Modelling the spatial distribution of snake species under changing climate scenario in Spain

Francis Kamau Muthoni
March, 2010

Course Title: Geo-Information Science and Earth Observation for Environmental Modelling and Management

Level: Master of Science (Msc)

Course Duration: September 2008 - March 2010

Consortium partners: University of Southampton (UK)
Lund University (Sweden)
University of Warsaw (Poland)
University of Twente Faculty of Geo-Information Science and Earth Observation (ITC) (The Netherlands)
GEM thesis number: 2010-18

Modelling the spatial distribution of snake species under changing climate scenario in Spain

By

Francis Kamau Muthoni

Thesis submitted to the University of Twente Faculty of Geo-information Science and Earth Observation (ITC) in partial fulfilment of the requirements for the degree of Master of Science in Geo-information Science and Earth Observation for Environmental Modelling and Management

Thesis Assessment Board

Chairman: Prof. Andrew Skidmore, University of Twente-ITC
External Examiner: Prof. T. P. Dawson, University of Southampton
First Supervisor: Dr. Bert Toxopeus, University of Twente-ITC
Second Supervisor: Dr. Thomas Groen, University of Twente-ITC
Course Director: M.Sc. Andre Kooiman, University of Twente-ITC

ITC
UNIVERSITY OF TWENTE.
FACULTY OF GEO-INFORMATION SCIENCE AND EARTH OBSERVATION

Disclaimer

Abstract

Climate change has been postulated to be one of the main drivers of biodiversity loss globally as it results to alteration of the species habitats. Hence, this study investigated the effect of climate change on the spatial distribution of four snake species *Coronella girondica, Natrix maura, Malpolon monspessulanus* and *Rhinechis scalaris* in Spain. The specific objectives were to; (1) identify the predictor variables that had the highest predictive power in the potential distribution models of the four snake species; (2) generate potential distribution models for the four snake species using the current climatic and biophysical explanatory variables; 3) project the future potential distribution of the four snakes using the projected year 2050 climatic and biophysical variables; and 4) investigate whether the projected range shifts among the specialist species was different than that of generalist species. Maxent algorithm was trained using species presence data and a set of climatic and biophysical environmental variables. To identify which set of predictors had the highest contribution to the model, two types of models were run; one with biophysical variables only and another with both climatic and biophysical variables. To assess the average behaviour of the algorithm, ten random partitions were run each comprising of 70% of presence data for training and 30% for testing. Jackknife test of variable importance was used to identify one variable that resulted to the least drop in the training gains when omitted from the models. This variable was eliminated and the process continued until only one variable remained. Mann-Whitney U statistic was used to test the statistical difference between the different sized models. The model with the least number of predictors and the training gains not significantly different from that of the full model was selected as the best model. Similarly, Mann-Whitney U statistic was used to test the statistical difference between the two sets of models. The best current conditions model from either of the two model suites was used to project the future ranges based on scenario A2 of the HadCM3 model. The models were evaluated using the area under the ROC curve (AUC), binomial tests and sensitivity. To reveal the future range shifts, the current and future maps were cross-tabulated to derive kappa index of agreement and crammers V statistic. Results showed that climatic variables had the highest predictive power suggesting that the distribution of these species at meso-scale is largely set by climate. Moreover, all species were projected to shift their ranges by the year 2050 due to changing climates. Furthermore the generalist's species range was projected to expand while that of specialist's species tended to contract. Nevertheless, factors such as biotic interactions, dispersal abilities and evolutionary adaptations need to be incorporated into the models before a concrete conclusion that climate is the main driver of the species range shifts. Moreover, re-testing of these hypotheses with higher resolution dataset that captures fine ecological details of these species was recommended.

Keywords: climate change, Maxent, specialist species, generalist species, range shifts, *Coronella girondica, Malpolon monspessulanus, Natrix maura, Rhinechis scalaris.*

Acknowledgements

My sincere thanks to the EU Erasmus Mundus consortium (University of Southampton, UK; University of Lund, Sweden; Warsaw University, Poland and ITC, The Netherlands) for awarding the scholarship to pursue such an outstanding programme. It was truly an enlightening experience.

Special thanks to my supervisors; Dr. Bert Toxopeus and Dr. Thomas Groen for their invaluable advice and expert guidance. It was really a splendid experience to working with them.

I'm equally indebted to my course lecturers in Southampton, Lund, Warsaw and ITC for their professionalism and enthusiasm to impart knowledge.

Thanks to Prof. Real Raimundo of University of Malaga for providing the Atlas data. I'm very grateful to PhD. Candidates; Aidin Niamir and Francisco Ferri for their valuable comments, sharing data and field experiences.

Big thanks to my fellow GEM students for their friendship and providing such a good company throughout the course. Thanks also to my fellow Kenyan students for their support and comradeship.

Am grateful to my family members and friends for their moral support and encouragement in the entire duration of the course. Lastly but not the least to, to the Almighty God for his grace and wisdom without which all these would not have been possible.

Table of contents

List of figures

List of tables

1. Introduction

1.1. Background and Significance

Climatic conditions have been reported as a major factor influencing the geographical distribution of global biodiversity (Prentice *et al.*, 1992, Sala *et al.*, 2000, Pearson and Dawson, 2003, Carey and Alexander, 2003, Thomas *et al.*, 2004, Araujo and Pearson, 2005, Sekercioglu *et al.*, 2008, Hole *et al.*, 2009, Baselga and Araujo, 2009). This is based on ecological niche theory (Hutchinson, 1957), that stipulates that each species has a defined set of environmental conditions under which it can survive and grow, the fundamental niche. However due to competition and ecological barriers, species are only able to inhabit some parts of their fundamental niche, thereby forming the realised niche (Guisan and Zimmermann, 2000). Hence, as stipulated by Pearson & Dawson (2003), species spatial distribution can be predicted effectively by using the empirical relationship between the observed species distribution and environmental variables that forms their 'climate space'.

However, various environmental variables influence species distribution differently depending on the modelling scale (Guisan & Hofer, 2003). (Austin and Smith, 1989) categorised environmental predictors into three classes (direct, indirect and resources) and demonstrated their varied predictive power depending on modelling scale. Direct predictors are environmental parameters that are not directly consumed but they exert substantial physiological importance to species survival e.g. temperature and precipitation, while indirect predictors do not have any direct physiological importance to species performance e.g. elevation and slope. Resource predictors are concerned with the matter and energy consumed by organisms e.g. food and water for faunal species (Guisan and Zimmermann, 2000). Direct predictors have been proved to be effective when modelling at small scale (large extent) while indirect predictors have been recommended for large scales (small extent) modelling (Guisan and Zimmermann, 2000). Patthey (2003) also attributed this to the fact that a study conducted at a small scale (large extent) can reveal environmental drivers that best characterise the overall species range. While a second nested analysis at a large scale (small extent) can reveal other features that best characterise habitat at population or home range level. This is because unlike indirect predictors that typically vary within short distances, direct predictors like climatic variables are relatively stable over larger areas hence models derived from them are more general and applicable over large areas (Guisan and Hofer, 2003). Evidently, therefore, for efficient distribution modelling, selection of relevant ecological parameters believed to be causal or driving forces for their distribution is imperative. However, despite the environmental factors, the distribution of species is also influenced by evolutionally changes, biotic interactions and the species dispersal abilities (Pearson and Dawson, 2003). Therefore predictive distribution models developed with environmental variables alone cannot be exhaustive and need to be interpreted in consideration of these other factors.

Several studies have used various predictive spatial distribution models to predict the effect of climate change on species on a global or continental scales (Gibbons *et al.*, 2000, Carey and Alexander, 2003, Collins and Storfer, 2003, Pearson and Dawson, 2003, Root *et al.*, 2003, Stuart *et al.*, 2004, Araujo *et al.*, 2006), meso-scale (Guisan and Hofer, 2003), national scale (Reading, 2007) and local scales (Pounds et al., 1999, Bosch et al., 2007). All these studies reveal that impacts of climate change on species distribution are already discernible. Evidently, Root *et al.* (2003), in a study of 143 species ranging from molluscs to mammals identified a steady and consistent shift in their distribution in concurrence with changing climate. Similarly, Thomas *et al.* (2004) demonstrated that between 15-37% of 1,103 plant and animal species in a sample region comprising 20% of the Earth's terrestrial surface, will be committed to extinction by year 2050 due to their shrinking range. On European scale, Araujo *et al.* (2006) modelled the spatial distribution of 42 amphibians and 66 reptiles using climate scenarios up to year 2050 and concluded that with limited dispersal ability, the geographic range of virtually all species evaluated will contract. Most of contraction was projected to occur in south-west Europe especially in the Iberian Peninsula due to increasing arid conditions and high levels of habitat fragmentation that will hamper their dispersal to keep track with changing climate.

Significantly also, (Araujo *et al.*, 2006) demonstrated that impacts of climate change on different species varies in magnitude depending on their taxonomic and life history traits. They observed that the range shift among the species in the taxonomic order Urodela was significantly different from those of the orders Anura, Ophidia and Sauria. These differences were attributed to the varying degree of specialisation of species within these taxonomic orders. The taxonomic order Ophidia comprised of 25 snake species. Generalist snake species tolerate a wide range of environmental conditions (Segura *et al.*, 2007), have wide variety of prey and exhibit good adaptability to altered habitats (Reed and Shine, 2002, Santos *et al.*, 2007b). In contrast, the specialist snake species occupy limited habitat types, depict low prey diversity, small range size and may exhibit life-history traits that increase their vulnerability such as sit-and-wait predation tactics (Reed and Shine, 2002, Santos *et* *al.*, 2007b). *Malpolon monspessulanus* is an excellent example of a generalist snake species as it inhabits almost all environmental conditions in Iberian Peninsula, has wide prey diversity, a high reproductive rate and can tolerate habitat alteration by human activities (Segura *et al.*, 2007). Contrastingly, *Vipera lastatei* is among the most threatened snake species in Iberian Peninsula (Santos *et al.*, 2007a) as it depends on ambush predation rather than actively searching for prey and has a low reproduction rate as it reproduces on a triennial basis (Santos *et al.*, 2007b). The snake species depicting sit-and-wait predation tactics depend on sites with specific land cover types making them highly vulnerable to extinction in-case of alteration of such habitats (Reed and Shine, 2002). They are also characterised by biological traits that involve low rates of feeding, growth and reproduction that consequently lower their population (Reed and Shine, 2002). Under changing climate scenario, vulnerability of such specialist species may increase considering that climatic conditions especially temperature directly influences almost all physiological processes in snakes (Teixeira and Arntzen, 2002) and the potential habitat changes as a result of changing climate. Evidently therefore, it is imperative to investigate the effect of climate change based on species physiological, specialization (habitat, diet) and taxonomic differences (Araujo *et al.*, 2006) to facilitate the design of relevant species specific conservation strategies.

Such an investigation can be achieved by using Species Distribution Models (SDM's). These models use quantitative methods to infer species ecological requirements from prevailing environmental conditions at locations where the species is known to occur and then use that to predict the species habitat suitability or probability of occurrence in un-sampled areas (Hernandez *et al.*, 2006, Wisz *et al.*, 2008). Consequently, to assess the effect of climate change on species distribution, SDM's are used to predict the current species range using current climatic conditions and then project future distributions based on projected future climate (Thuiller, 2004, Araujo *et al.*, 2006, Fitzpatrick *et al.*, 2008). This is based on assumption that the current species-climate relationships remains unchanged under changing climate (Fitzpatrick et al., 2008).

Several studies have shown that the ecological characteristics of modelled species affect the accuracy of the SDM's (Elith *et al.*, 2006, Phillips *et al.*, 2006, Franklin *et al.*, 2009). Generally, wide-ranging generalist species are more difficult to model than species with a compact range, due to their ability to survive in highly varied environmental conditions that are not easily defined by the presence data, independent variables or model design (Segurado and Araujo, 2004, Hernandez *et al.*, 2006, Evangelista *et al.*, 2008). Furthermore, generating accurate SDM's requires long-term continuous data set on the species distribution, which is generally lacking for most snake species as their population dynamics are poorly monitored (Santos *et al.*, 2007a). It is difficult to monitor snakes due their characteristic secretive behaviour, low population and patchy distribution (Segura *et al.*, 2007). In addition, most spatial distribution modelling algorithms requires species presence and absence data. Whereas presence data can be ascertained with higher confidence, the absence data has high inherent uncertainties, making it more difficult to ascertain (Anderson, 2003). Hence the use of a robust modelling method that requires only presence data and that is capable of predicting effectively with limited available data can eliminate some of these limitations. The Maxent (Maximum Entropy) algorithm, a novel method developed by Phillips *et al.* (2006) has shown these qualities as demonstrated by Hernandez et al. (2006) and Elith *et al.* (2006) through a comparative evaluation with other modelling techniques including the well established GARP (Stockwell and Peters, 1999), BIOCLIM (Busby, 1991) and DOMAIN (Carpenter *et al.*, 1993) methods. These two studies concluded that Maxent was the most capable of the four methods in producing results even with samples sizes as small as five occurrences in addition to its ability to model complex relationships and interactions between variables.

1.1.1. Climate change.

Climate change refers to variations in the mean state of climate or variability of its properties that extends for a long period usually decades or longer (IPCC, 2007). There is a consistent and unequivocal agreement between climate models pointing towards increasing warming trends globally (IPCC, 2007). For 50 years extending from 1956 to 2005 the global surface warming increased at a rate of 0.13°C per decade which was nearly double that experienced in 100 years from 1906 to 2005 (IPCC, 2007). The Mediterranean basin is ranked among the most vulnerable to climate change partly due to its location in a transitional area between the temperate central Europe and arid northern Africa climates (Giorgi and Lionello, 2008). Significant drying and warming is projected in this basin, especially in the summer season which is projected to experience a decrease in precipitation exceeding -30% and about 4°C warming by the year 2100 (Giorgi and Lionello, 2008). Similar trends are projected for Spain, which is located within this basin e.g. Santos *et al.* (2009) reported 20% reduction in annual rainfall over the 20th century in Spain. According to Hughes (2000) a 3°C change in mean annual temperature result to shift in isotherms of approximately 300 - 400 Km in latitude in the temperate zone or 500 m in elevation. Hence, species are expected to shift their ranges upwards altitudinally or pole-ward to track the changing climate.

1.1.2. Scenarios in climate change

According to IPCC (2007) climate change is mainly caused by increased atmospheric concentration of Greenhouse Gases (GHG's). Hence projecting the possible future outlook of GHG's emissions is imperative before projecting the future climate. However these emissions are driven by complex dynamic processes that are highly uncertain to project (IPCC, 2000). Hence, scenarios have been developed as tool of assessing how various driving forces may influence the future emissions. These scenarios represent plausible alternatives of how the future may unfold (IPCC, 2000). The IPCC Special Report on Emission Scenarios (SRES) (IPCC, 2000) detailed four families of future scenarios (A1, A2, B1 and B2) that explore alternative development pathways, covering a wide range of demographic, economic, technological, environmental and policies driving forces (Figure 1-1).

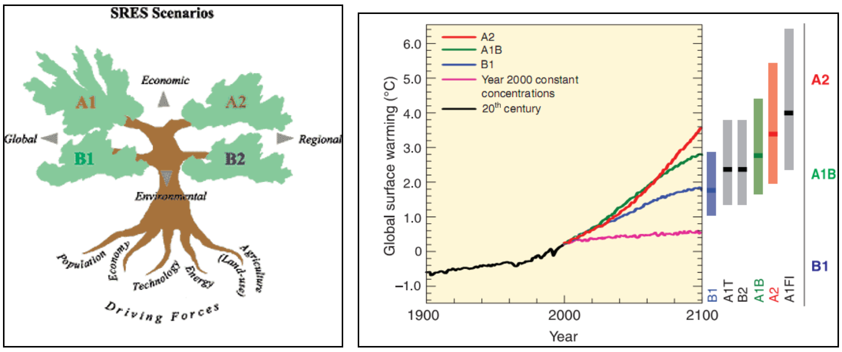


Figure 1-1. (a) Illustration of the four SRES scenario families and (b) projected global average temperature increases for different SRES scenarios (IPCC, 2000).

According to IPCC (2000) the A1 scenario projects a world with very rapid economic growth, a global population that peaks in mid 21st century and decline thereafter. This scenario is sub-divided into three sub-groups describing alternative directions of technological change: A1FI (fossil intensive), A1T (non-fossil energy resources with rapid introduction of new and more efficient technologies) and A1B (balance across all sources). The B1 scenario describes a convergent world, with the same global population as A1, but with more rapid changes in economic structures toward a service and information economy. The B2 scenario stipulates a world with intermediate population and economic growth, emphasizing on local solutions to economic, social, and environmental sustainability. The A2 scenario, which is used in this study, describes a very heterogeneous world with high population growth, slow economic development and slow technological change.

Significantly, the fossil fuel CO_2 emissions since year 2000 have increased at a higher rate than previous decades (Raupach *et al.*, 2007). Even the more fossil fuel intensive GHG's emission scenarios have underestimated the actual emissions growth for this period. In consideration of this, therefore, the use of more extreme scenarios A1 and A2 instead of conservative B1 and B2 scenarios has been recommended (Beaumont *et al.*, 2008). Consequently, the scenario A2 was preferred since only data for scenarios A2 and B2 was available.

1.1.3. Climate change models

After generation of future scenarios of GHG emissions, they are used together with observed past climatic variables to generate future climates using General Circulation Models (GCM's). These are mathematical models that describe the processes that are known to occur in the earth's climate system and their possible interactions. They are used to forecast the trend of climate over several decades (IPCC, 2009). These models maybe categorized based on the climate forcing that drive them. Atmosphere General Circulation Models (AGCM's), models the atmospheric processes such as convection, aerosols and cloud cover while the Ocean General Circulation Models (OGCM's) models the ocean processes influencing the climate. Coupling of the AGCM's and OGCM's yields the Atmosphere-Ocean General Circulation Models (AOGCM's) that are more robust in simulating the climatic processes especially at continental scales and above (IPCC, 2007). There is considerably high confidence on the capability of AOGCM's to provide credible estimates of future climate change as demonstrated by their ability to reproduce observed features of recent and past climate changes (IPCC, 2007). However, uncertainties in their projections still exist although they are significantly lower for some climatic variables like temperature but higher for others like precipitation (IPCC, 2007). Generally, the uncertainties of the projections increases with decreasing spatial and temporal scales hence changes in the regional climates are therefore more uncertain than changes in the global mean climates (IPCC, 2000).

The Hadley Centre Coupled Model version-3 (HADCM3) developed by Hadley Centre for Climate Prediction and Research (HCCPR) within United Kingdom's (UK) Meteorological Office was used. Its detailed parameterization and evaluation are discussed by Gordon *et al.* (2000) and Pope *et al.* (2000). However, it is one of the AOGCM's participating in IPCC's Fourth Assessment Report (AR4) (IPCC, 2007) and does not need flux adjustment (additional artificial heat and freshwater fluxes at the ocean surface) to produce good simulations (Gordon *et al.*, 2000). Moreover, it has been run for over a thousand years, showing little drift in its surface climate.

However, like all other GCM's, its simulations are global and hence with low resolution that does not capture regional climatic variability well (Beaumont *et al.*, 2008). To capture regional specific climate aspects, the GCM's need to be downscaled with Regional Climate Models (RCM) using dynamic or statistical methods (Beaumont *et al.*, 2008). The HADCM3 model data used in this research had been statistically downscaled to 30 arc-seconds resolution using the Anuspline interpolation algorithm of IPCC climate anomalies (CIAT, 2009) and the current distribution of climates in WorldClim database developed by Hijmans *et al.* (2005).

1.2. Research problem

Global climate has been experiencing an increasingly changing trend, with the warming of the last 30 years being estimated greater than any other time in the last 1,000 years (Walther *et al.,* 2002). The changing climate has been reported to affect the species distribution, physiology and phenology (Hughes, 2000). Consequently, climate change has emerged as a major driver of global biodiversity loss and has been linked to several species level extinction (Pounds *et al.*, 1999, Gibbons *et al.*, 2000) and numerous range shifts (Walther *et al.*, 2002, Carey and Alexander, 2003, Collins and Storfer, 2003, Pearson and Dawson, 2003, Root *et al.*, 2003, Thomas *et al.*, 2004, Araujo *et al.*, 2006, Sekercioglu *et al.*, 2008, Hole *et al.*, 2009). This is due to the fact that the changing climate in synergy with other biodiversity drivers, likes habitat fragmentation, may result to contraction of species climatic space with consequent local extinction. Contracting species ranges may lead to commitment of more species into extinction following the existing inverse relationship between species probability of extinction and their range size (Thomas *et al.,* 2004). Without exception, snake species are also susceptible to climate change partly due to their characteristic low population, patchy distribution, low dispersal rate and low reproduction rates (Segura *et al.*, 2007).

Moreover, the Mediterranean basin is projected to experience high biodiversity loss due to synergic combination of climate change and other drivers of biodiversity loss such as habitat fragmentation and invasive species (Sala *et al.,* 2000). Considering the high diversity of snake species in this biome, (107 species), of which 37 are endemic (Cox *et al.,* 2006), this raises serious conservation concern. Consequently, the existing snake species in Spain, located within the Mediterranean basin, may also be under serious threat. In addition to increasingly warming trends, Spain has also experienced widespread habitat fragmentation as a result of intensive agricultural and urban development (Segura *et al.,* 2007, Omolo, 2006) that may further jeopardize the limited dispersal rate of snake species in a bid to tract their changing habitats.

Despite these threats poised by climate change on snake species in Spain, there is limited research on the possible impacts of changing climate on the geographical range of these species. The magnitude and patterns of change in geographical range of these species and the corresponding response of generalists' and specialists' species to changing climate remain largely unknown. Hence this study investigates the impact of climate change on distribution of four snake species by the year 2050 and whether the response of specialists and generalists' species will be different.

1.3. Research objectives.

1.3.1. General objective.

This study investigates the effect of climate change on the spatial distribution of four snake species in Spain mainland.

1.3.2. Specific objectives.

The specific objectives were to:

i. Identify the predictor variables that have the highest predictive power in the potential distribution models of the four snake species.
ii. Generate potential distribution models for the four snake species using the current climatic and biophysical explanatory variables.
iii. Project the future potential distribution of the four snake species using the projected year 2050 climatic and biophysical variables.
iv. Investigate whether the projected range shifts among the specialist species will be different from that of generalist species.

1.4. Research questions.

The research questions to be addressed are:

i. Which variables contribute the highest predictive power in the potential distribution models of the four snake species in Spain?
ii. Will climate change result to shift in distribution of the four snake species by the year 2050 in Spain?
iii. Will the projected range shifts among the specialists' species be different from that of generalists' species?

1.5. Hypotheses.

Test the concept that the climatic variables have significantly higher predictive power than biophysical variables in potential distribution models of the four snake species in Spain.

H_0: Climatic variables do not have significantly higher predictive power than biophysical variables in potential distribution models of the four snake species in Spain.

H_1: Climatic variables have significantly higher predictive power than biophysical variables in potential distribution models of the four snake species in Spain.

Test the concept that climate change will result to shift in distribution of the four snake species in Spain by the year 2050.
H_0: Climate change will not result to shift in distribution of the four snake species in Spain by the year 2050.
H_1: Climate change will result to shift in distribution of the four snake species in Spain by the year 2050.

Test the concept that the projected range shifts among the specialist species will be different from that of generalist species?
H_0: The projected range shifts among specialist species will not be different from that of generalist species.
H_1: The projected range shifts among specialist species will be different from that of generalist species.

1.6. Selected snake species.

In this study, four snake species are considered namely: *Malpolon monspessulanus*, *Rhinechis scalaris*, *Coronella girondica* and *Natrix maura*. The selection of these species was based on their specialization and endemicity. Despite *Malpolon monspessulanus* all the other species are endemic to the Mediterranean basin (Cox *et al.*, 2006). Moreover, *Malpolon monspessulanus* and *Rhinechis scalaris* are generalists while *Coronella girondica* and *Natrix maura* are specialist's species. Species specialisation may either be in the form of habitat, diet or both (Santos *et al.*, 2007b, Segura *et al.*, 2007).

1.6.1. *Malpolon monspessulanus* (Hermann, 1804).

This species is commonly known as Montpellier snake. It is a generalist species inhabiting nearly all environmental conditions in the Iberian Peninsula. It preys upon over thirty vertebrate and invertebrate species (Moreno-Rueda *et al.*, 2009), has a high reproductive rate and depicts high tolerance to habitat alteration by human activities (Segura *et al.*, 2007). The population of this species has been reported to be increasing despite the general declining trend for most snakes in the region (IUCN, 2009). Altitudinally, its range extends from sea level up to 2,160m above sea level (a.s.l.). On the IUCN red list, it is listed as a species of Least Concern (LC) owing to its relatively wide distribution, tolerance to habitat modification, presumed large population, and the fact that it is unlikely to be declining fast enough to qualify for listing in a more threatened category (IUCN, 2009).

1.6.2. Rhinechis scalaris (Schinz, 1822)

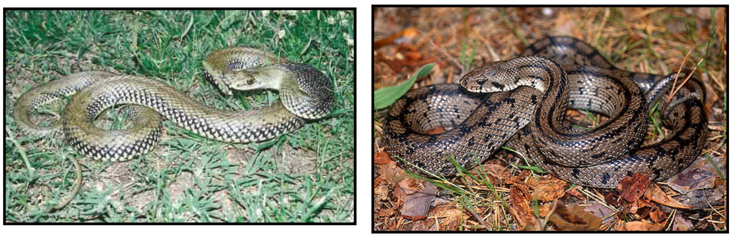
This species was earlier classified taxonomically as *Elaphe scalaris*. It's commonly known as the Ladder Snake relating to ladder-like pattern on the back during its juvenile stage. It is a generalist species mostly preferring sunny and stony Mediterranean type habitats with good vegetation cover (IUCN, 2009) such as open woodlands and scrubland, hedges, vineyards, olive groves, stone walls and ruins and south facing slopes with sparse vegetation or crops (Pleguezuelos, 2006). It preys almost exclusively on endotherms, mainly small mammals that represent nearly 95% of their diet in mass (Pleguezuelos *et al.*, 2007). It is an active forager, a trait that exposes it to high risk of predation especially by the short toed eagle (Gil and Pleguezuelos, 2001). In the IUCN red book, it is listed as Least Concern (LC) in relation to its wide distribution, tolerance to broad range of environmental conditions, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (IUCN, 2009).

1.6.3. Coronella Girondica (Daudin, 1803).

This species is commonly known as southern smooth snake. This species displays crepuscular and nocturnal tendencies as it spends much of the time below-ground or underneath stones and is active in the open only at night or at dusk (Luiselli *et al.*, 2001). Due to its crepuscular and nocturnal tendencies, the distribution of this species is little known. Moreover, it is a specialist predator of small lizards (Santos and Pleguezuelos, 2004). It employs active foraging tactics by searching their prey in their hiding places as their preys are mostly diurnal. Its habitat preferences includes scrublands, open woodlands, dry hedgerows, grasslands and rocky areas located in mountainous areas with cool and wet conditions (Santos and Pleguezuelos, 2004). It is known to avoid altered habitats (Segura *et al.*, 2007) and is markedly absence in large areas of intense agricultural activity, indicating their vulnerability to such practices (Santos and Pleguezuelos, 2004). Its altitudinal range extends from sea level up to 2,150 m a.s.l (Santos and Pleguezuelos, 2004). Its threat level in Spain has been proposed to be raised from Least Concern to vulnerable (Santos and Pleguezuelos, 2004, Segura et al., 2007, IUCN, 2009).

1.6.4. Natrix maura (Linnaeus, 1758).

The common name for this species is viperine snake due to its resemblance of vipers. It is the most common snake in Spain (Segura *et al.*, 2007) inhabiting exclusively aquatic environments both natural (rivers, lakes, ponds, marshes) and artificial (irrigation ponds, decorative fountains, canals and reservoirs) (Santos, 2004). Altitudinally, it extends from sea level to 2600 m a.s.l. (IUCN, 2009). Its prey items comprise mainly of amphibians and fish (Santos, 2004). Due to its aquatic habits it is highly threatened in parts of its range as a result of aquatic pollution. The organochlorine pesticides affect them indirectly as they result in loss of their prey species like fishes (IUCN, 2009). The overall reduction of water volume in its habitats has also been cited as a major threat (Santos, 2004). It is listed as Least Concern in consideration of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category (IUCN, 2009).



Malpolon monspessulanus *Rhinechis scalaris*

Natrix maura Coronella girondica

Figure 1-2. Photo of the selected snake species.

1.7. Modelling Asssumptions.

To generate SDM's of the snake species several assumptions were made. First, the biotic interactions between species such as competition and predation were not considered even though they are known to limit species distribution (Pearson and Dawson, 2003). Since natural systems involve a complex web of interactions and feedbacks between species, changes in distribution of one species could result to drastic impacts on the distributions of many other inter-related species.

Secondly, evolutionary adaptations of species to changing climate, that may lead to their continued persistence in some areas, are also not considered (Pearson and Dawson, 2003). It is therefore assumed that species will not be able to adapt to the changing climate within the time period considered. Although adaptation and evolutional changes of species mostly takes a considerable long time (Pearson and Dawson, 2003), some rapid adaptations has been reported (Thomas *et al.*, 2001).

Thirdly, it is assumed that the species have no constraints to dispersal (Araujo *et al.*, 2006) and hence they will be able to track the changing climate by colonising new areas that become suitable. However, snake species have been demonstrated to have limited dispersal abilities (Segura *et al.*, 2007), a fact that may be further aggravated by increased habitat fragmentation and aridity in Spain.

Fourthly, the projections of the future species ranges are made with assumptions that the current species-climate relationships will remain unchanged under changing climate (Fitzpatrick *et al.*, 2008). Lastly, the species are assumed to be in equilibrium with their environment i.e. occurring in all climatically suitable areas whilst being absent from all unsuitable ones (Araujo and Pearson, 2005).

2. Materials and methods

2.1. Research approach

As illustrated in Figure 2-1 the maxent model was trained using current climate and biophysical explanatory variables for the entire Spain mainland. The trained model was validated using threshold dependent and independent methods together with independently collected species occurrence data. The predicted current range was applied to project the future range (year 2050). For each species the current and future range maps were cross-tabulated to reveal the range shifts. Finally, the range shifts among generalist species was compared with those of specialist species.

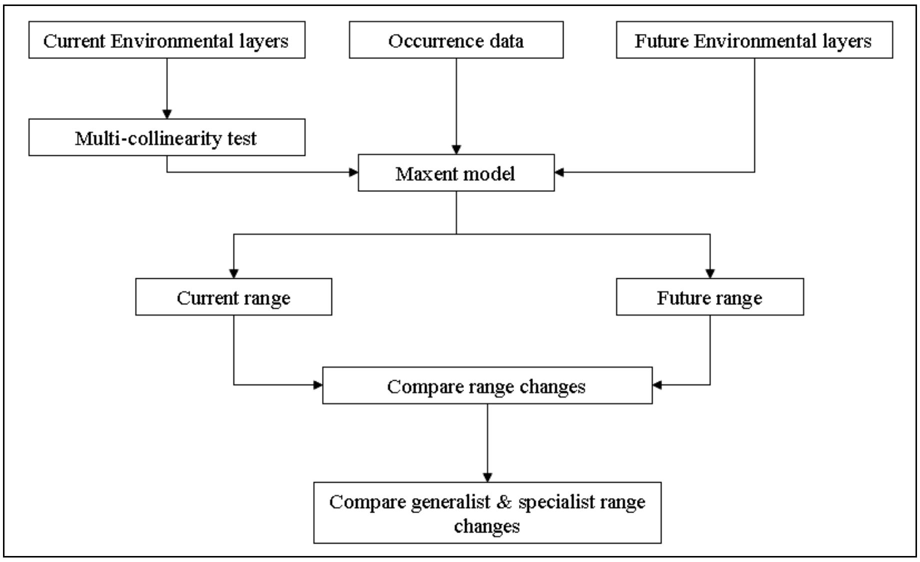


Figure 2-1. The general research approach.

2.2. Study area

The study area was the whole Spain mainland territory. Spain has been selected due to its high diversity of snake species and its location within the Mediterranean biome which is projected to be highly vulnerable to biodiversity loss due to a combination of several drivers that include climate change and habitat fragmentation (Sala et al., 2000). Spain is situated on the Iberian Peninsula in an area covering about 504,030 Km^2. It is located between latitudes 43° 47' 24" N and 36° 00' '3" N and between longitudes 7° 00' 29" E and 5° 36’ 40" W. It borders to the north the Bay of Biscay, France and Andorra; to the East the Mediterranean Sea; to the South the

Mediterranean Sea and the Atlantic Ocean and to the West by the Atlantic Ocean and Portugal.

The climate is characterised by mild and wet winter and hot and dry summer (Giannakopoulos *et al.*, 2005). The south-western and eastern coastline regions have the highest mean annual temperature (>15 °C) while the lowest are recorded in north-east, hence revealing a north-east to south-west temperature gradient (Hijmans *et al.*, 2005). The high altitude northern region in the Pyrenees receives the highest mean annual precipitation with records of higher than 1000 mm being recorded. Generally, much of the country is dry, especially the central parts that receives 500 or less mean annual precipitation. The country has witnessed historical pressures on land use changes mainly from agricultural intensification, pine afforestation and urbanization that lead to habitat fragmentation. Since Spain joined the European Union, agricultural intensification mainly dominated by olive growing has been boosted by subsidies, further accelerating habitats alteration (Omolo, 2006).

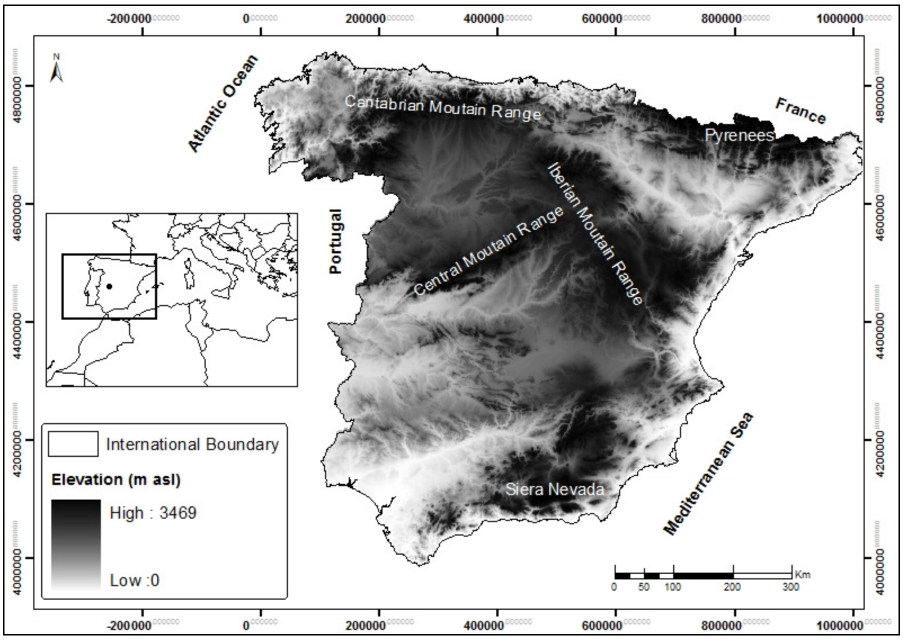


Figure 2-2. Showing map of the study area.

2.3. Species Distribution Data

Several datasets with different resolution were used in this study for various purposes. The main dataset utilised was obtained from the original database used to generate the “Atlas Y Libro Rojo De Los Anfibios Y Reptiles De Espana” (Atlas and Red Book of

Amphibians and Reptiles in Spain) (Pleguezuelos *et al.*, 2004). The majority of the atlas data was collected in the period 1981-1997 by various regional mapping projects. However, further surveys were conducted from year 2000 - 2002 to ground truth the earlier records and to add new observations especially in grids that were not previously covered (Pleguezuelos *et al.*, 2004). The database had seven main fields detailing the species scientific name, UTM 10x10 Km grid reference, UTM 1x1 Km grid reference, xy coordinates of the species location, the province and altitude in metres a.s.l. However, as illustrated in Table 2-1 the obtained database had only few records with UTM 1x1 Km grid and xy coordinates.

The data was up-scaled by generating central point of grids that recorded presence of each species using feature to point tool in ArcGIS 9.3.1 (ESRI, 2008). The generated centroids were used as presence localities following Brito *et al.* (2008), Bombi *et al.* (2009), Sillero *et al.* (2009) and Niamir (2009). 70% of random centroids were used to train the model while the rest 30% were used as test dataset. Table 2-1 below shows the distribution of the centroids used for model training.

Although the centroids generated from 1x1 Km grids had higher resolution, they did not represent all climatic zones adequately hence they could not be used for model training. All the available xy presence points (Table 2-1) were used to update the 1x1 Km grids. Hence they were overlaid on the 1x1 Km grids covering the whole Spain those grids that had one or more xy points falling within them and the species was not previously observed there were re-coded as presence. Finally all the 1x1 Km grids coded as presence for each species were selected and their central points generated as presence localities. This was done to ensure that the dataset is of same resolution and to avoid replication as some of the xy points had been used to generate the original atlas. The derived presence points from 1x1 Km grids for each species were used to compute the sensitivity of the models.

Although most of these datasets used were not collected using a spatially explicit sampling scheme that would be ideal for modelling species response to climatic gradients, they are the often the best data available for such elusive species (Franklin *et al.*, 2009) that are poorly monitored and covering such a scale used in this study.

Table 2-1. Species occurrence data.

Species	Fieldwork XY points	Secondary Data XY points	 1x1Km grids	 10x10Km grids
Coronella girondica	1	12	145	1144
Rhinechis scalaris	8	38	364	2012
Malpolon monspessulanus	14	65	461	2218
Natrix maura	5	130	675	2625

[1] Shows the total 1x1 Km grids after updating with the new xy datasets.

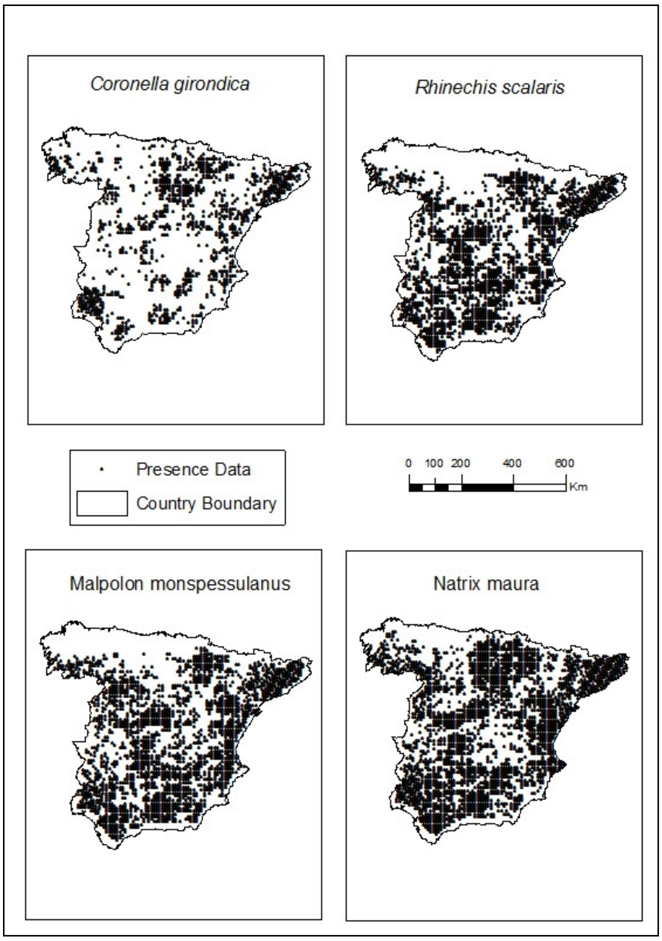


Figure 2-3. Species presence data used for model building

2.3.1. Field work

As shown in Table 2-1 above some of the xy points were collected during the fieldwork that was undertaken in Malaga province, Spain. Field sampling was based on corine land cover (EEA, 2000) whereby 18 out of 31 corine classes covering Malaga province were selected based on knowledge of snake habitat preferences and accessibility. Three polygons from each of the selected corine classes were selected randomly; hence the overall samples were 54 polygons. The selected corine sample classes together with geo-referenced roads map and QuickBird orthophotos (Digitalglobe, 2004) collected in year 2004 covering the whole of Malaga province were input into a HP-iPAQ hand-held PDA with a Bluetooth GPS receiver. The roads map was used to navigate to the selected sample polygons while orthophotos aided in interpreting the habitat types. Once in the sampling polygon searching was done along a random line transects cutting across the polygon. Sampling involved visual encounters of live snakes and signs of presence like skins. Stones were carefully overturned as snakes often shelter under the rocks. Moreover, GPS points of road kills spotted when driving were also recorded. When a snake was spotted the geographical coordinates, species, time of the day, weather conditions and the habitat type were recorded. The searches were done on warm and sunny days lasting from 0800 hours to 1800 hours. However during the hot midday hours it was difficult to spot live snakes as high temperatures made them to retreat into thermo-regulation sites mostly underneath rocks and bushes. Due to time, weather (e.g. rain in some days) and logistical limitations only 48 of the sample polygons were covered.

2.4. Environmental predictor Variables

Table 2-2 shows the pre-selected predictor variables and their sources. Since the datasets were obtained from multiple sources with different coordinate systems, they were all projected to ED50_UTM_30N coordinate system with a resolution of 1Km^2. Furthermore, all environmental variables were converted to ASCII format using conversion tool in ArcGIS 9.3.1 (ESRI, 2008).

The selection of the environmental variables was based on their demonstrated causal effect on snake species distribution e.g. in (Soares and Brito, 2007, Real *et al.*, 2009, Bombi *et al.*, 2009) and data availability. In addition to exerting direct physiological effects on the species, the climatic variables are also used to reflect the energy and water availability that influences the ecosystem productivity (Moreno-Rueda and Pizarro, 2007). Topographical variables has an indirect effect in influencing micro-climates within the species ranges (Guisan and Hofer, 2003). The westness and southness are used to reveal local variations in insolation and temperature (Deng *et* *al.*, 2009). Incorporating land cover facilitate discrimination of species habitat preferences while the proximity variables enables assessment of species behavioural responses such as avoidance, attraction or neutrality to habitat fragmentation (Suarez-Seoane *et al.*, 2008).

Table 2-2. Pre-selected Predictor variables

Predictor variable	Original Resolution	Source
Climatic		
Min. temperature of coldest month (10 x ^{o}C)	1 Km	WorldClim/CIAT
Temperature seasonality (C. of V.)	1 Km	`` ``
Precipitation seasonality (C. of V.)	1 Km	`` ``
Isothermality[2]	1 Km	`` ``
Precipitation in spring (mm)	1 Km	`` ``
Precipitation in autumn (mm)	1 Km	`` ``
Precipitation of warmest Quarter (mm)	1 Km	`` ``
Max. temperature autumn (10 x ^{o}C)	1 km	`` ``
Max. temperature summer (10 x ^{o}C)	1 Km	`` ``
Max. temperature spring (10 x ^{o}C)	1 Km	`` ``
Topographic		
DEM (STRM)	90 M	CGIAR
Slope	90 M	
Southness	90 M	
Westness	90 M	
Land cover		
Corine	1 Km	EEA
CLUE	1 Km	Verburg
Proximity		
Distance to rivers	1 Km	
Distance to urban centres	1 Km	

[1] Isothermality = mean diurnal range/temperature annual range*100

2.4.1. Climatic variables.

The current climatic layers were downloaded from the WorldClim website (WorldClim, 2005). WorldClim is a set of global climate layers with spatial resolution of 30 arc-seconds, generated using thin-plate smoothing spline interpolation of weather station data for the period 1950 to 2000 (Hijmans *et al.*, 2005).

Future climatic projections for the year 2050 based on HADCM3 model and A2 emission scenario were downloaded from International Centre for Tropical Agriculture (CIAT) database (CIAT, 2009). This dataset is part of the CIAT climate change downscaled data, developed in the Decision and Policy Analysis (DAPA) program. CIAT obtained the original climate data from the IPCC data portal (IPCC-DDC, 2009) before downscaling it using an empirical approach (CIAT, 2009). The downscaling procedure involved (1) calculation of anomalies (if not directly provided by IPCC) by subtracting each variable's future values with the baseline (both are provided by IPCC) (2) interpolation of anomalies to a 30 arc-seconds resolution using Anuspline interpolation algorithm and (3) addition of the interpolated anomalies to the current distribution of climates in the WorldClim database developed by Hijmans *et al.* (2005).

2.4.2. Topography

The Shuttle Radar Topographic Mission (SRTM) Digital Elevation Model (DEM) was downloaded from CGIAR (CGIAR, 2009) website. The original DEM had spatial resolution of 90 m but was aggregated using ArcGIS spatial Analyst aggregate tool to 1Km resolution. Slope and aspect were generated from this DEM using surface tools in ArcGIS 9.3.1 Spatial Analyst tool. Since aspect has circular dimensions, it was transformed into two distinct variables, the southness and westness following Chang *et al.* (2004) where:

$\text{Southness} = 180 - |\text{aspect} - 180|$ **Equation 1.**

$\text{Westness} = |180 - |\text{aspect} - 270||$ **Equation 2.**

This resulted to south facing slopes having a value 180 and while north facing slopes have a value 0. Similarly, the west facing slopes had value 180 and while the east facing slope had value 0.

2.4.3. Land cover

Corine Land Cover (CLC) 2000 was downloaded from the European Environmental Agency (EEA) website (EEA, 2000). The original map had a spatial resolution of 100 m but was aggregated to 1 Km resolution using ArcGIS 9.3.1 Spatial Analyst aggregate tool. For future climate model, a future land cover map projected using CLUE (Conversion of Land Use and its Effects) model (Verburg *et al.*, 2009, Verburg and Overmars, 2009) was used. CLUE is a spatially explicit land allocation model, with a spatial resolution of 1 Km that provides a typology of land use changes in Europe based on a series of different scenarios of land use change for the period 2000 - 2030. The model is based on four different scenarios of plausible changes in world economy, demography, technology and policies that may alter the European land use pattern (IPCC, 2000). The CLUE map used had 1Km^2 spatial resolution and was based on scenario A2 for year the 2030. However it had 17 land use classes while Corine map has 43 land cover classes. But in the accompanying CLUE legend (Appendix 1), the equivalent Corine classes were clearly indicated, which was used to re-classify the Corine map into 17 classes, matching those in the CLUE map.

2.4.4. Proximity variables

Two proximity variables, namely; distance to rivers and distance to urban centres were generated by calculating the linear distance to rivers, urban centres and highways, respectively, using ArcGIS 9.3.1 Spatial Analyst Euclidean distance tool.

2.4.5. Matching current and future variables.

To enable projections of future species ranges, environmental predictors were required to be in pairs, one for current and other for future conditions. Both current and future climatic layers were readily available with the same resolution. The Corine land cover was however matched with the CLUE model land use/cover classes for the year 2030 as the projections of year 2050 were not readily available. However, the linear distance to rivers and urban centres were assumed to be constant for both time periods due to high uncertainties in projecting their future conditions. This is despite the fact that the distances to these variables may change due to drying or decrease in water volume in rivers and increased urban sprawl. Since the topographical variables are not subject to change in the future, similar layers were hence used for both time periods.

2.4.6. Multi-collinearity diagnostics

Multi-collinearity refers to the state of very high inter-correlations amongst the explanatory variables used in a model. Existence of high multi-collinearity makes statistical inferences on the data unreliable since the confidence intervals of the coefficients become very wide and the statistics tend to be very small. Multi-collinearity diagnostics were calculated for all continuous variables by computing Variance Inflating Factors (VIF's) using Collinearity Diagnostics in SPSS 16. VIF is computed using the following formula:

$$VIF = \frac{1}{1-R^2} \quad \textbf{Equation 3.}$$

Where R2 is the coefficient of determination of the regression equation. VIF values greater than 10 suggest existence of multi-collinearity problems in the explanatory variables (Myers, 1990). Hence, for each diagnostic run, one explanatory variable with a VIF value greater 10 was eliminated. Expert knowledge was used to ensure that as many predictors as possible with different ecological meaning were retained. Consequently, the diagnostic was re-run again until none of the variable had VIF greater than 10. However, using the expert knowledge of snake species ecology, five variables were added in the model despite having multi-collinearity problems. However some were eventually eliminated after jackknife test of variables importance in Maxent hence reducing multi-collinearity. Table 2-3 show the VIF values for variables that remained after multi-collinearity test and also the final VIF values after the addition of the five variables with multi-collinearity problems. Moreover, Corine land cover layer (CLUE for future conditions), which is a categorical variable, was included into the final list of variables that were used to run the model.

Table 2-3. Remaining variables after multi-collinearity diagnostics

		VIF	
Abbreviation	**Full Name**	**Passed**	**All**
Southness	Southness	1.05	1.06
Rivers_Distance	Distance to rivers	1.05	1.06
Westness	Westness	1.02	1.14
Slope	Slope	1.40	1.45
Urban_Distance	Distance to urban	1.42	1.85
Isothermality	Isothermality	1.22	4.19
Prec_spring	Precipitation spring	2.68	8.74
Prec_Seasonality	Precipitation seasonality	6.17	11.71
Prec_autum	Precipitation in autumn	-	12.33
Prec_Warmest_Quarter	Precipitation of warmest quarter	7.46	15.15
DEM	DEM	2.33	17.51
Temp_Seasonality	Temperature seasonality	2.14	29.11
Tmin_coldest_quarter	Min. temperature of coldest month		31.69
Tmax_spring	Max. temperature in spring		77.80
Tmax_summer	Max. temperature in summer		156.40
Tmax_autum	Max. temperature in autumn		161.73

2.5. Maxent Model.

The maxent modelling algorithm Phillips *et al.* (2006) was used for modelling. This is a general purpose machine learning method that makes predictions from incomplete information since it requires only species presence data. This maybe advantageous considering that there are high uncertainties in identifying the absence of species in a particular location (Phillips *et al.*, 2006). Maxent uses a maximum likelihood method to generate probability distribution over pixels in the study area (Yost *et al.*, 2008). The estimated Maxent probability distribution is exponential in a weighted sum of environmental features divided by a scaling constant to ensure that the probability values range from 0 to 1 and sum to 1 (Phillips *et al.*, 2006). The Maxent probability distribution takes the form:

$$q_{\lambda}(x) = \frac{e^{\lambda . f(x)}}{z_{\lambda}} \qquad \textbf{Equation 4.}$$

Where: λ is a vector of *n* real valued coefficients or feature weights, f denotes the vector of all *n* features, and z_{λ} is a normalizing constant that ensures that q_{λ} sums to 1 (Phillips *et al.*, 2006).

The program starts with a uniform distribution and performs a number of iterations, each of which increases the probability of the sample locations for the species. The probability is expressed as 'gain' which is the log of the number of grid cells less the log loss (average of the negative log probabilities of sample locations) (Phillips *et al.*, 2006). The program starts with a uniform distribution which has zero gain. Then sequential iterations are undertaken, each of which increases the probability of locations for the species. The gain increases from one iteration to the next until the change from one iteration to the other is less than the set threshold or the maximum iterations set are reached, whichever is earlier. The gain is a measure of the likelihood of the samples as it indicates how much better the Maxent distribution fits the training data points than the uniform distribution which has a gain of zero (Phillips *et al.*, 2006). If for example the gain is 0.7, it means that the average sample likelihood is exp(0.7) ≈ 2 times higher than that of a random background pixel. The gain is closely related to deviance as used in generalized linear models. The sequential-update algorithm is guaranteed to converge to the optimum probability distribution and because the algorithm does not use randomness, the outputs are deterministic ((Phillips *et al.*, 2006). Maxent controls over fitting the model by using a regularization parameter that constrains the estimated distribution such that the average value for a given predictor is close to the empirical average instead of being equal to it (Phillips *et al.*, 2006).

The Maxent distribution is calculated over all pixels in the study area that have data for all explanatory environmental variables. However in the case of a large number of pixels, the process is slowed without any significant improvement to model performance. Hence if the number of pixels exceeds 10,000, a random sample of 10,000 "background" pixels is used to represent the variety of environmental conditions present in the data (Phillips *et al.*, 2006). The Maxent distribution is then computed by combination of the “background” pixels and the training sample points where the species was located. Maxent offers three output formats for the generated distribution maps i.e. the raw, cumulative and logistic outputs. For this study, logistic output was preferred as it gives the probability values ranging from 0 to 1 for each pixel. Hence the most suitable pixels are the ones with a value of 1 while the least suitable pixels have values zero (Phillips *et al.*, 2006).

The Maxent algorithm was selected as it offers several advantages as outlined by (Suarez-Seoane *et al.*, 2008) namely: (1) it requires only presence data together with environmental information covering whole study area (2) it is capable of using both continuous and categorical data and successively incorporate complex interactions between these variables and (3) over-fitting can be avoided by using regularization parameters.

However, it has a drawback when projecting species distributions to future environments that may require extrapolation beyond the limits observed in the training dataset (Phillips *et al.*, 2006). Since it uses an exponential model for probabilities, which is not inherently bounded above, it can therefore produce very large predicted values for environmental conditions outside the range present in the study area (Phillips *et al.*, 2006). However, this problem has been addressed by introduction of “Clamping” functionality (Phillips and Dudik, 2008) that automatically set the upper and lower bounds of future climate environmental variables to those observed under the current conditions. Hence if the future climate values for a variable used in the model exceed the maximum or is lower than the minimum recorded in the current climatic conditions, the “Clamping” functionality automatically set the future conditions values to either maximum or minimum of current conditions depending on the bounds they exceed.

2.5.1. Model building with Maxent.

Before running the models, the maximum iterations were set to 1000, convergence threshold to 10^{-5}, regularization multiplier to 1 and the “fade by clamping” option was used to control extrapolation beyond the range of training dataset. The linear, quadratic, product, hinge and threshold functions were used. For each species two suites of models were run: first with topographical, land cover and proximity variables (biophysical only model) and secondly with all variables in the first model plus climatic variables (all-inclusive model). This was done to assess the relative importance of climate in species distribution models.

Model building aimed at generating models with adequate performance using the best subset of predictors. To start with, a full model comprising of all preselected environmental variables for each species was run. Following Phillips *et al.* (2006) and Yost *et al.* (2008) ten random partitions were run using 70% of all presence points available for each species to training the models while the rest 30% for testing. This partitioning allowed assessment of the average behaviour of the algorithm and facilitated statistical testing of the performance of models run with different number of predictors for each species.

Using the jackknife test for variable importance, the variable with the lowest decrease to the average training gain when omitted was eliminated and the model re-run with the remaining variables. The process was repeated until only one variable remained. The Jackknife test calculates the gain for each variable when used alone and the drop in average gain when the variable is omitted from the model (Phillips *et al.*, 2006). Maxent also generated a heuristic percentage contribution of each variable in the respective species models. To determine this estimate, in each iteration of the training algorithm, the increase in regularized gain was added to the contribution of the corresponding variable or subtracted from it if the change to the absolute value of lambda is negative (Phillips *et al.*, 2006).

The Shapiro-Wilkson normality test was used to test whether the resulting training gains and test AUC values were normally distributed before choosing the statistical method to be used for testing their significance. Following Yost *et al.* (2008) the Mann-Whitney-U statistic was used to test for statistical difference between the training gains of the full model and those of the other models with some variables removed. The sample for this test comprised of n=10 training gains for each model emanating from 10 partitions. Hence for each species, the model with the least number of predictors and training gain not significantly different from that of full model was selected as the best model. The best model was run with all occurrence localities to take advantage of all available data following Phillips *et al.* (2006).

Furthermore to determine which of the two model suites was performing better; the Mann-Whitney-U statistic was used to test whether the test gains and test AUC values for the biophysical only model were statistically different from that of the all-inclusive model. Between the two model suites, the one having highest predictive power was used to project the future distribution. Moreover to assess the predictive power of the corine variable, Mann-Whitney-U statistic was used to compare the resulting training gains with and without corine variable in the model as reflected by the jackknife test of variable importance. The sample size for this test also comprised of 10 training gains emanating from the ten partitions for each model with certain number of predictors up-to when the corine variable was eliminated from the model.

2.6. Model evaluation.

As recommended by Hernandez *et al.* (2006), to determine the accuracy of the models generated with presence only data, multiple evaluation criteria's are necessary. This is because each measure provides only a portion of the elusive ''truth'' of the predictive ability of the models. Hence, the following evaluation techniques were used:

2.6.1. Threshold independent evaluation criteria.

The Area Under Curve (AUC) of the Receiver Operating Characteristic (ROC) function was used as the threshold independent evaluation. The AUC of the ROC function is an index of model performance that provide a single measure of overall accuracy that is independent of any particular threshold (Fielding and Bell, 1997). The AUC is the probability that a randomly chosen presence site is ranked above a random background site. A random model has AUC of 0.5 while a perfect model should have AUC of 1. However, as demonstrated by Phillips *et al.* (2006), when using the presence only data the maximum achievable AUC is less than 1 since it has been proved that:

$$\text{Maximum AUC} = 1 - {}^{a}\!/_{2} \quad \textbf{Equation 5.}$$

Where a = fraction of pixels covered by species true distribution that is normally not known. This is an artefact within the ROC evaluation method that essentially lowers the maximum achievable AUC values for habitat generalist species that have wide distribution.

The ROC analysis assigns a threshold to the modelled probability values by which sampling units are classified as positive or negative for species presence. The sensitivity for a particular threshold is the fraction of all positive instances that are classified as present and specificity is the fraction of all negative instances that are classified as not present (Phillips *et al.*, 2006). The Maxent model derive the ROC plot by plotting all sensitivity values on the y axis against their equivalent (1- specificity) values for all available thresholds on the x axis (Phillips *et al.*, 2006). Hence, any particular point (x, y) in the ROC plot shows the fraction x of negative examples that are classified as positive and fraction y of positive examples that are classified as positive given a particular probability threshold.

The Wilcoxon rank-sum test was used to test whether the derived test AUC values for each of the two type of models were significantly better than that of a random model following Phillips *et al.* (2006).

2.6.2. Threshold dependent evaluation

Since the models were run with only presence data, evaluation criteria's that does not require absence (or background data) was necessary (Hernandez et al., 2006). Consequently, two threshold dependent evaluation methods were used i.e. sensitivity and binomial tests. Before evaluating with these criteria's, a threshold for converting the logistic predictions into suitable and unsuitable areas for species had to be specified. Although there is no universally agreed threshold in species modelling, a threshold criteria that maximizes the sum of sensitivity and specificity has been recommended by Hernandez *et al.* (2006) and Liu *et al.* (2005) as it balances between the omission and commission errors. Hence maximum training sensitivity plus specificity threshold was used for both evaluation methods.

The models were also evaluated using the binomial tests to investigate whether they predicted the test data significantly better than a random model with the same fractional predicted area. When test data is provided, Maxent automatically calculates the binomial probabilities and reports their associated p-values.

Moreover the sensitivity was used to evaluate the prediction accuracy of the models. This method indicates the percentage of positive test occurrences correctly classified as positive (Hernandez *et al.*, 2006). Similarly, the maximum training sensitivity plus specificity threshold was applied on the generated current distribution maps to convert the continuous predictions into suitable or unsuitable habitats. Then presence points derived from 1x1 Km grids were overlaid on thresholded maps using ArcGIS 9.3.1 software. The sensitivity was then computed as the percentage of presence points that occurred in areas predicted as suitable.

2.7. Range shifts analysis.

To evaluate the species range shifts between the two time periods, the produced probability distribution maps were reclassified into four suitability categories based on the probability of occurrence i.e. 0 - 0.25 (low suitability), 0.25 - 0.5 (medium suitability), 0.5 - 0.75 (high suitability) and 0.75 - 1 (very high suitability) following Chefaoui *et al.* (2005) and Santos *et al.* (2009). Although threshold criteria's that classifies the species as either presence or absence (suitable or unsuitable) are mostly preferred (Liu *et al.*, 2005, Jimenez-Valverde and Lobo, 2007), they are still a form of generalization since species are rarely in equilibrium with their environment i.e.

occurring in all climatically suitable areas whilst being absent from all unsuitable ones (Araujo and Pearson, 2005). Hence this conservative approach was adopted.

The re-classified current and future distribution maps were Cross-tabulated using Idrisi Andes software (Clarklabs, 2006). Cross-tabulation is used for change analysis between two image pairs. Despite showing a map on changes between the two time periods, it also gives a cross-tabulation table that shows the frequencies with which classes have remained the same (frequencies along the diagonal) or have changed (off-diagonal frequencies) (Eastman, 2006). Moreover, to show the degree of agreement between the two maps, cross-tabulation also shows the Kappa Index of Agreement (KIA), both in overall sense and on per category basis. The higher the agreement, the less the impacts of climate change on that particular species range. Following Landis & Koch (1977) the Kappa values are interpreted as follows: < 0 no agreement, 0.0 - 0.2 slight agreement, 0.21- 0.4 fair agreement, 0.41 - 0.60 moderate agreement, 0.61 – 0.80 substantial and 0.81- 1 almost perfect agreement.

In addition, cross-tabulation also uses the Chi square to test the association between the two maps and if the association is found to be significant, the Crammers V statistic is used as a post-test to determine the strength of association (Cramer, 1999). Crammers V is derived by first calculating the Chi square then using the following calculation:

$$V = \sqrt{\left(\frac{x^2}{(n(k-1))}\right)}$$ **Equation 6.**

Where x^2 is chi-square and k is the number of rows or columns in the table. Cramer's V varies between 0 and 1, with values close to 0 indicating little association while those close to 1 indicating strong association between variables. Similarly, the higher the association between the two maps the less the changes in the distribution of that particular species between the two time periods.

Furthermore, the resulting cross-tabulation map was reclassified using ArcGIS 9.3.1 into three general classes showing areas of the species range that are projected to contract, expand or remain stable respectively, regardless of their suitability class. The areas experiencing decline in suitability was interpreted as contraction while areas experiencing increase in suitability was interpreted as expansion. The aggregation into three classes facilitated the comparison of range shift trends between the generalists and specialist's species.

3. Results

3.1. Species models optimization and evaluation

For each species two types of models were run; biophysical only and all-inclusive models. Modelling started with 5 and 15 variables respectively except for Natrix maura models that started with 7 and 17 variables respectively. For each model, ten random partitions were run starting with a full model with all preselected variables. Then the jackknife test of variable importance was used to identify the variable having the minimal drop in average training when omitted. Then a reduced model without that predictor was run and the process repeated until only one variable remained.

The order by which the variables were eliminated and their accompanying gains and AUC values is shown in Table 3-1, Table 3-2, Table 3-3 and Table 3-4 for *Rhinechis scalaris, Malpolon monspessulanus, Coronella girondica* and *Natrix maura* respectively. The all-inclusive models for all species showed that temperature seasonality (Temp_seasonality) was the variable that remained and hence it proved to be the most important in that category. On the other hand, the biophysical only models for all species revealed that corine land cover was the variable that had the highest predictive power in that category as it was the one that remained after elimination.

Despite for models with one variable that showed relatively higher decline in the average training gains, test gains and AUC values after elimination of variables, the other models recorded only slight decline. Since the training gains reveal the fit of the data to the predicted distribution, it was therefore used to select the best performing model. The model with the fewest number of predictors and training gains not significantly different from that of the full model was selected as the best model. Since the training gains from different sized models did not pass the Shapiro-Wilkson normality test ($p < 0.05$), a nonparametric method, Mann Whitney-U statistic, was used to test their significance. The resulting best models for each species and for the two model suites are shown in bold in Table 3-1, Table 3-2, Table 3-3 and Table 3-4 for *Rhinechis scalaris, Malpolon monspessulanus, Coronella girondica* and *Natrix maura* respectively. Consequently, the selected best model for each species was run with all occurrence points to produce the final current distribution maps that were used for evaluating the prediction success of the models with a set of quasi-independent xy presence data derived from 1x1 Km grids. The selected best model for each species was also used to project it's the future distribution.

Furthermore, the Wilcoxon rank-sum test of average test AUC values showed that all species models predicted significantly better than random model ($p < 0.05$) irrespective of the varying number of predictors and the two suites of models. Moreover, the p-values resulting from the binomial tests for all partitions and threshold categories of the two types of models were highly significant ($p < 0.0001$) for all species models as shown in Appendix 2 and Appendix 3 for all-inclusive and biophysical models respectively. This indicated that all predictions were significantly better than a random model with the same fractional predicted area.

To determine which of the two types of models had the highest predictive power, Mann Whitney-U test ($\alpha = 0.05$) was used to test whether the average test gains and test AUC values for the biophysical only models were significantly different from that of the all-inclusive models. Results for all species showed that the average test gains and AUC values for the biophysical only models were highly significantly different from that of all-inclusive models ($p = 0.001$). In addition, the all-inclusive models for all species had higher average test gains and AUC values than biophysical models indicating that they had higher fit to the training data and accuracy in prediction respectively (Table 3-1, Table 3-2, Table 3-3 and Table 3-4). Furthermore the derived sensitivity values revealed that the all-inclusive models had higher sensitivity than biophysical models for all species. This revealed that at the modelling scale used in this study the climatic variables were the most important factors influencing the distribution of these species.

In addition, the Mann-Whitney-U test ($\alpha = 0.05$) indicated that the training gains for models with and without corine variable were not significantly different for all species (Table 3-5). Similarly, this indicated that at the modelling scale used in this study land cover had low predictive power in all species models.

Table 3-1. Optimization and evaluation of Rhinechis scalaris models

# of Predictors	**Predictor removed**	**Training gain p value**	**Gains**		**AUC**	
			Training	**Test**	**Training**	**Test**
All-inclusive model						
15			0.1523	0.1742	0.674	0.647
14	Tmax_autumn	0.823	0.1516	0.1741	0.674	0.646
13	Prec_spring	0.123	0.1514	0.1722	0.675	0.647
12	DEM	0.684	0.1511	0.1716	0.671	0.645
11	Southness	0.529	0.1505	0.1723	0.67	0.644
10	Isothermality	0.052	0.1464	0.1739	0.664	0.646
9*	**Slope**	**0.096**	**0.146**	**0.1714**	**0.666**	**0.644**
8	Tmax_spring	0.002	0.1416	0.1706	0.662	0.645
7	Corine	0.002	0.1413	0.1664	0.661	0.642
6	Prec_autumn	0.001	0.1381	0.1633	0.661	0.642
5	Tmax_summer	<0.001	0.1295	0.1635	0.653	0.644
4	Urban_distance	<0.001	0.1248	0.1553	0.646	0.635
3	Prec_seasonality	<0.001	0.1071	0.1395	0.64	0.635
2	Prec_warmest quarter	<0.001	0.0976	0.1225	0.627	0.616
1	Tmin-coldest-month	<0.001	0.0697	0.0783	0.597	0.588
Biophysical model						
5*			**0.0537**	**0.0481**	**0.615**	**0.583**
4	Slope	0.001	0.0452	0.0503	0.606	0.580
3	Southness	<0.001	0.0404	0.0474	0.594	0.578
2	DEM	<0.001	0.0327	0.0394	0.58	0.570
1	Urban Distance	<0.001	0.0203	0.0223	0.545	0.537

* Selected best models

Table 3-2. Optimization and evaluation of *Malpolon monspessulanus* models

# of variables	Predictor removed	Training gain P-value	Training gain	Test gain	Training AUC	Test AUC
All-inclusive model						
15			0.1349	0.1551	0.676	0.634
14	Tmax_autumn	0.631	0.1356	0.1554	0.675	0.634
13	Isothermality	0.315	0.1378	0.1369	0.676	0.624
12	Tmax_spring	0.89	0.1317	0.1507	0.673	0.629
11	DEM	0.971	0.1332	0.1456	0.670	0.629
10	Prec_autumn	0.353	0.1328	0.1513	0.667	0.632
9*	**Corine**	**0.430**	**0.1284**	**0.1531**	**0.665**	**0.631**
8	Slope	0.003	0.1266	0.1474	0.661	0.628
7	Southness	< 0.001	0.1225	0.1434	0.655	0.626
6	Urban_distance	< 0.001	0.1183	0.1552	0.649	0.631
5	Tmax_summer	< 0.001	0.1163	0.1448	0.643	0.626
4	Prec_spring	< 0.001	0.1127	0.1306	0.636	0.615
3	Prec_warmest_quarter	< 0.001	0.1022	0.1229	0.631	0.618
2	Prec_seasonality	< 0.001	0.0940	0.1174	0.621	0.608
1	Tmin-coldest-quarter	< 0.001	0.0722	0.0903	0.593	0.575
Biophysical model						
5*			**0.0376**	**0.0346**	**0.599**	**0.566**
4	Southness	0.131	0.0348	0.0324	0.592	0.560
3	Slope	0.004	0.0310	0.0337	0.584	0.566
2	DEM	< 0.001	0.0240	0.0287	0.568	0.556
1	Urban-Distance	< 0.001	0.0169	0.0215	0.540	0.533

* Selected best models

Table 3-3. Optimization and evaluation of Coronella girondica models

# of Variables	Predictor removed	Training gain P-value	Training gain	Test gain	Training AUC	Test AUC
All-inclusive model						
15			0.2195	0.2272	0.743	0.688
14	Tmax_spring	0.035	0.2273	0.2067	0.745	0.681
13	Tmax_autumn	0.280	0.2147	0.2359	0.741	0.692
12	Prec_autumn	0.684	0.2202	0.2024	0.741	0.679
11*	**Corine**	**0.579**	**0.2209**	**0.2160**	**0.741**	**0.685**
10	Tmax_summer	0.003	0.2020	0.2269	0.733	0.690
9	Prec_spring	0.015	0.2117	0.2083	0.735	0.680
8	Isothermality	0.001	0.1989	0.2130	0.730	0.684
7	Slope	<0.001	0.1951	0.1954	0.728	0.674
6	Urban_distance	<0.001	0.1842	0.2047	0.721	0.679
5	Southness	<0.001	0.1698	0.2000	0.708	0.679
4	DEM	<0.001	0.1494	0.1814	0.691	0.670
3	Tmin_coldest_month	<0.001	0.1373	0.1736	0.681	0.662
2	Prec_seasonality	<0.001	0.1083	0.1187	0.653	0.632
1	Prec_warmest Quarter	<0.001	0.0577	0.0679	0.619	0.608
Biophysical model						
5			0.06	0.0431	0.633	0.593
4*	**Urban**	**0.750**	**0.0525**	**0.0428**	**0.623**	**0.592**
3	Slope	0.003	0.0494	0.028	0.615	0.572
2	Southness	<0.001	0.0344	0.0195	0.59	0.565
1	DEM	<0.001	0.0196	0.0204	0.561	0.561

* Selected best models

Table 3-4. Optimization and evaluation of Natrix maura models

# of variables	Variable removed	Training gain P-value	Training gain	Test gain	Training AUC	Test AUC
All-inclusive model						
17			0.0852	0.0915	0.658	0.613
16	Tmax_autumn	0.880	0.0850	0.0847	0.660	0.607
15	Tmax_spring	0.623	0.0856	0.0909	0.659	0.610
14	Tmax_summer	0.910	0.0844	0.0916	0.658	0.611
13	DEM	0.970	0.0845	0.0895	0.654	0.609
12	Southness	0.406	0.0817	0.0908	0.650	0.611
11*	**Rivers_distance**	**0.070**	**0.0822**	**0.0851**	**0.647**	**0.605**
10	Corine	0.004	0.0794	0.0892	0.646	0.608
9	Urban_distance	< 0.001	0.0769	0.0926	0.643	0.613
8	Prec_warmest_quarter	< 0.001	0.0752	0.0929	0.640	0.610
7	Westness	< 0.001	0.0729	0.0837	0.635	0.607
6	Prec_spring	< 0.001	0.0712	0.0849	0.630	0.605
5	Isothermality	< 0.001	0.0666	0.0756	0.624	0.599
4	Prec_seasonality	< 0.001	0.0608	0.0737	0.615	0.596
3	Slope	< 0.001	0.0533	0.0692	0.607	0.592
2	Tmin_coldest_month	< 0.001	0.0433	0.0522	0.593	0.576
1	Prec_autumn	< 0.001	0.0306	0.0412	0.564	0.554
Biophysical model						
7*			**0.0229**	**0.0101**	**0.593**	**0.546**
6	Westness	0.005	0.0197	0.0129	0.585	0.544
5	Rivers_distance	0.003	0.0192	0.0121	0.582	0.547
4	Southness	<0.001	0.0154	0.0151	0.573	0.544
3	DEM	<0.001	0.0129	0.0091	0.561	0.536
2	Urban_distance	<0.001	0.0095	0.0132	0.548	0.541
1	slope	<0.001	0.0071	0.0094	0.532	0.526

* Selected best models

Table 3-5. P values for models with and without corine

	P-Values			
# of Variables	Natrix maura	Rhinechis scalaris	Malpolon Monspessulanus	Coronella girondica
17	0.096	-		-
16	0.545	-		-
15	0.226	0.427	0.186	0.290
14	0.405	0.364	0.384	0.406
13	0.364	0.226	0.545	0.496
12	0.199	0.273	0.070	-
11	0.199	0.257	0.140	-
10	-	0.496	0.325	-
9	-	0.326	-	-
8	-	0.29	-	-

Table 3-6. Sensitivity of species models

		All-inclusive model		Biophysical model	
Species	Total points	Correctly predicted	Sensitivity (%)	Correctly predicted	Sensitivity (%)
R. scalaris	364	280	77	205	56
M. monspessulanus	461	366	79	217	47
C. girondica	145	98	68	95	66
N. maura	675	436	65	321	47

3.2. Analysis of variables contribution to species models

A heuristic estimate of relative contributions of the environmental variables to each species selected best model is shown in Table 3-7 below. Temperature seasonality (Temp_seasonality) was the variable with the highest percentage contribution except for *Coronella girondica* model where precipitation seasonality (Prec_Seasonality) had the highest contribution. Similarly, the results of jackknife test of variable importance for all species showed that temperature seasonality (Temp_seasonality) was also the variable with highest gain when used in isolation hence indicating that it had the most useful information by itself (Figure 3-1, Figure 3-2, Figure 3-3 and Figure 3-4). Moreover, except in *Coronella girondica,* temperature seasonality was still the variable that showed the highest decline in training gains when omitted in the three species models, hence indicating that it still had the most information that was not present in other variables. Contrastingly, for *Coronella girondica* precipitation seasonality was the variable that had the most information that was not present in other variables as it showed the highest decline in training gains when omitted in its model.

Table 3-7. Variables contribution to the species models.

	% Contribution			
Variable	***Rhinechis scalaris***	***Malpolon monspessulanus***	***Coronella girondica***	***Natrix Maura***
Temp_seasonality	38.2	58.3	18.3	41.1
Tmax_Summer	16.9	17.0	18.9	-
Tmax_Spring	10.5	-	-	-
Prec_Autum	10.0	-	-	12.8
Urban_Distance	6.5	4.9	2.4	2.7
Prec_Warmest Quarter	5.8	3.0	11.1	3.0
Prec_Seasonality	5.3	5.9	22.0	5.5
Tmin_Coldest Month	4.4	4.0	4.5	9.1
Corine	2.4	-	-	3.0
Prec_Spring	-	3.4	4.1	5.8
Slope	-	2.0	4.6	3.9
Southness	-	1.5	5.1	-
Isothermality	-	-	7.7	12.0
DEM	-	-	1.3	-
Westness	-	-	-	1.0
Total	100	100	100	100

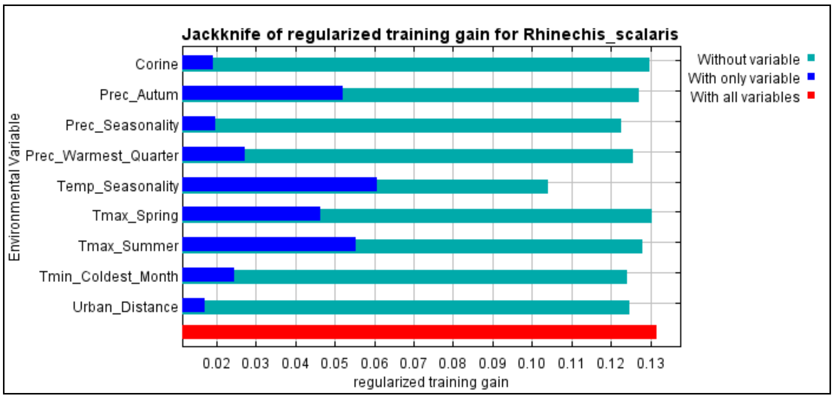


Figure 3-1. The jackknife test for Rhinechis scalaris all inclusive model.

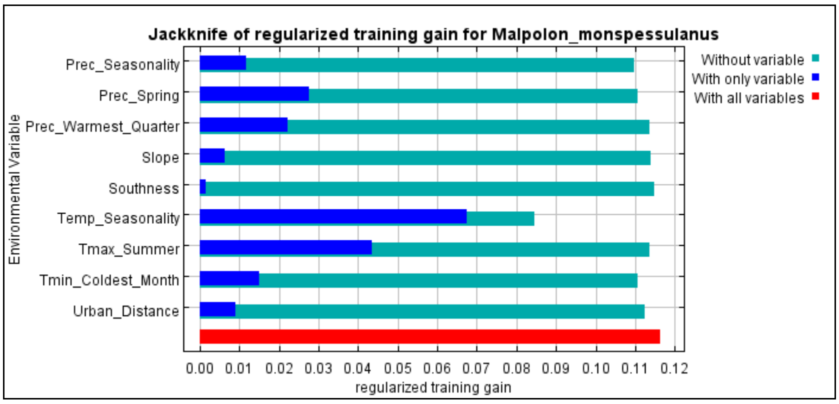


Figure 3-2. The jackknife test for Malpolon monspessulanus all-inclusive model.

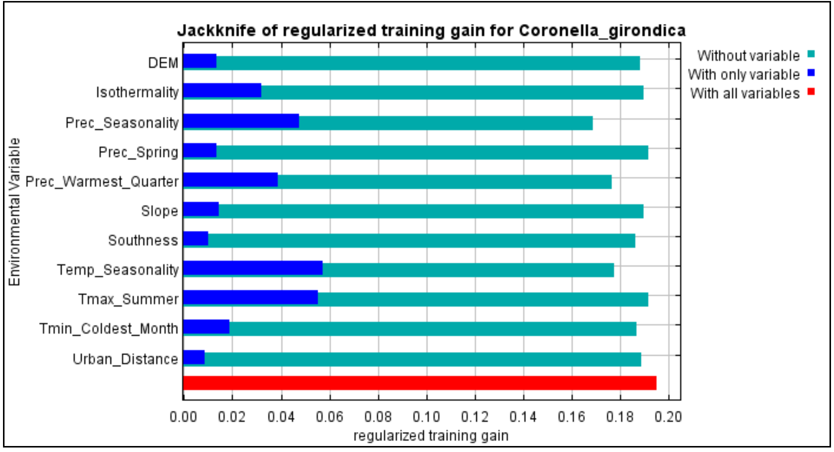


Figure 3-3. The jackknife test for Coronella girondica all-inclusive model.

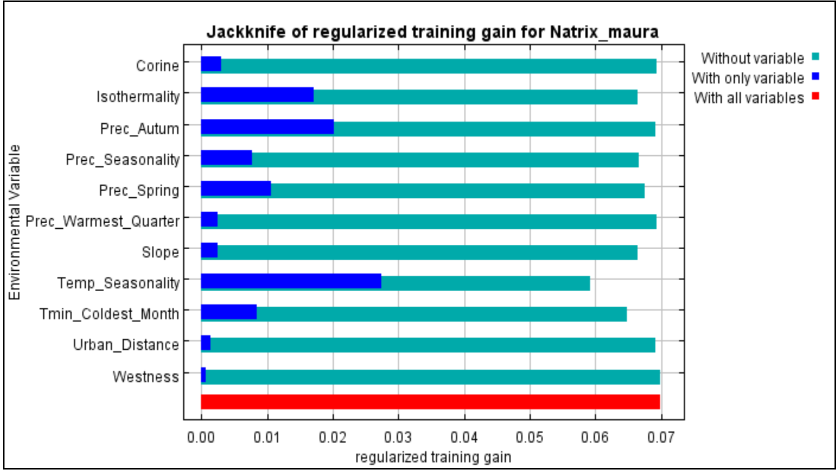


Figure 3-4. The jackknife test for Natrix maura all-inclusive model.

3.3. Species range shifts analysis

3.3.1. Predicted current and projected future ranges.

The predicted current and projected future distribution for *Rhinechis scalaris* is shown in Figure 3-5. For current climate, the high suitable range for this species occurred in the southern and central Spain while they avoided the colder north western part neighbouring the Atlantic Ocean. However, the future distribution showed remarkable expansion towards the north western tip as reflected by reduction in the low suitability region. Moreover, very high suitability emerged in south east Spain and eastern the coastal belt.

The predicted current and projected future distribution maps for Malpolon monspessulanus is shown in Figure 3-6. The current distribution revealed that much of the high suitability range for this species was concentrated in south and central Spain. This species range is highly sympatric with that of Rhinechis scalaris. In the future the considerable range shift from high to very high suitability was projected in the south-western Spain. A remarkable northward expansion is also evident especially in the north-western region in response to increasing temperatures. However some high and medium ranges in central Spain were projected to decline to low suitability in response to projected warming and aridity in this region.

Figure 3-7 below shows the predicted current and projected future distribution for Coronella girondica. In the current map, high suitability range for this species occurs in north-eastern and some patches in south-western Spain. The future distribution map revealed a drastic decrease in suitability in the southern and central regions in tandem with increased aridity and warming. However, its high suitability range in the cool and moist high elevation areas in the north east were projected to remain stable or expand.

The predicted current and projected future distribution for Natrix maura is shown in Figure 3-8. In the current map, high suitability range for this species occurs in north-eastern and south-western Spain. The future distribution map showed a significant decline in suitability in the southern and central Spain in concordance with increased aridity and warming but may also be attributed to high clamping of environmental variables that had their projected values higher than those encountered in the training as shown in Figure 3-11. Moreover, a remarkable northwards expansion of high suitability habitats is evident in the north-west tip.

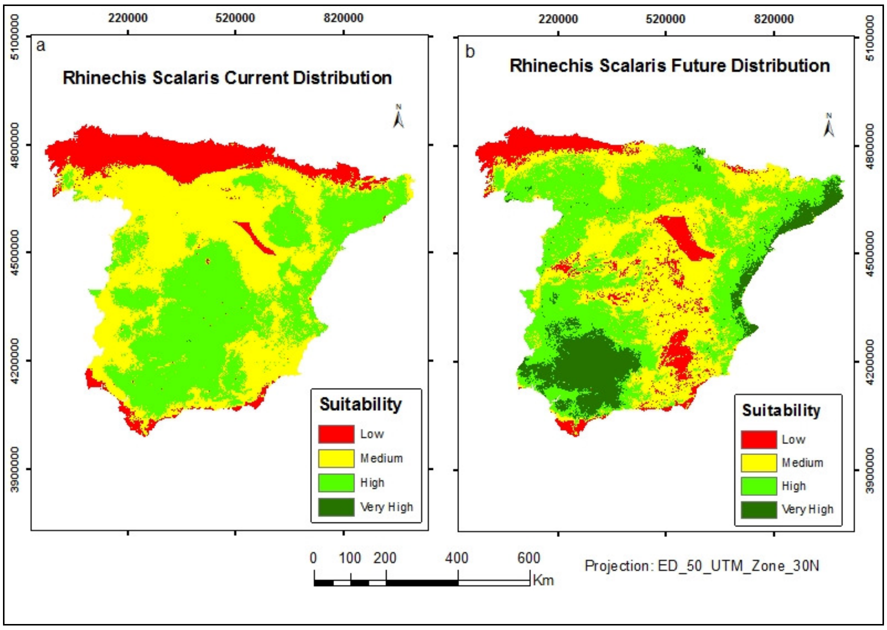


Figure 3-5. The current and future ranges for *Rhinechis scalaris*.

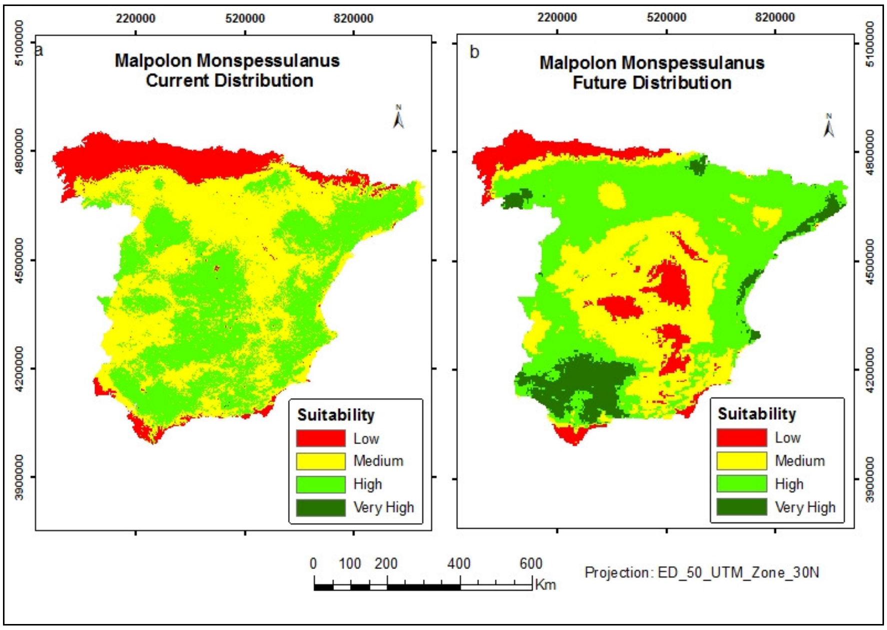


Figure 3-6. The current and future ranges for *Malpolon monspessulanus*.

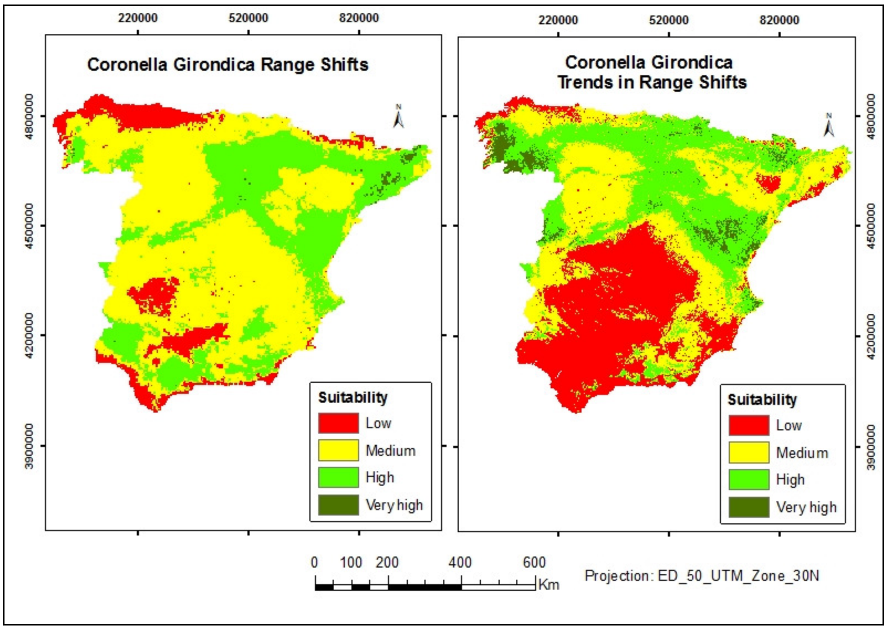


Figure 3-7. The current and future ranges for *Coronella girondica*

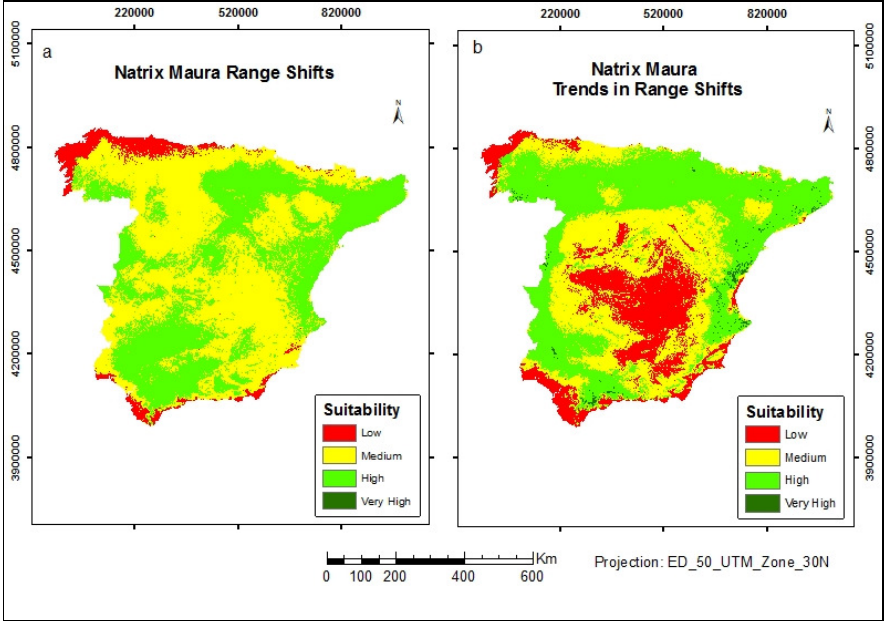


Figure 3-8. The current and future ranges for *Natrix maura*.

3.3.2. Clamping

Clamping means that the values of the future environmental variables are restricted to the range of values in the current environmental variables that were used for model training. Figure 3-9, Figure 3-10, Figure 3-11 and Figure 3-12 below shows where the prediction were most affected by variables being outside their training range when projecting the *Rhinechis scalaris, malpolon monspessulanus, Coronella girondica* and *Natrix maura* models respectively onto the year 2050 environmental variables. The values show the absolute difference in predictions when using and not using clamping respectively. Warmer colours show the areas where the treatment of values outside their training ranges had a large effect on predicted suitability hence higher associated uncertainty in projection.

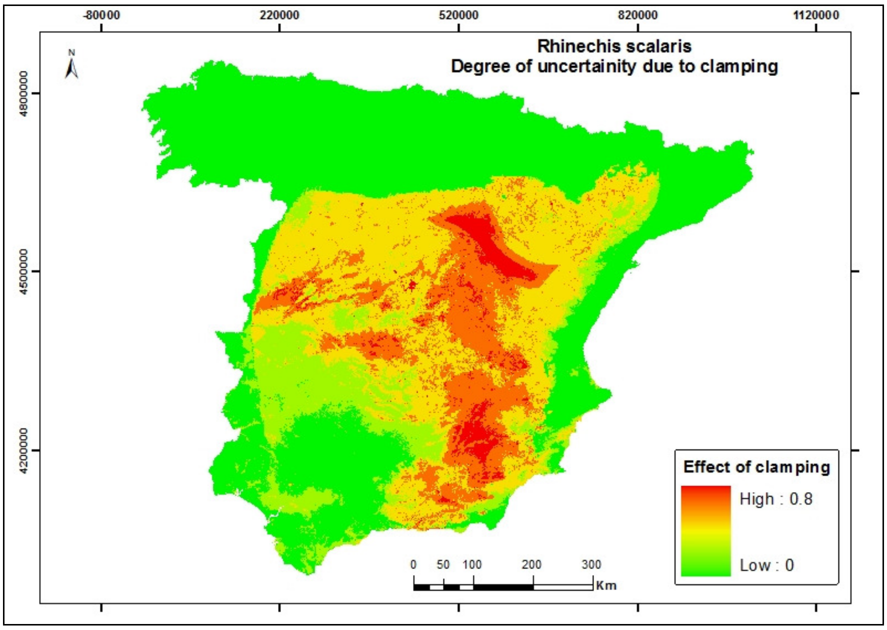


Figure 3-9. Degree of uncertainty in projecting *Rhinechis scalaris* future range due to clamping.

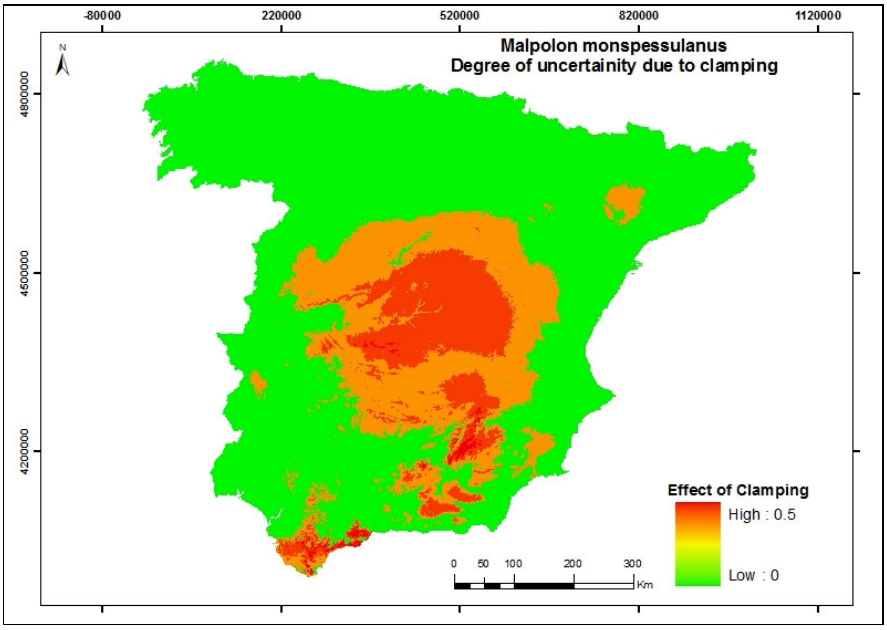


Figure 3-10. Degree of uncertainty in projecting *Malpolon monspessulanus* future range due to clamping.

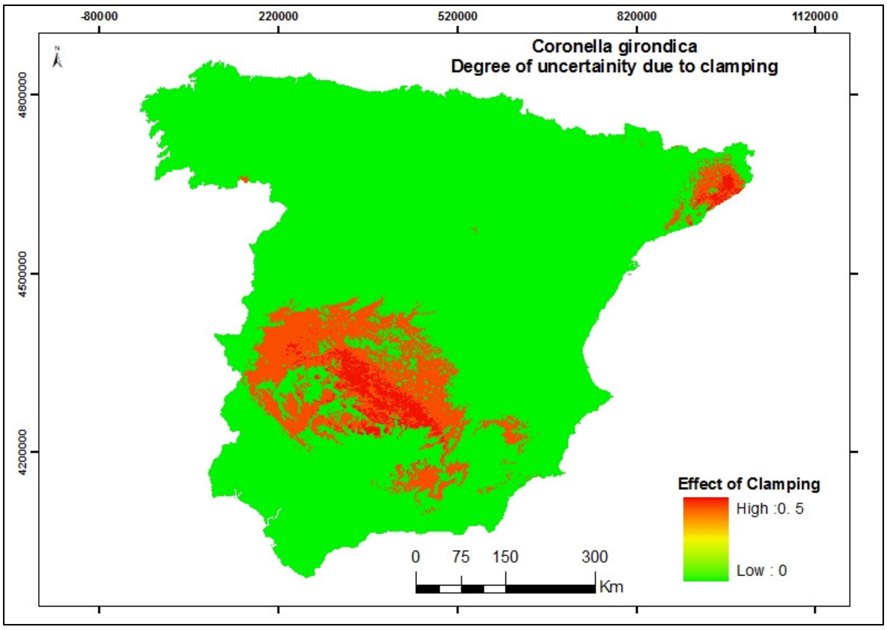


Figure 3-11. Degree of uncertainty in projecting *Coronella girondica* future range due to clamping.

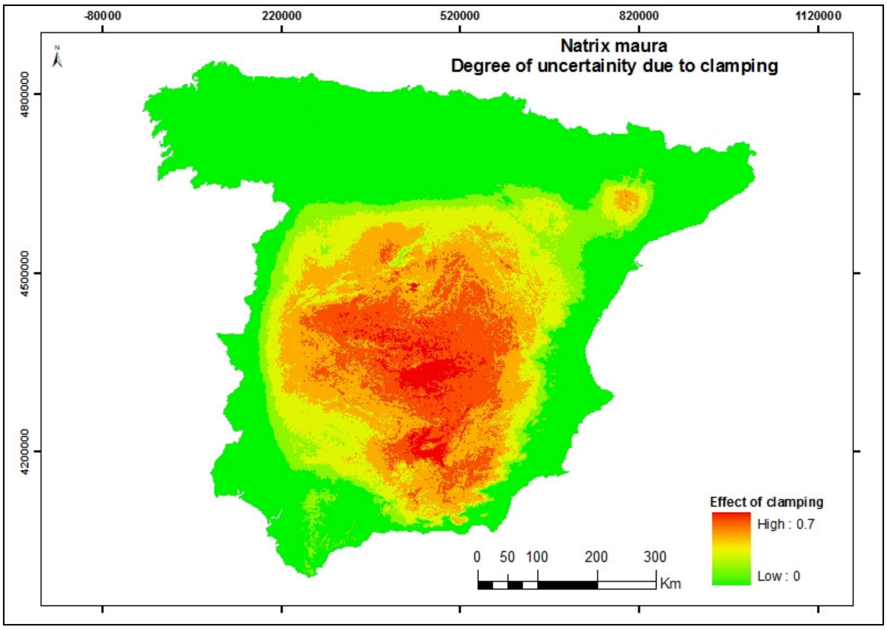


Figure 3-12. Degree of uncertainty in projecting *Coronella girondica* future range due to clamping

3.3.3. Species range shifts.

The results of cross-tabulating the current and future maps are shown in Figure 3-13, Figure 3-14, Figure 3-15 and Figure 3-16 for *Rhinechis scalaris, malpolon monspessulanus, Coronella girondica* and *Natrix maura* respectively. The suitability classes in the maps are coded as: 1 (low), 2 (medium), 3 (high) and 4 (very high). Moreover, the corresponding cross-tabulation tables that shows the frequencies with which classes remained the same (along the diagonal) or changed (off-diagonal) are shown in Table 3-8, Table 3-9, Table 3-10 and Table 3-11 for *Rhinechis scalaris, malpolon monspessulanus, Coronella girondica* and *Natrix maura* respectively. The percentage changes within the suitability classes shown in the cross-tabulation tables' reveals that the areal range changes in the two generalist species (*Rhinechis scalaris* and *malpolon monspessulanus*) will be driven mainly by shifting of medium suitability (2) to very high suitability range (4) in future whereas that of the two specialists' species (*Coronella girondica* and *Natrix maura*) will be driven mainly by shifting of medium suitability range (2) to low suitability (1) range.

Furthermore, for better illustration of the trends in range shifts between the four suitability classes, the species ranges were aggregated into three categories depending on whether their suitability will increase or decrease or remain stable in the future. The classes experiencing increase in suitability are interpreted as expanding while those decreasing in suitability are interpreted as contracting. This is shown in Figure 3-13b, Figure 3-14b, Figure 3-15b and Figure 3-16b for *Rhinechis scalaris, malpolon monspessulanus, Coronella girondica* and *Natrix maura* respectively and summarized in Table 3-12. The aggregation revealed that in overall the generalists' species range will tend to expand while that of specialist species will contract. This suggests that in overall the generalists' species will expand their range as it tended to become more suitable while the specialists' species range will contract their range as it tended to become less suitable. Furthermore the slightly higher area that will remain stable in the specialist species than in generalist species suggests that the rate of expansion will be higher than that of contraction.

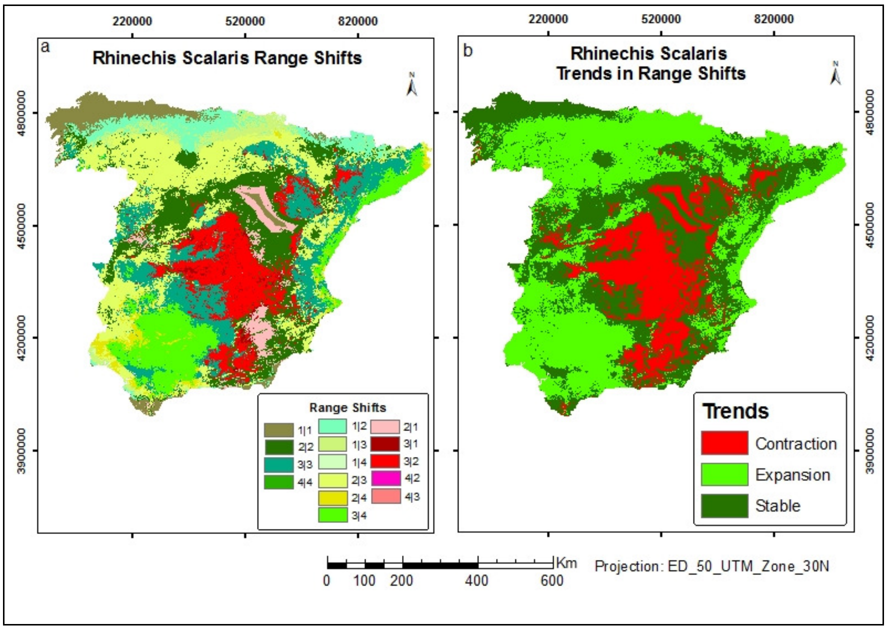


Figure 3-13. Range shifts and associated trends for Rhinechis scalaris

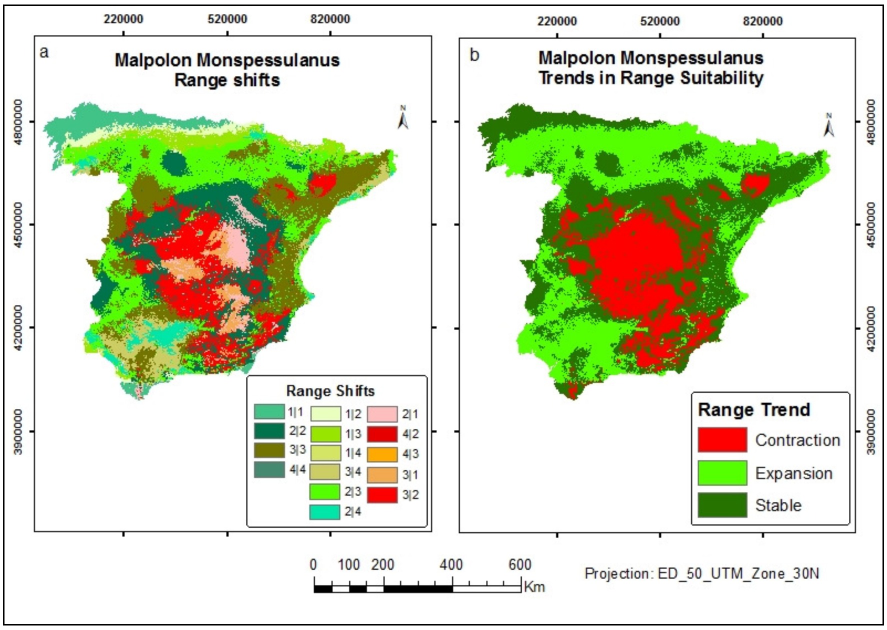


Figure 3-14. Range shifts and associated trends for Malpolon monspessulanus.

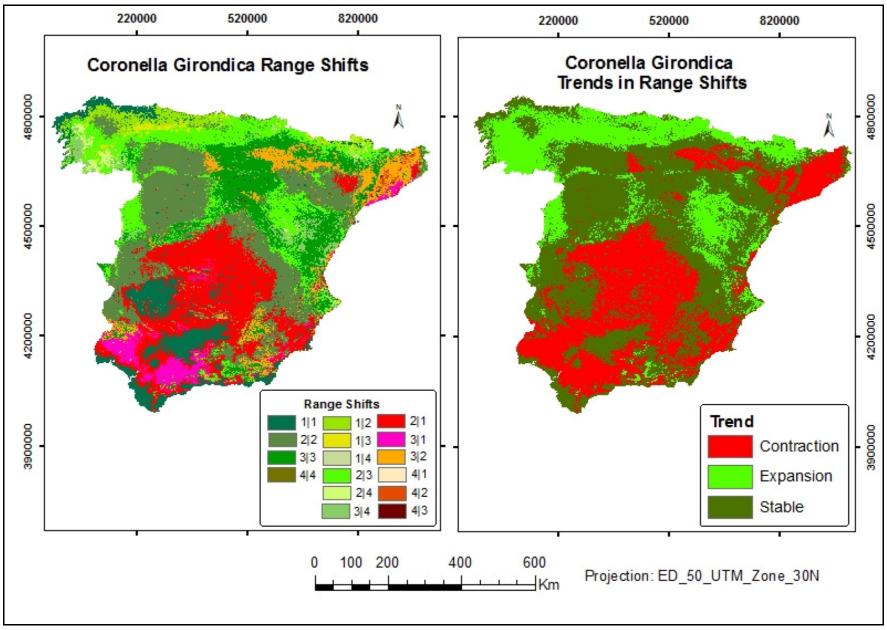


Figure 3-15. Range shifts and associated trends for *Coronella girondica*.

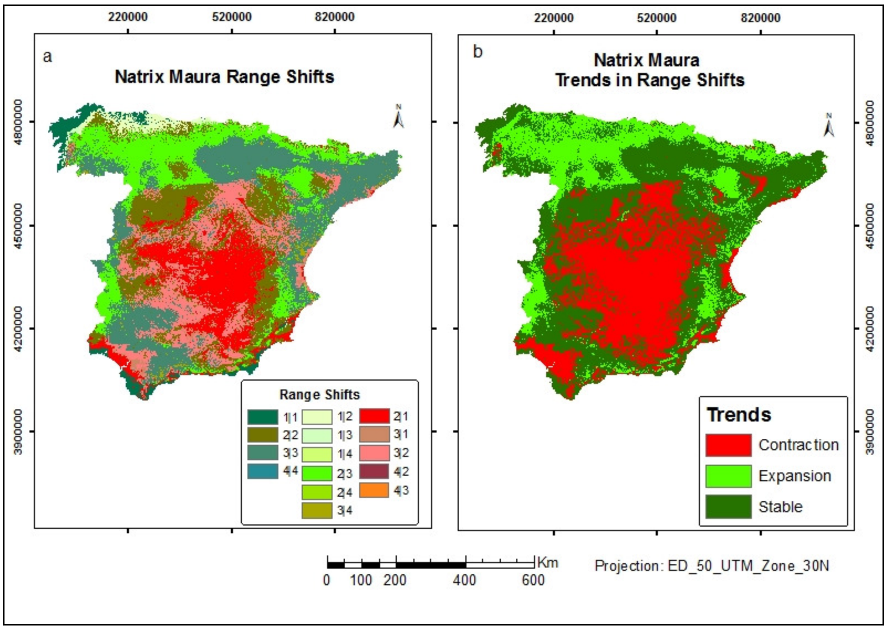


Figure 3-16. Range shifts and the associated trends for *Natrix maura.*

Table 3-8. Rhinechis scalaris range shifts

	Current range (Km^2)							
Future range (Km^2)	**Classes**	**1**	**2**	**3**	**4**	**Total**	**% Total**	**% Change**
	1	28219	17938	5843	0	52000	11	-4
	2	27461	80857	61012	8	169338	34	-10
	3	17035	107274	81390	10	205709	42	1
	4	614	11178	50824	6	62622	13	13
	Total	73329	217247	199069	24	489669	100	
	% Total	15	44	41	0	100		

Table 3-9. Range shifts for Malpolon monspessulanus.

	Current range (Km^2)							
Future range (Km^2)	Classes	1	2	3	4	Total	% Total	% Change
	1	28782	18488	15798	0	63068	13	0
	2	15139	86421	70438	28	172026	35	-10
	3	20501	101079	92462	5	214047	44	2
	4	725	15193	24606	4	40528	8	8
	Total	65147	221181	203304	37	489669	100	
	% Total	13	45	42	0	100		

Table 3-10. Range shifts for Coronella girondica

	Current range (Km^2)							
Future range (Km^2)	Classes	1	2	3	4	Total	% Total	% Change
	1	43621	97191	19175	73	160060	33	20
	2	13571	122822	32498	1326	170217	35	-24
	3	5283	64621	70101	743	140748	29	2
	4	33	6328	12040	243	18644	4	4
	Total	62508	290962	133814	2385	489669	100	
	% Total	13	59	27	0	100		

Table 3-11. Range shifts for Natrix maura

	Current range (Km^2)							
Future range (Km^2)	Classes	1	2	3	4	Total	% Total	% Change
	1	16438	73930	7585	0	97953	20	14
	2	11037	94419	70001	1	175458	36	-16
	3	1247	86967	123603	2	211819	43	1
	4	1	259	4178	1	4439	1	1
	Total	28723	255575	205367	4	489669	100	
	% Total	6	52	42	0	100		

Table 3-12. Trends in species range shifts

	Rhinechis scalaris		**Malpolon monspessulanus**		**Coronella girondica**		**Natrix maura**	
Suitability Trend	Area	% Area	Area	% Area	Area	% Area	Area	% Area
Contracting	84811	17	104757	21	151006	31	151519	31
Expanding	214386	44	177243	36	101876	21	103689	21
Stable	190472	39	207669	43	236787	48	234461	48
Total	489669	100	489669	100	489669	100	489669	100

Moreover, to measure the degree of agreement and association between the current and future ranges, cross-tabulation also showed the overall Kappa, per category Kappa, and the crammers-V values as shown Table 3-13 below. From the Chi square test, the association between the current and future range sizes for all species were highly significant ($p < 0.0001$, d.f. = 16). Consequently, the resulting Cramer's V values after post test showed moderate association between the current and future range sizes for all species (Table 3-13). Similarly, the resulting overall Kappa values for all species showed moderate agreement between the current and future maps indicating that the species will experience moderate range shifts between the two time periods (Table 3-13). The overall Kappa values for specialist species were slightly higher than that of generalists' species. However, the per category Kappa values for specialists' species showed higher agreement in low and high suitability ranges than in generalists' species. This suggests that the slightly higher overall Kappa values in the specialist species is as a result of the corresponding higher agreement in their low and high suitability ranges. This was also clearly evident in the predicted and projected distributions for these species in Figure 3-7 and Figure 3-8 above whereby the high suitability ranges of the two specialists species in the predominantly moist and cool high altitude ranges in north-eastern Spain remained stable or expanded. The higher agreement in high suitability range may be attributed to high elevation mountainous areas (Figure 2-2) that remain moist and cool under current and future conditions hence favouring the persistence of the two specialists' species.

Table 3-13. Degree of agreement and association between the current and future species ranges

	Per category Kappa index of agreement			
Suitability	**Rhinechis scalaris**	**Malpolon monspessulanus**	**Coronella girondica**	**Natrix maura**
Low	0.3478	0.4005	0.6338	0.5210
Medium	0.2296	0.2496	0.2900	0.2198
High	0.2374	0.2883	0.4373	0.4819
Very high	0.1949	0.0668	0.0832	0.2463
Overall Kappa	0.5237	0.5478	0.5996	0.5858
Cramer’s V	0.5578	0.5353	0.5517	0.5447

4. Discussion

4.1. Predictor variables

Results revealed that climatic variables predicted significantly better than biophysical variables for all species as shown by better fit to the training data and the accuracy of predictions. This suggests that at meso-scale the distribution limits of the four snake species in Spain are mainly influenced by climate especially the temperature related gradients. The observed superiority of the temperature gradients is in concordance with the expected behaviour of ectotherms as almost all of their physiological processes are influenced by body temperature that is in itself is determined by the temperature from the surrounding physical environment (Aubret and Shine, 2010). The physiological processes in snakes that are dependent on their body temperature includes: reproduction, metabolic reactions (Teixeira and Arntzen, 2002), rates and efficiency of digestion (Hailey and Davies, 1988) and locomotion that affect their foraging performance and ability to escape from predators (Moreno-Rueda *et al.*, 2009).

Hence, the distributional limits of these species are highly dependent on availability of optimal temperatures that would be able to maintain their preferred body temperatures required for these physiological processes (Aubret and Shine, 2010). Evidently, Saint Girons (1982) showed that the isotherm of 22^{o}C in the summer mean temperature to be the thermo-climatic limit of *Malpolon monspessulanus* species in relation to its vernal reproduction cycle (spermatogenesis and mating occur in the same calendar year). Species exhibiting vernal cycles are restricted to warm regions where longer activity periods allow successful completion of reproductive cycle within a calendar year (Feriche *et al.*, 2008). However, with climate warming this species is expected to expand its range upwards altitudinally and northwards in latitude. Moreover, Lourdais *et al.* (2004) demonstrated that latitudinal and altitudinal distribution limits of an oviparous snake species, *Vipera aspis,* is influenced by thermal requirements for embryogenesis. This is because actively thermo-regulating females avoid cold areas where the minimum thermal requirements for embryonic development may not be met.

Furthermore, climatic variables have been shown to have higher predictive power when modelling at meso-scale (Guisan and Zimmermann, 2000, Austin, 2002, Guisan and Hofer, 2003, Santos *et al.*, 2009). Guisan and Hofer (2003) attributed this to the fact that climate is relatively stable over larger areas hence making models generated with climatic variables to be more general and therefore applicable over a large area.

In contrast, biophysical variables like altitude, slope and land cover varies within short distances, hence models generated from them can only be applied within a limited geographical extent without significant errors (Guisan and Zimmermann, 2000). Moreover, the low predictive power of the biophysical variables may also be attributed to their aggregation to a coarser 1 Km resolution that reduces the amount of details they add in the models (Guisan and Hofer, 2003). Hence the predictive power of the biophysical variables may increase when modelling at local scale and higher grain size (Yost *et al.*, 2008) as this may ensure better discrimination of local variations in species micro-habitats. However it is still possible that some climatic predictors may remain important regardless of modelling scale (Guisan and Hofer, 2003, Soares and Brito, 2007, Penman *et al.*, 2010).

Nonetheless, although the climatic variables emerged as the most important predictors it should be recognised that correlation does not necessarily imply causation (Teixeira and Arntzen, 2002). Therefore the results should be interpreted in consideration of the known ecological traits of the species in question. In this regard, the response of the *Natrix maura* should be interpreted with caution because this species inhabit aquatic habitats and therefore its distribution was expected to be in close proximity to water bodies. However the results were contrary to this as evidenced by low contribution of distance to rivers variable to its model. Hence some areas predicted as climatically suitable for this species may in essence be inhabitable as they do not have water bodies in their vicinity. This may be attributed to the coarse resolution of the presence data used for modelling as the centroids derived from the 10 x10 Km grids were not necessarily located on the water bodies. It may also be attributed to the scale (extent) of this study that does not allow capturing of fine ecological aspects for this species and also due to its trait as widespread specialist species that makes it difficult for the algorithm to discriminate its habitat.

4.2. Species ecological traits and models accuracy.

The results showed that the models gains and AUC values for *Coronella girondica* were higher compared with those of the other three species that are widely distributed. Whereas *Malpolon monspessulanus* and *Rhinechis scalaris* are habitat generalist, *Natrix maura* is a widespread specialist species inhabiting aquatic habitats. In agreement with this, various studies e.g. (Elith *et al.*, 2006, Phillips *et al.*, 2006, Evangelista *et al.*, 2008, Franklin *et al.*, 2009) have demonstrated that the accuracy of the distribution models are affected by the species ecological traits. Hence models for wide ranging species have lower accuracy than those generated for species with small range size. This is attributed to the generalist's ability to persevere in wide range of environmental conditions that are not easily discriminated by the models (Evangelista *et al.,* 2008). In contrast the specialist species have sharply defined niches and environmental barriers that are easily discriminated by the models (Evangelista et al., 2008). Moreover as argued by Stockwell & Peterson (2002) and supported by Hernandez *et al.,* (2006), local ecological adaptations can reduce the accuracy of models generated for widespread species. This is because the widespread species often displays local or regional variations in ecological characteristics that may result to emergence of local or regional sub-populations of the same species but with varying habitat preferences in different parts of the species range. Hence generating models for all these sub-populations together effectively overestimate the species' ecological breadth and consequently reduce the model accuracy.

Moreover, poor performing models are usually interpreted as lacking important variables that are necessary in discriminating the species suitable habitats (Gibson et al., 2004) or relied on inconclusive field data (Hernandez *et al.,* 2006). In contrast, well performing models are interpreted as having indentified key predictor variables explaining the habitat suitability of the species (Gibson *et al.,* 2004). Even though these are rational interpretations, broader interpretations that incorporate the species ecological traits are vital (Evangelista *et al.*, 2008). This is because poor performing models may be as a result of species traits rather than shortcoming in methodology, selected explanatory variables or the completeness of occurrence data (Evangelista *et al.*, 2008, Hernandez *et al.*, 2006, Wisz *et al.*, 2008).

4.3. Climate change and species distributional shifts.

The resulting overall Kappa and Cramers V values revealed that all species will experience moderate range shifts by the year 2050. These suggest that climate change will affect the distribution of these species. This is in agreement with the general theory that species are expected to shift their ranges upwards in elevation and pole-wards in latitude in response to shifting climatic zones (Hughes, 2000, Walther *et al.*, 2002). Similar climatic related snake species range and phenological shifts has been reported in Spain. In agreement with this, Santos *et al.* (2009) reported altitudinal expansion of *Malpolon monspessulanus* snake in previously cold habitats in Sierra Nevada mountains, Spain, that consequently resulted to increased predation of *Coronella austriaca snake.*. Moreover, Moreno-Rueda & Pleguezuelos (2007) and Moreno-Rueda *et al.* (2009) reported an increase in seasonal activity periods of *Malpolon monspessulanus* at a rate of 2-3 days/year between 1983 and 2004 in tandem with 0.07°C per year increase in mean annual temperatures in south eastern Spain. They showed that rise in mean annual temperatures made the snakes to be active earlier in spring and enter hibernation later in autumn. The extended seasonal activity periods may offer additional selective advantages such as more opportunity to feed, grow, reproduce and possibly wider distribution (Chamaille-Jammes *et al.*, 2006, Moreno-Rueda *et al.*, 2009). These observations suggest that the effects of climate change on the snake species in Spain are already discernible.

4.4. Generalist and specialist species response to climate change.

The resulting Cramers V values for all species did not reveal difference between the generalists and specialists' species. Moreover, even though the overall kappa values for the specialists' species were slightly higher compared to that of generalists' species, the difference was negligible to conclude that there was difference in their response to changing climate. The slightly higher overall Kappa values in the specialist species was as a result of the corresponding higher agreement in their low and high suitability ranges. Contrastingly, the trends in the range shifts revealed that generalist species ranges will be dominated by expansion while that of the specialists' species will be dominated by contraction. This suggests that climate change will favour the distribution of the two generalist species while the two specialist species will suffer from range contraction. This supports the view that species ecological traits such as habitat and dietary specialisation influence their response to changing climate and their vulnerability to local extinction (Araujo *et al.*, 2006, Santos *et al.*, 2009). In consistent with the results, Penman *et al.* (2010) attributed the high vulnerability to climatically induced contraction in suitable habitats of Australia's broad-headed snake (Hoplocephalus bungaroides) to its specialized habitat requirements, slow life-histories such as delayed maturation and low reproductive rate that reduce their ability to recover from population declines and pressure from anthropogenic processes. These qualities fits that of *Coronella girondica* as it is a highly specialized predator of small lizards that comprise 82% of its diet frequency (Santos and Pleguezuelos, 2004), have low reproduction rate, population size and patchy distribution within its range (Segura et al., 2007). Moreover, it is known to avoid altered habitats (Segura *et al.*, 2007) and is markedly absence in large areas of intense agricultural activity, indicating its vulnerability to such practices (Santos and Pleguezuelos, 2004). It also prefers cool and wet habitats mostly located in mountainous areas. These life history traits have been pointed out to increase this species vulnerability to local extinction in southern Spain (Segura *et al.*, 2007) where the models projected drastic contraction of its range. Owing to this, its conservation status in Spain has been proposed to be raised from Least Concern (LC) to vulnerable (Santos and Pleguezuelos, 2004, Segura *et al.*, 2007, IUCN, 2009).

Similarly, the aquatic habits of *Natrix maura* may contribute to the projected contraction of its range. The increased warming and the accompanied aridity projected in some parts of Spain (Giorgi and Lionello, 2008), is expected to reduce water volume or in worse case scenario cause drying of some of its aquatic habitats. In agreement with this, the results projected contraction of most of its range in central Spain where extreme arid conditions are projected (Giorgi and Lionello, 2008). However its range in mountainous northern-east Spain where it is cooler and experiencing higher precipitation was projected to expand or to stabilise. However as argued by (Araujo *et al.*, 2006) the ability of this species to disperse in order to track the changing climate will be greatly hampered by massive draining and alteration of aquatic habitats. Moreover, increased irrigation farming where the water flow is regulated in certain seasons of the year and the pollution from organo-chlorine pesticides had greatly affected this species as they lead to killing of its prey species mostly fishes and amphibians (Santos, 2004, Santos and Llorente, 2009, IUCN, 2009).

In contrast, the expansionary trend revealed by the two generalists species is in agreement with Araujo *et al.* (2006) who projected that a great proportion of reptile species in Europe including snakes will increase their range by 2050 in response to increased warming if a scenario of unlimited dispersal is considered. Their range expansion is related to their tolerance to wide ranging environmental conditions (Segura *et al.*, 2007), wide variety of prey and ability to persist in altered habitats (Reed and Shine, 2002, Santos *et al.*, 2007b). It has been reported that due to high tolerance to extreme temperatures by *Malpolon monspessulanus,* the increased warming may boost their foraging performance (more time to forage and improved strike speed) and their capacity to escape from predators (Moreno-Rueda *et al.*, 2009). Hence, temperature rise especially in winter may favour the breeding and juvenile survival of *Malpolon monspessulanus* that may result to increased population size and possibly wide distribution. In support of this, Moreno-Rueda and Pleguezuelos (2007) reported that this species has increased its dominance in snake community in Southern Spain from 27% to 50% with a 22 years period (1983-2004) as a result of increasing warming trend.

Significantly also, *Rhinechis scalaris* has be shown to be a highly active forager with high mobility as it searches for mainly stationary preys in their nest (Pleguezuelos *et al.*, 2007). Evidently, in a study of the spatial ecology of snake species using radio-tracking, Blázquez (1993) found that the mean home range of active *Rhinechis scalaris* individuals was 1.83 ha. This was larger than those recorded in *Malpolon monspessulanus* (0.39 ha) and *Natrix maura* (0.177- 0.18 ha.). In agreement with this, the results showed that this species will have the largest expansion in its range (44%).

4.5. Sources of errors and uncertainities in the models.

There are several sources of errors and uncertainties when predicting the current and projecting the future ranges respectively. According to Beaumont *et al.* (2008) they can be categorized into three broad classes i.e. those originating from (a) species traits and location data (biological) (b) climate scenarios and (c) species distribution models.

4.5.1. Uncertainties originating from species traits and location data.

Despite climate and habitat changes there are other factors not considered in this study that may limit the distribution of these species, namely: biological interactions, dispersal abilities, geographical barriers, evolutional adaptations and negative stochastic events (Guisan and Zimmermann, 2000, Pearson and Dawson, 2003, Araujo *et al.*, 2005, Araujo *et al.*, 2006, Araujo and Pearson, 2005). Biotic interactions between species such as competition and predation are known to exert limits to species distribution (Pearson and Dawson, 2003). This emanate from the fact that natural systems involve complex web of interactions and feedbacks between species, hence changes in distribution of one species could result to drastic impacts on the distributions of many other inter-related species (Pearson and Dawson, 2003). However, as argued by Guisan & Zimmermann (2000), the impact of biotic interactions can be minimised in models generated at macro or meso-scales where the influence of climate on species distributions have been shown to be dominant.

Moreover, it is assumed that the species have unlimited dispersal abilities and hence they will be able to track the changing climate. However, snake species are poor dispersers and highly philopatric (Araujo *et al.*, 2006), hence this assumption is an over-generalization. Indeed, their limited dispersal rate is expected to be further hampered by high rate of habitat fragmentation in Spain. Related also, it is assumed that the species are in equilibrium with climate, hence they are present in all climatically suitable areas and absent from all unsuitable ones (Araujo *et al.*, 2005, Araujo and Pearson, 2005). The species-climate equilibrium has been shown to be inversely related to species' ability to track future climate changes (Araujo and Pearson, 2005). Therefore due to their low dispersal abilities, this species depict very low levels of equilibrium with climate which is reflected by their high rates of endemism in comparison with other terrestrial vertebrates in Europe (Williams, 2000). Indeed, as demonstrated by Araujo & Pearson (2005), this can explain why the distribution of herpetile species in Europe coincide more with the location of past glacial refugia e.g. Iberian Peninsula, rather than with current climates. Moreover, molecular studies have demonstrated their evolutionary adaptations to changing climates since ice ages (Brito *et al.*, 2008, Santos *et al.*, 2009) while the possibility of species rapid adaptations to climate change within shorter periods have been supported (Pearson and Dawson, 2003). Related also, these species have continued to persist in North Africa (IUCN, 2009) despite the apparent extreme arid conditions.

Critically therefore, these observations seriously challenge the notion that climate change per se would cause major distributional shifts among the snake species. In this regard, before a concrete conclusion that climate change is the main driver for range shifts for these species, all the other alternative hypotheses need to be discarded (Moreno-Rueda *et al.*, 2009). However, accomplishing such a task will be greatly hampered by the general lack of long-term dataset on these species as their population dynamics are poorly monitored (Santos *et al.*, 2007a) due to their elusiveness and patchy distribution (Segura *et al.*, 2007). The available datasets, as used in this study, are usually from museum collections or observational studies mostly lacking a well designed sampling strategy. However the accuracy of SDM's has been shown to be highly sensitive to sample size and biases in the data (Hernandez *et al.*, 2006, Pearson *et al.*, 2007). Moreover, the presence data used for model training was derived from 10x10 Km resolution grids, therefore the presence localities had low precision that may not capture fine ecological details of some species e.g. *Natrix maura*.

Furthermore when projecting the future species ranges, it is assumed that the current species-climate relationships will remain unchanged under changing climate (Fitzpatrick *et al.*, 2008). However since the modelled system is not closed, other factors such as limited dispersal ability, biotic interactions and possible rapid evolutionary adaptations may hinder maintenance of climatic niches in both space and time (Pearson and Dawson, 2003). Consequently, as demonstrated by Araujo *et al* (2005), good model fit in the current climate do not necessarily translate to good predictions of future ranges.

4.5.2. Uncertainties originating from climate scenarios

The future climate and land cover changes scenarios are based on projected changes in population, technology, socio-economic and policies (IPCC, 2000). Although the projections represents plausible alternatives that are likely to occur, high uncertainty still exist in determining the likelihood of their eventual occurrence (IPCC, 2000). The climate models also suffer from inadequate understanding of some physical processes driving them (Randall *et al.*, 2007). Moreover, the climatic variables input in the SDM's were generated by interpolation of weather stations data that is prone to interpolation errors and biases associated with uneven spatial and temporal distribution of weather stations (Guisan and Zimmermann, 2000, Hijmans *et al.*, 2005). Furthermore, the GCM's data has coarse resolution that is not readily suitable for ecological applications therefore necessitating downscaling to regional climate models (Beaumont *et al.*, 2008). Generally, the uncertainties of the projections increases with decreasing spatial and temporal scales hence the down-scaling introduce more uncertainties than the original global surfaces (Randall *et al.*, 2007).

In addition, this study is based on single climate model (HADCM3) and scenario (A2). Since projections of different climate models and scenarios vary, the use of a single model or scenario may not capture the variability of climatic projections (Araujo *et al.*, 2006, Beaumont *et al.*, 2008). Incorporating multiple climate models and scenarios (ensemble modelling) is recommended as it reduces biases of individual models (Randall *et al.*, 2007). Nevertheless, the ensemble modelling has its own disadvantages as averaging result to loss of higher order variability (extreme values) that are known to exert higher influence on species distribution (Beaumont *et al.*, 2008). Moreover, an ensemble average may not reflect an observable or existing state e.g. a system that is either very wet (1000 mm) or very dry (100 mm) will have an average (550 mm) that represent a system that does not exist in nature.

4.5.3. Uncertainties originating from species distribution models

A potential problem in projecting future ranges arises when extrapolating beyond the environmental conditions encountered during model training. Since Maxent uses an exponential model which is not inherently bounded above, it can give very large predicted values for environmental conditions outside the range observed under current conditions (Phillips *et al.*, 2006). To solve this, Phillips & Dudik (2008) introduced "clamping" functionality that automatically set the upper and lower bounds of environmental variables to those observed under the current conditions (Phillips and Dudik, 2008). Nevertheless, projection in the regions experiencing climatic changes beyond the current maximum or below the current minimum remains highly uncertain.

Moreover, appropriate modelling grain size (resolution) and scale (extent) need to be established as this affect the results of the model (Guisan and Hofer, 2003). Aggregation of topographical variables to 1 Km resolution greatly reduces the amount of information especially in mountainous regions where topography varies within a short distance. Furthermore, the choice of the threshold for converting the predicted probability distribution into suitable or unsuitable could affect the accuracy of the models (Thuiller, 2004, Hernandez *et al.*, 2006). Although several thresholds have been recommended to yield high predictive success (Liu *et al.*, 2005), there is no single agreed threshold yet. Using different thresholds could result to differing model accuracy (Hernandez *et al.*, 2006).

In addition, the climatic surfaces generated by interpolation of weather station data may have spatial auto-correlation since closer stations are more likely to have same climatic conditions. Existence of auto-correlation has been shown to inflate model predictive ability (Franklin *et al.*, 2009, Araujo and Pearson, 2005).

5. Conclusions and recommendations

Climate change has been advanced as one of the main factors contributing to alteration of global biodiversity patterns by exerting shifts in spatial distributions of species (Araujo *et al.*, 2006). To evaluate the magnitude of such shifts, maxent model was used to predict current and project future distribution of four snake species in Spain using current and future climatic and biophysical variables respectively.

The first objective was to determine the predictor variables having the highest predictive power in each species distribution model. Results revealed that climatic variables had the highest predictive power compared to the biophysical variables. The second objective was to generate the spatial distribution models for the four snake species for the current climate. The current distribution models were generated and evaluated using ROC AUC, binomial tests and sensitivity. The models were optimized based on training gains in order to select the best models with the fewest predictors to enhance ecological interpretation of the results. The third objective was to project the future distribution (year 2050) for the species. Hence the selected best models for the current conditions were run with future environmental variables to project their future distributions. The fourth objective was to establish whether the projected range shifts among the specialist species were greater than that of generalist species. The current and future maps for each species were cross-tabulated. The resulting Kappa index of agreement and Crammers V statistic values revealed moderate agreement and association between the current and future distribution maps for all species. However the overall range shift trends for generalists was shown to expand while that of the specialist species was to contracting.

The results suggested that climate is the main factor that set the distributional limits of these species at meso-scale. However it is still probable that other non-climatic factors that were not incorporated in the models such as biotic interactions, dispersal abilities and evolutionary adaptations may have significant influence in setting the distribution of these species. Nevertheless, the results provided a first assessment of the potential impact of climate change on four snake species in Spain that is necessary for formulating appropriate conservation strategies.

5.1. Specific conclusions

1. At meso-scale the distribution of the four snake species is largely set by climate.
2. Climate change will result to shift in the distribution of the four species by the year 2050. However the effect of climate change in influencing the shifts in the distribution of these species is still inconclusive until all the factors that influence their distribution are incorporated in the models e.g. biotic interactions, dispersal abilities, geographic barriers and evolutionary adaptations.
3. Under changing climate, the generalists' species range will expand while that of specialists' species will contract. This reveals that species life-history traits such as habitat and dietary specialization influence their response to changing climates and vulnerability to local extinction.

5.2. Recommendations

1. Re-test the hypotheses with higher resolution species presence data that may facilitate capturing fine ecological details of the four Species. To reduce the uncertainties in projections, multiple future climate scenarios (ensemble modelling) and other factors influencing species distribution such as biotic interactions, dispersal abilities and evolutional adaptations should be incorporated in the modelling process.
2. Assess the species turnover in the protected areas due to climate change. This will identify the proportion of the species range that will shift into or out of the protected areas networks in future. This will help in gauging the continued efficiency of protected area networks in conserving these species under changing climate.
3. Transferability of this method to other snake species in Spain should be explored to assess their vulnerability to climate change.
4. Conservation strategies should be formulated in recognition of species natural history traits with the priority given to the specialist species that are more vulnerable to environmental changes.

6. References

Anderson, R. P. (2003) Real vs. artefactual absences in species distributions: Tests for Oryzomys albigularis (Rodentia: Muridae) in Venezuela. *Journal of Biogeography,* 30**,** 591-605.

Araujo, M. B. & Pearson, R. G. (2005) Equilibrium of species' distributions with climate. *Ecography,* 28**,** 693-695.

Araujo, M. B., Pearson, R. G., Thuiller, W. & Erhard, M. (2005) Validation of species-climate impact models under climate change. *Global Change Biology,* 11**,** 1504-1513.

Araujo, M. B., Thuiller, W. & Pearson, R. G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography,* 33**,** 1712-1728.

Aubret, F. & Shine, R. (2010) Thermal plasticity in young snakes: how will climate change affect the thermoregulatory tactics of ectotherms? *The Journal of Experimental Biology* 213**,** Pg. 242 - 248.

Austin, M. P. (2002) Spatial prediction of species distribution: An interface between ecological theory and statistical modelling. *Ecological Modelling,* 157**,** 101-118.

Austin, M. P. & Smith, T. M. (1989) A new model for the continuum concept. *Vegetatio* 83**,** Pg. 35-47.

Baselga, A. & Araujo, M. B. (2009) Individualistic vs community modelling of species distributions under climate change. *Ecography,* 32**,** 55-65.

Beaumont, L. J., Hughes, L. & Pitman, A. J. (2008) Why is the choice of future climate scenarios for species distribution modelling important? *Ecology Letters,* 11**,** 1135-1146.

Blázquez, M. C. (1993) Ecology of two species of colubrids, Malpolon monspessulanus and Elaphe scalaris in Doñana (Huelva). Sevilla, Sevilla University.

Bombi, P., Luiselli, L., Capula, M. & Salvi, D. (2009) Predicting elusiveness: potential distribution model of the Southern smooth snake, Coronella girondica, in Italy. *Acta Herpetologica 4(1): 7-13.*

Bosch, J., Carrascal, L. M., Duran, L., Walker, S. & Fisher, M. C. (2007) Climate change and outbreaks of amphibian chytridiomycosis in a montane area of Central Spain; is there a link? *Proceedings of the Royal Society B: Biological Sciences,* 274**,** 253-260.

Brito, J. C., Santos, X., Pleguezuelos, J. M. & Sillero, N. (2008) Inferring evolutionary scenarios with geostatistics and geographical information systems for the viperid snakes Vipera latastei and Vipera monticola. *Biological Journal of the Linnean Society,* 95**,** 790-806.

Busby, J. R. (1991) BIOCLIM - a bioclimate analysis and prediction system. IN MARGULES, C. R. & AUSTIN, M. P. (Eds.) *Nature conservation: cost effective biological surveys and data analysis* Canberra, ACT, Australia., CSIRO.

Carey, C. & Alexander, M. A. (2003) Climate change and amphibian declines: is there a link? *Diversity and Distributions,* 9**,** 111-121.

Carpenter, G., Gillison, A. N. & Winter, J. (1993) DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity and Conservation,* 2 667- 680.

CGIAR (2009),Shuttle Radar Topographic Mission (STRM) Digital Elevation Model (DEM), http://strm.csi.cgiar.org, accessed on: 20th September 2009

Chamaille-Jammes, S., Massot, M., Aragon, P. & Clobert, J. (2006) Global warming and positive fitness response in mountain populations of common lizards Lacerta vivipara. *Global Change Biology,* 12**,** 392-402.

Chang, C. R., Lee, P. F., Bai, M. L. & Lin, T. T. (2004) Predicting the geographical distribution of plant communities in complex terrain: a case study in Fushian Experimental Forest, northeastern Taiwan. *Ecography 27: 577 - 588.*

Chefaoui, R. M., Hortal, J. & Lobo, J. M. (2005) Potential distribution modelling, niche characterization and conservation status assessment using GIS tools: A case study of Iberian Copris species. *Biological Conservation,* 122**,** 327-338.

CIAT (2009), Downscaled GCM Data Portal, http://gisweb.ciat.cgiar.org/GCMPage/, accessed on: 20th November 2009

Clarklabs (2006) Idrisi 15: The Andes Edition. Worcester, MA, USA, Clark University.

Collins, J. P. & Storfer, A. (2003) Global amphibian declines: Sorting the hypotheses. *Diversity and Distributions,* 9**,** 89-98.

Cox, N., Chanson, J. & Stuart, S. (2006) *The Status and Distribution of Reptiles and Amphibians of the Mediterranean Basin.,* Gland, Switzerland and Cambridge, UK. , IUCN.

Cramer, H. (1999) *Mathematical Methods of Statistics*, Princeton University Press.

Deng, Y., Goodchild, M. F. & Chen, X. (2009) Using NDVI to define thermal south in several mountainous landscapes of California. *Computers and Geosciences,* 35**,** 327-336.

Digitalglobe (2004) QuickBird Orthophoto imagery.

Eastman, J. R. (2006) Idrisi Andes Guide to GIS and Image Processing. Worcester, MA, USA, Clarke University.

EEA (2000),Corine Land Cover 2000, http://dataservice.eea.europa.eu/dataservice, accessed on: 25 th september 2009

Elith, J., H. Graham, C., P. Anderson, R., Dudik, 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., Soberon, J., Williams, S., S. Wisz, M. & E. Zimmermann, N. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography,* 29**,** 129-151.

ESRI (2008) ARCMAP 9.3.1. Redlands, California, USA., ESRI.

Evangelista, P. H., Kumar, S., Stohlgren, T. J., Jarnevich, C. S., Crall, A. W., Norman Iii, J. B. & Barnett, D. T. (2008) Modelling invasion for a habitat generalist and a specialist plant species. *Diversity and Distributions,* 14**,** 808-817.

Feriche, M., Pleguezuelos, J. M. & Santos, X. (2008) Reproductive Ecology of the Montpellier Snake, Malpolon monspessulanus (Colubridae), and Comparison with Other Sympatric Colubrids in the Iberian Peninsula. *Copeia* No. 2**,** pp 279-285.

Fielding, A. H. & Bell, J. F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. . *Environmental Conservation,* 24**,** 38-49.

Fitzpatrick, M. C., Gove, A. D., Sanders, N. J. & Dunn, R. R. (2008) Climate change, plant migration, and range collapse in a global biodiversity hotspot: The Banksia (Proteaceae) of Western Australia. *Global Change Biology,* 14**,** 1337-1352.

Franklin, J., Wejnert, K. E., Hathaway, S. A., Rochester, C. J. & Fisher, R. N. (2009) Effect of species rarity on the accuracy of species distribution models for reptiles and amphibians in southern California. *Diversity and Distributions,* 15**,** 167-177.

Giannakopoulos, C., Bindi, M., Moriondo, M., LeSager, P. & Tin, T. (2005) Climate change impacts in the Mediterranean resulting from a 2^{o}C global temperature rise. Gland, Switzerland, WWF.

Gibbons, J. W., Scott, D. E., Ryan, T. J., Buhlmann, K. A., Tuberville, T. D., Metts, B. S., Greene, J. L., Mills, T., Leiden, Y., Poppy, S. & Winne, C. T. (2000) The global decline of reptiles, Deja Vu amphibians. *Bioscience,* 50**,** 653-666.

Gibson, L. A., Wilson, B. A., Cahill, D. M. & Hill, J. (2004) Spatial prediction of rufous bristlebird habitat in a coastal heathland: A GIS-based approach. *Journal of Applied Ecology,* 41**,** 213-223.

Gil, J. M. & Pleguezuelos, J. M. (2001) Prey and prey-size selection by the short-toed eagle (Circaetus gallicus) during the breeding season in Granada (south-eastern Spain). *Journal of Zoology,* 255**,** 131-137.

Giorgi, F. & Lionello, P. (2008) Climate change projections for the Mediterranean region. *Global and Planetary Change,* 63**,** 90-104.

Gordon, C., Cooper, C., Senior, C. A., Banks, H., Gregory, J. M., Johns, T. C., Mitchell, J. F. B. & Wood, R. A. (2000) The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. *Climate Dynamics,* 16**,** 147-68.

Guisan, A. & Hofer, U. (2003) Predicting reptile distributions at the mesoscale: Relation to climate and topography. *Journal of Biogeography,* 30**,** 1233-1243.

Guisan, A. & Zimmermann, N. E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling,* 135**,** 147-186.

Hailey, A. & Davies, P. M. C. (1988) Activity and thermoregulation of the snake Natrix maura: A synoptic model of the thermal biology and the physiological ecology of performance *J. Zool.,* 214.

Hernandez, P. A., Graham, C. H., Master, L. L. & Albert, D. L. (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography,* 29**,** 773-785.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology,* 25**,** 1965-78.

Hole, D. G., Willis, S. G., Pain, D. J., Fishpool, L. D., Butchart, S. H. M., Collingham, Y. C., Rahbek, C. & Huntley, B. (2009) Projected impacts of climate change on a continent-wide protected area network. *Ecology Letters,* 12**,** 420-431.

Hughes, L. (2000) Biological consequences of global warming: Is the signal already apparent? *Trends in Ecology and Evolution,* 15**,** 56-61.

Hutchinson, G. E. (1957) Concluding remarks. *Cold Spring Harbor Symp. Quantitative Biol. ,* 22**,** 415-427.

IPCC-DDC (2009),Climate model projections and simulations, http://www.ipcc-data.org/, accessed on: 29th September 2009

IPCC (2000) IPCC Special Report on Emissions Scenarios. Cambridge, UK, Cambridge University Press.

IPCC (2007) Climate Change 2007: The Physical Science Basis. IN SOLOMON, S., QIN, D., MANNING, M., CHEN, Z., MARQUIS, M., AVERYT, K. B., TIGNOR, M. & MILLER, H. L. (Eds.) *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge, United Kingdom

IPCC (2009),Climate model projections and simulations, http://www.ipcc-data.org/, accessed on: 29th September 2009

IUCN (2009) IUCN Red List of Threatened Species. *http://www.iucnredlist.org*. Version 2009.1. ed.

Jimenez-Valverde, A. & Lobo, J. M. (2007) Threshold criteria for conversion of probability of species presence to either-or presence-absence. *Acta Oecologica,* 31**,** 361-369.

Liu, C., Berry, P. M., Dawson, T. P. & Pearson, R. G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography,* 28**,** 385-393.

Lourdais, O., Shine, R., Bonnet, X., Guillon, M. & Naulleau, G. (2004) Climate affects embryonic development in a viviparous snake, Vipera aspis. *Oikos,* 104**,** Pg. 551-560.

Luiselli, L., Pleguezuelos, J. M., Capula, M. & Villafranca, C. (2001) Geographic variation in the diet composition of a secretive Mediterranean colubrid snake: Coronella girondica from Spain and Italy. *Italian Journal of Zoology,* 68**,** 57-60.

Moreno-Rueda, G. & Pizarro, M. (2007) The relative influence of climate, environmental heterogeneity and human population on the distribution of vertebrate species richness in south-eastern Spain. *Acta oecologica* 32 Pg. 50-58.

Moreno-Rueda, G. & Pleguezuelos, J. M. (2007) Long-term and short-term effects of temperature on snake detectability in the wild: A case study with Malpolon monspessulanus *Herpetological Journal,* 17**,** pp. 204 - 207.

Moreno-Rueda, G., Pleguezuelos, J. M. & Alaminos, E. (2009) Climate warming and activity period extension in the Mediterranean snake Malpolon monspessulanus. *Climatic Change,* 92**,** 235-242.

Myers, R. (1990) *Classical and modern regression with applications,* Boston, MA, Duxbury.

Niamir, A. (2009) Distribution modelling of the short - toed eagle in relation to potential food availability. Enschede, ITC.

Omolo, D. P. (2006) Biodiversity patterns in changing mediterranean landscapes : a modelling perspective. Enschede, ITC.

Patthey, P. (2003) Habitat and corridor selection of an expanding red deer (Cevus elaphus) population. *Unpublished PhD.* Lausanne, Switzerland, University of Lausanne.

Pearson, R. G. & Dawson, T. P. (2003) Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography Letters,* 12**,** 361-371.

Pearson, R. G., Raxworthy, C. J., Nakamura, M. & Townsend Peterson, A. (2007) Predicting species distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. *Journal of Biogeography,* 34**,** 102-117.

Penman, T. D., Pike, D. A., Webb, J. K. & Shine, R. (2010) Predicting the impact of climate change on Australia's most endangered snake, Hoplocephalus bungaroides. *Diversity and Distributions* 16 Pg. 109-118.

Phillips, S. J., Anderson, R. P. & Schapire, R. E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling,* 190**,** 231-259.

Phillips, S. J. & Dudik, M. (2008) Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography,* 31**,** 161-175.

Pleguezuelos, J. M. (2006) *Rhinechis scalaris* IN CARRASCAL, L. M. & SALVADOR, A. (Eds.) *Encyclopedia of Vertebrates Virtual Spanish.* Madrid, Museo Nacional de Ciencias Naturales.

Pleguezuelos, J. M., Fernández-Cardenete, J. R., Honrubia, S., Feriche, M. & Villafranca, C. (2007) Correlates between morphology, diet and foraging mode in the Ladder Snake Rhinechis scalaris (Schinz, 1822). *Contributions to Zoology,* 76 (3)**,** pp. 179 -186

Pleguezuelos, J. M., Marquez, R. & Lizana, M. (Eds.) (2004) *Atlas y Libro Rojo de los Anfibios y Reptiles de Espana,* Madrid, Ministerio De Medio Ambiente.

Pope, V. D., Gallani, M. L., Rowntree, P. R. & Stratton, R. A. (2000) The impact of new physical parametrizations in the Hadley Centre climate model: HadAM3. *Climate Dynamics,* 16**,** 123-46.

Pounds, J. A., Fogden, M. P. L. & Campbell, J. H. (1999) Biological response to climate change on a tropical mountain. *Nature,* 398**,** 611-615.

Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Monserud, R. A. & Solomon, A. M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography,* 19**,** 117-134.

Randall, D. A., Wood, R. A., Bony, S., Colman, R., Fichefet, T. & Fyfe, J. (2007) Climate models and their evaluation. IN SOLOMON, S., QIN, D., MANNING, M., CHEN, Z., MARQUIS, M., AVERYT, K. B., TIGNOR, M. & MILLER, H. L. (Eds.) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the*

Intergovernmental Panel on Climate Change. Cambridge, UK and NY, USA, Cambridge University Press.

Raupach, M., Marland, G., Ciasis, P., Que´re´, C., Canadell, J. & Klepper, G. (2007) Global and regional drivers of accelerating CO2 emissions. *Proc. Natl. Acad. Sci.* , 104**,** 10288–10293.

Reading, C. J. (2007) Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia,* 151**,** 125-131.

Real, R., Marquez, A. L., Estrada, A. & Olivero, J. (2009) Modeling potential impacts of climate change on the distribution of mountain species in Peninsular Spain. *The International Biogeography Society.*

Reed, R. N. & Shine, R. (2002) Lying in wait for extinction: Ecological correlates of conservation status among Australian elapid snakes. *Conservation Biology,* 16**,** 451-461.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. & Pounds, J. A. (2003) Fingerprints of global warming on wild animals and plants. *Nature,* 421**,** 57-60.

Saint Girons, H. (1982) Reproductive cycles of male snakes and their relationships with climate and female reproductive cycles. *Herpetologica* 38**,** Pg. 5 -16.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M. & Wall, D. H. (2000) Biodiversity - Global biodiversity scenarios for the year 2100. *Science,* 287**,** 1770-1774.

Santos, X. (2004) Viperine snake - Natrix maura. IN CARRASCAL, L. M. & SALVADOR, A. (Eds.) *Encyclopedia of Vertebrates Virtual Spanish.* Madrid, Museo Nacional de Ciencias Naturales

Santos, X., Brito, J. C., Caro, J., Abril, A. J., Lorenzo, M., Sillero, N. & Pleguezuelos, J. M. (2009) Habitat suitability, threats and conservation of isolated populations of the smooth snake (Coronella austriaca) in the southern Iberian Peninsula. *Biological Conservation,* 142**,** 344-352.

Santos, X., Brito, J. C., Pleguezuelos, J. M. & Llorente, G. A. (2007a) Comparing Filippi and Luiselli's (2000) method with a cartographic approach to assess the conservation status of secretive species: The case of the Iberian snake-fauna. *Amphibia Reptilia,* 28**,** 17-23.

Santos, X. & Llorente, G. A. (2009) Decline of a common reptile: case study of the viperine snake Natrix maura in a Mediterranean wetland. *Acta Herpetologica 4(1): 7-13,* 4(2)**,** 161-169.

Santos, X., Llorente, G. A., Pleguezuelos, J. M., Brito, J. C., Fahd, S. & Parellada, X. (2007b) Variation in the diet of the Lataste's viper Vipera latastei in the Iberian Peninsula: Seasonal, sexual and size-related effects. *Animal Biology,* 57**,** 49-61.

Santos, X. & Pleguezuelos, J. M. (2004) Southern smooth snake - *Coronella girondica*. IN CARRASCAL, L. M. & SALVADOR, A. (Eds.) *Enciclopedia Virtual de los Vertebrados Españoles.* Madrid, Museo Nacional de Ciencias Naturales.

Segura, C., Feriche, M., Pleguezuelos, J. M. & Santos, X. (2007) Specialist and generalist species in habitat use: Implications for conservation assessment in snakes. *Journal of Natural History,* 41**,** 2765-2774.

Segurado, P. & Araujo, M. B. (2004) An evaluation of methods for modelling species distributions. *Journal of Biogeography,* 31**,** 1555-1568.

Sekercioglu, C. H., Schneider, S. H., Fay, J. P. & Loarie, S. R. (2008) Climate change, elevational range shifts, and bird extinctions. *Conservation Biology,* 22**,** 140-150.

Sillero, N., Brito, J. C., Skidmore, A. K. & Toxopeus, A. G. (2009) Biogeographical patterns derived from remote sensing variables: the amphibians and reptiles of the Iberian Peninsula. *Amphibia-Reptilia,* 30**,** 185-206.

Soares, C. & Brito, J. C. (2007) Environmental correlates for species richness among amphibians and reptiles in a climate transition area. *Biodiversity and Conservation,* 16**,** 1087-1102.

Stockwell, D. & Peters, D. (1999) The GARP modelling system: problems and solutions to automated spatial prediction. *Int. J. Geo-graph. Inform. Sci.,* 13**,** 143-158.

Stockwell, D. R. B. & Peterson, A. T. (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling,* 148**,** 1-13.

Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S. L., Fischman, D. L. & Waller, R. W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science,* 306**,** 1783-1786.

Suarez-Seoane, S., Garcia de la Morena, E. L., Morales Prieto, M. B., Osborne, P. E. & de Juana, E. (2008) Maximum entropy niche-based modelling of seasonal changes in little bustard (Tetrax tetrax) distribution. *Ecological Modelling,* 219**,** 17-29.

Teixeira, J. & Arntzen, J. W. (2002) Potential impact of climate warming on the distribution of the Golden-striped salamander, Chioglossa lusitanica, on the Iberian Peninsula. *Biodiversity and Conservation,* 11**,** 2167-2176.

Thomas, C. D., Bodsworth, E. J., Wilson, R. J., Simmons, A. D., Davies, Z. G., Musche, M. & Conradt, L. (2001) Ecological and evolutionary processes at expanding range margins. *Nature,* 411**,** 577-581.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., Ferreira De Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L. & Williams, S. E. (2004) Extinction risk from climate change. *Nature,* 427**,** 145-148.

Thuiller, W. (2004) Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology,* 10**,** 2020-2027.

Verburg, P. H., Berkel, D. B., Doorn, A. N., Eupen, M. & Heiligenberg, H. A. (2009) Trajectories of land use change in Europe: a model-based exploration of rural futures. *Landscape Ecol.*

Verburg, P. H. & Overmars, K. P. (2009) Combining top-down and bottom-up dynamics in land use modeling: exploring the future of abandoned farmlands in Europe with the Dyna-CLUE model. *Landscape Ecol,* (in press).

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature,* 416**,** 389-395.

Williams, P. H. (2000) Endemism and important areas for representing European biodiversity: a preliminary exploration of atlas data for plants and terrestrial vertebrates. *Bel. J. Entomol* 2**,** Pg. 21- 46.

Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., Guisan, A., Elith, J., Dudik, M., Ferrier, S., Huettmann, F., Leathwick, J. R., Lehmann, A., Lohmann, L., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. M., Phillips, S. J., Richardson, K. S., Scachetti-Pereira, R., Schapire, R. E., Soberon, J., Williams, S. E. & Zimmermann, N. E. (2008) Effects of sample size on the performance of species distribution models. *Diversity and Distributions,* 14**,** 763-773.

WorldClim (2005),WorldClim - Global Climate Data, http://www.worldclim.org, accessed on: 20th August 2009

Yost, A. C., Petersen, S. L., Gregg, M. & Miller, R. (2008) Predictive modeling and mapping sage grouse (Centrocercus urophasianus) nesting habitat using Maximum Entropy and a long-term dataset from Southern Oregon. *Ecological Informatics,* 3**,** 375-386.

7. Appendices

Appendix 1. CLUE and Corine land cover legend

Code	CLUE Class name	Corine Equivalent
0	Built-up area	Artificial surfaces
1	Arable land (non-irrigated)	Arable land (non-irrigated)
2	Pasture	Pasture
3	(Semi) Natural vegetation	(Semi) Natural vegetation
4	Inland wetlands	Inland wetlands
5	Glaciers and snow	Glaciers and perpetual snow
6	Arable land (irrigated)	Permanently irrigated land & Rice fields
7	Recently abandoned arable land	No equivalent Corine class. Most of it classified as arable land or permanent crops.
8	Permanent crops	Permanent crops
9	Arable land devoted to the cultivation of (annual) biofuel crops	No equivalent Corine class. Contained within "Non-irrigated arable land"
10	Forest	Forest
11	Sparsely vegetated areas	Sparsely vegetated areas
12	Beaches, dunes and sands	Beaches, dunes and sands
13	Salines	Salines
14	Water and coastal flats	Water bodies
15	Heather and moorlands	Moors and heathland
16	Recently abandoned pasture land	No equivalent Corine class, most classified as pasture
17	Perennial biofuel crop cultivation	No Corine equivalent part of arable land

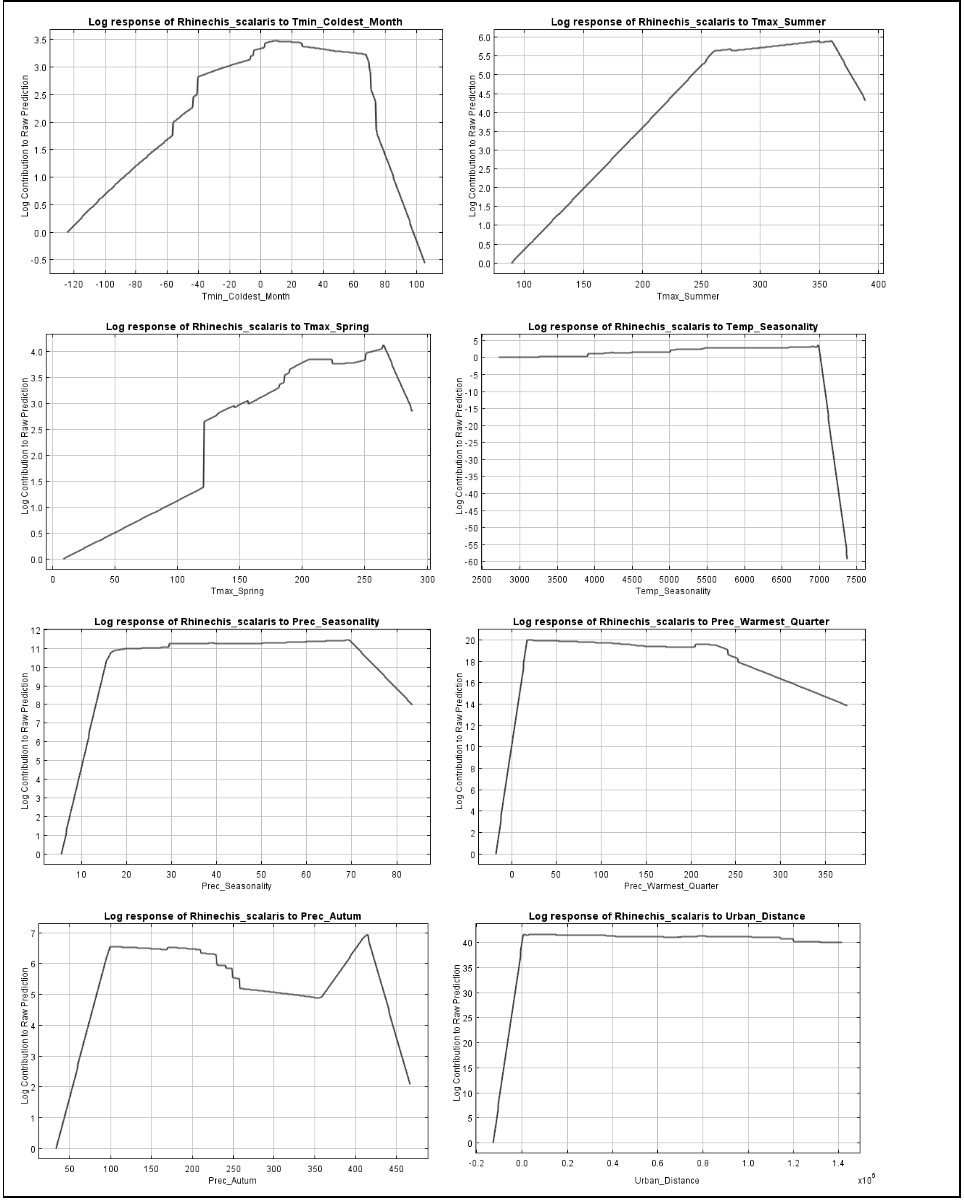
Appendix 2. P- Values from the binominal test for all-inclusive models.

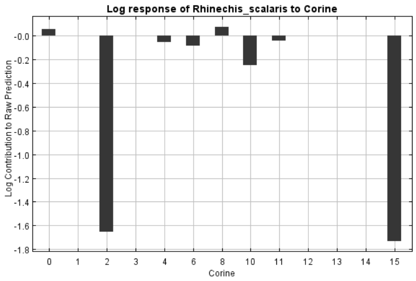
	P-Values for			
Variables	**Natrix maura**	**Rhinechis scalaris**	**Malpolon Monspessulanus**	**Coronella girondica**
17	2.26E-13	-	-	-
16	3.05E-13	-	-	-
15	2.70E-16	3.31E-20	3.62E-16	8.59E-20
14	1.27E-13	7.98E-24	1.41E-17	1.15E-16
13	4.16E-16	1.70E-22	2.97E-13	3.05E-22
12	3.41E-17	3.60E-18	1.65E-13	4.06E-21
11	7.87E-13	1.72E-16	8.17E-17	2.50E-20
10	1.20E-13	2.51E-20	1.40E-14	2.51E-22
9	2.59E-15	1.32E-15	1.64E-18	3.10E-20
8	3.91E-19	1.00E-21	2.56E-17	2.73E-20
7	7.00E-14	7.55E-15	1.16E-18	2.65E-19
6	7.83E-13	1.17E-20	1.82E-18	2.66E-19
5	2.19E-12	6.02E-21	7.41E-14	1.27E-17
4	1.64E-12	1.77E-18	1.35E-14	5.25E-16
3	1.28E-12	1.04E-16	1.60E-12	6.98E-21
2	2.60E-07	2.72E-16	3.04E-11	4.72E-13
1	1.81E-03	1.92E-13	4.18E-15	4.11E-07

Appendix 3. P- values from the binominal test for biophysical only models

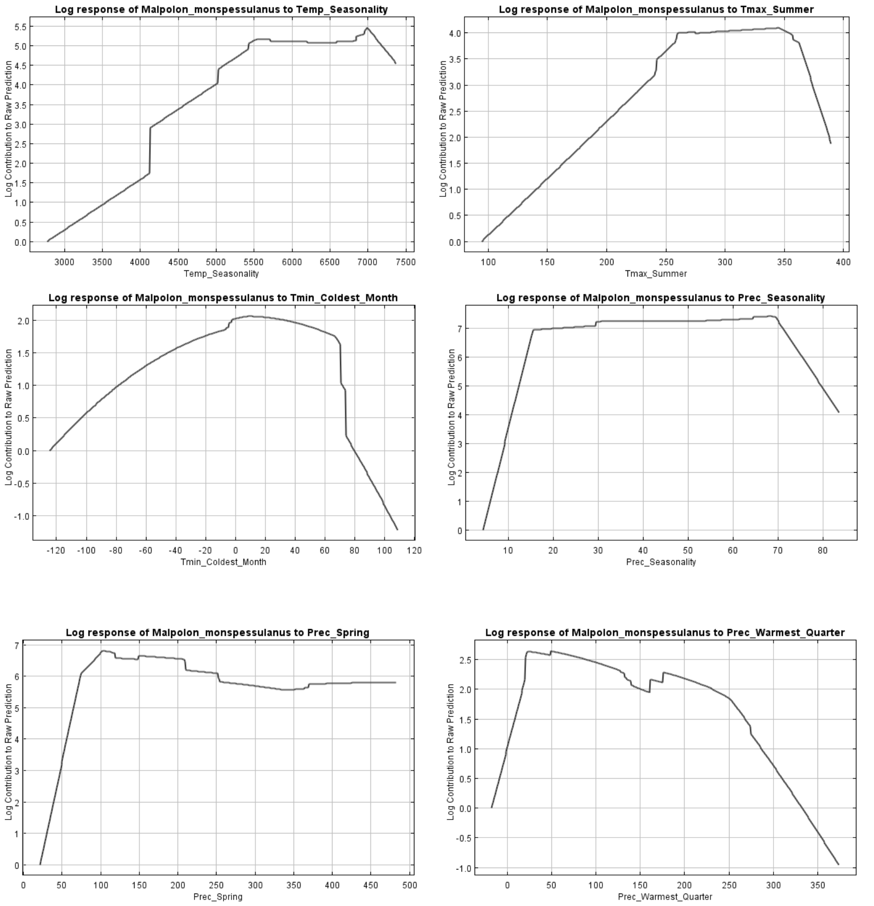
	P-Values for			
Variables	**Natrix maura**	**Rhinechis scalaris**	**Malpolon Monspessulanus**	**Coronella girondica**
7	4.42E-03			
6	2.45E-03			
5	7.70E-04	4.99E-07	6.90E-05	2.42E-06
4	7.88E-03	1.42E-06	6.16E-05	4.49E-05
3	1.46E-02	1.62E-07	1.54E-04	1.44E-04
2	2.99E-03	8.64E-05	1.02E-03	1.46E-03
1	9.01E-02	9.58E-04	4.14E-03	4.86E-04

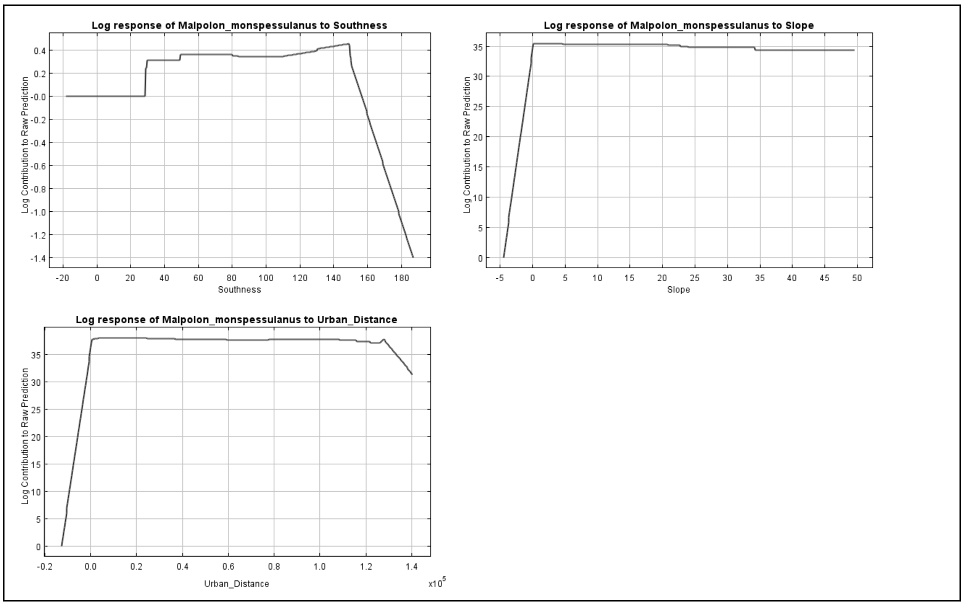
Appendix 4. Rhinechis scalaris response curves



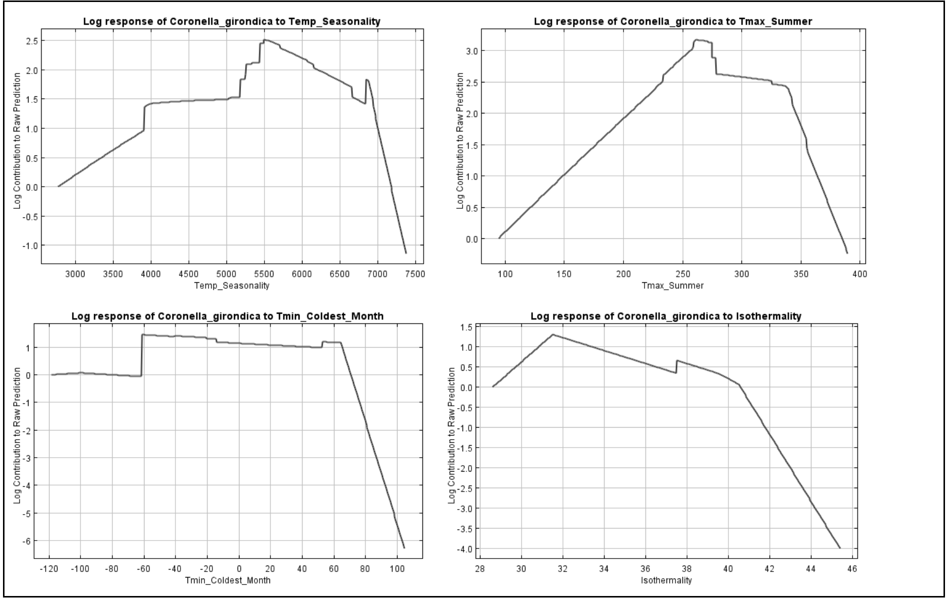


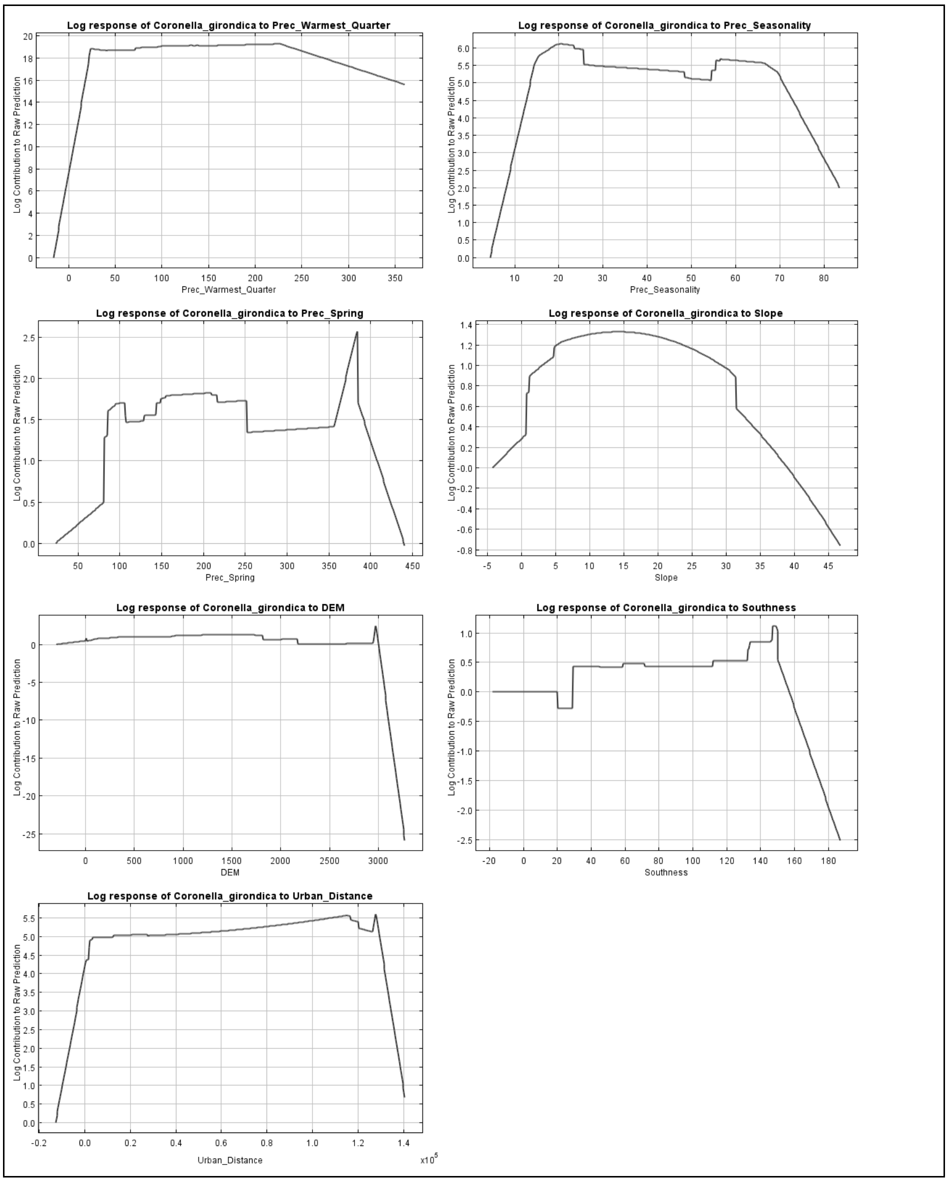
Appendix 5. Malpolon monspessulanus response curves



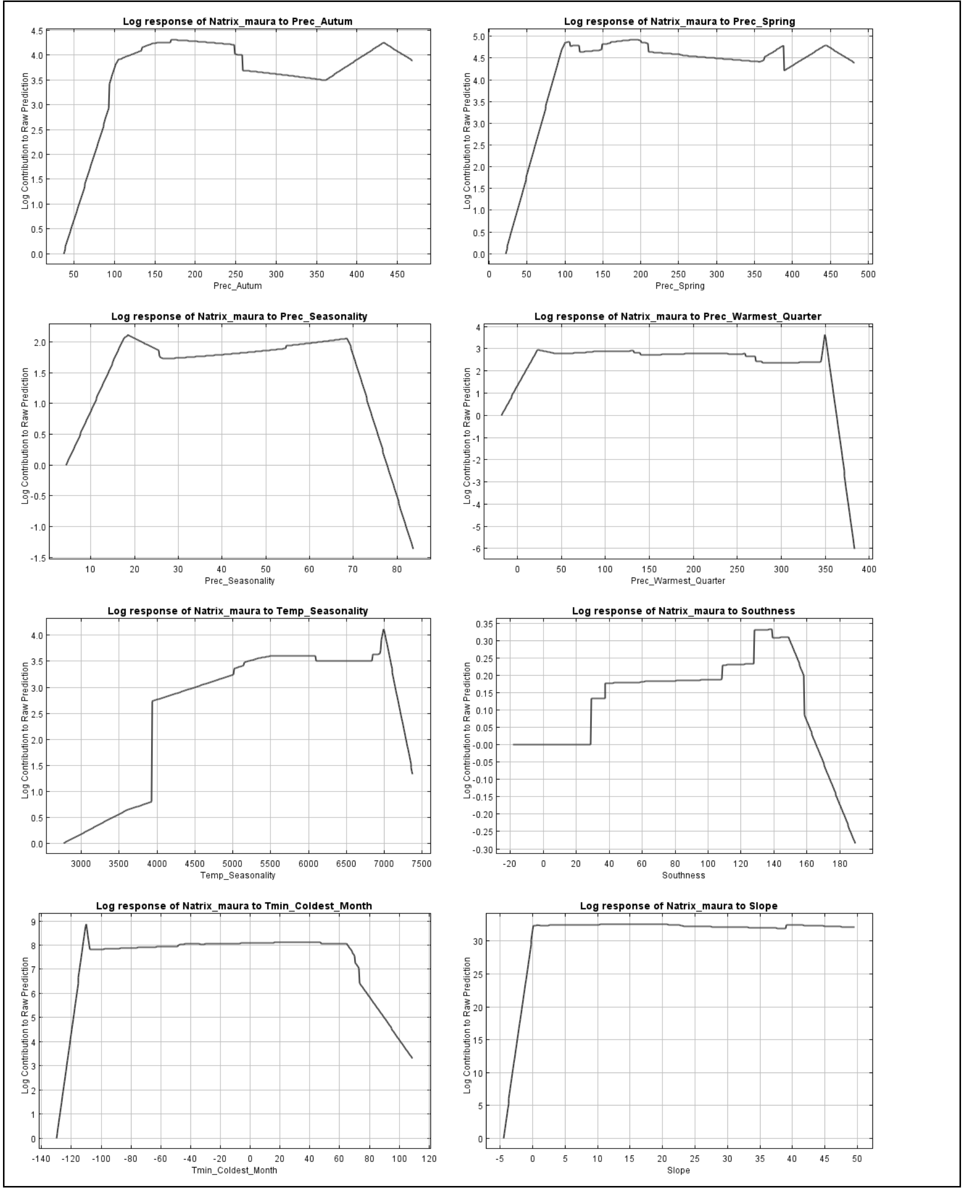


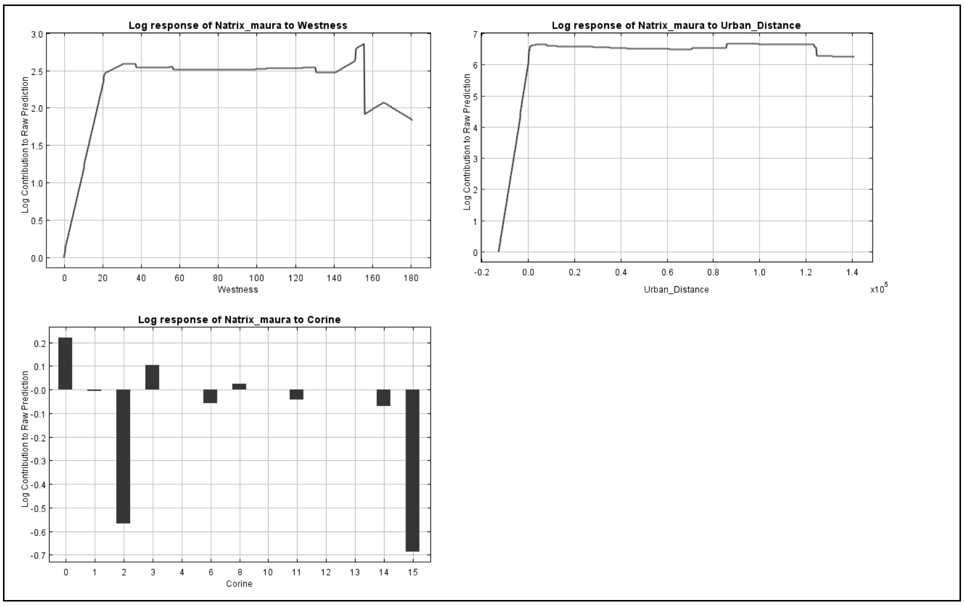
Appendix 6. Coronella girondica response curves




Log response of Coronella_girondica to Prec_Warmest_Quarter
Log Contribution to Raw Prediction
0 2 4 6 8 10 12 14 16 18 20
0 50 100 150 200 250 300 350
Prec_Warmest_Quarter
Log response of Coronella_girondica to Prec_Seasonality
Log Contribution to Raw Prediction
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0 4.5 5.0 5.5 6.0
10 20 30 40 50 60 70 80
Prec_Seasonality
Log response of Coronella_girondica to Prec_Spring
Log Contribution to Raw Prediction
0.0 0.5 1.0 1.5 2.0 2.5
50 100 150 200 250 300 350 400 450
Prec_Spring
Log response of Coronella_girondica to Slope
Log Contribution to Raw Prediction
-0.8 -0.6 -0.4 -0.2 -0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4
-5 0 5 10 15 20 25 30 35 40 45
Slope
Log response of Coronella_girondica to DEM
Log Contribution to Raw Prediction
-25 -20 -15 -10 -5 0
0 500 1000 1500 2000 2500 3000
DEM
Log response of Coronella_girondica to Southness
Log Contribution to Raw Prediction
-2.5 -2.0 -1.5 -1.0 -0.5 0.0 0.5 1.0
-20 0 20 40 60 80 100 120 140 160 180
Southness
Log response of Coronella_girondica to Urban_Distance
Log Contribution to Raw Prediction
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0 4.5 5.0 5.5
-0.2 0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4
Urban_Distance
x10^5

Appendix 7. Natrix maura response curves




Log response of Natrix_maura to Westness
Log Contribution to Raw Prediction
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
20
40
60
80
100
120
140
160
180
Westness
Log response of Natrix_maura to Urban_Distance
Log Contribution to Raw Prediction
7
6
5
4
3
2
1
0
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Urban_Distance
x10^5
Log response of Natrix_maura to Corine
Log Contribution to Raw Prediction
0.2
0.1
-0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
0
1
2
3
4
6
8
10
11
12
13
14
15
Corine