Biodiversity Patterns in Changing Mediterranean Landscapes:

A Modelling Perspective

Dan Peter Omolo
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Biodiversity Patterns in Changing Mediterranean Landscapes: A Modelling Perspective

by

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I certify that although I have conferred with others in preparing for this assignment, and drawn upon a range of sources cited in this work, the content of this thesis report is my original work.

Dan P. Omolo
“It is not the strongest of the species, or the most intelligent, that survives. It is the one that is most adaptable to change”.

Charles Darwin (1809 – 1882).

Dedicated to my loving parents,

Jack and Esther Omolo

My eternal gratitude for your love, care and support.
Abstract

Understanding biodiversity patterns and processes through predictive modelling of potential species distributions remains at the vanguard of modern-day conservation strategies. The aim of this study is to explore the respective predictive powers of NDVI indices versus climatic parameters to model the distributions of herpetofaunal species at mesoscale level in the Mediterranean (Spain).

Generalised Linear Models (GLMs) were used to derive predictive herpetofauna species distribution models from a set of respective eco-geographic parameters (NDVI and climate) in a GIS. The quality of the respective potential species distribution maps were assessed and compared using Cohen’s Kappa and threshold-independent Receiver Operating Characteristics (ROC) analysis. Mann-Whitney U statistic was used to determine if one model prediction was significantly better than the other.

The amount of deviance explained by integrated eco-climatic models for individual herp species ranged from 8.8 - 35.3 %. Comparatively, NDVI explained substantially less deviance ranging from 1.5 – 25.3% for individual species. However, NDVI predictors were superior to climatic predictors for two amphibian species; *S. salamandra* and *T. boscai*. Both predictors performed poorly (< 10%) for *H. arborea*. Overall, computed as a mean of relative differences between adjusted deviances $D^2$ across all species, climate explained 10.4% more deviance than NDVI. Low Kappa and AUC accuracy values were obtained when evaluating potential species distribution maps derived from NDVI predictors vs. climatic parameters. In comparing the two predictors, the area under the ROC curve (AUC) for 7 out of 10 species modelled by climatic predictors were significantly better ($z$-test; $z > 2$, $p < 0.05$) compared to NDVI. Our analysis revealed that the two measures of accuracy used to assess prediction map quality (Kappa & AUC$_{0.1}$) were in good agreement for both calibration and evaluation data sets ($r = 0.8$).

Overall, the models derived from eco-climatic parameters more closely match actual herp distributions than those based on NDVI. This contradicts our hypothesis and established ecological theory. These results suggest that the distributional limits of herp species and their assemblages in the Mediterranean may be largely set by climatic parameters. Conservation strategies for the increasingly vulnerable herpetofauna species in the Mediterranean must therefore respond to challenges posed by rapid habitat changes at landscape scale and climate change at continental and global scales.

**Keywords**: Predictive models, GLMs, herpetofauna, species richness, climate, NDVI, Spain, Mediterranean.
"If I have seen farther than others, it is because I was standing on the shoulders of giants"; Isaac Newton, 1642 – 1727.

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1. Introduction

1.1 General background

Human activities are altering global landscapes more rapidly than ever before. A significant modification is the formation of isolated and fragmented habitats, which can interrupt landscape connectivity, and increase species extinction rates (Osborne et al., 2001). At continental scale, Europe’s biodiversity is subject to serious decline as a result of these modifications including climate change, changes in land use, land abandonment, agricultural expansion, loss of habitat due to urbanisation or industrialisation, fragmentation by infrastructure, change in land management and pollution (Bouwma et al., 2002). In Europe, most regions are characterised by high level of economic development hence most natural ecosystems have been destroyed and pushed to the margins by dominant land uses such as agriculture and urban development. Further at sub-continental scale, the Mediterranean landscape, considered to be one of the world’s biodiversity hotspots, faces even greater challenges owing to its unique tapestry of culture, climate, economy and biogeography. The IUCN reports that Mediterranean ecosystems are relatively nutrient-poor, seasonally-stressed yet species-rich ecosystems. A majority of the taxa exhibit high levels of diversity, at both specific and sub-specific levels. For instance, within the 2.3 million km2 of the Mediterranean Basin occur at least 30,000 plant taxa implying that 1.6% of Earth’s land surface contains approximately 10% of all plant species. Half of these species are reported to be endemic to the area with approximately 4,800 endemic to individual countries that comprise the region (IUCN-MED, 2005).

Much of the historical reasoning and evolutionary mechanisms of such diversification has been largely attributed to the changes occasioned by environmental peculiarities related to geographic location and configuration of the area (e.g. insularity, existence of peninsulas, climatic variability, habitat heterogeneity, etc.) and also to the long history of varying land-use by people in the area that has created and maintained a wide range of habitats (IUCN-MED, 2005). These peculiarities have actually intensified the anthropogenic threats to biodiversity in the Mediterranean environment. Thus, the Basin is ranked among those areas where the severity of biodiversity erosion is expected to reach its maximum. For instance, approximately 14-15% of the flora is threatened with extinction (IUCN-MED, 2005). However, of prime concern is the rapid decline of European herpetofauna (amphibians and reptiles) since they are the most
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biologically vulnerable species to these rapid habitat changes. Most herpetofauna have very small home ranges, little ability and no instinct to migrate away from machinery or fire, are flightless and do not have comparable resting phases such as seeds or spores (Gasc J.-P. et al., 2004). Further, existing conservation measures are largely insensitive or even harmful to herpetofauna in cases where local habitat features and vegetation structures are seldom recognised. This could be attributed to the political reasoning that surrounds their perception as relatively unpopular species and thus, their conservation needs have been largely overlooked by a bias towards charismatic species such as birds, flowering plants and flagship mammals.

Spain, a Mediterranean state and the focus of this study, is experiencing most of the challenges mentioned above. Changes in land use resulting from marginalisation of traditional pastoralism and dryland agriculture may affect biodiversity conservation either directly or indirectly. The recent introduction of artificial irrigation systems in Spain (Op cit) has led to displacement of natural ecosystems and consequently loss of biodiversity (UNEP, 2000). Spain encompasses a significant portion of the 47 taxa prioritised by IUCN’s Species Survival Group for European Herpetofauna (IUCN, 2000). Further, as an EU member state, it is subject to EU-wide policy changes that may affect landuse and therefore impact on biological diversity. There is a well documented and growing need for research aimed at addressing the questions of impact of global change on Mediterranean diversity, knowledge on current patterns of species distribution and the role of diversity on ecosystem function in these rapidly changing landscapes (EU FP6 “Global Change and Ecosystems” www.cordis.lu). Emphasis is placed on understanding biodiversity and ecosystems patterns, processes and dynamics at European and global scales, in a changing environment through the development of earth systems analysis and modelling initiatives.

1.2 Patterns and theories of species distribution

Explaining the spatial and temporal variation in species diversity at local, regional and global scales is considered as one of the key problems of biology (Groombridge, 1992; Oindo, 2001; Owen, 1989). Species richness is considered a component of the concept of species diversity and explanations of its geographical variation have led to much discussion and debate leading to the advancement of several
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hypotheses (Owen, 1989). The task is complicated further by the fact that species diversity is determined by the outcome of many different interacting factors and processes with the prospect that one factor may be superseded by others (Diamond, 1988). Groombridge (1992) contends that the explanation of the patterns of species diversity must involve both historical events and current ecological processes. Understanding ecological systems therefore depends on the awareness that patterns and processes are strongly scale-dependent hence emphasizing the spatial scale at which species richness is to be estimated (Cody, 1975; Levin, 1992). Nevertheless, biodiversity – a fundamentally multidimensional concept - has to be first quantified. The most commonly considered facet of biodiversity is “species richness” – the number of species in a site or habitat. Considering that biodiversity surveys are expensive and time-consuming, conservationists are faced with the challenge of identifying important areas for biodiversity quickly and cheaply (Williams & Gaston, 1994). Rapid appraisals over large areas therefore demand the use of suitable diversity indices based on binary (presence-absence) data that are easy to measure and capable of capturing the variation between species (Oindo, 2001; Oindo & Skidmore, 2002).

Species-energy relationships (also referred to as diversity-productivity relations) have formed much of hotly contested ecological debates with many fundamental issues as yet unresolved. Ecological theory indicates that at sub-continental (areas > $10^6$ km²) or continental scales, productivity or energy flow through an ecosystem is considered a major determinant of species diversity (Currie, 1991; Rosenzweig & Abramsky, 1993; Said, 2003; Said et al., 2003; Wright et al., 1993). This energy is often estimated from models or indirectly from other variables and often used interchangeably with ‘net primary productivity’ (NPP) (Gaston, 2000). However, the direct estimation of energy is difficult at continental or sub-continental scales (Box et al., 1989; Currie, 1991; Owen, 1988; Said et al., 2003). Consequently, at regional scales, NPP is typically estimated from climatic data collected at scattered (and often biased) sampling points that are extrapolated in order to characterize productivity over a large region. However, such climatic-based models assume that vegetation cover is ‘natural’ and ipso facto under the control of climate (ibid). Further, at similar scales, it is argued that vegetation productivity is also influenced by non-climatic factors such as soil nutrient and structure, topography, disturbance and landuse. Therefore, the maximum Normalised Difference Vegetation Index (NDVI) derived from satellite data seems to provide a more accurate index of ecosystem processes and productivity compared to climate-based models due to the fact that it is spatially-explicit (Box
et al., 1989; Currie, 1991; Owen, 1988). NDVI, and increasingly other related ecosystem variables e.g. Leaf Area Index (LAI) have been related to distribution of plant and animal species diversity (Jorgensen & Nohr, 1996; Oindo et al., 2000; Oindo & Skidmore, 2002; Said, 2003; Said et al., 2003; Walker et al., 1992) Fig. 1 illustrates the variation of species numbers across different productivity levels with maxima reached at intermediate levels (Oindo & Skidmore, 2002; Said et al., 2003)

1.3 Geo-information science and species distribution modelling – a conceptual framework

Several approaches exist to identify areas of ecological interest ranging from landscape to conservation biology perspectives (Corsi et al., 2000; Forman, 1983; Gustafson & Gardener, 1996). The advent of new statistical techniques e.g. Generalised Linear Models (GLMs) and GIS tools have increasingly led to the development of predictive habitat distribution models in ecology (Guisan & Zimmermann, 2000). GIS expert-based species distribution models are considered as cost effective and efficiently address species conservation (Corsi, 2004; Corsi et al., 2000). Classifications have been made for the different distribution models based on their conceptual basis and/or applicability for conservation (Stoms et al., 1992; Norton & Possingham, 1993 in Corsi et al., 2000). This study largely adopts an ‘inductive-analytical approach’ which relies on samples of locations

1 See Corsi et al., 2000 for a detailed review of logical frameworks for species distribution modelling with GIS.
that are analysed using a statistical procedure (GLMs). However, we also incorporate elements of a 'deductive approach' where we have a priori knowledge on species-environment relationships e.g. in the selection of appropriate environmental predictor variables. Fig. 2 summarises our overall modelling conceptual framework. Remote sensing applications for mapping species distributions are increasing as the technology continues to evolve (higher spatial, temporal and spectral resolutions) and become readily available. Nonetheless, there have been few successful applications (de Leeuw et al., 2002).

1.4 Problem statement and justification

Human-induced changes to the landscape tend to cause loss of natural habitat and increased fragmentation, and this is generally believed to decrease the quantity and quality of habitats available. Although distributions of many plant and animal species have been modelled e.g. for animals: (Aspinall, 1992; Augustin et al., 1996; Corsi et al., 1999; Corsi et al., 2000; Güisan & Zimmerman, 2000; Manel et al., 1999; Mastrorillo et al., 1997; Mladenhoff et al., 1999; Oindo et al., 2000; Oindo & Skidmore, 2002; Owen, 1988, 1990; Pereira & Itami, 1991; Said et al., 2003; Toxopeus et al., 1994; Xuehua et al., 2001), there are few papers in literature which have predicted herpetofauna distributions (Guisan & Ulrich, 2003; Nix, 1986; Owen, 1989; Teixeira & Arntzen, 2002). Threats to vulnerable taxa such as herpetofauna have therefore been exacerbated by modest research and conservation interest. Applied conservation must therefore provide solutions for the conservation of such species in modern landscapes where prime habitats are continuously being fragmented and altered and where species are restricted to small, non-viable populations (Palomeras et al., 2000). Since species distribution is considered to be correlated to population size (Corsi et al., 2000; Gaston, 1994; Mace, 1994) conservation primarily focuses on fragmentation and reduction of distribution as an indicator of population viability (Corsi et al., 2000; Maurer, 1994).

Often, wildlife species distribution maps are derived from direct observations in the field of the animal species or their artefacts using conventional methods such as ground surveys, aerial surveys, aerial photography, radio telemetry and satellite tracking (de Leeuw et al., 2002; Said et al., 2003). Increasingly, species distribution modelling with GIS has been used to describe the distribution and density of biodiversity from ground or aerial observations (de Leeuw et al., 2002; Said et al., 2003). Despite long-standing scientific interest, the potential of remote sensing technology to measure, map, monitor and model spatial patterns and trends in species diversity have been
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little explored (Oindo, 2001; Stoms & Estes, 1993). Such information becomes invaluable in managing the resource base to preserve biological diversity, especially in increasingly fragmented landscapes.

Ecological theory indicates that at sub-continental (areas > 10^6 km^2) or continental scales, productivity or energy flow through an ecosystem is considered a major determinant of species diversity (Currie, 1991; Oindo & Skidmore, 2002; Rosenzweig & Abramsky, 1993; Said et al., 2003; Wright et al., 1993). However, there seems to be a paucity in literature regarding testing this ecological theory of species distribution and applying the relevant approaches in increasingly fragmented and intensely human dominated landscapes such as those present in Mediterranean where it is probable that other ecological, historical or anthropogenic factors could be more pervasive. Information and maps describing habitat suitability and wildlife distributions in such landscapes are therefore essential to habitat conservation and wildlife management. This is consistent with EU Framework Programme 6 (FP6) Policy under “Global Ecosystems and Change” (www.cordis.lu/fp6) where emphasis for research is focused upon understanding biodiversity and ecosystems patterns, processes and dynamics at European and global scales, in a changing environment.

1.5 Research objectives

The general objective of this research is to assess the relative predictive powers of remotely-sensed productivity indices (NDVI) and climatic parameters in modelling and understanding biodiversity distributions in a Mediterranean landscape. In order to achieve this general objective, the accomplishment of the following specific objectives is proposed;

1. Determine the relationship between climatic parameters and herpetofauna species distribution and richness in a Mediterranean landscape.
2. Determine the relationship between NDVI and herpetofauna species distributions and richness in a Mediterranean landscape.
3. Compare the effectiveness of remotely-sensed productivity indices and climatic parameters in determining herpetofauna species distribution and richness.
4. Predict the spatial distribution of herpetofauna species based on the ‘best-fit’ models.
5. Validate the accuracy of the potential herpetofauna species distribution maps.
1.5.1 Research hypotheses

Hypothesis 1

Testing the concept that climate influences species distribution and richness in Mediterranean landscapes where climate is represented by bioclimatic variables (Mean Annual Temp, Annual Precipitation, etc.)

$H_0$: There is no significant relationship between bioclimatic parameters and herpetofauna species distribution and richness in Mediterranean landscapes.

$H_a$: There is a significant relationship between bioclimatic parameters and herpetofauna species distribution and richness in Mediterranean landscapes.

Hypothesis 2

Testing the concept that productivity influences species distribution and richness in Mediterranean landscapes where productivity is represented by NDVI indices - Maximum average NDVI and its Standard deviation.

$H_0$: There is no significant relationship between NDVI indices and herpetofauna species distribution and richness in Mediterranean landscapes.

$H_a$: There is a significant relationship between NDVI indices and herpetofauna species distribution and richness in Mediterranean landscapes.

Hypothesis 3

Testing the concept that NDVI indices are better predictors of herpetofauna species distribution and richness compared to climatic parameters (Temperature, Precipitation)

$H_0$: There is no significant difference between NDVI indices and climatic parameters in predicting herpetofauna species distribution in Mediterranean landscapes.

$H_a$: There is a significant difference between NDVI indices and climatic parameters in predicting herpetofauna species distribution in Mediterranean landscapes.
Figure 2: Conceptual framework for species distribution modelling (adapted from Corsi et al, 2000).
2. Methods and Materials

2.1 Study area

The Mediterranean climate is characterised by mild wet winters and by warm to hot, dry summers between about 30° and 40° latitude. The climate is exposed to the South Asian Monsoon in summer and the Siberian high-pressure system in winter. The southern part of the region is mostly under the influence of the descending branch of the Hadley cell, while the northern part is more linked to the mid-latitude variability (Giannakopoulos et al., 2005). This study focuses on Spain which lies in the Iberian Peninsula and occupies a considerable part of the Mediterranean basin. Spain, together with Portugal, forms the westernmost of the three major peninsulas of southern Europe, an enormous octagonal headland, at the extreme southwest of the continent. It borders to the North on the Bay of Biscay, France and Andorra; to the East, on the Mediterranean; to the South, on the Mediterranean and the Atlantic, and to the West on the Atlantic and Portugal.

It is situated in a temperate area, between latitudes 43 47’ 24”N. (Estaca de Bares) and 36 00’ 3” S. (Punta de Tarifa) and between longitudes 7 00’ 29” E. (Cabo de Creus) and 5 36’ 40” W. (Cabo Tourinan) (Bario, 2006). With only 26% of the land arable, dive growing features as the main agricultural output of the region followed by other perennial crops such as citrus, almond and more recently, vines. Since Spain’s incorporation in the European Union, agriculture has been boosted by subsidies, with citrus and olive...
production being promoted. The plains are covered by grassland followed in altitudinal range by the typical Mediterranean shrubland dominated by *Quercus* and *Olea spp* communities, commonly referred to as *matorral* in Spanish (ITC, 2002).

### 2.2 Herpetofauna species distribution data

Amphibian and Reptile species distribution maps were derived from the "*Anfibios y Reptiles de España*" Atlas (Pleguezuelos et al., 2004). The majority of the species data was collected in the period 1981 – 1997, originating from regional mapping projects. Further surveys were conducted in the summer of 2000 to “ground truth” the records and include new observations which culminated in the publication of a concise atlas in 2004 (Pleguezuelos et al., 2004). A total of 67 scanned distribution maps of selected herp species were acquired from this database (See Annex 3 for a full species list). 10 herp species (4 reptiles and 6 amphibians – Table 1) were selected from these of which species-specific models were fitted. The species were selected on the basis of either their rarity (restricted range) (e.g. *L. schreibei*) or widespread distribution (e.g. *S. salamandra*). To model overall species richness, the herpetofauna data was divided into two main groups for analysis purposes: *Amphibia*, *n* = 27 species and; *Reptilia*, *n* = 47 species. A further subdivision following Owen (1989) was used: Salamanders (*Amphibia: Caudata*, *n* = 9 species), frogs and toads (*Amphibia: Anura*, *n* =18 species, Lizards (*Reptilia: Squamata*, Suborder *Sauria*, *n* =9 species), and snakes (*Reptilia: Squamata*, Suborder *Serpentes*, *n* =12 species). This taxonomic approach is considered superior in both evolutionary and ecological aspects compared to previous studies where they were grouped together (Owen, 1989).

For each species, the distributional data was aggregated at a 10 x 10 km UTM resolution sampling grid following the European network of meshes approach, albeit at 10 km$^2$ resolution (Gasc J. -P. et al., 2004). The observations are coded in a binary format i.e. presence/absence (1 & 0). The database contains > 5,000 observations pertaining to the 67 herp species. Species richness for each taxonomic grouping was calculated by summing the total number of species present in each sampling grid. The study assumes that species not found in a given 10 x 10 km sampling grid were considered absent, supposing a quasi-exhaustive sampling was carried out for most squares. However, given the large sampling grain size hence need for more sampling effort and; considering the fact that herpetofauna are cryptic and mobile species, this may be too strong an assumption. Nevertheless, this approach remains better
than generating pseudo-absences (e.g. in Zaniewski et al, 2002) as shown in similar studies of rare plant species (Guisan et al, 2000, Guisan & Ulrich, 2003). The models were calibrated using a subset of 1000 randomly selected squares. From the remaining data, 1000 randomly selected squares were used to evaluate the predictions of the models on a quasi-independent basis.

Table 1: List of 10 herpetofauna species in Spain whose distributions are modelled by GLM

<table>
<thead>
<tr>
<th>Order</th>
<th>Acronym</th>
<th>Scientific name</th>
<th>Common name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphibia</td>
<td>Alycis</td>
<td>Alytes cisternasii (Boscá, 1879)</td>
<td>Iberian midwife toad</td>
</tr>
<tr>
<td></td>
<td>Alyobs</td>
<td>Alytes obstetricans (Laurenti, 1768)</td>
<td>Midwife toad</td>
</tr>
<tr>
<td></td>
<td>Hylarb</td>
<td>Hyla arborea (Linnaeus, 1758)</td>
<td>Common tree frog</td>
</tr>
<tr>
<td></td>
<td>Hylmer</td>
<td>Hyla meridionalis (Boettger, 1874)</td>
<td>Mediterranean treefrog</td>
</tr>
<tr>
<td></td>
<td>Salsal</td>
<td>Salamandra salamandra (Linnaeus, 1758)</td>
<td>Spotted salamander</td>
</tr>
<tr>
<td>Reptilia</td>
<td>Tribos</td>
<td>Triturus boscai (Lataste, 1879)</td>
<td>Bosca's newt</td>
</tr>
<tr>
<td></td>
<td>Blacin</td>
<td>Blanus cinereus (Vandelli, 1797)</td>
<td>Iberian worm lizard</td>
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<tr>
<td></td>
<td>Lacsh</td>
<td>Lacerta schreiberi (Bedriaga, 1878)</td>
<td>Schreiber's green lizard</td>
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<tr>
<td></td>
<td>Maccuc</td>
<td>Macroprotodon cucullatus (Geoffrey Saint-Hilaire, 1827)</td>
<td>Balearic false smooth snake</td>
</tr>
<tr>
<td></td>
<td>Viplat</td>
<td>Vipera latasti (Boscá, 1878)</td>
<td>Lataste's viper</td>
</tr>
</tbody>
</table>

2.3 Environmental predictors

A) Normalised Difference Vegetation Index (NDVI)

As indicated in literature (Section 1.2), at sub-continental, mesoscale (areas > 10^6 km^2) and continental scales, productivity or energy flow through an ecosystem is considered a major determinant of species diversity (Currie, 1991; Oindo & Skidmore, 2002; Rosenzweig & Abramsky, 1993; Said et al., 2003; Wright et al., 1993). Since this cannot be estimated directly, proxies such as integrated maximum average NDVI - *indicator of ecosystem productivity* -; its standard deviation and coefficient of variation - *indicators of habitat heterogeneity* - are often used to model species distributions (Oindo & Skidmore, 2002; Said et al., 2003). NDVI data was acquired from the "Global Inventory Modelling and Mapping Studies (GIMMS) Satellite Drift Corrected and NOAA - 16 incorporated Normalised Difference Vegetation Index, Monthly 1981" digital dataset. The GIMMS NDVI datasets were generated from Advanced Very High Resolution Radiometer (AVHRR) imagery and contain global, composited and monthly NDVI over land areas for the period 1981–2003 available at a coarse spatial resolution of 8 x 8 Km. NDVI is the difference in reflectance between the AVHRR near-infra red and visible bands divided by the sum of these two bands. The datasets
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have been corrected for calibration, view geometry, volcanic aerosols and other effects not related to actual vegetation change. For a full description, see Tucker et al., (2004). Only datasets (15-day composites) covering the period 1993 – 2003 were used in this study since a 10 year time series was deemed sufficient. To derive the NDVI spatial datasets, 3 indices were calculated as follows;

Max Avg. NDVI (MavNd)  \[ MavNd = \frac{\sum (p_v)}{n} \]  

Where \( p_v \) is the individual pixel values (i.e. for all 240 composites calculated maximum NDVI images) and \( n \) is the number of 15-day composites. Its standard deviation was calculated as;

StDev. NDVI (SD)  \[ SD = \sqrt{\frac{1}{n-1} \sum (x_i - x)^2} \]  

Where \( n \) is the number of observations (i.e. 240 composites), \( x \), is the deviations from the average and \( x \) is the maximum average NDVI for individual pixels. The coefficient of variation was calculated by dividing the standard deviation by average NDVI expressed as a percentage.

Coefficient of Variation (CV)  \[ CV = \left( \frac{SD}{MavND} \right) \times 100 \]  

B) Climatic parameters

Temperature and precipitation-related indices are important for explaining the distribution of herp species diversity and their assemblages in the Mediterranean (Gasc J. -P. et al., 2004). Generally in ecology, two main hypotheses have been advanced that relate species diversity to climatic parameters; (i) *Climatic stability hypothesis* whereby stable climates permit a constant influx of resources leading to increased densities of species (Pianka, 1983) and (ii) *Intermediate disturbance hypothesis* whereby irregular or unpredictable climatic variation may function biologically as a form of disturbance and maintain herpetofauna species and their assemblages away from the equilibrium (Connell, 1978). In this study, annual mean temperature, annual mean precipitation and precipitation seasonality (coefficient of variation) were employed as measurements of climatic stability. Although they are temporally variable, they are nevertheless predictable since they are cyclic in nature (Owen, 1989). Likewise, measures of irregular or stochastic variability of climate were estimated by the maximum and minimum
temperatures of record. Climatic data layers for this study were obtained from the WORLDCLIM database which consists of precipitation records from 47,554 locations, mean temperature from 24,542 locations and minimum and maximum temperature for 14,835 locations. The climatic measurements are interpolated using mainly thin plate smoothing splines. All the layers were obtained at 8 x 8 km and in geodetic coordinate system. The relevant layers were then clipped using the study area boundary. For a full description of the database, see Hijmans et al., (2004).

All environmental predictors were subsequently aggregated in ArcGIS® to the 10 x 10 Km UTM standard sampling grid (See Section 2.2) by specifying: Max as the operation to perform on aggregated values of Maximum Average NDVI and Maximum temperature of record; Mean as the operation for annual mean temperature and precipitation; Min operation for the minimum temperature of record and; the value of the centre pixels was taken for the derived variables e.g. standard deviation. The climatic and NDVI predictors used are described in table 2 below.

Table 2: List of environmental predictors used to model herp species distributions in Spain

<table>
<thead>
<tr>
<th>Name</th>
<th>Description</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Climatic predictors</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIO 1</td>
<td>Annual mean temperature</td>
<td>°C</td>
</tr>
<tr>
<td>BIO 5</td>
<td>Maximum temperature of the warmest month</td>
<td>°C</td>
</tr>
<tr>
<td>BIO 6</td>
<td>Minimum temperature of the coldest month</td>
<td>°C</td>
</tr>
<tr>
<td>BIO 12</td>
<td>Annual mean precipitation</td>
<td>mm</td>
</tr>
<tr>
<td>BIO 15</td>
<td>Precipitation seasonality (Coefficient of variation)</td>
<td></td>
</tr>
<tr>
<td>(B) NDVI predictors</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MavND</td>
<td>Maximum average NDVI</td>
<td></td>
</tr>
<tr>
<td>SD</td>
<td>Standard deviation of NDVI</td>
<td></td>
</tr>
<tr>
<td>CV</td>
<td>Coefficient of variation</td>
<td>%</td>
</tr>
</tbody>
</table>
2.3.1 Multi-collinearity

Also referred to as ‘co-dependence’, multi-collinearity occurs in a multiple regression when several predictors (regressors) are highly correlated hence the inflation of regression parameter estimates e.g. variance (Fox, 1997). Such an issue is more of a problem when one’s intention is to explain a phenomenon rather than conducting a simple prediction of a phenomenon (Leahy, 2001). Sets of environmental variables often exhibit varying amounts of linear dependencies which results in a form of ill-conditioning in the correlation matrix. Subsequently, the usual least squares analysis of a regression model can dramatically become inadequate (Owen, 1989). Since linear dependencies may not be restricted to only two predictors, analysis of pairwise correlations between variables may not suffice. Variance Inflation Factor (VIF) is a common way used to detect multi-collinearity (Montgomery & Peck, 1982) and is denoted by the following mathematical expression;

\[
VIF = \sqrt{1/(1-R^2)}
\]  

VIFs represent the inflation that each regression coefficient experiences above what it would experience if the correlation matrix were an identity matrix i.e. if multi-collinearity was not present in the data (Owen, 1989). In general, VIFs exceeding 10 provide an indication that regression coefficients may have been poorly estimated due to multi-collinearity (Montgomery & Peck, 1982).

A unimodal method of ordination, Canonical Correspondence Analysis (CCA), was undertaken in CANOCO 4.5® software (Ter Braak & Smilauer, 2002) to detect multi-collinearity in the selected environmental variables. From the resulting VIFs (Table 3), it was concluded that the existence of multi-collinearity was not significantly high since none exceeded 10 as suggested by Montgomery & Peck, (1982) and hence all the variables could be used in subsequent analysis.

Table 3: Multi-collinearity analysis for environmental parameters

<table>
<thead>
<tr>
<th>Acronym</th>
<th>Description</th>
<th>VIF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bio 1</td>
<td>Annual mean temperature</td>
<td>8.7</td>
</tr>
<tr>
<td>Bio 5</td>
<td>Maximum temperature of warmest month</td>
<td>4.5</td>
</tr>
<tr>
<td>Bio 6</td>
<td>Minimum temperature of coldest month</td>
<td>6.7</td>
</tr>
<tr>
<td>Bio 12</td>
<td>Annual precipitation</td>
<td>2</td>
</tr>
<tr>
<td>Bio 15</td>
<td>Precipitation seasonality</td>
<td>1.9</td>
</tr>
<tr>
<td>MaxND</td>
<td>Maximum average NDVI</td>
<td>2.4</td>
</tr>
<tr>
<td>SD</td>
<td>Standard deviation of NDVI</td>
<td>1.3</td>
</tr>
<tr>
<td>CV</td>
<td>Coefficient of variation of NDVI</td>
<td>2.4</td>
</tr>
</tbody>
</table>
2.4 Statistical analyses

Generalised Linear Models (Chambers & Hastie, 1992; Gill, 2000; McCullagh & Nelder, 1989) were used to fit different models using the S-Plus® software (Insightful Corp). GLMs are an extension of the classical linear or multiple regression models where model coefficients are estimated by a Maximum-Likelihood (ML) algorithm or some variant of it, instead of the classical ordinary least squares (OLS). This allows one to specify distributional properties of the stochastic component, and also the transformation function, which transforms the scale of the predictor variable onto the scale of the response variable via an appropriate link function (Fox, 1997, 2002). GLMs are increasingly used in ecology to summarise the relationships between species distributions and environmental variables (Austin et al., 1984; Corsi et al., 1999; Guisan et al., 2002; Guisan et al., 1999; Nicholls, 1989). GLMs offer a powerful method to test ecological hypotheses about the distribution of organisms (Birks, 1996; Leathwick, 1998; Mourell & Ezcurra, 1996) and assess possible consequences of environmental changes e.g. climate change on these distributions (Guisan & Theurillat, 2000; Teixeira & Arntzen, 2002).

To model the individual herp species distributions and taxon-specific species richness, the GLMs were fitted by specifying a binomial distribution with a logistic link function (Logit) and a Poisson distribution with a log link function (Log) respectively. This has been similarly carried out in ecological studies using presence-absence data (Binomial distribution) and count data such as species richness (Poisson distribution) (Guisan et al., 1998; Guisan et al., 2002; Guisan & Ulrich, 2003; Guisan et al., 1999; Guisan & Zimmermann, 2000; Manel et al., 1999). In GLMs, the model is optimised through deviance reduction, which is converted to an estimated $\hat{D}^2$ – the equivalent to $R^2$ in OLS models – using the following formula:

$$\hat{D}^2 = \frac{\text{Null deviance} - \text{Residual deviance}}{\text{Null deviance}}$$  \hspace{1cm} (5)

Where the null deviance is the deviance of the model with the intercept only, and the residual deviance is the deviance that remains unexplained by the model after all final variables have been included (Guisan & Zimmermann, 2000). However, an adjusted $\hat{D}^2$ (similar to adjusted $R^2$) which takes the number of observations $n$ and the number of predictors $p$ in the model into account is considered an ideal measure and is representative of a real model fit (Nagelkerke, 1991; Weisberg, 1980). The adjusted deviance is thus calculated as follows;
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Adjusted $D^2 = 1 - \left(\frac{n - 1}{n - p}\right) \times [1 - D^2]$ \hspace{1cm} (6)

Two series of models were fitted; (1) models including only eco-climatic predictors and (2) models including only NDVI predictors (See table 2). In either case, model building was undertaken by first fitting linear and quadratic terms specified for all quantitative predictors. For each species and taxon group, final predictive models included only those terms, linear or quadratic, that satisfied two main criteria; (a) included terms must be significant at the 0.05 confidence level from a chi-square test of deviance reduction and; (b) significant terms must explain at least 1% of the deviance. The motivation to set these constraining factors was to ensure model parsimony by reducing complexity (Guisan & Zimmermann, 2000). These criteria follow a similar study carried out by Guisan & Hofer in 2003. A 1% deviance reduction with large datasets such as the one used in this study is considered a highly significant result. Guisan & Hofer (2003) contend that this provides a strong result and makes a permutation test unnecessary in most cases. Further, they argue that such a rigorous deviance reduction criterion combined with large datasets both contribute to limit problems caused by spatial autocorrelation in species occurrence data (i.e. when specimens are collected from several nearby locations in a restricted area). As such, autocorrelation aspects were not investigated in this study.

2.4.1 Model evaluation and comparison

Evaluating model predictions remain a fundamental objective in allowing its proper use in ecological applications, particularly when species and habitat conservation remains a priority (Corsi, 2004; Corsi et al., 2000; Guisan & Ulrich, 2003). Consequently, this aspect of predictive modelling has been widely researched and several techniques proposed from which optimal model evaluation can be successfully conducted (Corsi et al., 2000; Guisan & Zimmermann, 2000; Manel et al., 2001). Two main approaches emerge when evaluating the predictive power of models. The first approach, considered as ideal, involves the use of two independent data sets – one for calibration and the other for evaluation - also called training and evaluation data sets e.g. (Guisan et al., 1998; Guisan et al., 1999; Guisan & Zimmermann, 2000; Manel et al., 1999; Manel et al., 2001). However, this method is only optimal when two different datasets, originating from two distinct sampling strategies, are available upfront or the original dataset is sufficiently large to be split into subsets (so called ‘split-sample approach’). Often, when these conditions cannot be met, resampling techniques such as ‘Jack-knife’
or cross-validation, provide alternative possibilities for model evaluation (Guisan & Ulrich, 2003; Guisan & Zimmermann, 2000; Manel et al., 1999). Since the species dataset used in this study was sufficiently large (> 5,000 observations), we could use a quasi-independent dataset for evaluation purposes. This was obtained by randomly splitting the original dataset into a training (n = 1000) and test (n = 1000) set – ‘split-sample approach’ (Guisan & Zimmermann, 2000). This approach was considered appropriate compared to other resampling techniques such as ‘Jack-knifing’ which may be slow with large datasets (Guisan & Ulrich, 2003). Nevertheless, these datasets cannot be considered fully independent since they cover the same study area.

Two statistical measures were employed to compare individual species predictions with ‘ground truth’; (1) Kappa statistics (Cohen, 1960) by detecting the optimal threshold (i.e. maximum Kappa) for cutting the probabilistic predictions into presence-absence on the calibration dataset and using this optimal threshold for calculating Kappa on the evaluation (test) dataset (Guisan & Ulrich, 2003; Guisan et al., 1999; Guisan & Zimmermann, 2000) and; (2) the threshold-independent Receiver Operating Characteristic (ROC) approach, by calculating the area under the ROC curve (AUC) as the measure of the prediction success. Cohen’s provides a measure of the proportion of all possible cases of presence or absence that are correctly predicted after accounting for chance effects. It is thus considered as a simple, effective, standardised and appropriate statistic for evaluating or comparing presence-absence models (Manel et al., 2001). The ROC curve is obtained by plotting sensitivity (true positives) on the y axis and 1 – specificity (false positives) on the x axis for all possible thresholds. ROC analysis was initially developed for signal processing and clinical medicine (Fieldings & Bell, 1997). Its main advantage over other adequacy measures is that the AUC provides a single measure of model performance independent of any particular choice of threshold (Phillips et al., 2006). Since the AUC takes values between 0.5 and 1, making it difficult to compare to other accuracy measures, a modified version of AUC - Gini Coefficient AUC' - was calculated to take values between 0 and 1 (Copas, 1999; Guisan & Ulrich, 2003).

AUC' = 2*(AUC – 0.5)  

Finally, to compare the two model prediction AUC’s, AccuROC® Version 2.5 (Vida, 1993) was used. It uses a ties-corrected Mann-Whitney-U statistic which it approximates using a z-statistic. It employs a non-parametric test (DeLong et al., 1988) to determine if
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one model prediction is significantly better than another when using either quasi-independent or correlated samples (i.e. when both predictions are evaluated using the same evaluation sets) and reports the result either as a \( z \) or \( X^2 \) statistic, respectively, with a corresponding \( p \) value.
3. Results

3.1 Introduction

This section describes the main findings of the study and these are presented as follows;

- General spatial distribution of herpetofauna species richness in Spain
- Climatic parameters and herpetofauna species distribution and richness patterns
- NDVI indices and herpetofauna species distribution and richness patterns
- Model evaluation and comparison of relative predictive powers

3.2 General herpetofauna species richness distribution patterns

The general spatial distribution patterns of amphibians and reptiles in Spain are illustrated in Figure 4. These were calculated by summing the number of concurrent species per 10 km$^2$ sampling grid. A longitudinal gradient seems to be evident with higher amphibian species richness (> 10 spp per grid) in the north-east Pyrenees region to the south-west region. This longitudinal gradient is less apparent for reptile species richness although maxima occur in the south and along the eastern coastline. For both groups, species densities are highest in the north east Pyrenees and Catalonia region, along Basque country, Burgos and Salamanca region in the west, mountains of the central system and the south west. Conversely, the central region of Spain appears to be relatively ‘species-poor’ with low numbers per grid (< 5 spp).
Results

Figure 4: Spatial distribution of herp. species richness in Spain (10x10 Km). (a) Amphibians (b) Reptiles

3.3 Climatic parameters and herp species distribution in the Mediterranean

Figure 5: Spatial distribution of climatic parameters (10x10 Km). (a) Annual mean temperature (b) Annual precipitation
The south-western and eastern coastline of Spain receive the highest mean temperature (> 15 °C) revealing a north-east to south-west temperature gradient as illustrated in Figure 5 (a). This depicts the climatic influence of the descending branch of the Hadley cell which affects the southern part of the European continent in which Spain lies. The northern part of the country however has comparatively cooler temperatures, especially in the high altitude areas of the Pyrenees. Much of the country, especially central Spain, is dry with annual precipitation records of 500 mm or less (See Fig. 5 b). However, the northern high altitude regions traversing Basque country and the Pyrenees are quite humid with annual records above 1000 mm.

For all the selected species, climatic models could be fitted that fulfilled the 2 main criteria; (a) included terms significant at the 0.05 alpha level and (b) final model terms explained at least 1% of the deviance. Overall, the amount of deviance explained by the integrated eco-climatic models ranged from 8.8 to 35.3 % (Table 3). Low values of explained deviance (< 10%) were obtained for two amphibian species whose distributions are largely limited to the north-west of Spain, *H. arborea* and *T. boscai*. The maxima (> 30%) were reached for two herp species with widely differing distributions; *A. obstetricans* with a distribution limited to the relatively humid north and north-east Pyrenees and *B. cinereus* limited to the warmer southern Andalusia region of Spain. Temperature-related parameters explained a higher proportion of deviance (1.4 – 23%) for the reptile species (*L. schreiberi, B. cinereus & M. cucullatus*) compared to precipitation-related parameters which only explained 2.2 – 9.4 %. The only exception is *V. latasti* where precipitation seasonality explained a higher proportion of deviance (10.8%) compared to 1.4 % explained by annual mean temperature. Contrary to expectation, precipitation-related parameters were only important for 2 out of 6 amphibian species. These included *A. cisternasii* (~ 18%), limited to the south-west and *S. salamandra* (17.8%) with a comparatively widespread distribution. (See appendix 1 for selected species response curves to a climatic parameter)
Table 4: Selected climatic predictors and their proportion of explained deviance for individual species.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Lacsh</th>
<th>Blacin</th>
<th>Viplat</th>
<th>Maccuc</th>
<th>Alycis</th>
<th>Alyobs</th>
<th>Hylarb</th>
<th>Hylmer</th>
<th>Salsal</th>
<th>Tribos</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual mean temp</td>
<td>9.5</td>
<td>9.8</td>
<td>1.4</td>
<td>17.8</td>
<td>-</td>
<td>15.4</td>
<td>7.6</td>
<td>19</td>
<td>1.6</td>
<td>6.7</td>
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<td>Max temp of record</td>
<td>1.3</td>
<td>13.2</td>
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<td>-</td>
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<td>14.3</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Min temp of record</td>
<td>3.3</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.1</td>
<td>2.2</td>
<td>1.2</td>
<td>-</td>
<td>-</td>
<td>2.2</td>
</tr>
<tr>
<td>Annual precip.</td>
<td>-</td>
<td>-</td>
<td>10.8</td>
<td>-</td>
<td>4.1</td>
<td>-</td>
<td>-</td>
<td>9.7</td>
<td>17.8</td>
<td>-</td>
</tr>
<tr>
<td>Prec. seasonality</td>
<td>9.4</td>
<td>7.8</td>
<td>2.2</td>
<td>8.5</td>
<td>14.6</td>
<td>3.3</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>(D^2(%))</td>
<td>23.5</td>
<td>30.8</td>
<td>14.4</td>
<td>26.3</td>
<td>19.8</td>
<td>35.2</td>
<td>8.8</td>
<td>28.7</td>
<td>19.4</td>
<td>8.9</td>
</tr>
<tr>
<td>Adjusted (D^2(%))</td>
<td><strong>23.6</strong></td>
<td><strong>30.9</strong></td>
<td><strong>14.4</strong></td>
<td><strong>26.3</strong></td>
<td><strong>19.8</strong></td>
<td><strong>35.3</strong></td>
<td><strong>8.8</strong></td>
<td><strong>28.7</strong></td>
<td><strong>19.4</strong></td>
<td><strong>8.9</strong></td>
</tr>
<tr>
<td>Threshold</td>
<td>0.40</td>
<td>0.55</td>
<td>0.22</td>
<td>0.27</td>
<td>0.25</td>
<td>0.42</td>
<td>0.20</td>
<td>0.38</td>
<td>0.37</td>
<td>0.20</td>
</tr>
<tr>
<td>Kappa cal</td>
<td>0.60</td>
<td>0.45</td>
<td>0.27</td>
<td>0.31</td>
<td>0.35</td>
<td>0.56</td>
<td>0.28</td>
<td>0.50</td>
<td>0.44</td>
<td>0.30</td>
</tr>
<tr>
<td>Kappa eva</td>
<td>0.58</td>
<td>0.37</td>
<td>0.29</td>
<td>0.35</td>
<td>0.31</td>
<td>0.49</td>
<td>0.25</td>
<td>0.47</td>
<td>0.42</td>
<td>0.34</td>
</tr>
<tr>
<td>AUC cal</td>
<td>0.95</td>
<td>0.87</td>
<td>0.76</td>
<td>0.86</td>
<td>0.84</td>
<td>0.87</td>
<td>0.71</td>
<td>0.86</td>
<td>0.79</td>
<td>0.73</td>
</tr>
<tr>
<td>AUC eva</td>
<td>0.94</td>
<td>0.83</td>
<td>0.76</td>
<td>0.86</td>
<td>0.81</td>
<td>0.82</td>
<td>0.68</td>
<td>0.86</td>
<td>0.79</td>
<td>0.74</td>
</tr>
<tr>
<td>AUC' cal</td>
<td>0.89</td>
<td>0.74</td>
<td>0.52</td>
<td>0.72</td>
<td>0.68</td>
<td>0.74</td>
<td>0.42</td>
<td>0.72</td>
<td>0.58</td>
<td>0.46</td>
</tr>
<tr>
<td>AUC' eva</td>
<td>0.88</td>
<td>0.66</td>
<td>0.52</td>
<td>0.72</td>
<td>0.62</td>
<td>0.64</td>
<td>0.36</td>
<td>0.72</td>
<td>0.58</td>
<td>0.48</td>
</tr>
</tbody>
</table>

Values of explained deviance adjusted for the number of predictors and occurrences, hence a realistic estimate of model fit are set in bold. Cal = measured on the calibration data set, eva = measured on the evaluation data set, Threshold = probability threshold used to cut predictions into presence-absence.
At *Suborder* species richness level (Table 5), climatic influences were much reduced with the proportion of explained deviance ranging between 3.3 and 18%. Precipitation-related parameters explained proportionately less deviance (1.6 – 5.2%) compared to temperature (1 – 11.7%). However, when aggregated to *Order* level; *Amphibia* and *Reptilia*, there is a clear dichotomy with precipitation (8.4%) and temperature (2.8%) emerging as important, for each group respectively.

Table 5: Selected climatic predictors and their proportion of explained deviance for herp taxon groups.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Specie richness</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Suborder</td>
</tr>
<tr>
<td></td>
<td>Anura</td>
</tr>
<tr>
<td>Annual mean temp</td>
<td>-</td>
</tr>
<tr>
<td>Max temp of record</td>
<td>-</td>
</tr>
<tr>
<td>Min temp of record</td>
<td>-</td>
</tr>
<tr>
<td>Annual precip.</td>
<td>1.7</td>
</tr>
<tr>
<td>Prec. seasonality</td>
<td>1.6</td>
</tr>
<tr>
<td>$D^2$ (%)</td>
<td>3.3</td>
</tr>
<tr>
<td>Adjusted $D^2$ (%)</td>
<td><strong>3.3</strong></td>
</tr>
</tbody>
</table>

Realistic estimates of model fit are set in bold
3.3 NDVI and herp species distribution and richness in the Mediterranean

Maximum average NDVI – an indicator of ecosystem productivity – is highest (> 0.5) in the North and western parts of the Spain as indicated in Fig. 6 (a). Vegetation variability, represented by standard deviation of NDVI, however depicts a relatively sparse pattern but with clusters of highly heterogeneous habitats in the north-west and south-west regions (Fig. 6 b). At least one or more of the 3 NDVI indices could be fitted based on the main criteria (i.e. significant at the 0.05 alpha level and explained at least 1% of the deviance). However, only the maximum average NDVI (MavND) was important for all species (Table 5). Standard deviation of NDVI (SD) only partially explained the deviances of *A. cisternasii* and *H. arborea*, a tree frog. *T. boscai* had a small proportion of its deviance explained by coefficient of variation (CV) of NDVI (1.6%). Overall, the amount of deviance explained by the NDVI models ranged from 1.5 to 25.3 % (Table 5). Low values of explained deviance (< 10%) were obtained for 3 reptile species (*B. cinereus*, *V. latasti* & *M. cucullatus*) and 3 amphibian species (*A. obstetricans*, *H. arborea* & *H. meridionalis*). The maxima (> 20%) were reached for three herp species with disparate distributions; *L. schreiberi* & *T. boscai*, limited to the relatively humid and ‘biomass-rich’ north-western Spain and; *S. salamandra*, a comparatively widespread species.
Table 6: NDVI predictors and their proportion of explained deviance for individual species.

<table>
<thead>
<tr>
<th>Parameters</th>
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<th>Blacin</th>
<th>Viplat</th>
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Values of explained deviance adjusted for the number of predictors and occurrences, hence a realistic estimate of model fit are set in bold. Cal = measured on the calibration data set, eva = measured on the evaluation data set, Threshold = probability threshold used to cut predictions into presence-absence.
Considering aggregated species richness (Table 7); at suborder taxon level, maximum average NDVI emerged as the most important variable with the exception of Serpentes which had CV as its only important predictor (1.5%). At Order taxon level species aggregation, only the maximum average NDVI emerged as the most important index, explaining 11.6 and 3% of deviance for Amphibia and Reptilia respectively. (See appendix 1 for the species richness response curves to NDVI)

Table 7: NDVI predictors and their proportion of explained deviance for herp taxon groups.

<table>
<thead>
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<tr>
<td></td>
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<td>Adjusted $D^2$ (%)</td>
<td><strong>5.3</strong></td>
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</table>

Realistic estimates of model fit are set in bold
3.4 Climate vs. NDVI for predicting herpetofauna species distribution

Figure 7: Spatial distribution of *Salamandra salamandra* in Spain (a) documented distribution on 10 x 10 Km UTM square, 1981 – 1997 (b) predicted distribution by climatic model (10 x 10 Km resolution), (c) predicted distribution by NDVI model (10 x 10 km resolution)

For all species, both eco-climatic and NDVI models could be fitted as indicated in Tables 4 and 6. Eco-climatic models explained a substantially higher proportion of deviance (8.8 – 35.3%) compared to NDVI-based models (1.5 – 25.3%). Nevertheless, NDVI predictors were superior to climatic parameters for two amphibian species; *S. salamandra* (25.3 vs. 19.4%) and *T. boscai* (23 vs. 8.9%). Since humidity and thermic inertia is generally more important for amphibian species, this is not unexpected. Both species’ observed distributions are highly concurrent with areas having high vegetation cover known to integrate radiation, temperature and humidity factors (Gasc J. -P. *et al.*, 2004). Further, in instances where NDVI predictors closely matched eco-climatic parameters in terms of proportion of explained deviance e.g. *L. schreiberi, A. cisternasii & S. salamandra*, precipitation-related predictors emerged as important (9.4, 18.7 and
17.8% respectively). However, both predictors performed poorly (< 10%) for H. arborea, a common tree frog mainly restricted to the north-western regions of Spain. This is an indicator that other eco-geographic parameters e.g. leaf area index, solar radiation etc. could be more salient for this species.

Computed as the mean of relative differences between adjusted $D^2$ across all species, climate explained 10.4% more deviance than NDVI. Figure 8 illustrates this by indicating that most species points fall above the 1:1 line into the upper triangle. Guisan and Ulrich, 2003 obtained similar results when they compared the relative powers of climate and topography in predicting reptile distributions in Switzerland.

Model evaluations using Kappa (Cohen, 1960) and ROC - AUC analysis (Fieldings & Bell, 1997) confirm the trend shown by explained deviances. Comparatively low accuracy values (both Kappa and AUC) were obtained when evaluating potential species distribution maps derived from NDVI predictors compared to eco-climatic parameters using the GLM approach (See Tables 4 and 6 above). All the potential distribution maps derived from eco-climatic models performed significantly better than random using the ROC-AUC analysis ($z$-test; $z = 21.7$, $p < 0.05$). However, NDVI-derived potential distribution maps for 6 species (B. cinereus, V. latasti, M. cuculatus, A. obstetricans, H. arborea & H. meridionalis) did not perform significantly better than random ($z$-test; $z = -2.4$, $p > 0.05$).
The results of the analysis also reveal that the two measures of adequacy used to assess prediction map quality (Kappa and re-scaled AUC0-1) are in good agreement for both calibration and evaluation data sets (Pearson correlation coefficient $r = 0.9$ and $r = 0.8$, respectively in Figure 9). This has similarly been observed by Guisan & Ulrich (2003) and Manel et al. (2001).

Further pairwise AUC comparisons of the potential distribution maps (climate vs. NDVI) using the non-parametric Mann-Whitney-U statistic revealed that 7 out of the 10 species ($L. \text{schreiberi}$, $B. \text{cinereus}$, $V. \text{latasti}$, $M. \text{cuculatus}$, $A. \text{cisternasii}$, $A. \text{obstetricans}$ & $H. \text{meridionalis}$) modelled by eco-climatic parameters had significantly better maps compared to NDVI-derived maps (Table 8). Conversely, NDVI performed significantly better for two amphibian species; $S. \text{salamandra}$ (z-test; $z = 1.76$, $p < 0.05$) and $T. \text{boscai}$ (z-test; $z = 2.12$, $p < 0.05$). However, there was no significant difference between the map accuracies for $H. \text{arborea}$ produced by either models (z-test; $z = 1.06$, $p = 0.14$).
Figure 10: Spatial distribution of *Lacerta schreibeii* in Spain (a) documented distribution on 10 x 10 Km UTM Square, 1981 – 1997 (b) predicted distribution by climatic model (10 x 10 Km resolution), (c) predicted distribution by NDVI model (10 x 10 km resolution)

Overall, throughout Spain (mesoscale), 7 out of 10 potential species distribution maps derived from selected eco-climatic predictors, more closely match actual herpetofauna distributions compared to those derived from NDVI predictors. The potential distribution maps of two species with distinct distribution patterns; Spotted salamander, *S. salamandra* and Schreiber’s green lizard, *L. schreibeii* (Figs. 7 and 10) exemplify the relative differences. Maps illustrated in appendix 2 indicate the comparative differences between climate and NDVI in predicting species richness for amphibians and reptiles.
Results
4. Discussion

4.1 From Patterns to processes; Climatic parameters vs. remotely-sensed NDVI

The results from this study reveal that remotely-sensed NDVI indices were less accurate predictors of herp species distributions compared to eco-climatic parameters. This concurs with Said et al., (2003) who found similar results when comparing climate vs. NDVI in predicting mammalian species richness in East Africa. This is contrary to our hypothesis (Section 1.5.2), and contradicts established ecological theory of species distribution at mesoscales (Los, 1998b; Rosenzweig & Abramsky, 1993; Said et al., 2003; Stoms & Estes, 1993; Walker et al., 1992). Statistically, models fitted with eco-climatic parameters, except for S. salamandra and T. boscai, proved superior to those fitted by remotely-sensed NDVI indices. This was demonstrated by (a) better fits in terms of explained proportion of deviance and; (b) higher values obtained from independent evaluations using two measures of adequacy, Kappa and AUC. As such, potential distribution maps calculated from eco-climatic predictors reflected more realistic distributions, as illustrated by maps in Fig. 10. However, when considering the species assemblages, NDVI explained more deviance for amphibians; Anura (5.3 vs. 3.3 %) and Caudata (25 vs. 18%) compared to climatic predictors. Conversely, climatic predictors were more important to reptiles; Sauria (15.8 vs. 7.4%) and Serpentes (6.9 vs. 1.5%). These results are consistent with natural history for these taxon groups as temperature is known to be important for explaining reptile distributions while humidity (and vegetation cover) plays the same role for amphibians (Gasc J. -P. et al., 2004). Visually, maps based on NDVI indices also appear less smooth compared to those based on climate. This could be attributed to the fact that climate depicts less variation over short distances compared to the high variability of vegetation cover which manifests itself by more contrasted values over proximate cells in the NDVI images.

Direct vs. indirect predictors

From a mechanistic standpoint, it is desirable to predict the spatial distribution of biotic entities based on ecological parameters believed to be causal, driving forces for their distribution and abundance (Guisan & Zimmermann, 2000). However these parameters are often sampled from digital maps as they are difficult or expensive to
measure and tend to be less precise. For instance, most bioclimatic parameters such as those used in this study are developed by elevation-sensitive spatial interpolations of climate station data (Hijmans et al., 2004) which introduce spatial uncertainties. As such, climate based models fail to reveal biologically important microclimates (e.g. soil, nutrients etc.). Remotely-sensed NDVI, at similar scales, is however considered more biologically relevant as it is spatially explicit – i.e. it integrates soils, topography, radiation etc. (Box et al., 1989; Currie, 1991; Owen, 1988). Austin and his co-workers (Austin, 1980, 2002; Austin et al., 1984) consider climate as a direct predictor (distal) thus posing strong distributional limits whereas vegetation/habitat type (NDVI) could be considered as an indirect (proximal) predictor since it does not have direct physiological relevance for a species’ performance. In spite of their low biological relevance, climatic models due to their direct physiological influence have been shown to predict species distributions more accurately in some cases (Guisan & Ulrich, 2003; Owen, 1988, 1989, 1990; Rosenzweig & Abramsky, 1993; Said et al., 2003). Our results are consistent with these studies as the selected eco-climatic parameters explained 7 out of 10 herp species distributions more efficiently than NDVI indices at mesoscale. NDVI is certainly a good proxy for important environmental features other than climate (e.g. moisture, soil etc.). Nevertheless, at our study scale, it explained less deviance than climate alone. It is plausible that relative to climate, these environmental features are of secondary importance to the herp species considered.

**Scale matters!**

Questions on species distribution must adequately tackle the issue of resolution (grain size) and scale (referring to the extent of the study area) (Guisan & Ulrich, 2003; Murwira, 2003). A possible explanation as to why NDVI models were not as predictive in this study could be that the integrity of the indices and their possible combinations might not have been retained when aggregated to 10 x 10 square kilometre resolution (grain size). This might have resulted in their effect remaining contained in the unexplained deviance. Patthey (2003) contends in his work that a modelling study conducted at a small scale (large extent) can reveal environmental drivers that best characterise the overall species range whereas, a second nested analysis at a large scale (small extent) can reveal other features that best characterise habitat at population or home range level. Nevertheless, it is important to note that some predictors could remain important at all scales. Multi-scale perspectives on herp species distribution were, however, not considered in this study.
Limitations of estimating productivity from remotely-sensed NDVI

Much of the Spanish territory could be considered as arid to semi-arid with only 30% of its land arable hence the reliance on irrigated systems. There are known issues with vegetation indices in such areas largely attributed to soil-vegetation spectral mixing (Heute & Tucker, 1991; Nicholson & Farrar, 1994). In such sparsely vegetated areas, cover is insufficient to yield a near infra red (NIR) reflectance response. Conversely, NDVI has been found to saturate in humid areas above certain thresholds (e.g. 1000 mm) and consequently becomes insensitive to precipitation variations (Box et al., 1989; Nicholson et al., 1990; Said et al., 2003; Sellers, 1985). Further, it has been observed that atmospheric conditions and underlying soil material can reduce the accuracy of estimating ecosystem productivity through NDVI. Studies have revealed that in sparsely vegetated areas (~ 40 – 75% green cover) such as those in Spain, soil darkening either due to moisture content or the soil type itself can increase the estimation of NDVI by 25% (Heute & Tucker, 1991; Nicholson & Farrar, 1994). Conversely, aerosols and water vapour have been reported to significantly reduce NDVI by up to 60% (Justice et al., 1991; Los, 1998b). The above factors discussed in this study highlight the main limitations posed by using NDVI-derived indices to estimate ecosystem productivity and hence species distributions. These may have contributed significantly to the fact that NDVI did not perform better than eco-climatic parameters in predicting herp species distributions. Similar investigations have reported lower correlations between plant or mammalian species richness and NDVI (Oindo, 2001; Oindo et al., 2000; Oindo & Skidmore, 2002; Said, 2003; Said et al., 2003; Walker et al., 1992) compared to those that employed climatic variables as indicators of ecosystem productivity (Guisan & Ulrich, 2003; Owen, 1989, 1990).

New sensors, new indices ...

Improvements in spectral, spatial and temporal resolutions of RS satellites (e.g. MODIS, hyperspectral sensors etc.) offer possibilities to investigate species-environment relationships and offer a uniform platform upon which to test ecological hypotheses such as those tackled in this study. The advent of hyperspectral remote sensing has ushered in fresh opportunities of estimating single species or biodiversity distribution and finer habitat units through improved productivity (biomass) and more importantly forage quality indices -
Discussion

foliar chemicals e.g. N, P etc. (Aspinall, 1992; Ferwerda et al., In press; Guisan & Zimmermann, 2000; Mutanga & Skidmore, 2004). The use of these new indices in predictive modelling may add new perspectives on species-environment relationships and provide further argument for the use of remotely-sensed vegetation indices over other eco-geographic predictors.

4.2 Herpetofaunal distribution patterns and implications for conservation

Evidence from this study suggests that eco-climatic parameters, predominantly temperature-related, may set the distributional limits of most herp species in Spain. However, higher correlation does not necessarily imply causation (Texeira & Arntzen, 2002). Climatic features, though dominant, are not the only factors influencing the distribution of herpetofauna; other ecological and historic factors have a similar or even greater influence on distribution (Gasc J.-P. et al., 2004). For instance, the results of this study show that NDVI indices performed equally-well or better for amphibian species and their assemblages (Tables 4 – 7). Whereas temperature-related parameters are important for explaining the distribution of reptile species, humidity (and plant cover) plays a similar role for amphibians although this is often manifested in a complex pattern (Gasc J.-P. et al., 2004). This lends credence to the findings of this study which indicated that precipitation was significantly correlated to maximum average NDVI (Fig. 11) with a correlation coefficient $r = 0.6$. Both factors explained a higher proportion of deviance for amphibian species and their assemblages which reveal the species’ relative thermic inertia and preponderance in wet areas.

Figure 11: Relationship between maximum average NDVI and precipitation
Further, the Iberic area which encompasses Spain, Portugal and South of France, is considered as ‘Warm Europe’ including the Mediterranean area. Here, the influence of climate is thought to be secondary and the distribution of herpetofauna is mainly due to historic processes such as the differentiation of species in the Mediterranean peninsulas resulting in the presence of endemic species e.g. *L. schreiberi* in the region (Gasc J.-P. *et al.*, 2004).

Do these results show any association between particular habitat types and herpetofauna? Perhaps not directly but the general herp species richness patterns (Fig. 4); spatial distribution of maximum average NDVI and annual precipitation (Fig. 6) and; their proportion of explained deviance (Tables 4–7) hint towards this and provide a basis upon which such inference can be made. Results show that amphibian assemblages are highly concurrent with relatively wet and ‘green’ areas which encompass upland habitat types such as Open Mediterranean forests comprising of *Quercus ilex*, *Q. rotundifolia* and *Q. suber*; riverine forests and; juniper bushes. Conversely, reptile assemblages are concurrent with the relatively lowland, dry and sparsely vegetated regions characterised by habitat types such as maquis; phygrama; garrigue, heaths; tussocky meadows; sandy soils; sandy dunes; sandy nesting beaches; offshore sea grass beds and; calcareous rocks e.g. karst (See (Gasc J.-P. *et al.*, 2004), for a full vegetation description).

Since Spain’s incorporation in the EU, it has been subject to EU-wide policy changes which have invariably affected such habitats and the biological diversity therein. UNEP (2000) reports that the recent introduction of artificial irrigation systems and marginalisation of traditional pastoralism and dryland agriculture have led to displacement of natural ecosystems and consequent loss of biodiversity. It is therefore not surprising that herp species considered in this study e.g. *H. arborea*, a common tree frog, is threatened by intensive land use (agriculture, forestry, infrastructure, drainage etc.) and is currently decreasing over much of its range (Gasc J.-P. *et al.*, 2004). In addition to the anthropogenic pressures, climate change is expected to cause dramatic changes in vegetation communities (Crumpacker *et al.*, 2001; Sykes *et al.*, 1996; Tchebakova *et al.*, 1995) thus affecting micro-habitat and micro-climate which in turn affect the physiology, demography, distribution, behaviour and phenology of associated species (Gibbs & Breisch, 2001; Teixeira & Arntzen, 2002). Conservation for vulnerable herp species in Mediterranean landscapes experiencing such rapid changes must therefore not only respond to immediate threats of local habitat modification from intense land use, but also to mesoscale, continental
and global challenges of greenhouse emissions and resultant climate change. Areas having high herp species richness such as those depicted in the maps and the accompanying species distribution models developed in this study provide a context upon which such conservation interventions can be designed and implemented.

4.3 Efficacy and limitations of predictive statistical models

The methodological framework adopted in this study is simple, robust and replicable. Generalized Linear Models (GLMs) have expanded the range of data types that can be readily modelled including dichotomous data such as presence-absence and counts data employed in this study. The main advantage of this statistical model is that the assumptions are most likely to apply to the data (Nicholls, 1989). Further, they provide a better fit of the non-normal error structures of ecological data and as such are better suited for analysing ecological relationships, which can be poorly represented by classical Gaussian distributions (Austin, 2002; Austin et al., 1984; Guisan et al., 2002). We can therefore have increased confidence on our predictions based on the associated standard errors (Fig. 12). GLMs can also be readily integrated into a GIS to enable spatial (and temporal) modelling of biogeographic phenomena as demonstrated by the potential distribution maps (Fig. 7 and 10).

Nonetheless, there are limitations to our approach. To be able to fit our models using GLMs, we made certain assumptions about the data (Section 2.2). It is probable that species coded as ‘absent’ using the binary approach may have not been observed during the survey. This may lead to incorrect predictions (false negatives i.e. that a species is absent yet in reality it exists in that particular grid). However, our approach is pragmatic and remains better than generating ‘pseudo-absences’ as done in (Zaniowski et al., 2002) since accurate data on absences is difficult to obtain, especially for mobile or cryptic species such as herpetofauna (Brotons et al., 2004). The second limitation arises from interpreting predictions from modelled binary data. The probability that the response (presence of the modelled species) will be positive ranges from near zero to near one. However, on any particular piece of land (or grid), a species can only be present or absent. Therefore, the interpretation placed upon the predicted probabilities must be that over a sample of sites with similar predictor environmental attributes, a proportion of sites equal to the predicted probability will contain the species in question (Nicholls, 1989).
Thirdly, GLMs effectively model ecological (realised) rather than fundamental niches due to their intrinsic empirical nature and thus implicitly incorporate biotic interactions and negative stochastic effects (Guisan et al., 2002; Guisan & Zimmermann, 2000). These can vary spatially and temporally hence models fitted for the same species but in different areas and/or at different resolutions can be difficult to compare (Guisan & Theurillat, 2000). Consequently, the predictive capability of such models may be lowered and most have limited transferability to other sampling locations (Pearce & Ferrier, 2000; Power, 1993). Our predictive models are therefore only valid for the study scale, temporal and spatial resolution under which they have been developed.

Figure 12: Spatial prediction error for species distribution models in Spain (a) *S. salamandra* (b) *L. schreibei*
Discussion
5. Synthesis and Conclusions

Knowledge on biodiversity distribution patterns at small scales (sub-continental to continental) makes it easier to understand the general ecological requirements of species and their assemblages. Predicting their potential distributions in unsampled locations may lead to their discovery or reveal factors that might explain their absence. More importantly from a conservation standpoint, it provides the opportunity to assess the possible disturbances that may keep species away from the area and thus design appropriate conservation measures. Whereas the relevance and disparate methodologies for species distribution modelling are not in doubt, intrinsic species-environment relationships at mesoscales still remain contentious. A key debate amongst ecologists has been the notion that at small scales, remotely-sensed vegetation indices (NDVI) are better predictors of potential species distributions when compared to other eco-geographic parameters such as climate and topography. Using herpetofauna occurrence records in Spain and statistical predictive techniques (GLMs), we embarked on specific objectives to test this hypothesis as outlined below;

The first and second objectives aimed at establishing if there were significant relationships between the herpetofauna species distributions and both eco-geographic parameters; climate and NDVI respectively. Our results revealed, through significance tests and proportions of explained deviance, that both sets of predictors were significantly correlated with herpetofauna species distributions. The third objective, which formed the crux of our study, was to compare the relative predictive powers of NDVI indices versus climatic parameters. Overall, our results indicated that climatic parameters explained a higher proportion of deviance for most herpetofauna species distributions compared to NDVI indices. The fourth and fifth objectives were to make spatial predictions of the selected herp species based on the ‘best-fit’ models and assess their accuracies. The results of model validation and comparisons concur with results found in objective three. Overall, using Kappa and AUC statistics, potential species distribution maps derived from climatic parameters were significantly better than those derived from NDVI. In summary, these results are contrary to our expectations and do not support established ecological theory that NDVI is a better predictor of species distributions at small scales. Nevertheless, we offer some key perspectives from this study and these are highlighted as follows;
5.1 Specific conclusions

1. At the study scale, NDVI is not a better predictor of species distributions compared to climate – the evidence does not support our hypothesis and established ecological theory.

2. Overall, models derived from eco-climatic parameters more closely match actual herpetofauna distributions than those based on NDVI. These results suggest that the distributional limits of herpetofauna species and their respective assemblages in the Mediterranean may be largely set by eco-climatic parameters.

3. High correlation does not imply causation. Other ecological and historic factors have a similar or even greater influence on herpetofauna species distribution. NDVI proved as much for two amphibian species and amphibian assemblages.

4. The relative predictive powers of NDVI may have been hampered by a number of factors including: aggregation of NDVI values to larger resolutions (10 x 10 Km); study scale (extent of study area) and; geometric and radiometric limitations which degrade NDVI quality from remote-sensing platforms.

5. New high-resolution/hyperspectral sensors and vegetation indices together with perspectives gained from this study, add to the argument that remotely-sensed vegetation indices have a great potential to be used as environmental predictors over other eco-geographic parameters thus providing evidence to support established ecological theory.

6. The issues raised above leads us to the conclusion that hypothesis of species distributions, at least as herein interpreted and tested, is inconclusive until fundamental issues of scale, resolution and taxon under consideration are adequately resolved.

7. The methodological framework adopted in this study is simple, robust and replicable. Generalized Linear Models (GLMs) provide a powerful basis for testing ecological hypotheses about the distribution of species and assess possible impacts of changing landscapes on their distributions. However,
underlying ecological and statistical assumptions must be carefully considered to yield valid model outputs.

5.2 **Recommendations**

1. Re-test the hypothesis using high resolution vegetation indices and/or new vegetation indices (e.g. LAI) from hyperspectral imagery that may have physiological relevance for individual herpetofauna species and/or their assemblages.

2. In addition, a second nested analysis at a large scale (small extent) can reveal other features that best characterise habitat (species distribution) at population or home range level. A multi-scale perspective may thus add new insights to our current knowledge base.

3. Conservation efforts for these species must aim at tackling rapid habitat changes (especially at landscape level) as well as mitigating the impacts of climate-change at sub-continental, continental and global scales.
References


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regression models vs. new field data. *Ecological Application*, 9, 37 - 44.


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Appendices

Appendix 1: Species response curves to environmental predictors

1(a) Amphibian and reptile species richness response to max average NDVI

1 (b) Selected herp species response to annual mean temperature

\[^2\text{Temperature values have been scaled by a factor of x 10}\]
Appendix 2: Species richness maps and spatial prediction error estimates

(a) Reptiles_{Climate}  (b) Reptiles_{NDVI}  (c) Amphibians_{Climate}  (d) Amphibians_{NDVI}
### Appendix 3: Herpetofauna species list

<table>
<thead>
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<th>Order</th>
<th>Sub-order</th>
<th>Family</th>
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### Appendix

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