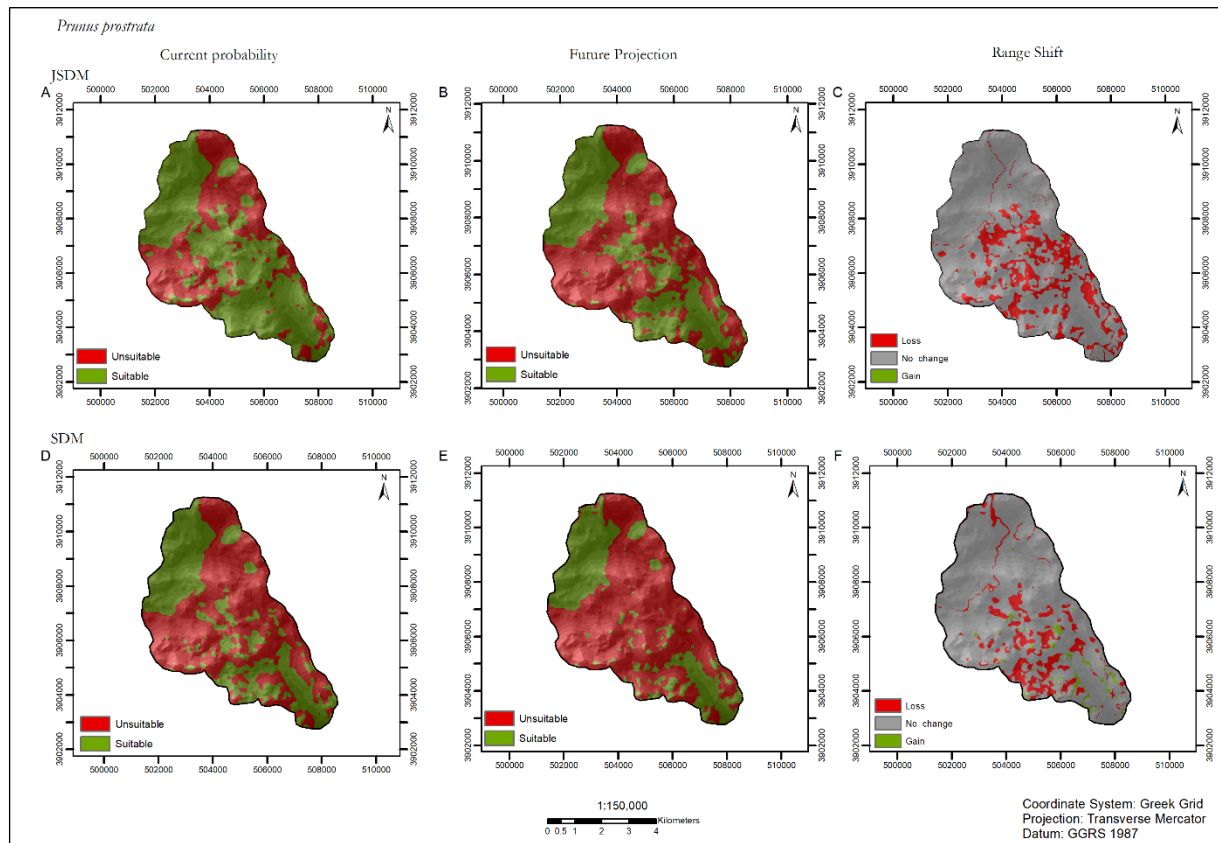


Figure 3-9: The current prediction (A and D), future projection (B and E), and range shift (C and F) of *Prunus prostrata* in JSDM (upper section) and SDM (lower section).

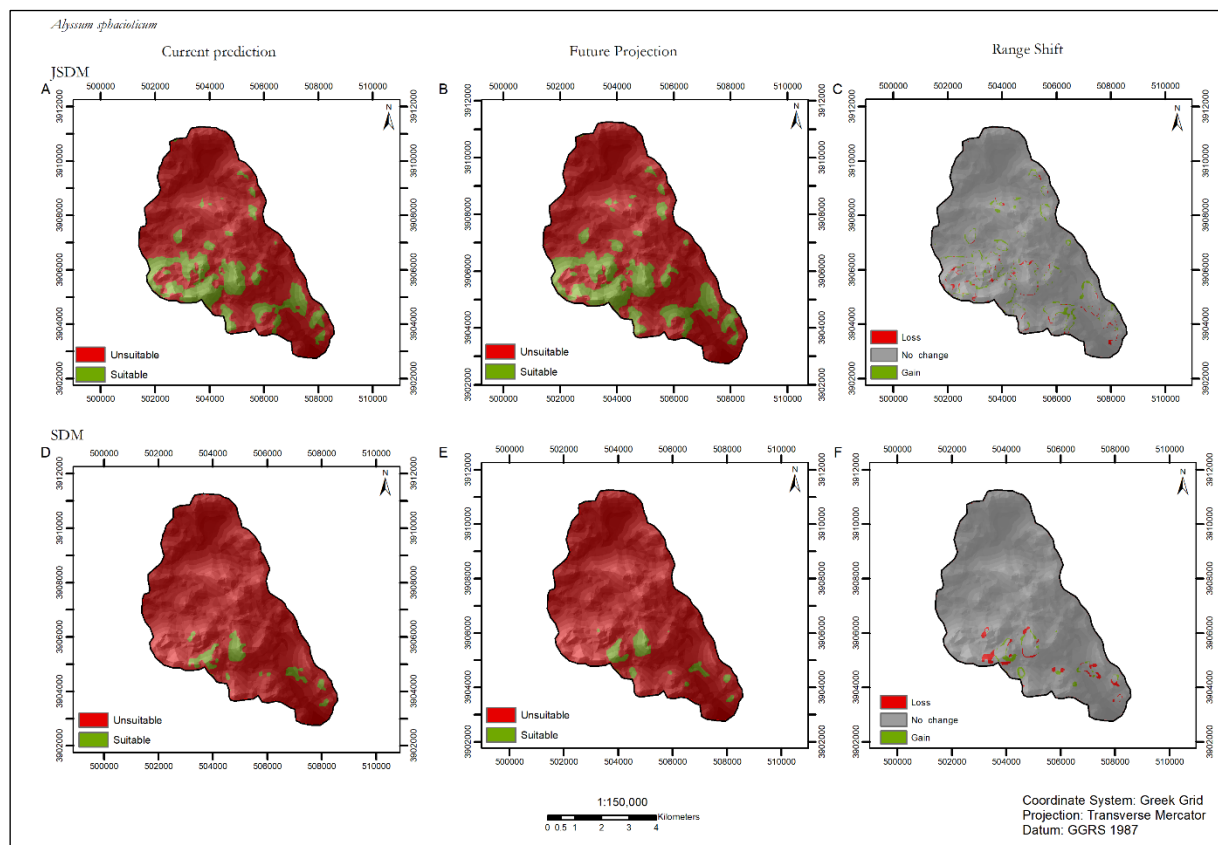


Figure 3-10: The current prediction (A and D), future projection (B and E), and range shift (C and F) of *Alysium sphacioticum* in JSDM (upper section) and SDM (lower section).

Subsequently, the two non-co-occurring species result shows that *Anchusa cespitosa* in Figure 3-11 will have more suitable areas in SDM as shown in Figure 3-12B than JSDM in Figure 3-11E (see Table 3-7). Likewise, the potential range shift in JSDM shown in Figure 3-11C and SDM in Figure 3-11F indicate approximately 12.1 - 21.95 % will be lost, and 0 - 0.17 % will be gained in the suitable area from 2012 to 2112 see Table 3-6. Similarly, *Berberis cretica* in Figure 3-12 will have more suitable areas in SDM shown in Figure 3-12B than SDM in Figure 3-12E. Also, approximately 8.5 - 13.29% in the suitable range area will be lost, and a gain of 0.10 - 0.32% is projected in 100 years. For these non-co-occurring species, I expected more suitable areas in the future scenario in the SDMs than JSDMs.

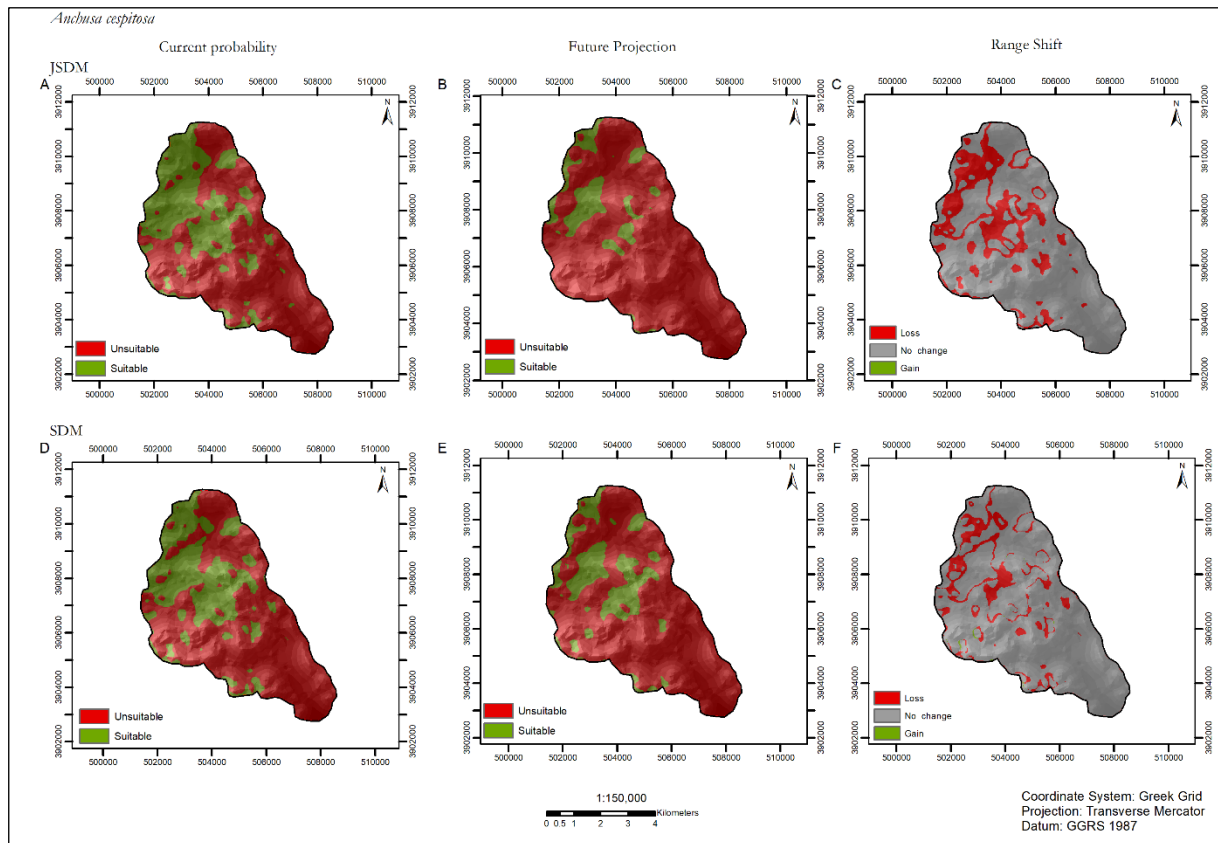


Figure 3-11: The current prediction (A and D), future projection (B and E), and range shift (C and F) of *Anchusa cespitosa* in JSDM (upper section) and SDM (lower section).

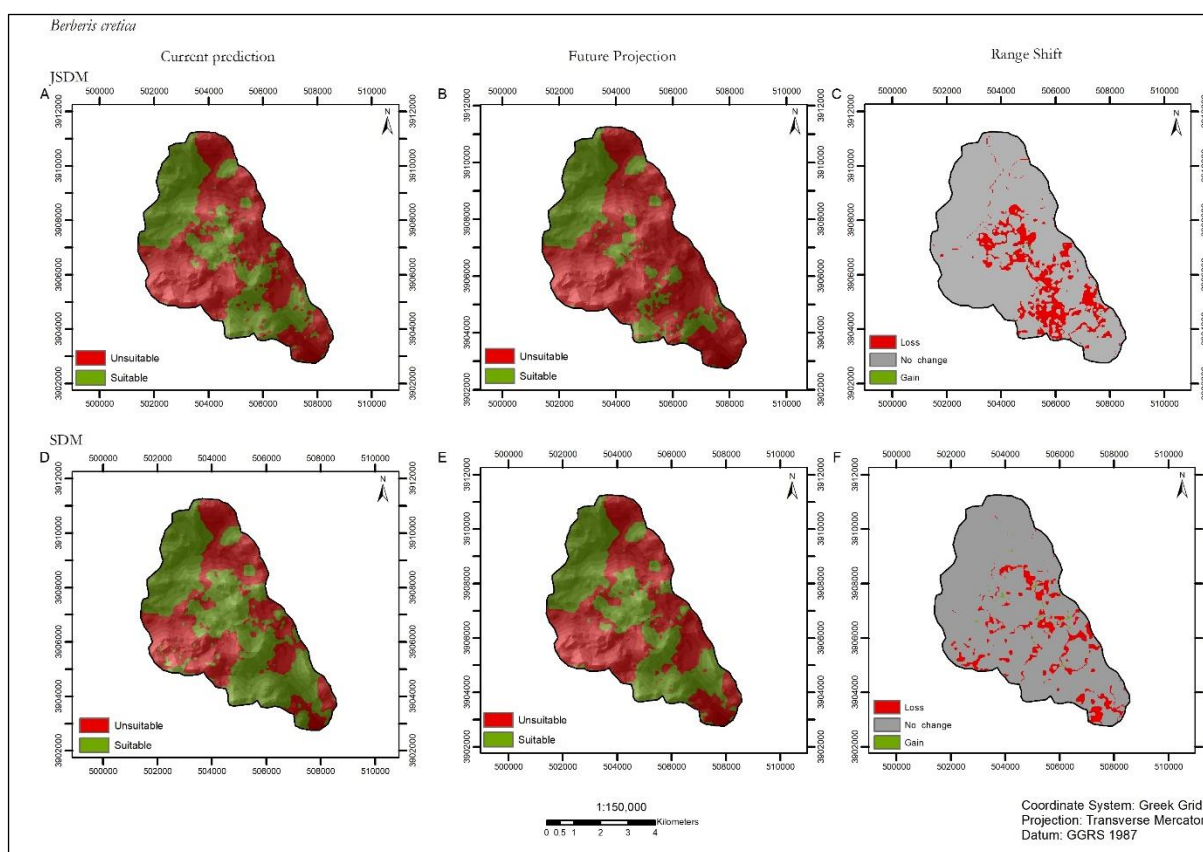


Figure 3-12: The current prediction (A and D), future projection (B and E), and range shift (C and F) of *Berberis cretica* in JSDM (upper section) and SDM (lower section).

Generally, the projected range shift of the species from the maps and Table 3-6 indicates the approximated loss of species suitable niche is more significant in JSDMs (2858.18 ha) than SDMs (1596.20 ha). Also, areas of no change are smaller in JSDMs (13544.16 ha) than SDMs (14680.87 ha) irrespective of species occurrence status (Appendix 10).

Research hypothesis three of this study deals with identifying if the projected range shift of species suitable areas will differ in JSDMs and SDMs. The total suitable niche area from 2012 and 2112 in Table 3-7 shows a variation of suitable areas irrespective of occurrence status.

Therefore, the results of the summarized current suitable niche areas in Table 3-7 show that suitable areas of *Acantholimon androsaceum* are larger in SDM than JSDM. In contrast, the suitable areas for *Alyssum sphacioticum* and *Prunus prostrata* are larger in JSDM than SDM. These species co-occur, and the variations in suitable areas are not model specific. Similarly, for species that do not co-occur, the suitable area for *Anchusa cespitosa* is larger in JSDM than SDM. In contrast, for *Berberis cretica* the suitable niche areas are larger in SDMs than JSDMs. Generally, the total suitable areas in JSDMs (7313.08 ha) are larger than the SDMs (6593.44 ha).

The results of the summarized projected suitable niche areas in Table 3-7 show differences irrespective of occurrence status. The suitable areas of *Acantholimon androsaceum* are larger in SDM than JSDM, whereas the suitable areas for *Alyssum sphacioticum* and *Prunus prostrata* are larger in JSDM than SDM. However, for *Anchusa cespitosa* and *Berberis cretica* that do not co-occur, the suitable niche areas are larger in SDMs than JSDMs. The results identify that the projected range shift differs in JSDMs and SDMs, and these differences are species-specific, not based on occurrence status. Also, the Total suitable area for all species in 2012 is approximately 7566.98 ha, and it decreases to 6333.90 ha in 2112 (Appendix 10).

Table 3-6: JSDM and SDM species projected range shift

	Species range shift											
	JSDM range shift (2112-2012)						SDM range shift (2112-2012)					
	areas lost		areas gained		common area		areas lost		areas gained		common area	
	area (ha)	percentage	area (ha)	percentage	area (ha)	percentage	area (ha)	percentage	area (ha)	percentage	area (ha)	percentage
<i>Acantholimon androsaceum</i>	1045.16	31.60%	46.83	1.40%	2214.81	16.35%	466.77	14.10%	131.26	4%	2709.45	18.46%
<i>Alyssum sphacioticum</i>	25.16	0.93%	75.72	2.64%	3207.01	23.63%	46.11	1.40%	32.22	1.01%	3229.60	22%
<i>Prunus prostrata</i>	622.41	18.82%	7.88	0.24%	2676.96	19.76%	401.19	12.12%	79.84	2.41%	2826.47	19.25%
<i>Anchusa cespitosa</i>	725.98	21.95%	0	0	2580.45	19.05%	400.53	12.11%	5.8	0.17%	2900.79	19.76%
<i>Berberis cretica</i>	439.47	13.29%	3.4	0.10%	2864.93	21.15%	281.69	8.51%	10.67	0.32%	3014.56	20.53%
Total	2858.18		133.83		13544.16		1596.29		259.79		14680.87	

Table 3-7: Current and Projected suitable niche area

	Suitable niche area											
	JSDM-SDM (Current)						JSDM-SDM (Projected)					
	2012 modelled suitable niche area (ha)						2112 modelled suitable niche area (ha)					
	JSDM only	SDM only	Suitable Area (JSDM & SDM)	JSDM-SDM	Unchanged area	Percentage of unchanged area	JSDM only	SDM only	Suitable Area (JSDM & SDM)	JSDM-SDM	Unchanged area	Percentage unchanged
<i>Acantholimon androsaceum</i>	2009.04	2157.02	2260.60	147.98	1905.47	30.05%	1009.61	1821.73	1849.39	812.12	981.96	28.10%
<i>Alyssum sphacioticum</i>	644.93	142.32	140.25	502.61	647.00	10.20%	699.13	128.52	700.69	570.61	126.97	3.63%
<i>Prunus prostrata</i>	2080.56	1370.96	2106.01	153.31	1345.51	21.22%	1460.46	1048.91	1528.35	411.55	981.03	28.08%
<i>Anchusa cespitosa</i>	1118.22	1054.90	1164.13	63.31	1009.00	15.91%	391.61	656.87	659.08	265.26	389.41	11.14%
<i>Berberis cretica</i>	1460.33	1868.24	1895.98	110.98	1433.59	22.61%	1017.09	1594.21	1596.40	577.12	1014.91	29.04%
Total	7313.08	6593.44	7566.98				4577.90	5250.24	6333.90			

4. DISCUSSION

To compare autecological and synecological approaches in species modelling, I initially started implementing all the parameters identified within the HMSC framework in Section 2.5.1. Such as the traits matrix, which indicates how the traits of species are related to the environmental variables. At first, I assumed traits as the life form and plant form of the plants. However, these assumed traits for the species are based on secondary sources and subjective assumptions, not the plot level's measured traits. Hence it did not make much difference in the model. Subsequently, using the HMSC modelling framework by Ovaskainen et al., 2017 as depicted in Figure 2-3, I modelled species in SDMs (autecology) and JSDMs (synecology) using similar parameters for both models.

4.1. Species interactions in modelling the distribution of alpine plant species

JSDM produces inferences of biotic interactions after accounting for species environmental relationships, which is an advantage of the model (Pollock et al., 2014; Zurell et al., 2020a). The residual correlation matrix in JSDM in Section 3.2, which is the synecological approach, identified fifteen co-occurring species within the alpine plant community. Studies affirm that JSDMs can identify negative correlations between species that may be attributed to competition. However, in a sparsely alpine vegetated zone like the white mountains, resources are probably scarce. Therefore, competition will be essential for species survival, but evidence may be less due to the sparse vegetation. Likewise, a joint response of species to an unaccounted environmental variable may depict positive correlations (Opedal and Hegland, 2020; Poggiato et al., 2021). I expected that spiny *Berberis cretica*, which is well defended against grazing by thorns, with a relatively open structure on Lefka Ori (Bergmeier, 2002), will positively correlate with other plant species. However, the results in Figure 3-1 did not depict this association in the matrix.

Also, I assume that a positive association will result in a facilitative relationship between species. For instance, *Acantholimon androsaceum* and *Prunus prostrata*, both relatively larger shrubs, should act as facilitators to other species and thus have a more positive association with other species in the matrix. From the matrix, *Prunus prostrata* has a more positive association (six) than negative association (two) with other species. While *Acantholimon androsaceum* has a more negative association (eight) than a positive association (one) with other species, as shown in Figure 3-1 and Appendix 3. Pollock et al. (2014) views that residual correlations depicting possible species interactions should be explored further. Likewise, Ovaskainen et al. (2017) state that the species association matrix is not a proven ecological interaction on the field but gives insights into what may be attainable. Nevertheless, a limitation to this result is that a field validation is not possible to verify these co-occurrences.

Furthermore, most of the co-occurring species depicted in the residual matrix are mainly hemicryptophyte and chamaephytes and are identified as the dominant species lifeforms on Lefka Ori (Bergmeier, 2002; Vogiatzakis et al., 2003). Also, a few of the co-occurrences detected by the matrix are synonymous with identified communities from previous studies (Bergmeier, 2002; Vogiatzakis and Griffiths, 2001).

Bergmeier (2002) used the Two-way indicator species analysis (TWINSPAN), a traditional synecological approach in vegetation science, to classify the plant community in Lefka Ori. A cluster of co-occurring species was identified, with these species reflecting responses to similar environmental conditions. The result identifies eleven species as dominating most plant communities, and these include *Berberis cretica* (77%), *Prunus prostrata* (74%) and *Acantholimon androsaceum* (56%). Whereas the species association matrix results in Figure 3-1 failed to identify the co-occurrences of *Berberis cretica* found in most plant communities in Lefka Ori. Which maybe because of the high confidence interval (95%) set for the species association matrix used in this study. However, the association matrix identified *Prunus prostrata* and *Acantholimon androsaceum* as co-occurring with other species. Irrespective of these associations, all species co-occur within communities, and these species co-occurrences may be due to randomness, species responses to similar environmental variables, dispersal limitations caused by the mountain or some form of biotic interaction between species (D'Amen et al., 2018; Pollock et al., 2014).

4.1.1. Are species that depend on other species modelled better by JSDMs than SDMs?

The predictive performances of JSDMs and SDMs of species that do and do not co-occur are evaluated based on predictions made from an independent dataset (Araújo and Guisan, 2006). Also, Elith et al. (2006) evaluated the predictive performance of models using AUC to discriminate species habitat and views that mean AUC variations indicate actual differences between models. Interestingly the AUC values in Figure 3-3 of two co-occurring species are higher in JSDMs than SDMs. Likewise, the AUC values of the two species that do not co-occur are also higher in JSDMs than SDMs (Section 3.3.1). The test results also indicate a statistically significant difference in the mean AUC values in JSDMs and SDMs (Appendix 5). Similarly, the predictive performance by AUC in JSDMs is slightly higher than SDMs in this study. Zurell et al. (2020b) used AUC and TSS to compare the predictive performance of JSDMs and stacked SDMs in testing the accuracy of species assemblage predictions. They identified that in comparing single species performances in SDMs and JSDMs, SDMs provided better predictions than JSDMs. However, this was not noticed in the results in Figure 3-3 of this study. The mean AUC values in JSDMs are higher than the SDM values for four species except for *Prunus prostrata*.

Similarly, the results of RMSE values in Figures 3-2 and Appendix 4 shows that the co-occurring species RMSE values in SDMs are lower than the JSDMs. These differences, although slight, indicate improved accuracies in SDMs. In contrast, *Anchusa cespitosa*, a non-co-occurring species, had lower RMSE values in JSDMs than SDMs. Similarly, Boulangeat et al. (2012) results show that the inclusion of biotic interaction to model plant species in the Alps improved model performances although not relevant for all species, which is also indicated in the present study results. Also, it is assumed that accuracies in JSDMs predictions of rare species should improve due to the association with other species (Pollock et al., 2014). For instance, the RMSE values of *Anchusa cespitosa*, a rare endemic, is lower in JSDM than SDM, therefore, depicting a better accuracy in JSDM. However, *Anchusa cespitosa* is a non-co-occurring species, as indicated in the residual correlation matrix. Thus, it is assumed to have limited interactions, but it occurs within species communities in Lefka Ori in other studies (Bergmeier, 2002; Vogiatzakis and Griffiths, 2001). Therefore, I would infer from section 3.3.1 that there are slight differences in the accuracy of species predictions in JSDMs and SDMs. However, there is no clear pattern as to which model produces higher accuracy measured by AUC and RMSE. The lack of a clear pattern maybe because all the variables needed in the modelling framework are not included. Also, maybe appropriate variables that explain these

differences, for instance, measured traits of individual plants other than the assumed model default settings, were used in modelling.

4.2. Autecological and synecological approaches in modelling plant species distribution

4.2.1. Species responses to environmental variables in JSDMs and SDMs

Species responses to environmental variables should be more pronounced in JSDMs than SDMs, because of the joint contribution of environmental variables from multiple species in JSDMs. In comparing the regression coefficient results in JSDMs and SDMs of the candidate species as presented in Figure 3-5. *Acantholimon androsaceum*, *Alyssum sphacioticum* and *Prunus prostrata*, the three co-occurring species, show different strengths in responses to specific environmental variables, indicating different factors such as biotic interactions between these species, underlying geology or location as defining their co-occurrences. Moreover, Warton et al. (2015) view that species with positive correlations should respond to similar environmental variables. Furthermore, Pollock et al. (2014) found that co-occurring species should also respond to environmental conditions similarly. In this study, the co-occurring species did not have similar strength or direction in environmental variables responses. However, the regression coefficient matrix results as presented in Figure 3-5 shows that the strength and direction of species responses to environmental variables in JSDMs and SDMs are different.

Similarly, the graphs of both models in Figure 3-5 revealed *Acantholimon androsaceum* (co-occurring) and *Anchusa cespitosa* (non-co-occurring) as having similar responses to geology and snow. Therefore, these species are expected to have a positive residual correlation, but this is not the case, maybe because the threshold I set is not strong enough to detect the positive association. However, I noticed that lowering the threshold from 95% credible interval to 85% identified more species co-occurrences. Also, Poggiato et al. (2021) view that regression coefficients only estimate species niches and not much residual results to infer biotic interactions.

In comparison, the general regression coefficient pattern indicates that the influences of snow, curvature, geology, altitude, northness and eastness are more pronounced in SDMs than JSDM for species that do and do not co-occur (Figure 3-5). Nevertheless, I do not infer that the autecological approach (SDM) has more strength in identifying the important environmental variables than the synecological approach (JSDM). The results of this study are affirmed by Poggiato et al. (2021), where the regression coefficient estimates of 65 alpine plants elucidate that these values are similar in SDMs and JSDMs, and there is difficulty in verifying which model produces a higher correlation coefficient of plant species with environmental variables.

4.2.2. Explained variances in JSDMs and SDMs

Generally, the environmental variables modelled as the fixed effects are the main factors attributed to species distribution compared to the random effects in Figures 3-4 and Appendix 6. These environmental factors are supposed to contribute significantly to species variances.

The results of the total portioning of variance in Figure 3-4F and Appendix 6 shows that for two co-occurring species, namely *Acantholimon androsaceum* and *Alyssum sphacioticum*, the environmental variables contribution is higher in SDMs than JSDMs. Of which I expect the interactions between these species to lead to higher contributions in JSDMs. In contrast, the two species that do not co-occur, namely *Anchusa cespitosa* and *Berberis cretica*, have higher environmental variable contributions in JSDMs than SDMs. I would expect a reverse result because these species do not indicate co-occurrences with the selected threshold for this study. The random effect contributions of species in both models are lower than the environmental variables, which is expected because the environmental variables are significant determinants for species distribution and plant growth (Appendix 6).

4.2.3. Important variables in plant species modelling and differences in JSDM and SDMs

The regression coefficient matrix indicates that geology, snow, curvature, and road are the important environmental variables contributing to the distribution of the five candidate species as identified in the graphs in Figure 3-5 and Appendix 7. Therefore, from this study, I infer slight differences exist in non-biotic variable contribution from both models but may not be ecologically meaningful.

Similarly, the variance proportions show that geology, snow, curvature, and road are the significant drivers for the distribution of these species as identified from previous studies and this study (Bergmeier, 2002; Nyktas, 2012; Vogiatzakis et al., 2003) and shown in Figure 3-4 and Appendix 6. However, the variations in the contribution of each variable to the distribution of species show no consistent pattern in JSDMs and SDMs. I expected species responses to environmental variables to be more pronounced in JSDMs than SDMs. Because of the combined joint responses of multiple species to these environmental variables in JSDM.

4.3. Climate change impact on species distribution and comparison in JSDMs and SDMs

The findings of this study indicate that the potential impact of climate change differs among species and models, as shown in Section 3.5. These were also confirmed by Thuiller et al. (2005), stating that species migration due to climate change is species-specific. Poggiato et al. (2021) view that the regression coefficient estimates, representing environmental factors, remain unchanged in JSDMs or SDMs. Also, in this study, the environmental variables affecting species distribution are similar in JSDMs and SDMs. Therefore, the differences observed from current predictions in JSDMs and SDMs are projected into the future climate change scenario, leading to the same variations observed from the current predictions in future climate projections. Similar patterns were observed in suitable niche areas in JSDMs and SDMs predictions and future climate projection of species that do and do not co-occur in Section 3.5, Table 3-7. *Acantholimon androsaceum*, *Anchusa cespitosa* and *Berberis cretica* have larger suitable areas in SDMs than JSDMs in 2012 also have larger suitable areas in 2112. Similarly, *Prunus prostrata* and *Alyssum sphacioticum*, with larger suitable areas in JSDM than SDMs in 2012, have the same in 2112.

Due to climate change, the upward shift of plant species towards mountain tops is expected in alpine plant communities. These shifts are expected because species follow altitudinal and latitudinal shifts, resulting from climate change (Songer et al., 2012). Also, Lenoir and Svenning (2015) found that species are constrained to shift upwards due to the dispersal barriers referred to as climatic traps. In this study, the future climate scenario projected into 2112 assumes a 61m species upward range shift in the studies of

Parmesan and Yohe (2003). The findings in Section 3.5 and Table 3-7 indicate that in 2112 the potential range shift will lead to more loss of suitable area in JSDMs than in SDMs (Appendix 10).

Thuiller et al. (2005) identified that Mediterranean mountains are very sensitive to climate change climate and would experience an average of 62% loss in range size by 2080. Similarly, the results of the species range shift in JSDMs indicate that between 0.93 - 31.60% of suitable areas will be lost in 2112, while in SDMs, it is between 1.40 - 14.10% (Table 3-6). These results indicate that the loss in suitable niche areas within a century is more pronounced in JSDM than in SDM (Appendix 9 and 10). Furthermore, a loss in the projected suitable niche area is expected for four species in 2112 in JSDMs and SDMs, except for *Alyssum sphacioticum*. Although losses are attributed to suitable habitats, these will also lead to a potential loss of species. Some species' increased loss of suitable habitat may be due to warmer climatic conditions on the mountain modelled by the future climate scenario. Though a significant drawback in evaluating the predictive performance of the future climate scenario models is that these anticipated changes are yet to occur and thus cannot be evaluated (Araújo and Guisan, 2006). Other studies have also confirmed that species range reduction and loss of suitable habitat are anticipated from the potential impact of climate change (Araújo et al., 2011; Barbet-Massin et al., 2012).

Matteodo et al. (2016) study on 65 alpine plant species in the Swiss Alps noticed after 50 years that changes in the snow cover impacted snowbed species. In this study, the future climate scenario depicting reduced snow persistence shows that four snow-dependent species of *Acantholimon androsaceum*, *Anchusa cespitosa*, *Berberis cretica* and *Prunus prostrata* in Figure 3-6 and Table 3-7 are anticipated to lose suitable habitat than gain, confirming that they are vulnerable to climate change. Consequently, conservation efforts should be geared towards protecting these rare endemics on Lefka Ori. Also, species with a preference for warmer conditions are expected to colonized alpine plant communities due to the warming climate (Vittoz et al., 2013). The combined suitable area of *Alyssum sphacioticum* in Table 3-7 in JSDM and SDM is expected to increase in 2112 compared to other species having reduced suitable areas in the future. Moreover, this is a species with low occurrence points in the study area. Also, the species prefers low snow persistence, as indicated in the snow gradient plot in JSDM and SDM in Figure 3-6 C, D. Therefore, the warming climate is anticipated to be favourable to this species compared to the others.

4.4. Limitations

A significant limitation to this study is that JSDMs are computationally efficient and deals with large volumes of data, likewise, assumed to provide better predictions due to their increased complexity. However, the computational time needed to run the model has a linear increase with the number of species fitted into the model (Tikhonov et al., 2020a). Therefore, fitting the 42 species into the HMSC framework used for this study took four to five days. However, for single species, it was under 3 hours.

In addition, the decision about the type of random effect to be included in the HMSC modelling framework to capture biotic interactions connoting species co-occurrences in Figure 2-3 was a challenge because I had no field observation to confirm species interactions in situ. However, this led to a subjective decision in selecting the random effect; nevertheless, this is still a challenge in the model used for this study. Similarly, understanding the type of biotic interactions derived from the residual correlation matrix without prior knowledge of the species co-occurrences on the field hindered practical explanation of the observed occurrence patterns.

5. CONCLUSION AND RECOMMENDATION

5.1. Conclusion

This study compared autecology and synecological approaches (JSDMs and SDMs) in plant species distribution predictions. The accuracies in RMSE and AUC in JSDMs and SDMs had slight variations but not enough to conclude which model yields higher accuracy. Furthermore, environmental variables contributed more to species variances than random factors in JSDMs and SDMs, although slightly higher in JSDMs than SDMs. Also, a loss of suitable habitat for these species in the future scenario is anticipated due to climate change. This research had three questions, and the conclusions are presented below:

Question 1: In modelling species that are dependent on other species, do they perform better in JSDM than SDMs?

- The RMSE values of 3 co-occurring species (dependent) are lower in SDMs than JSDMs
- The RMSE values of 2 non-co-occurring species (independent) are lower in JSDM than SDMs
- The result of the statistical analysis proved there is a significant difference in the mean AUCs of the 5 modelled species in JSDMs and SDMs ($p > 0.05$).

Question 2: Which variables are important for the modelling of plant species, and is there a difference in JSDM and SDMs?

- The important variables are geology, snow, curvature, road and altitude
- The proportioned variances in SDMs are slightly higher than the proportions in JSDMs

Question 3: What is the effect of not accounting for species community interactions in future climate projections?

- Biotic interactions are assumed to remain the same in the future scenario model for this study. The results show that species range loss will be more pronounced in JSDMs (which captures biotic interactions) than SDMs. Similarly, the suitable niche area will decline for four out of the five species within a century.

5.2. Recommendation

The HMSC framework utilizes data on traits and phylogenies. Therefore, I propose that in future studies of these unique alpine communities with the HMSC framework, traits and phylogenies should be included to utilise the model's capabilities entirely.

LIST OF REFERENCES

- Abrego, N., Norberg, A., Ovaskainen, O., 2017. Measuring and predicting the influence of traits on the assembly processes of wood-inhabiting fungi. *J. Ecol.* 105, 1070–1081. <https://doi.org/10.1111/1365-2745.12722>
- Allen, M., 2017. Post Hoc Tests: Tukey Honestly Significant Difference Test, in: *The SAGE Encyclopedia of Communication Research Methods*. SAGE Publications, Inc, 2455 Teller Road, Thousand Oaks California 91320. <https://doi.org/10.4135/9781483381411.n452>
- Anderson, R.P., 2013. A framework for using niche models to estimate impacts of climate change on species distributions. *Ann. N. Y. Acad. Sci.* 1297, 8–28. <https://doi.org/10.1111/nyas.12264>
- Anderson, S., 1994. Area and endemism. *Q. Rev. Biol.* 69, 451–471. <https://doi.org/10.1086/418743>
- Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D., Thuiller, W., 2011. Climate change threatens European conservation areas. *Ecol. Lett.* 14, 484–492. <https://doi.org/10.1111/j.1461-0248.2011.01610.x>
- Araújo, M.B., Guisan, A., 2006. Five (or so) challenges for species distribution modelling. *J. Biogeogr.* 33, 1677–1688. <https://doi.org/10.1111/j.1365-2699.2006.01584.x>
- Austin, M.P., 2002. Spatial prediction of species distribution: An interface between ecological theory and statistical modelling. *Ecol. Modell.* 157, 101–118. [https://doi.org/10.1016/S0304-3800\(02\)00205-3](https://doi.org/10.1016/S0304-3800(02)00205-3)
- Barbet-Massin, M., Thuiller, W., Jiguet, F., 2012. The fate of European breeding birds under climate, land-use and dispersal scenarios. *Glob. Chang. Biol.* 18, 881–890. <https://doi.org/10.1111/j.1365-2486.2011.02552.x>
- Bergmeier, E., 2002. The vegetation of the high mountains of crete - A revision and multivariate analysis. *Phytocoenologia* 32, 205–249. <https://doi.org/10.1127/0340-269X/2002/0032-0205>
- Bevans, R., 2021. Two-way ANOVA | When and How to Use It (With Examples). Scribbr.
- Boulangéat, I., Gravel, D., Thuiller, W., 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecol. Lett.* 15, 584–593. <https://doi.org/10.1111/j.1461-0248.2012.01772.x>
- Brooks, S.P., Gelman, A., 1998. General methods for monitoring convergence of iterative simulations)? *J. Comput. Graph. Stat.* 7, 434–455. <https://doi.org/10.1080/10618600.1998.10474787>
- Bystrova, D., Poggiato, G., Arbel, J., Thuiller, W., 2021. Latent factor models : a tool for dimension reduction in joint species distribution models. HAL.
- Campaign, P., Groups, S., Species, I., Commission, S., Mediterranean, T., Plant, Island, Group, S., Foundation, M., World, T., Union, C., Species, T., Commission, S., Mediterranean, T., Plant, Islands, Group, S., Plans, A., 2005. The Top 50 Mediterranean Island Plants, The Top 50 Mediterranean Island Plants. <https://doi.org/10.2305/iucn.ch.2005.8.en>
- Cantor, S.B., Sun, C.C., Tortolero-Luna, G., Richards-Kortum, R., Follen, M., 1999. A comparison of C/B ratios from studies using receiver operating characteristic curve analysis. *J. Clin. Epidemiol.* 52, 885–892. [https://doi.org/10.1016/S0895-4356\(99\)00075-X](https://doi.org/10.1016/S0895-4356(99)00075-X)
- Clark, J.S., Gelfand, A.E., Woodall, C.W., Zhu, K., 2014. More than the sum of the parts: Forest climate response from joint species distribution models. *Ecol. Appl.* 24, 990–999. <https://doi.org/10.1890/13-1015.1>
- Cruse, B., Liedloff, A.C., Wintle, B.A., 2012. A new method for dealing with residual spatial autocorrelation in species distribution models. *Ecography (Cop.)*. 35, 879–888. <https://doi.org/10.1111/j.1600-0587.2011.07138.x>
- D’Amen, M., Mod, H.K., Gotelli, N.J., Guisan, A., 2018. Disentangling biotic interactions, environmental filters, and dispersal limitation as drivers of species co-occurrence. *Ecography (Cop.)*. 41, 1233–1244. <https://doi.org/10.1111/ecog.03148>
- Díaz, S., Settele, J., Brondízio, E., Ferrier, S., Ninan, K.N., Leadley, P., Alkemade, R., Acosta, L.A., Akçakaya, H.R., Brotons, L., Cheung, W., Christensen, V., Harhash, K.A., Kabubo-Mariara, J., Lundquist, C., Obersteiner, M., Pereira, H., Peterson, G., Pichs-Madruga, R., Ravindranath, N.H., Rondini, C., Wintle, B. (eds.), 2019. Summary for policymakers of the methodological assessment of scenarios and models of biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. *Secr. Intergov. Sci. Platf. Biodivers. Ecosyst. Serv.* 39. <https://doi.org/10.1590/1676-0611201600010001>
- Dormann, C., Schymanski, S.J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M., Morin, X.,

- Römermann, C., Schröder, B., Singer, A., 2012. Correlation and process in species distribution models: Bridging a dichotomy. *J. Biogeogr.* 39, 2119–2131. <https://doi.org/10.1111/j.1365-2699.2011.02659.x>
- Dormann, C.F., Bobrowski, M., Dehling, D.M., Harris, D.J., Hartig, F., Lischke, H., Moretti, M.D., Pagel, J., Pinkert, S., Schleuning, M., Schmidt, S.I., Sheppard, C.S., Steinbauer, M.J., Zeuss, D., Kraan, C., 2018. Biotic interactions in species distribution modelling: 10 questions to guide interpretation and avoid false conclusions. *Glob. Ecol. Biogeogr.* 27, 1004–1016. <https://doi.org/10.1111/geb.12759>
- Drummond, A.J., Ho, S.Y.W., Phillips, M.J., Rambaut, A., 2006. Relaxed Phylogenetics and Dating with Confidence. *PLoS Biol.* 4, e88. <https://doi.org/10.1371/journal.pbio.0040088>
- Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L., A. Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC. M. Overton, J., Townsend Peterson, A., J. Phillips, S., Richardson, K., Scachetti-Pereira, R., E. Schapire, R., Soberón, J., Williams, S., S. Wisz, M., E. Zimmermann, N., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography (Cop.)*. 29, 129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- Enquist, B.J., Feng, X., Boyle, B., Maitner, B., Newman, E.A., Jørgensen, P.M., Roehrdanz, P.R., Thiers, B.M., Burger, J.R., Corlett, R.T., Couvreur, T.L.P., Dauby, G., Donoghue, J.C., Foden, W., Lovett, J.C., Marquet, P.A., Merow, C., Midgley, G., Morueta-Holme, N., Neves, D.M., Oliveira-Filho, A.T., Kraft, N.J.B., Park, D.S., Peet, R.K., Pilet, M., Serra-Diaz, J.M., Sandel, B., Schildhauer, M., Šimová, I., Violle, C., Wieringa, J.J., Wisser, S.K., Hannah, L., Svenning, J.C., McGill, B.J., 2019. The commonness of rarity: Global and future distribution of rarity across land plants. *Sci. Adv.* 5, 1–14. <https://doi.org/10.1126/sciadv.aaz0414>
- Evert, K.-J., Ballard (deceased), E.B., Elsworth, D.J., Oquiñena, I., Schmerber, J.-M., Stipe (deceased), R.E. (Eds.), 2010a. 273 autecology [n], in: *Encyclopedic Dictionary of Landscape and Urban Planning*. Springer Berlin Heidelberg, Berlin, Heidelberg, p. 47. https://doi.org/10.1007/978-3-540-76435-9_728
- Evert, K.-J., Ballard (deceased), E.B., Elsworth, D.J., Oquiñena, I., Schmerber, J.-M., Stipe (deceased), R.E. (Eds.), 2010b. 6266 synecology [n], in: *Encyclopedic Dictionary of Landscape and Urban Planning*. Springer Berlin Heidelberg, Berlin, Heidelberg, p. 1010. https://doi.org/10.1007/978-3-540-76435-9_14423
- Fernandez-Calzado, R., Ghosn, D., Gottfried, M., Kazakis, G., Mesa, J.M., Pauli, H., Merzouki, A., 2013. Patterns of endemism along an elevation gradient in sierra nevada (Spain) and lefka ori (Crete, Greece). *Pirineos* 168, 7–24. <https://doi.org/10.3989/Pirineos.2013.168001>
- Foggi, B., Viciani, D., Baldini, R.M., Carta, A., Guidi, T., 2015. Conservation assessment of the endemic plants of the Tuscan Archipelago, Italy. *ORYX* 49, 118–126. <https://doi.org/10.1017/S0030605313000288>
- Forman, R.T.T., Alexander, L.E., 1998. Roads and their Major Ecological Effects. *Annu. Rev. Ecol. Syst.* 29, 207–231. <https://doi.org/10.1146/annurev.ecolsys.29.1.207>
- Franklin, J., 2012. *Species distribution modeling, Mapping species distributions*. Cambridge University Press, New York. <https://doi.org/10.1017/cbo9780511810602.003>
- Franklin, J., 2010. *Mapping Species Distributions: Spatial Inference and Prediction, Ecology, Biodiversity and Conservation*. Cambridge University Press, Cambridge. <https://doi.org/DOI:10.1017/CBO9780511810602>
- Frost, J., 2019. Using Post Hoc Tests with ANOVA - Statistics By Jim [WWW Document]. URL <https://statisticsbyjim.com/anova/post-hoc-tests-anova/> (accessed 7.8.21).
- Gelman, A., Rubin, D.B., 1992. Inference from Iterative Simulation Using Multiple Sequences. *Stat. Sci.* 7, 457–472. <https://doi.org/10.1214/ss/1177011136>
- Giorgi, F., Lionello, P., 2008. Climate change projections for the Mediterranean region. *Glob. Planet. Change* 63, 90–104. <https://doi.org/10.1016/j.gloplacha.2007.09.005>
- Godsoe, W., Franklin, J., Blanchet, F.G., 2017. Effects of biotic interactions on modeled species' distribution can be masked by environmental gradients. *Ecol. Evol.* 7, 654–664. <https://doi.org/10.1002/ece3.2657>
- Goedecke, F., Bergmeier, E., 2018. Ecology and potential distribution of the {Cretan} endemic tree species *Zelkova abelicea*. *J. Mediterr. Ecol.* 16, 15–26.
- Google Earth [WWW Document], n.d. URL <https://earth.google.com/web/@35.34698897,24.11119306,-81799.04808029a,116536.42963557d,35y,->

- 0.0223901h,4.70612624t,0.0038r?utm_source=earth7&utm_campaign=vine&hl=en (accessed 4.23.21).
- Grabherr, G., Gottfried, M., Pauli, H., 1994. Climate effects on mountain plants. *Nature* 369, 448–448. <https://doi.org/10.1038/369448a0>
- Graham, M.H., 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84, 2809–2815. <https://doi.org/10.1890/02-3114>
- Guisan, A., Theurillat, J.-P., Kienast, F., 1998. Predicting the Potential Distribution of Plant Species in an Alpine Environment, Source: *Journal of Vegetation Science*.
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: Offering more than simple habitat models. *Ecol. Lett.* 8, 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecol. Modell.* 135, 147–186. [https://doi.org/10.1016/S0304-3800\(00\)00354-9](https://doi.org/10.1016/S0304-3800(00)00354-9)
- Hagen, J.B., 2010. History of Plant Ecology, in: *Encyclopedia of Life Sciences*. John Wiley & Sons, Ltd, Chichester, UK. <https://doi.org/10.1002/9780470015902.a0003288.pub2>
- Hamid, M., Khuroo, A.A., Charles, B., Ahmad, R., Singh, C.P., Aravind, N.A., 2019. Impact of climate change on the distribution range and niche dynamics of Himalayan birch, a typical treeline species in Himalayas. *Biodivers. Conserv.* 28, 2345–2370. <https://doi.org/10.1007/s10531-018-1641-8>
- Hamra, G., MacLehose, R., Richardson, D., 2013. Markov Chain Monte Carlo: an introduction for epidemiologists. *Int. J. Epidemiol.* 42, 627–634. <https://doi.org/10.1093/ije/dyt043>
- Harrington, S.M., Wishingrad, V., Thomson, R.C., 2020. Properties of Markov Chain Monte Carlo Performance across Many Empirical Alignments. *Mol. Biol. Evol.* <https://doi.org/10.1093/molbev/msaa295>
- Heegaard, E., 2002. A model of alpine species distribution in relation to snowmelt time and altitude. *J. Veg. Sci.* 13, 493–504. <https://doi.org/10.1111/j.1654-1103.2002.tb02076.x>
- HMSC | Statistical Ecology | University of Helsinki [WWW Document], 2020. URL <https://www2.helsinki.fi/en/researchgroups/statistical-ecology/hmsc> (accessed 5.9.21).
- Huston, M.A., 1995. *Biological diversity: the coexistence of species on changing landscapes*, Repr. ed. Cambridge: Cambridge university press.
- Inouye, D.W., 2020. Effects of climate change on alpine plants and their pollinators. *Ann. N. Y. Acad. Sci.* <https://doi.org/10.1111/nyas.14104>
- IPCC, 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Ippc. Intergovernmental Panel on Climate Change, Geneva.
- Işik, K., 2011. Rare and endemic species: why are they prone to extinction? *. *Turk J Bot* 35, 411–417. <https://doi.org/10.3906/bot-1012-90>
- IUCN, 2010. *Biodiversity, it's now or never* | IUCN [WWW Document]. URL <https://www.iucn.org/content/biodiversity-its-now-or-never> (accessed 6.3.20).
- IUCN, 2003. *Iucn Definitions — English*.
- Jeschke, J.M., Strayer, D.L., 2008. Usefulness of Bioclimatic Models for Studying Climate Change and Invasive Species. <https://doi.org/10.1196/annals.1439.002>
- Katsaounis, C., 2012. *Habitat use of the endangered and endemic Cretan Capricorn and impact of domestic goats* (Master's Thesis). University of Twente.
- Kazakis, G., Ghosn, D., Vogiatzakis, I.N., Papanastasis, V.P., 2007. Vascular plant diversity and climate change in the alpine zone of the Lefka Ori, Crete. *Biodivers. Conserv.* 16, 1603–1615. <https://doi.org/10.1007/s10531-006-9021-1>
- Keller, F., Goyette, S., Beniston, M., 2005. Sensitivity analysis of snow cover to climate change scenarios and their impact on plant habitats in alpine terrain. *Clim. Change* 72, 299–319. <https://doi.org/10.1007/s10584-005-5360-2>
- Kelly, A.E., Goulden, M.L., 2008. Rapid shifts in plant distribution with recent climate change. *Proc. Natl. Acad. Sci. U. S. A.* 105, 11823–11826. <https://doi.org/10.1073/pnas.0802891105>
- Körner, C., 1999. *Alpine Plant Life*, *Alpine Plant Life*. Springer Berlin Heidelberg. <https://doi.org/10.1007/978-3-642-98018-3>
- Kougioumoutzis, K., Kokkoris, I.P., Panitsa, M., Trigas, P., Strid, A., Dimopoulos, P., 2020. Spatial phylogenetics, biogeographical patterns and conservation implications of the endemic flora of Crete (Aegean, Greece) under climate change scenarios. *Biology (Basel)*. 9, 1–22. <https://doi.org/10.3390/biology9080199>
- Krespi, D., 2018. Slope stability and rock fall rates in a Mediterranean mountain range (Lefka Ori, Crete).

Wageningen University.

- Kutner, M.H., Nachtsheim, C.J., Neter, J., Li, W., McGraw-Hill, W., Burr Ridge, B., Dubuque, I., Madison, I., New York San Francisco St Louis Bangkok Bogota Caracas Kuala Lumpur Lisbon London Madrid Mexico City Milan Montreal New Delhi Santiago Seoul Singapore Sydney Taipei Toronto, W., 2005. *Applied Linear Statistical Models Fifth Edition* Irwin.
- Lanfear, R., Hua, X., Warren, D.L., 2016. Estimating the effective sample size of tree topologies from Bayesian phylogenetic analyses. *Genome Biol. Evol.* 8, 2319–2332. <https://doi.org/10.1093/gbe/evw171>
- Lazarina, M., Kallimanis, A.S., Dimopoulos, P., Psaralexi, M., Michailidou, D.E., Sgardelis, S.P., 2019. Patterns and drivers of species richness and turnover of neo-endemic and palaeo-endemic vascular plants in a Mediterranean hotspot: The case of Crete, Greece. *J. Biol. Res.* 26, 1–13. <https://doi.org/10.1186/s40709-019-0106-x>
- Leach, K., Montgomery, W.I., Reid, N., 2016. Modelling the influence of biotic factors on species distribution patterns. *Ecol. Modell.* 337, 96–106. <https://doi.org/10.1016/j.ecolmodel.2016.06.008>
- Lenoir, J., Svenning, J.-C., 2013. Latitudinal and Elevational Range Shifts under Contemporary Climate Change, in: *Encyclopedia of Biodiversity*. Elsevier, pp. 599–611. <https://doi.org/10.1016/B978-0-12-384719-5.00375-0>
- Lenoir, J., Svenning, J.C., 2015. Climate-related range shifts - a global multidimensional synthesis and new research directions. *Ecography (Cop.)*. 38, 15–28. <https://doi.org/10.1111/ecog.00967>
- Li, X., Hijazi, I., Xu, M., Lv, H., El Meouche, R., 2016. Implementing two methods in GIS software for indoor routing: an empirical study. *Multimed. Tools Appl.* 75, 17449–17464. <https://doi.org/10.1007/s11042-015-3156-6>
- Liu, C., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography (Cop.)*. 28, 385–393. <https://doi.org/10.1111/j.0906-7590.2005.03957.x>
- Magory Cohen, T., Dor, R., 2019. The effect of local species composition on the distribution of an avian invader. *Sci. Rep.* 9, 1–9. <https://doi.org/10.1038/s41598-019-52256-9>
- Marcantonio, M., Rocchini, D., Geri, F., Bacaro, G., Amici, V., 2013. Biodiversity, roads, & landscape fragmentation: Two Mediterranean cases. *Appl. Geogr.* 42, 63–72. <https://doi.org/10.1016/j.apgeog.2013.05.001>
- Marquardt, D.W., 1970. Generalized inverses, ridge regression, biased linear estimation, and nonlinear estimation. *Technometrics* 12, 591–612. <https://doi.org/10.1080/00401706.1970.10488699>
- Matteodo, M., Ammann, K., Verrecchia, E.P., Vittoz, P., 2016. Snowbeds are more affected than other subalpine–alpine plant communities by climate change in the Swiss Alps. *Ecol. Evol.* 6, 6969–6982. <https://doi.org/10.1002/ece3.2354>
- Médail, F., 2017. The specific vulnerability of plant biodiversity and vegetation on Mediterranean islands in the face of global change. *Reg. Environ. Chang.* <https://doi.org/10.1007/s10113-017-1123-7>
- Médail, F., Quézel, P., 1997. Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. *Ann. Missouri Bot. Gard.* 84, 112–127. <https://doi.org/10.2307/2399957>
- Meier, E.S., Kienast, F., Pearman, P.B., Svenning, J.C., Thuiller, W., Araújo, M.B., Guisan, A., Zimmermann, N.E., 2010. Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography (Cop.)*. 33, 1038–1048. <https://doi.org/10.1111/j.1600-0587.2010.06229.x>
- Meineri, E., Skarpaas, O., Vandvik, V., 2012. Modeling alpine plant distributions at the landscape scale: Do biotic interactions matter? *Ecol. Modell.* 231, 1–10. <https://doi.org/10.1016/j.ecolmodel.2012.01.021>
- Menteli, V., Krigas, N., Avramakis, M., Turland, N., Vokou, D., 2019. Endemic plants of Crete in electronic trade and wildlife tourism: Current patterns and implications for conservation. *J. Biol. Res.* 26, 1–14. <https://doi.org/10.1186/s40709-019-0104-z>
- Mod, H.K., Chevalier, M., Luoto, M., Guisan, A., 2020. Scale dependence of ecological assembly rules: Insights from empirical datasets and joint species distribution modelling. *J. Ecol.* 108, 1967–1977. <https://doi.org/10.1111/1365-2745.13434>
- Morin, X., Thuiller, W., 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology* 90, 1301–1313. <https://doi.org/10.1890/08-0134.1>
- Nagy, L., Grabherr, G., 2009. *The Biology of Alpine Habitats*. Oxford University Press (OUP), Oxford.
- Naimi, B., Skidmore, A.K., Groen, T.A., Hamm, N.A.S., 2011. Spatial autocorrelation in predictors

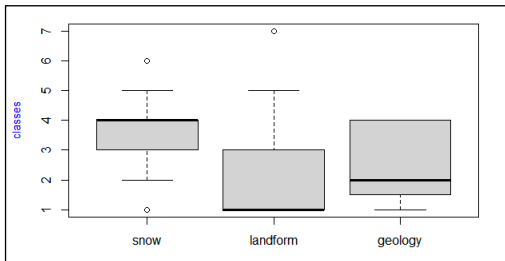
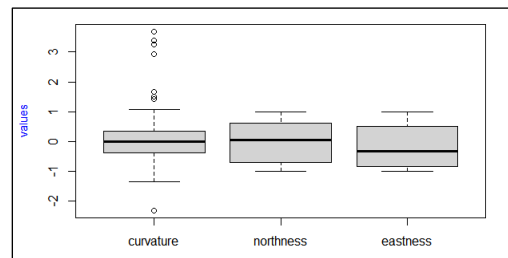
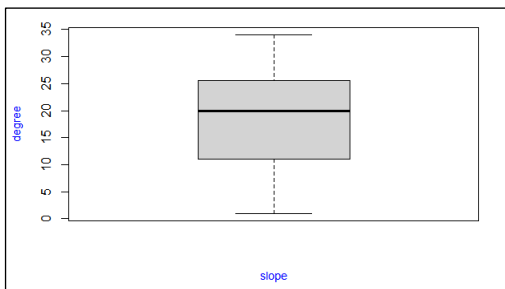
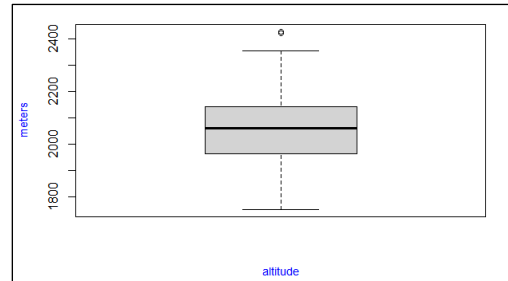
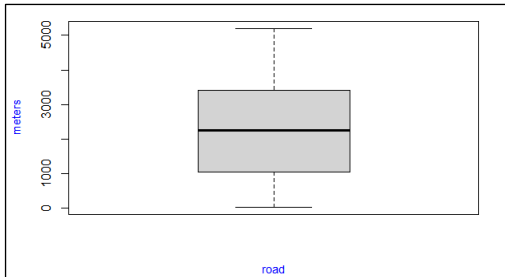
- reduces the impact of positional uncertainty in occurrence data on species distribution modelling. *J. Biogeogr.* 38, 1497–1509. <https://doi.org/10.1111/j.1365-2699.2011.02523.x>
- National Research Council, 1992. The Values of Biodiversity 2.1, in: National Research Council (US) Committee on Noneconomic and Economic Value of Biodiversity. *Perspectives on Biodiversity: Valuing Its Role in an Everchanging World*. National Academies Press (US), Washington (DC), pp. 13–17. <https://doi.org/https://doi.org/10.17226/9589>
- Neumann, W., Martinuzzi, S., Estes, A.B., Pidgeon, A.M., Dettki, H., Ericsson, G., Radeloff, V.C., 2015. Opportunities for the application of advanced remotely-sensed data in ecological studies of terrestrial animal movement. *Mov. Ecol.* 3, 8. <https://doi.org/10.1186/s40462-015-0036-7>
- Niskanen, A., Luoto, M., Väre, H., Heikkinen, R.K., 2017. Models of Arctic-alpine refugia highlight importance of climate and local topography. *Polar Biol.* 40, 489–502. <https://doi.org/10.1007/s00300-016-1973-3>
- Nyktas, P., 2012. Dynamic feedbacks between landform, landscape Processes and vegetation patterns. A modelling framework to predict the distribution of plant species in Lefka Ori, Crete, Greece. University of Reading.
- Opedal, Ø.H., Hegland, S.J., 2020. Using hierarchical joint models to study reproductive interactions in plant communities. *J. Ecol.* 108, 485–495. <https://doi.org/10.1111/1365-2745.13301>
- Ovaskainen, O., Abrego, N., 2020. Joint Species Distribution Modelling, Joint Species Distribution Modelling. Cambridge University Press. <https://doi.org/10.1017/9781108591720>
- Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T., Abrego, N., 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecol. Lett.* 20, 561–576. <https://doi.org/10.1111/ele.12757>
- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42. <https://doi.org/10.1038/nature01286>
- Pearce, J., Ferrier, S., 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Modell.* 133, 225–245. [https://doi.org/10.1016/S0304-3800\(00\)00322-7](https://doi.org/10.1016/S0304-3800(00)00322-7)
- Pescador, D.S., Sierra-Almeida, Á., Torres, P.J., Escudero, A., 2016. Summer freezing resistance: A critical filter for plant community assemblies in mediterranean high mountains. *Front. Plant Sci.* 7. <https://doi.org/10.3389/fpls.2016.00194>
- Pianka, E.R., 2008a. Synecology, in: *Encyclopedia of Ecology*. Elsevier, pp. 3458–3461. <https://doi.org/10.1016/B978-008045405-4.00550-4>
- Pianka, E.R., 2008b. Autecology, in: *Encyclopedia of Ecology*. Elsevier, pp. 285–287. <https://doi.org/10.1016/B978-008045405-4.00458-4>
- Poggiato, G., Münkemüller, T., Bystrova, D., Arbel, J., Clark, J.S., Thuiller, W., 2021. On the Interpretations of Joint Modeling in Community Ecology. *Trends Ecol. Evol.* 36, 391–401. <https://doi.org/10.1016/j.tree.2021.01.002>
- Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O'Hara, R.B., Parris, K.M., Vesk, P.A., Mccarthy, M.A., 2014. Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods Ecol. Evol.* 5, 397–406. <https://doi.org/10.1111/2041-210X.12180>
- Pringle, E.G., 2000. Orienting the Interaction Compass: Resource Availability as a Major Driver of Context Dependence. OPEN ACCESS Cit. Pringle EG 14, 2000891. <https://doi.org/10.1371/journal.pbio.2000891>
- Randin, C., Vuissoz, G., Liston, G., Vittoz, P., Guisan, A., 2009. Introduction of snow and geomorphic disturbance variables into predictive models of alpine plant distribution in the western swiss alps. *Arctic, Antarct. Alp. Res.* 41, 347–361. <https://doi.org/10.1657/1938-4246-41.3.347>
- Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M., Guisan, A., 2006. Are Niche-Based Species Distribution Models Transferable in Space?, Source: *Journal of Biogeography*.
- Rinawati, F., Stein, K., Lindner, A., 2013. Climate Change Impacts on Biodiversity—The Setting of a Lingering Global Crisis. *Diversity* 5, 114–123. <https://doi.org/10.3390/d5010114>
- Schöb, C., Kammer, P.M., Choler, P., Veit, H., 2009. Small-scale plant species distribution in snowbeds and its sensitivity to climate change. *Plant Ecol.* 200, 91–104. <https://doi.org/10.1007/s11258-008-9435-9>
- Shi, X., Li, M., Hunter, O., Guetti, B., Andrew, A., Stommel, E., Bradley, W., Karagas, M., 2019. Estimation of environmental exposure: interpolation, kernel density estimation or snapshotting. *Ann. GIS* 25, 1–8. <https://doi.org/10.1080/19475683.2018.1555188>
- Soberon, J., Peterson, A.T., 2005. Interpretation of Models of Fundamental Ecological Niches and

- Species' Distributional Areas. *Biodivers. Informatics* 2. <https://doi.org/10.17161/bi.v2i0.4>
- Sofaer, H.R., Jarnevich, C.S., Pearse, I.S., Smyth, R.L., Auer, S., Cook, G.L., Edwards, T.C., Guala, G.F., Howard, T.G., Morisette, J.T., Hamilton, H., 2019. Development and Delivery of Species Distribution Models to Inform Decision-Making. *Bioscience* 69, 544–557. <https://doi.org/10.1093/biosci/biz045>
- Songer, M., Delion, M., Biggs, A., Huang, Q., 2012. Modeling impacts of climate change on giant panda habitat. *Int. J. Ecol.* 2012, 1–12. <https://doi.org/10.1155/2012/108752>
- Spanos, I., Platis, P., Meliadis, I., Tsiontis, A., 2008. A review on the ecology and management of the Samaria Gorge, a Greek biosphere reserve. *J. Geogr. Reg. Plan.* 1, 19–33.
- Stebbins, G.L., 1942. The Genetic approach to problems of rare and endemic species, Source: Madroño.
- Taylor-Rodríguez, D., Kaufeld, K., Schliep, E.M., Clark, J.S., Gelfand, A.E., 2017. Joint species distribution modeling: Dimension reduction using Dirichlet processes. *Bayesian Anal.* 12, 939–967. <https://doi.org/10.1214/16-BA1031>
- Taylor, R., 1990. Interpretation of the Correlation Coefficient: A Basic Review. *J. Diagnostic Med. Sonogr.* 6, 35–39. <https://doi.org/10.1177/875647939000600106>
- Thuiller, W., Albert, C., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, A., Hickler, T., Midgley, G.F., Paterson, J., Schurr, F.M., Sykes, M.T., Zimmermann, N.E., 2008. Predicting global change impacts on plant species' distributions: Future challenges. *Perspect. Plant Ecol. Evol. Syst.* 9, 137–152. <https://doi.org/10.1016/j.ppees.2007.09.004>
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. *Proc. Natl. Acad. Sci. U. S. A.* 102, 8245–8250. <https://doi.org/10.1073/pnas.0409902102>
- Tikhonov, G., Abrego, N., Dunson, D., Ovaskainen, O., 2017. Using joint species distribution models for evaluating how species-to-species associations depend on the environmental context. *Methods Ecol. Evol.* 8, 443–452. <https://doi.org/10.1111/2041-210X.12723>
- Tikhonov, G., Duan, L., Abrego, N., Newell, G., White, M., Dunson, D., Ovaskainen, O., 2020a. Computationally efficient joint species distribution modeling of big spatial data. *Ecology* 101. <https://doi.org/10.1002/ecy.2929>
- Tikhonov, G., Opedal, Ø.H., Abrego, N., Lehikoinen, A., de Jonge, M.M.J., Oksanen, J., Ovaskainen, O., 2020b. Joint species distribution modelling with the r-package Hmsc. *Methods Ecol. Evol.* 11, 442–447. <https://doi.org/10.1111/2041-210X.13345>
- Treml, V., Chuman, T., 2015. Ecotonal Dynamics of the Altitudinal Forest Limit are Affected by Terrain and Vegetation Structure Variables: An Example from the Sudetes Mountains in Central Europe. *Arctic, Antarct. Alp. Res.* 47, 133–146. <https://doi.org/10.1657/AAAR0013-108>
- Trigas, P., Panitsa, M., Tsiftsis, S., 2013. Elevational Gradient of Vascular Plant Species Richness and Endemism in Crete-The Effect of Post-Isolation Mountain Uplift on a Continental Island System) Elevational Gradient of Vascular Plant Species Richness and Endemism in Crete-The Effect of Post-Iso. *PLoS One* 8, 59425. <https://doi.org/10.1371/journal.pone.0059425>
- Trombulak, S.C., Frissell, C.A., 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conserv. Biol.* 14, 18–30. <https://doi.org/10.1046/j.1523-1739.2000.99084.x>
- UNESCO, 2014. Gorge of Samaria National Park - UNESCO World Heritage Centre [WWW Document]. URL <https://whc.unesco.org/en/tentativelists/5865/> (accessed 6.14.20).
- Vieira, K.S., Montenegro, P.F.G., Santana, G.G., Vieira, W.L. da S., 2018. Effect of climate change on distribution of species of common horned frogs in South America. *PLoS One* 13, e0202813. <https://doi.org/10.1371/journal.pone.0202813>
- Vinutha, H.P., Poornima, B., Sagar, B.M., 2018. Detection of Outliers Using Interquartile Range Technique from Intrusion Dataset, in: Satapathy, S.C., Tavares, J.M.R.S., Bhateja, V., Mohanty, J.R. (Eds.), *Information and Decision Sciences*. Springer Singapore, Singapore, pp. 511–518.
- Vittoz, P., Cherix, D., Gonseth, Y., Lubini, V., Maggini, R., Zbinden, N., Zumbach, S., 2013. Climate change impacts on biodiversity in Switzerland: A review. *J. Nat. Conserv.* 21, 154–162. <https://doi.org/10.1016/j.jnc.2012.12.002>
- Vogiatzakis, I.N., Griffiths, G.H., 2006. A GIS-Based Empirical Model for Vegetation Prediction in Lefka Ori. *Ecology* 184, 311–323. <https://doi.org/10.1007/sl>
- Vogiatzakis, I.N., Griffiths, G.H., 2001. Vegetation-environment relationships in Lefka Ori (Crete, Greece) : ordination results from montane-mediterranean and oro-mediterranean communities. *Ecol. Mediterr.* 27, 1–13. <https://doi.org/10.3406/ecmed.2001.1903>
- Vogiatzakis, I.N., Griffiths, G.H., Mannion, A.M., 2003. Environmental factors and vegetation

- composition, Lefka Ori massif, Crete, S. Aegean. *Glob. Ecol. Biogeogr.* 12, 131–146.
<https://doi.org/10.1046/j.1466-822X.2003.00021.x>
- Wallace, C.S., Gass, L., 2008. Elevation Derivatives for Mojave Desert Tortoise Habitat Models, USGS Open File Report.
- Warton, D.I., Blanchet, F.G., O'Hara, R.B., Ovaskainen, O., Taskinen, S., Walker, S.C., Hui, F.K.C., 2015. So Many Variables: Joint Modeling in Community Ecology. *Trends Ecol. Evol.*
<https://doi.org/10.1016/j.tree.2015.09.007>
- Weiskopf, S.R., Rubenstein, M.A., Crozier, L.G., Gaichas, S., Griffis, R., Halofsky, J.E., Hyde, K.J.W., Morelli, T.L., Morissette, J.T., Muñoz, R.C., Pershing, A.J., Peterson, D.L., Poudel, R., Staudinger, M.D., Sutton-Grier, A.E., Thompson, L., Vose, J., Weltzin, J.F., Whyte, K.P., 2020. Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. *Sci. Total Environ.* <https://doi.org/10.1016/j.scitotenv.2020.137782>
- Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A., Snyder, M.A., 2009. Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19729–19736. <https://doi.org/10.1073/pnas.0901639106>
- Wilkinson, D.P., Golding, N., Guillera-Arroita, G., Tingley, R., McCarthy, M.A., 2021. Defining and evaluating predictions of joint species distribution models. *Methods Ecol. Evol.* 12, 394–404.
<https://doi.org/10.1111/2041-210X.13518>
- Wilkinson, D.P., Golding, N., Guillera-Arroita, G., Tingley, R., McCarthy, M.A., 2019. A comparison of joint species distribution models for presence–absence data. *Methods Ecol. Evol.* 10, 198–211.
<https://doi.org/10.1111/2041-210X.13106>
- Williams, J.N., Seo, C., Thorne, J., Nelson, J.K., Erwin, S., O'Brien, J.M., Schwartz, M.W., 2009. Using species distribution models to predict new occurrences for rare plants. *Divers. Distrib.* 15, 565–576.
<https://doi.org/10.1111/j.1472-4642.2009.00567.x>
- WWF, 2020. Living Planet Report 2020 - Bending the curve of biodiversity loss, WWF.
- Yu, F., Wang, T., Groen, T.A., Skidmore, A.K., Yang, X., Ma, K., Wu, Z., 2019. Climate and land use changes will degrade the distribution of Rhododendrons in China. *Sci. Total Environ.* 659, 515–528.
<https://doi.org/10.1016/j.scitotenv.2018.12.223>
- Yule, G.U., 1938. Notes of Karl Pearson's Lectures on the Theory of Statistics, 1884–96. *Biometrika* 30, 198. <https://doi.org/10.2307/2332238>
- Zobel, M., 1997. The relative role of species pools in determining plant species richness: An alternative explanation of species coexistence? *Trends Ecol. Evol.* 12, 266–269.
[https://doi.org/10.1016/S0169-5347\(97\)01096-3](https://doi.org/10.1016/S0169-5347(97)01096-3)
- Zurell, D., Franklin, J., König, C., Bouchet, P.J., Dormann, C.F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J.J., Leitão, P.J., Park, D.S., Peterson, A.T., Rapacciuolo, G., Schmatz, D.R., Schröder, B., Serra-Diaz, J.M., Thuiller, W., Yates, K.L., Zimmermann, N.E., Merow, C., 2020a. A standard protocol for reporting species distribution models. *Ecography (Cop.)*. 43, 1261–1277. <https://doi.org/10.1111/ecog.04960>
- Zurell, D., Zimmermann, N.E., Gross, H., Baltensweiler, A., Sattler, T., Wüest, R.O., 2020b. Testing species assemblage predictions from stacked and joint species distribution models. *J. Biogeogr.* 47, 101–113. <https://doi.org/10.1111/jbi.13608>

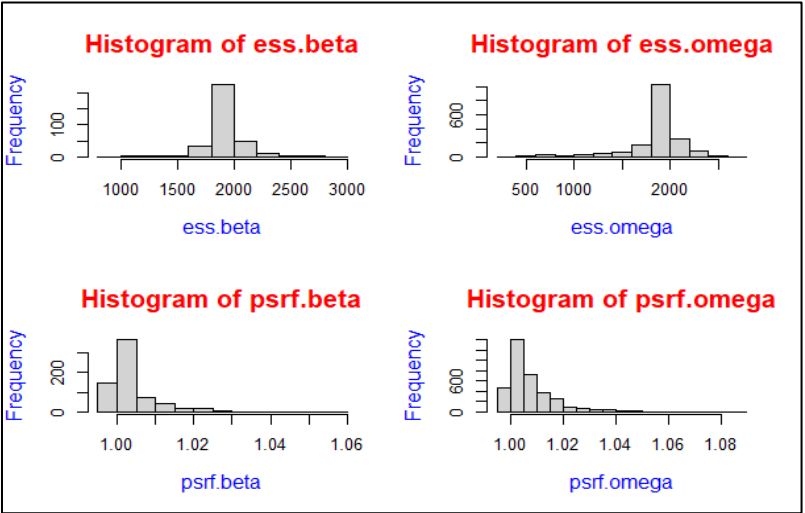
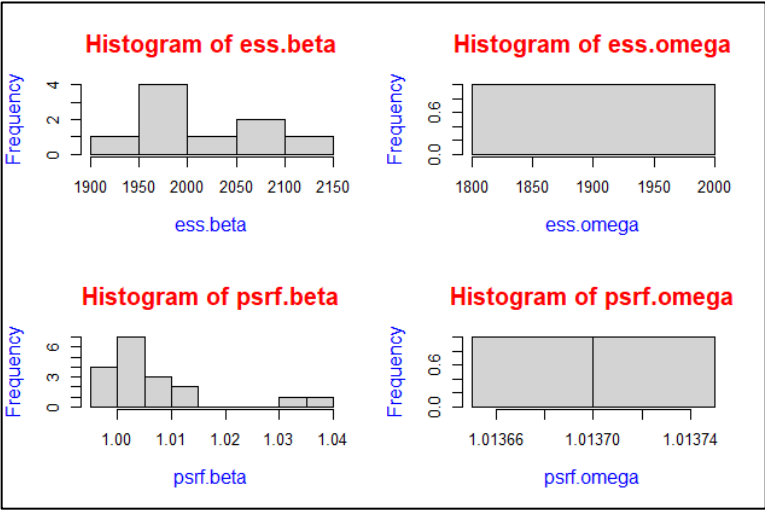
APPENDICES

Appendix 1 Environmental variables exploration

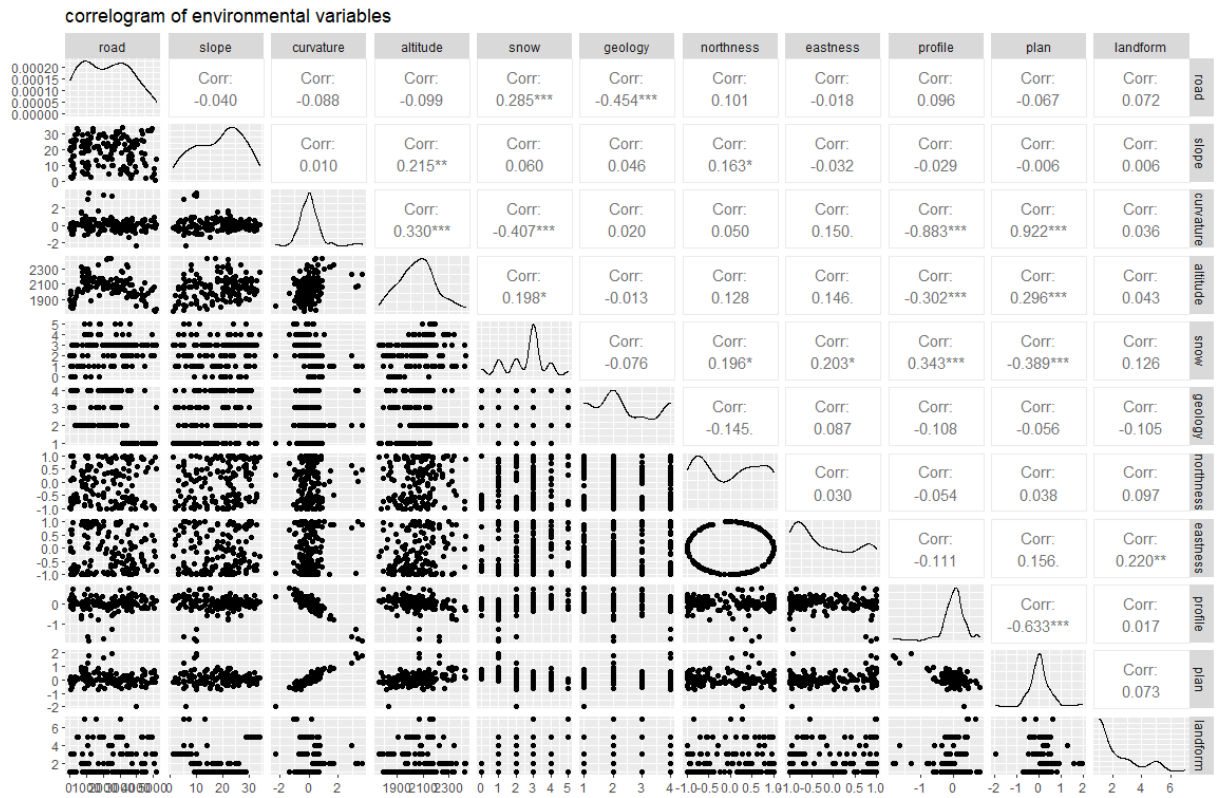


Example of MCMC convergence beta parameter estimates of *Acantholimon androsaceum* in SDM and JSMD

SDM					JSMD						
psrf.beta					psrf.beta						
Variables	Species			Point est.	Uppprt C.I.	Variables	Species			Point Estimate	Upper C.I
B[(Intercept)	(C1),	ACANAN	(S1)]	1.001	1.008416	B[(Intercept)	(C1),	ACANAN	(S1)]	1.000041	1.003869
B[env_data\$curv	(C2),	ACANAN	(S1)]	0.999732	1.002353	B[env_data\$curv	(C2),	ACANAN	(S1)]	0.999861	1.000296
B[env_data\$snow	(C3),	ACANAN	(S1)]	1.001739	1.003991	B[env_data\$snow	(C3),	ACANAN	(S1)]	0.99932	0.999476
B[env_data\$road	(C4),	ACANAN	(S1)]	1.003462	1.020324	B[env_data\$road	(C4),	ACANAN	(S1)]	1.002032	1.013764
B[env_data\$dem	(C5),	ACANAN	(S1)]	1.00017	1.004299	B[env_data\$dem	(C5),	ACANAN	(S1)]	1.00041	1.004114
B[env_data\$slope	(C6),	ACANAN	(S1)]	1.00057	1.0013	B[env_data\$slope	(C6),	ACANAN	(S1)]	1.000079	1.003617
B[env_data\$geo	(C7),	ACANAN	(S1)]	1.001881	1.013003	B[env_data\$geo	(C7),	ACANAN	(S1)]	1.00389	1.004699
B[env_data\$north	(C8),	ACANAN	(S1)]	1.002151	1.00859	B[env_data\$north	(C8),	ACANAN	(S1)]	1.000802	1.001253
B[env_data\$east	(C9),	ACANAN	(S1)]	0.999922	1.00158	B[env_data\$east	(C9),	ACANAN	(S1)]	1.006542	1.009693
ess.beta					ess.beta						
B[(Intercept)	(C1),	ACANAN	(S1)]	2134.806		B[(Intercept)	(C1),	ACANAN	(S1)]	2000	
B[env_data\$curv	(C2),	ACANAN	(S1)]	2000		B[env_data\$curv	(C2),	ACANAN	(S1)]	2000	
B[env_data\$snow	(C3),	ACANAN	(S1)]	2000		B[env_data\$snow	(C3),	ACANAN	(S1)]	1981.507	
B[env_data\$road	(C4),	ACANAN	(S1)]	2000		B[env_data\$road	(C4),	ACANAN	(S1)]	1461.937	
B[env_data\$dem	(C5),	ACANAN	(S1)]	2127.247		B[env_data\$dem	(C5),	ACANAN	(S1)]	1842.414	
B[env_data\$slope	(C6),	ACANAN	(S1)]	2065.478		B[env_data\$slope	(C6),	ACANAN	(S1)]	2000	
B[env_data\$geo	(C7),	ACANAN	(S1)]	1593.464		B[env_data\$geo	(C7),	ACANAN	(S1)]	1877.913	
B[env_data\$north	(C8),	ACANAN	(S1)]	2505.927		B[env_data\$north	(C8),	ACANAN	(S1)]	2382.912	
B[env_data\$east	(C9),	ACANAN	(S1)]	2000		B[env_data\$east	(C9),	ACANAN	(S1)]	2000	

JSDM	SDM
	
<p>Psrf: compares the ratio of variance within and among chains from the model parameters. When the variance ratio is towards 1.0 , it indicates the variance within chain is almost same with the variance among chains</p>	<p>ess: evaluates the autocorrelation structure within MCMC chains. If consecutive samples are independent, then the effective number of samples equals the actual number of samples</p>

Appendix 2 Correlation plot of Environmental Variables



Appendix 3 Residual correlation matrix of co-occurring species

	ACANAN	ALYSPH	CIRSMO	CREPSI	DRABCRE	FESTIP	HYPOTEN	PARMAC	PRUNPRO	SATUALP	SILEVA	TARABITH	VALANAPR	VERARV
ACANAN														
ALYSPH	-0.89466													
CIRSMO		-0.909614												
CREPSI		0.9250924	-0.86022											
DRABCRE	-0.899556	0.9867872	-0.91184	0.92875										
FESTIP		0.8819844			0.88205339									
HYPOTEN	-0.878105	0.9653319	-0.89161	0.90753	0.96977822									
PARMAC	-0.895494	0.983865	-0.91088	0.92539	0.98802485	0.966842	0.96684193							
PRUNPRO	-0.89333	0.9819228	-0.9086	0.92517	0.98622627	0.966259	0.96625912	0.9837968						
SATUALP	-0.880875		-0.89149	0.90928	0.96849268	0.948266	0.94826599	0.9658036	0.96370014					
SILEVA		-0.875692			-0.8782459		-0.8604195	-0.875377	-0.87368744	-0.86162172				
TARABITH		0.8857915			0.88856125		0.87221868	0.8857306	0.88355281	0.86778352				
VALANAPR	-0.885394	0.9733571				0.872579	0.95587327	0.9752422	0.97345261	0.95726304	-0.87006	0.87853762		
VERARV	0.8904442	-0.979039	0.906206	-0.9254	-0.9839471	-0.87787	-0.9627157	-0.980844	-0.98137997	-0.96154028	0.87273	-0.880097	-0.97133341	
VEROTHYM	-0.885572	0.9674673	-0.89504	0.91176	0.97209112	0.866435	0.95248108	0.9693087	0.96813339	0.951252	-0.8639	0.87610871	0.95992436	-0.964567

Positive associations are red and negative associations are blue

Residual correlation matrix of 42 showing species . Selected species are in green, and positive associations are red and negative associations are blue

Residual correlation matrix of 42 showing species. Selected species are in green, and positive associations are red and negative associations are blue.

Appendix 4 Accuracy results in JSDBM and SDM from 10 Model Runs

<i>Acantholimon androsaceum</i>					<i>Alyssum sphacioticum</i>				
Model	JSDM_RMSE	SDM_RMSE	JSDM_AUC	SDM_AUC	Model	JSDM_RMSE	SDM_RMSE	JSDM_AUC	SDM_AUC
M1	0.3921	0.3770	0.7667	0.7502	M1	0.2597	0.2432	0.9222	0.9011
M2	0.3924	0.3770	0.7667	0.7500	M2	0.2591	0.2415	0.9236	0.9047
M3	0.3922	0.3766	0.7664	0.7517	M3	0.2595	0.2440	0.9227	0.8979
M4	0.3929	0.3766	0.7667	0.7505	M4	0.2590	0.2428	0.9227	0.9011
M5	0.3924	0.3769	0.7662	0.7500	M5	0.2599	0.2435	0.9222	0.8993
M6	0.3913	0.3764	0.7676	0.7510	M6	0.2587	0.2429	0.9236	0.9015
M7	0.3919	0.3776	0.7669	0.7495	M7	0.2598	0.2438	0.9231	0.9033
M8	0.3922	0.3768	0.7679	0.7505	M8	0.2595	0.2419	0.9227	0.9060
M9	0.3924	0.3769	0.7679	0.7507	M9	0.2591	0.2446	0.9236	0.8975
M10	0.3916	0.3765	0.7671	0.7490	M10	0.2596	0.2427	0.9227	0.9024
Average	0.3921	0.3768	0.7670	0.7503	Average	0.2594	0.2431	0.9229	0.9015

<i>Anchusa cespitosa</i>					<i>Prunus prostrata</i>				
Model	JSDM_RMSE	SDM_RMSE	JSDM_AUC	SDM_AUC	Model	JSDM_RMSE	SDM_RMSE	JSDM_AUC	SDM_AUC
M1	0.4270	0.4519	0.8020	0.7606	M1	0.4662	0.4420	0.7034	0.7536
M2	0.4263	0.4521	0.8044	0.7602	M2	0.4652	0.4429	0.7050	0.7481
M3	0.4270	0.4522	0.8025	0.7601	M3	0.4661	0.4423	0.7037	0.7492
M4	0.4270	0.4520	0.8020	0.7607	M4	0.4656	0.4419	0.7034	0.7510
M5	0.4276	0.4516	0.8022	0.7611	M5	0.4661	0.4425	0.7018	0.7492
M6	0.4272	0.4516	0.8024	0.7611	M6	0.4663	0.4420	0.7016	0.7519
M7	0.4275	0.4517	0.8019	0.7601	M7	0.4656	0.4422	0.7034	0.7517
M8	0.4263	0.4523	0.8054	0.7602	M8	0.4659	0.4422	0.7041	0.7504
M9	0.4268	0.4523	0.8022	0.7599	M9	0.4657	0.4426	0.7048	0.7504
M10	0.4264	0.4518	0.8040	0.7604	M10	0.4663	0.4428	0.7002	0.7499

Average	0.4269	0.4520	0.8029	0.7604	Average	0.4659	0.4424	0.7031	0.7505
<i>Berberis cretica</i>									
	SDM								
Model	JSDM_RMSE	_RMSE	JSDM_AUC	SDM_AUC					
M1	0.4769	0.5382	0.6794	0.5412					
M2	0.4767	0.5387	0.6818	0.5414					
M3	0.4769	0.5371	0.6798	0.5424					
M4	0.4770	0.5383	0.6806	0.5412					
M5	0.4767	0.5379	0.6810	0.5421					
M6	0.4765	0.5379	0.6801	0.5412					
M7	0.4769	0.5376	0.6781	0.5419					
M8	0.4768	0.5390	0.6813	0.5391					
M9	0.4769	0.5370	0.6803	0.5410					
M10	0.4772	0.5383	0.6787	0.5397					
Average	0.4769	0.5380	0.6801	0.5411					

Appendix 5 Two-way ANOVA and Tukey HSD results

A comparison between AUC means of species and model type, and the interaction between species and model type

Two-Way ANOVA test result of AUC and Interaction effects for species and model.

Source of Variation	SS	df	MS	F value	P-value	F crit
Species	0.9405	4	0.23513	133412	<2e-16***	3.968
Model	0.0296	1	0.02963	16813	<2e-16***	
Species * Model	0.0909	4	0.02272	12894	<2e-16***	

***0.001

Tukey HSD post hoc test of Species

Multiple Comparisons	Mean Difference	95% Confidence Interval		p-value
		Lower Bound	Upper Bound	
alysph-acana	0.154	0.152	0.155	0
anches-acana	0.023	0.022	0.024	0
bercre-acana	-0.148	-0.149	-0.147	0
prupro-acana	-0.032	-0.033	-0.031	0
anches-alysph	-0.131	-0.132	-0.129	0
bercre-alysph	-0.302	-0.303	-0.300	0
prupro-alysph	-0.185	-0.187	-0.184	0
bercre-anches	-0.171	-0.172	-0.170	0
prupro-anches	-0.055	-0.056	-0.054	0
prupro-bercre	0.116	0.115	0.117	0

* The mean difference is significant at the 0.05 level.

Tukey HSD post hoc test of Model type

Multiple Comparisons	Mean Difference	95% Confidence Interval		p-value
		Lower Bound	Upper Bound	
SDM-JSDM	-0.034	-0.035	-0.034	0

* The mean difference is significant at the 0.05 level.

Tukey HSD post hoc test of interactions of Species and Model type

Multiple Comparisons	Mean Difference	95% Confidence Interval		p-value
		Lower Bound	Upper Bound	
alysph:JSDM-acana:JSDM	0.156	0.154	0.158	0
anches:JSDM-acana:JSDM	0.036	0.034	0.038	0

bercre:JSDM-acana:JSDM	-0.087	-0.089	-0.085	0
prupro:JSDM-acana:JSDM	-0.064	-0.066	-0.062	0
acana:SDM-acana:JSDM	-0.017	-0.019	-0.015	0
alysph:SDM-acana:JSDM	0.134	0.133	0.136	0
anches:SDM-acana:JSDM	-0.007	-0.008	-0.005	0
bercre:SDM-acana:JSDM	-0.226	-0.228	-0.224	0
prupro:SDM-acana:JSDM	-0.016	-0.018	-0.015	0
anches:JSDM-alysph:JSDM	-0.120	-0.122	-0.118	0
bercre:JSDM-alysph:JSDM	-0.243	-0.245	-0.241	0
prupro:JSDM-alysph:JSDM	-0.220	-0.222	-0.218	0
acana:SDM-alysph:JSDM	-0.173	-0.175	-0.171	0
alysph:SDM-alysph:JSDM	-0.021	-0.023	-0.019	0
anches:SDM-alysph:JSDM	-0.162	-0.164	-0.161	0
bercre:SDM-alysph:JSDM	-0.382	-0.384	-0.380	0
prupro:SDM-alysph:JSDM	-0.172	-0.174	-0.170	0
bercre:JSDM-anches:JSDM	-0.123	-0.125	-0.121	0
prupro:JSDM-anches:JSDM	-0.100	-0.102	-0.098	0
acana:SDM-anches:JSDM	-0.053	-0.055	-0.051	0
alysph:SDM-anches:JSDM	0.099	0.097	0.101	0
anches:SDM-anches:JSDM	-0.042	-0.044	-0.041	0
bercre:SDM-anches:JSDM	-0.262	-0.264	-0.260	0
prupro:SDM-anches:JSDM	-0.052	-0.054	-0.050	0
prupro:JSDM-bercre:JSDM	0.023	0.021	0.025	0
acana:SDM-bercre:JSDM	0.070	0.068	0.072	0
alysph:SDM-bercre:JSDM	0.221	0.219	0.223	0
anches:SDM-bercre:JSDM	0.080	0.078	0.082	0
bercre:SDM-bercre:JSDM	-0.139	-0.141	-0.137	0
prupro:SDM-bercre:JSDM	0.070	0.069	0.072	0
acana:SDM-prupro:JSDM	0.047	0.045	0.049	0
alysph:SDM-prupro:JSDM	0.198	0.196	0.200	0
anches:SDM-prupro:JSDM	0.057	0.055	0.059	0
bercre:SDM-prupro:JSDM	-0.162	-0.164	-0.160	0
prupro:SDM-prupro:JSDM	0.047	0.045	0.049	0
alysph:SDM-acana:SDM	0.151	0.149	0.153	0
anches:SDM-acana:SDM	0.010	0.008	0.012	0
bercre:SDM-acana:SDM	-0.209	-0.211	-0.207	0
prupro:SDM-acana:SDM	0.000	-0.002	0.002	1
anches:SDM-alysph:SDM	-0.141	-0.143	-0.139	0
bercre:SDM-alysph:SDM	-0.360	-0.362	-0.358	0
prupro:SDM-alysph:SDM	-0.151	-0.153	-0.149	0
bercre:SDM-anches:SDM	-0.219	-0.221	-0.217	0
prupro:SDM-anches:SDM	-0.010	-0.012	-0.008	0
prupro:SDM-bercre:SDM	0.209	0.207	0.211	0

* The mean difference is significant at the 0.05 level.

Appendix 6 Percentage of predictor variable contribution in JSDM and SDM (variance partitioning)

<i>Acantholimon androsaceum</i>			<i>Alyssum sphacioticum</i>			<i>Anchusa cespitosa</i>		
	JSDM	SDM		JSDM	SDM		JSDM	SDM
snow	21%	27%	snow	6%	6%	snow	19%	24%
slope	4%	3%	slope	10%	7%	slope	3%	3%
curvature	23%	21%	curvature	3%	4%	curvature	16%	14%
geology	13%	13%	geology	24%	11%	geology	39%	34%
altitude	9%	4%	altitude	5%	3%	altitude	7%	9%
road	7%	14%	road	14%	48%	road	3%	3%
northness	6%	5%	northness	11%	10%	northness	2%	1%
eastness	8%	5%	eastness	6%	8%	eastness	10%	11%
Random:operator	10%	6%	Random:operator	21%	4%	Random:operator	2%	2%

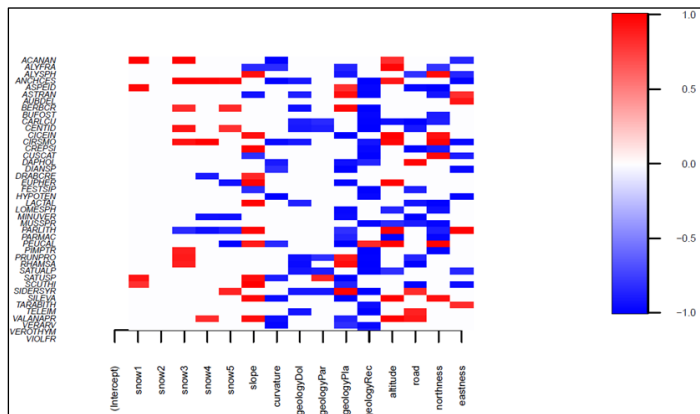
<i>Berberis cretica</i>			<i>Prunus prostrata</i>		
	JSDM	SDM		JSDM	SDM
snow	6%	7%	snow	6%	9%
slope	1%	2%	slope	3%	4%
curvature	3%	3%	curvature	2%	3%
geology	73%	69%	geology	40%	33%
altitude	3%	5%	altitude	2%	2%
road	7%	6%	road	8%	9%
northness	3%	2%	northness	2%	1%
eastness	1%	1%	eastness	2%	1%
Random:operator	2%	4%	Random:operator	36%	38%

Total percentage of predictor variable contribution in JSMD and SDM

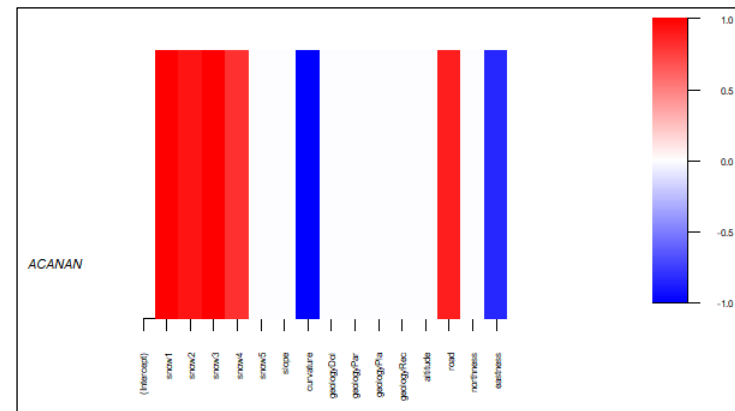
	Co-occurring species						Non-co-occurring			
	<i>Acantholimon androsaceum</i>		<i>Alyssum sphacioticum</i>		<i>Prunus prostrata</i>		<i>Anchusa cespitosa</i>		<i>Berberis cretica</i>	
	JSDM	SDM	JSDM	SDM	JSDM	SDM	JSDM	SDM	JSDM	SDM
Fixed effect	90.3	93.6	78.9	95.8	64	62	98.3	97.9	98.4	95.78
Random effect	9.7	6.4	21.1	4.2	36	38	1.7	2.1	1.6	4.2

Appendix 7 Regression coefficients heat map in JSMD and SDM

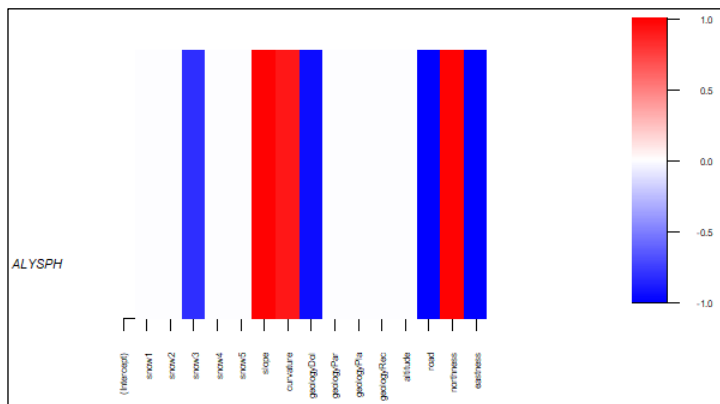
A: Regression coefficient plot in JSMD



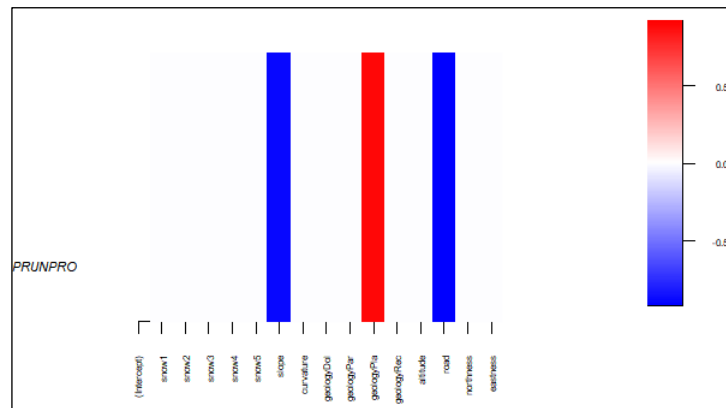
B *Acantholimon androsaceum*



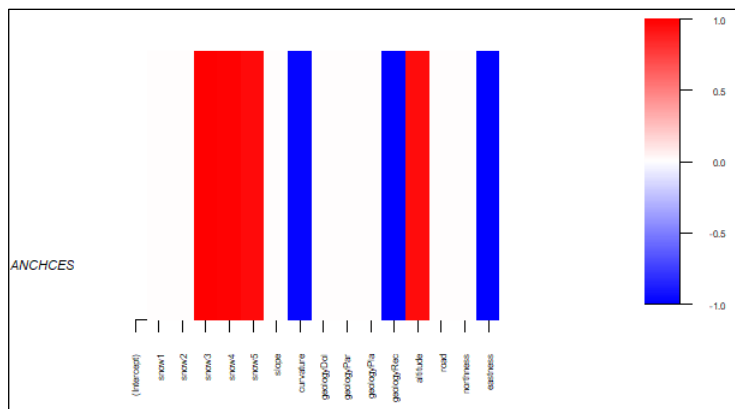
C *Alyssum sphacioticum*



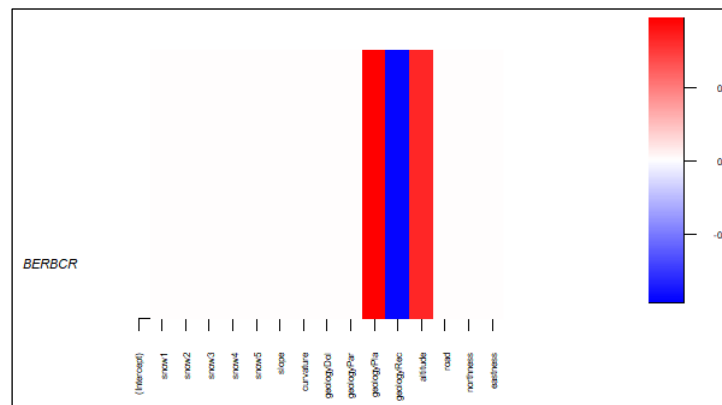
D *Prunus prostrata*



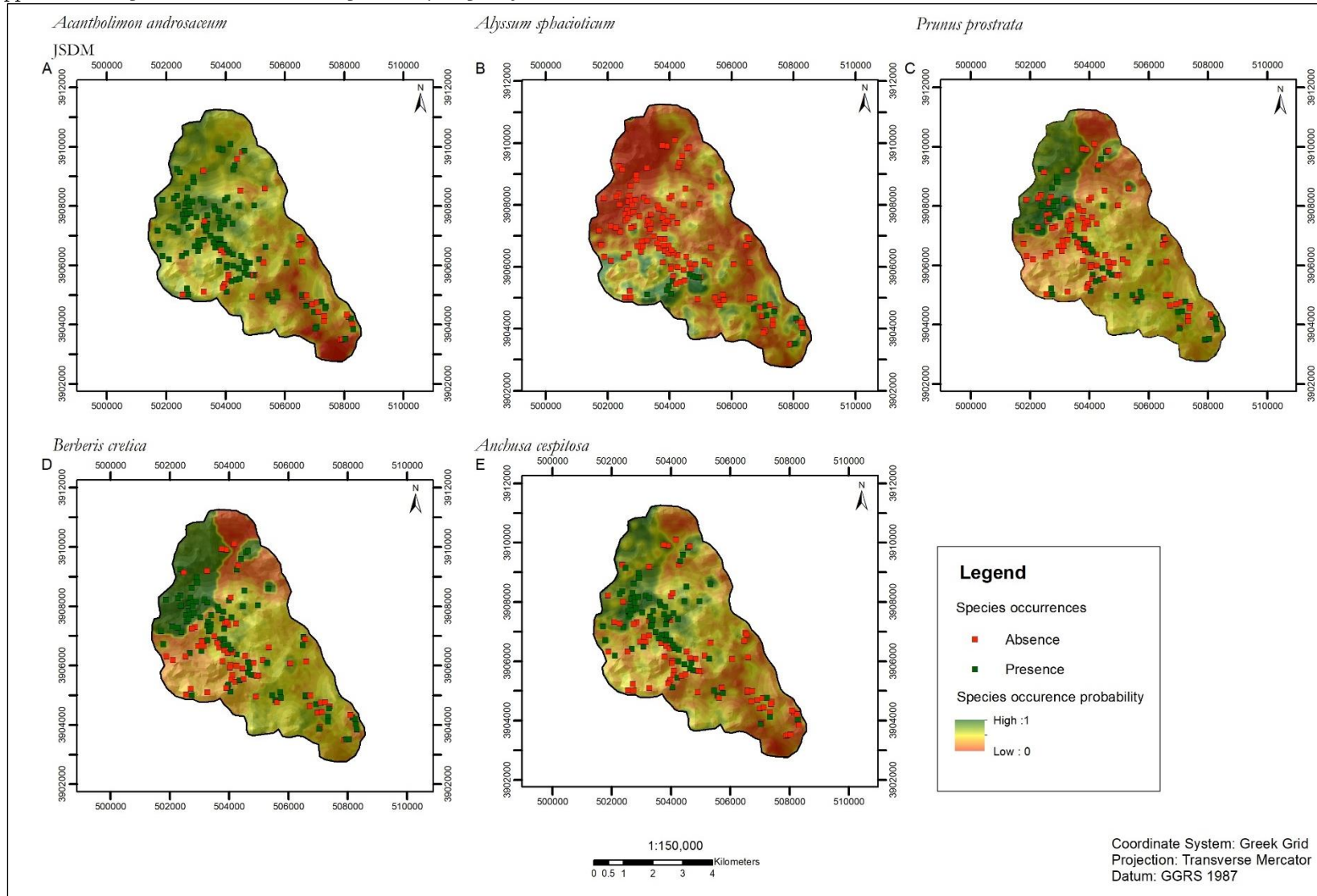
E *Anchusa cespitosa*



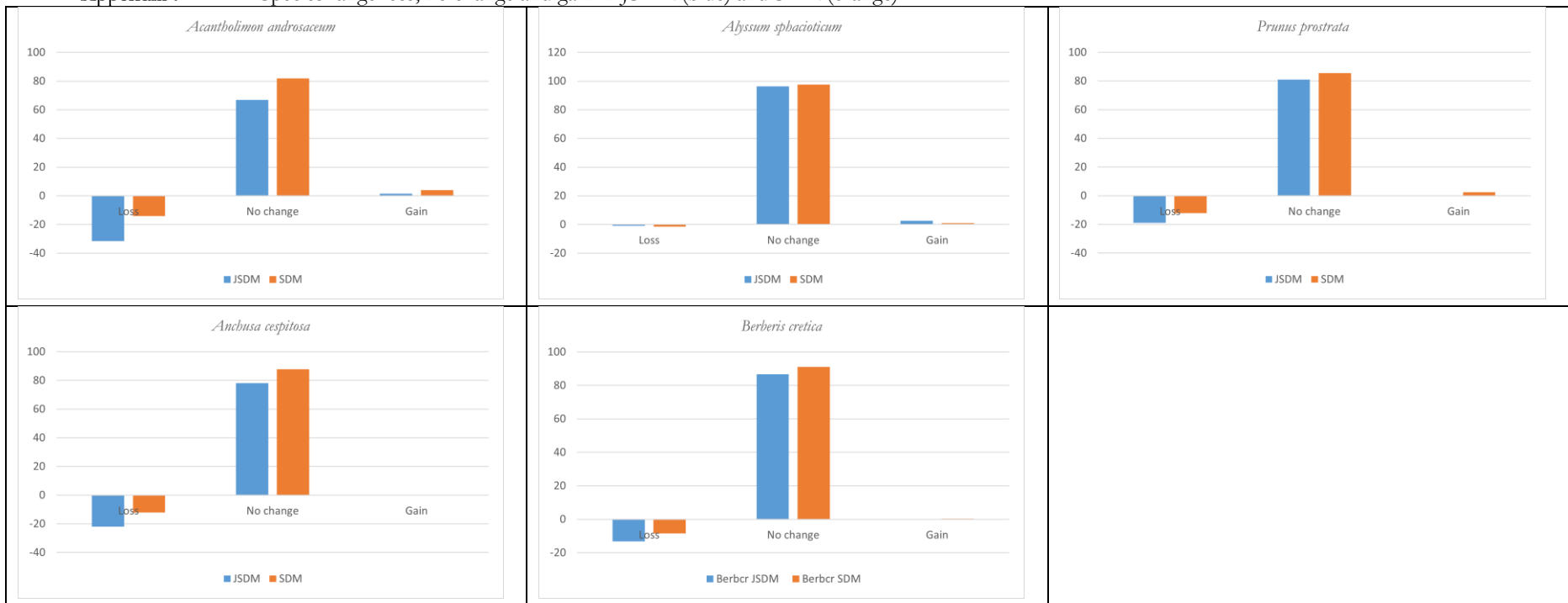
F: *Berberis cretica*



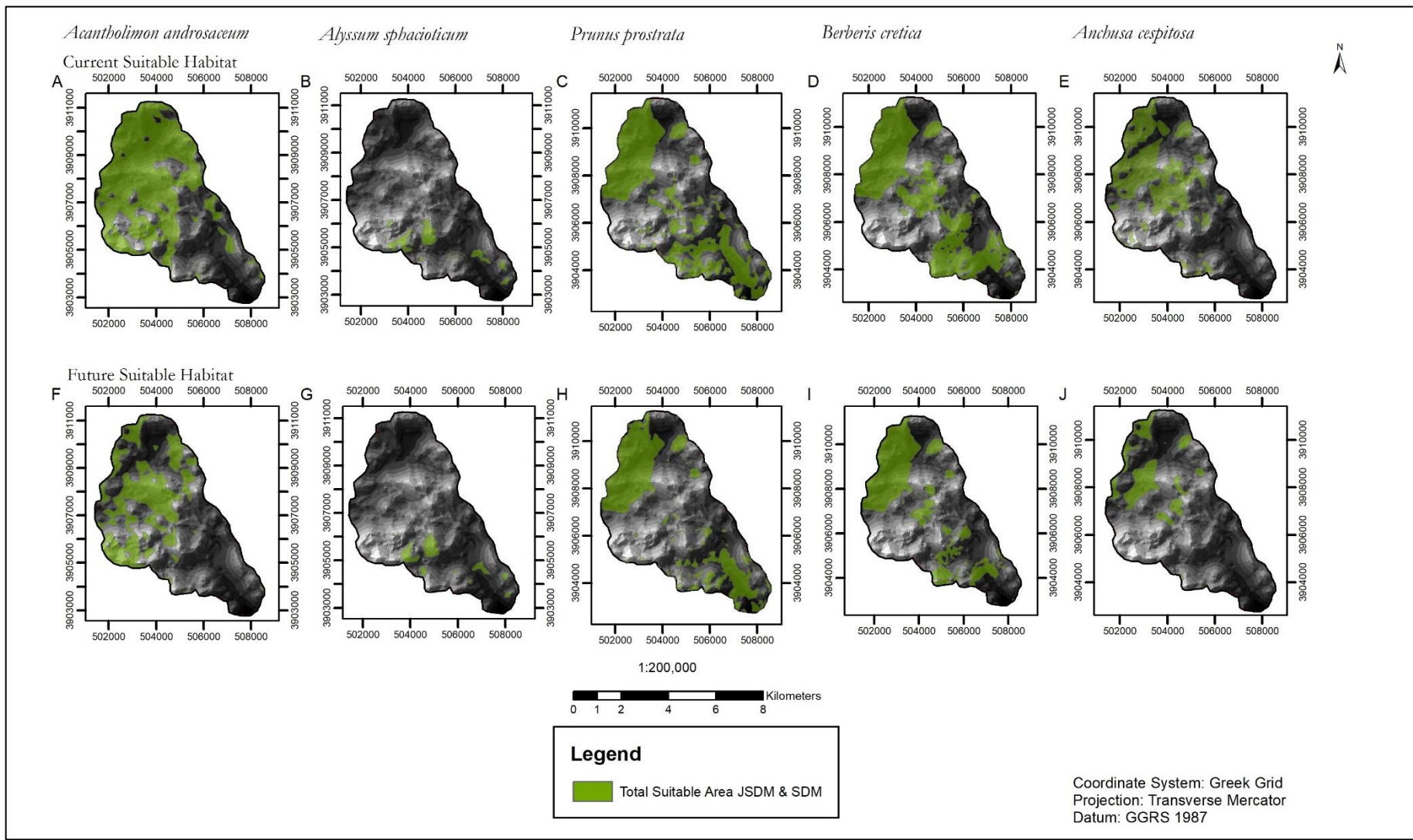
Appendix 8 Species current occurrence probability maps in JSDM



Appendix 9 Species range loss, no change and gain in JSDM (blue) and SDM (orange)



Appendix 10 Total suitable habitat in JSDM and SDM in current and future climate scenario



Appendix 11 Unchanged suitable habitat in JSDM and SDM in current and future climate scenario

