THE VALUE OF SPECIES DISTRIBUTION MODELS AS A TOOL FOR CONSERVATION AND ECOLOGY IN EGYPT AND BRITAIN

Tim Newbold, Bsc. (Hons.)

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Abstract

Knowledge about the distribution of species is limited, with extensive gaps in our knowledge, particularly in tropical areas and in arid environments. Species distribution models offer a potentially very powerful tool for filling these gaps in our knowledge. They relate a set of recorded occurrences of a species to environmental variables thought to be important in determining the distributions of species, in order to predict where species will be found throughout an area of interest. In this thesis, I explore the development, potential applications and possible limitations of distribution models using species from various taxonomic groups in two regions of the world: butterflies, mammals, reptiles and amphibians in Egypt, and butterflies, hoverflies and birds in Great Britain. Specifically I test: 1) which modelling methods produce the best models; 2) which variables correlate best with the distributions of species, and in particular whether interactions among species can explain observed distributions; 3) whether the distributions of some species correlate better with environmental variables than others and whether this variation can be explained by ecological characteristics of the species; 4) whether the same environmental variables that explain species' occurrence can also explain species richness, and whether distribution models can be combined to produce an accurate model of species richness; 5) whether the apparent accuracy of distribution models is supported by ground-truthing; and 6) whether the models can predict the impact of climate change on the distribution of species. Overall the use of distribution models is supported; my models for species in both Egypt and Britain explained observed occurrence very well. My results shed some light on factors that may be important in

determining the distributions of species, particularly on the importance of interactions among species. As they currently stand, distribution models appear unable to predict accurately the impacts of climate change.

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Publications

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Newbold T., Reader T., El-Gabbas A., Berg W., Shohdi, W.M., Zalat S., Baha El Din S. & Gilbert F. (in press). Testing the accuracy of species distribution models using species records from a new field survey. *Oikos*.

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Chapter 1. Introduction: ecological niches, distributions and species distribution modelling[1]

1.1 Abstract

Statistical models which combine data on species occurrence with environmental variables to predict the distributions of species have gained prominence in ecology in recent years. Species distribution models have their grounding in niche theory. In the first part of this chapter, I provide a very brief review of niche theory with some discussion of recent developments. In the second part, I introduce species distribution models, their relationship to niche theory and some of the challenges associated with them. I review some of the applications for which distribution models have been used in the past, and the relative merits and limitations of these applications. Finally, I introduce records of species occurrence from museums, natural history collections and literature as a valuable source of data on species' distributions, discussing some of the problems with data from these sources and the implications of these problems for developing distribution models.

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[1] Parts of this chapter were used in a paper published in *Progress in Physical Geography*

1.2 Niche theory

1.2.1 Formulation of the niche concept

Joseph Grinnell (1917, 1924) is credited with first using the term “niche” to describe the environmental conditions within which a species can survive and reproduce; these could include abiotic factors, such as temperature or rainfall, or interactions with other species (Grinnell 1924; Vandermeer 1972). Charles Elton (1927), on the other hand, saw a species’ niche as its place or role within the ecological community, placing less emphasis on the abiotic conditions and more on relationships with other species (Vandermeer 1972) and the impact that species have on the environment (Leibold 1995; Chase & Leibold 2003). Niche theory was first properly formalized by G Evelyn Hutchinson (1957). He described a species’ fundamental niche as a space in an ‘n-dimensional hypervolume’ defined by numerous (abiotic) environmental axes. Hutchinson’s (1957) fundamental niche describes the environmental conditions within which a species *could* survive and reproduce in the absence of interactions with other species (Figure 1.1a). The realized niche describes the environmental conditions within which a species *actually* lives, taking into account interactions with other species (Figure 1.1b). Species distribution models deal with Grinnellian or Hutchinsonian fundamental niches, rather than Eltonian niches (Peterson 2006), and so I focus on these here.

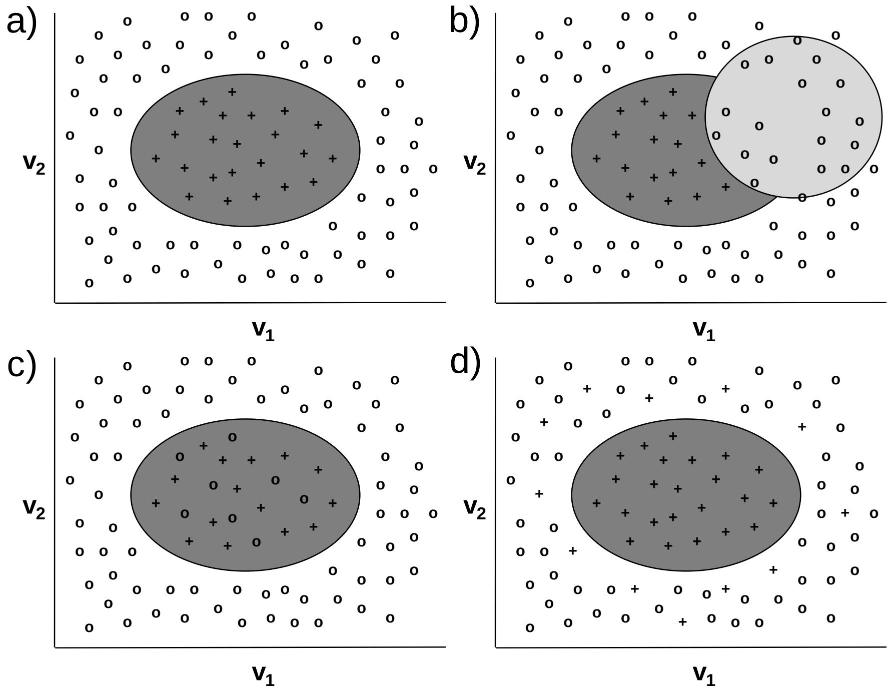


Figure 1.1 – Various plausible relationships between the fundamental niche, shown here by dark grey shading, and the actual distribution of species, shown here as hypothetical instances of species presence (+) or absence (o), modified from Pulliam (2000). For simplicity, the niche is assumed to be a simple function of two environmental variables, v_1 and v_2: (a) the species occupies its entire fundamental niche; (b) the presence of a superior competitor (light grey shading) excludes the species from part of its fundamental niche, leaving it to occupy the realized niche; (c) dispersal limitation means that the species is unable to reach all environmentally-suitable areas; (d) continued migration from areas of suitable habitat (sources) allows the species to persist in areas of unsuitable habitat (sinks).

Grinnell (1917) suggested that two species with exactly the same niche cannot persist together in the same place indefinitely. This idea, now termed 'competitive exclusion', has been demonstrated empirically using microcosm experiments where two or more species were made to compete for the same resource, first by Gause (1934) using protozoan species, and later by Park (1948) using flour beetles (*Tribolium* sp.). Testing competitive exclusion in the field has been much harder. Assuming that closely related species have more similar niches than more distantly related species, it has been predicted that competition will result in communities being composed of more distantly related species than one would expect by chance (den Boer 1986, but see Kraft *et al.* 2007). On the other hand, similar ecological requirements may cause closely related species to co-occur more often than expected (den Boer 1986; Kraft *et al.* 2007). A large number of studies have developed this idea, using measures of phylogenetic community structure in an attempt to disentangle the mechanisms driving the composition of ecological communities (see e.g. Webb 2000). One such study (Helmus *et al.* 2007), focusing on sunfish in the United States, showed that there was no overall phylogenetic signal in communities. However, after accounting for the effects of shared environmental requirements among related species, communities were shown to be composed of more distantly related species than expected by chance, consistent with effects of competition (Helmus *et al.* 2007). I return to the importance of competition in shaping species distributions later.

In recent years, a number of important developments have been made to niche theory. I briefly discuss these developments in the following paragraphs.

1.2.2 Dispersal limitation

Species may be absent from suitable climatic areas or habitats because they are unable to reach them, either because the distance is too far, or because there are geographical barriers to dispersal (Figure 1.1c; Pulliam 2000). Several studies have attempted to demonstrate dispersal limitation at local scales in natural populations. A large proportion of these studies has focused on aquatic species, either measuring the distance that individuals disperse between water bodies (Gulve 1994; Petersen *et al.* 2004), or showing that the similarity of species composition among water bodies is a function of the distance between them (Cottenie *et al.* 2003). Tests for dispersal limitation in terrestrial species have been fewer, although dispersal limitation is a key assumption of metapopulation models, which have been applied successfully to a number of species (e.g. Hanski et al., 1995; James et al., 2003). One study (Linares-Palomino & Kessler 2009) showed that differences in the plant species composition of Andean mountain valleys could be explained both by environmental differences and by the distance between valleys.

The aforementioned studies were all observational. The problem with this approach is that the observed patterns could be the result of interactions among species or could be driven by environmental factors that were not considered (Cottenie *et al.* 2003). This has led some authors to perform experimental tests of dispersal limitation. In one study (McCauley 2006), artificial ponds were placed in areas of similar habitat, separated by varying distances, and colonization by dragonfly species was recorded. Species richness in the artificial ponds after colonization decreased with increasing distance to the nearest natural ponds (McCauley 2006). Moore *et al.* (2008) conducted an experimental test of dispersal ability in rainforest birds by trapping birds from forested islands, and then releasing them at varying distances from those islands. Birds with high dispersal ability in these experiments were shown to have larger natural distributions (Moore *et al.* 2008).

Dispersal limitation has also been demonstrated at much larger spatial scales. Munguía *et al.* (2008) showed that Mexican mammals generally inhabit only a relatively small proportion of the area containing suitable climate. At an even larger scale, European plant species have not expanded to fill the full extent of their potential distribution since the last ice age (Svenning & Skov 2004) and distributions can be explained in part by distance to the nearest glacial refuge (Svenning *et al.* 2008). Furthermore, spatial turnover in the composition of plant communities in North America can be explained to some extent by geographical distance, further suggesting dispersal limitation (Qian & Ricklefs

2007). In a study of multiple taxonomic groups (Araújo & Pearson 2005), the distributions of plant and bird species showed a relatively strong correlation with climate, interpreted as showing a high degree of equilibrium with climate, while the distributions of reptiles and amphibians showed poorer correspondence with climate, possibly owing to dispersal limitation. As with the observational studies at smaller scales, the results of these studies could be artefactually caused by unidentified environmental factors or by interactions among species (Svenning & Skov 2004).

Dispersal ability is expected to vary among species, and several studies have reported substantial such variation (Petersen *et al.* 2004; Beck & Kitching 2007; Moore *et al.* 2008; Munguía *et al.* 2008). Beck & Kitching (2007) showed that the dispersal ability of hawkmoth (Sphingidae) species is a function of wing morphology. In a meta-analysis of dispersal ability across species from very diverse taxa, Jenkins *et al.* (2007) found that the dispersal ability of active dispersers showed a positive relationship with body size, while no such relationship existed for passive dispersers.

1.2.3 Source-sink dynamics

While dispersal limitation can cause species to be absent from otherwise suitable habitat, the dispersal of individuals between areas may result in a species being found in habitat that would not ordinarily support it (Figure 1.1d; Pulliam 1988). Theoretical models have shown that, with sufficient dispersal, populations can persist over long periods of time in areas where the population growth rate would, in the absence of immigration, be below the level required for replacement (Pulliam 1988, 2000). Areas with net *emigration* are termed ‘sources’ and areas with net *immigration* are termed ‘sinks’ (Pulliam 1988).

There have been several attempts to demonstrate source-sink dynamics empirically in natural populations. The approach most commonly used is to compare demographic rates among different habitats thought to be either sources or sinks. If it appears that a population would not sustain itself without immigration, then it is concluded to be a sink. Tests of this kind have been conducted for a variety of taxa, including plants (Watkinson *et al.* 1989; Moore 2009), mammals (Kreuzer & Huntly 2003; Johnson *et al.* 2005; Marshall 2009) and birds (Holmes *et al.* 1996). An interesting alternative to comparing birth and death rates among habitats is to use genetic parentage assignments to quantify the proportion of individuals that are born in a habitat vs. the proportion that immigrate from other habitats (e.g. Peery *et al.* 2008).

The problem with any approach that simply compares observed demographic rates among habitats is that fitness (survival and reproductive success) may be reduced in some habitats *because* of immigration, through the effects of density-dependence (Watkinson & Sutherland 1995). Observing that immigration increases population growth rate above the level required for replacement does not necessarily mean that the population would become extinct in the absence of immigration. Habitats that appear to be sinks, but which could persist in the absence of immigration, are termed ‘pseudo-sinks’ (Watkinson & Sutherland 1995). Watkinson *et al.* (1989) explicitly accounted for density-dependence when testing for source-sink dynamics in a grass *Sorghum intrans*, demonstrating the existence of true sink habitat (Watkinson & Sutherland 1995). An alternative approach would be to artificially prevent migration between habitats, and then to compare demographic rates.

1.2.4 Neutral theory

Neutral theory (Hubbell 1997, 2001) brings into question whether niches are important at all in explaining observed spatial patterns of biodiversity. It provides a null model in which niche differences among species are not important in determining their occurrence and abundance; instead it assumes that species are essentially identical in terms of birth, death, dispersal and extinction rates. The regional community consists of species that arise there by speciation and that, through chance demographic events, eventually become extinct. Local communities consist of individuals from any species in the regional species pool that arrive there through dispersal from other local communities (Hubbell 1997, 2001; Bell 2001). Neutral theory assumes that species are dispersal-limited (Hubbell 1997) and that extinction is slow enough that it is balanced by speciation (Adler *et al.* 2007). Changes in the composition of local communities come about through stochastic demographic events (birth, death, immigration and emigration). Predictions made by neutral theory about the distribution of abundances among species, and about relationships between area and species richness, show a remarkably close fit to observed patterns, at least for communities in tropical forests and coral reefs (Hubbell 1997). This suggests that niche theory, in its current state, often falls short of explaining observed patterns.

On the other hand, McGill (2003) found that observed abundance distributions of birds in North America and trees on Barro Colorado Island fitted predictions made by traditional niche-based models rather better than those made by neutral models. Similarly, while observed abundances of marine benthic communities fitted neutral models very well, when the dominant species in a community was experimentally removed, neutral models predicted changes in the abundance of the other species poorly (Wootton 2005). Further, some authors have suggested that the fundamental assumption of neutral theory, that species are demographically identical, is highly unrealistic (Enquist *et al.* 2002; Tilman 2004).

Increasingly, niche and neutral models are being seen as extremes of a continuum along which models of real communities lie (Gaston & Chown 2005; Leibold & McPeek 2006; Kelly *et al.* 2008; Leibold 2008). Neutral processes may be important in shaping community composition for some species and in some regions (Gaston & Chown 2005; Leibold & McPeek 2006; Kelly *et al.* 2008), while niche differences may be more important in other cases. When two co-occurring species are similar in terms of demographic rates (and thus overall fitness), then smaller niche differences will be required for them to coexist stably than if there are larger differences between the species in demogarphic rates (Chesson 2000). Several authors have successfully incorporated some aspects of neutral theory, such as dispersal limitation (Snyder & Chesson 2003) and demographic stochasticity (Tilman 2004), into niche-based models to help explain observed patterns.

Neutral theory serves as an important null model against which observed data can be compared. A niche-based model that captures the mechanisms driving patterns of species occurrence and abundance should be able to explain observed patterns much better than do neutral models (Hubbell 2005).

1.3 Using niche theory to model the distributions of species

1.3.1 Species distribution models

Species distribution models relate recorded species occurrences to variables describing the environment to predict distributions over an entire area of interest (for good recent reviews, see Guisan & Thuiller 2005; Wintle *et al.* 2005; Hirzel & Le Lay 2008). The use of species distribution models has increased rapidly in the last two decades (Figure 1.2) and recent years have seen the development of several new modelling techniques (Stockwell & Noble 1992; Phillips *et al.* 2006; see Chapter 2 for more details). While distribution models have been applied primarily to terrestrial species, there have also been several attempts to model marine species (Wiley *et al.* 2003; Hawkes *et al.* 2007).

Although species distribution models are based on niche theory, the theory is often lost in the statistics. Since distribution models are correlative, it may be possible to develop a seemingly accurate model for a species without capturing causal relationships between species occurrence and the environment (Hirzel & Le Lay 2008). These concerns have prompted several authors to call for a greater consideration of ecological theory when developing distribution models (Austin 2002; Guisan & Thuiller 2005; Soberón & Peterson 2005; Austin 2007; Hirzel & Le Lay 2008).

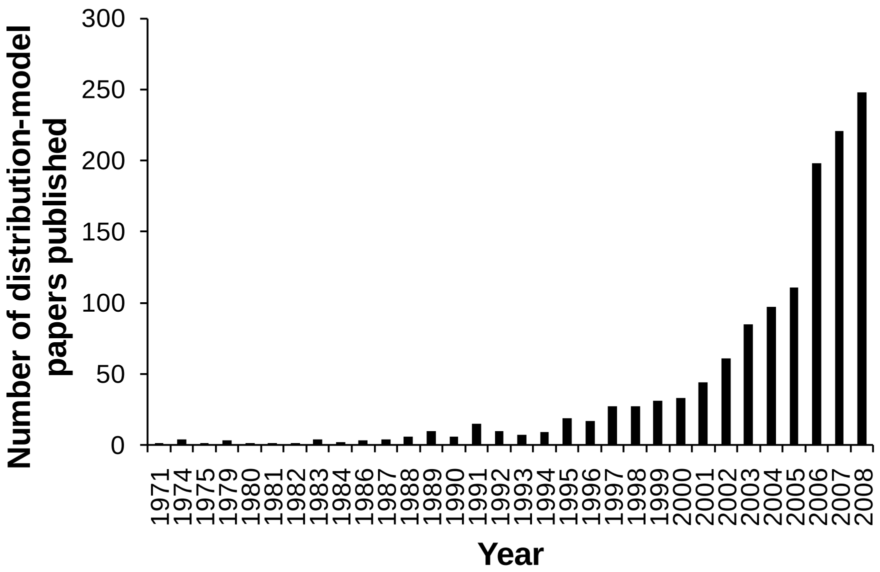


Figure 1.2 – Frequency of papers considering species distribution models published in the years since 1971. Papers were searched for in the ISI Web of Knowledge database using the following search term in the 'Topic' field: "species distribution model" or "species distribution modelling" or "species distribution modeling" or "ecological niche model" or "ecological niche modelling" or "ecological niche modeling" or "niche model" or "niche modelling" or "niche modeling" or "habitat model" or "habitat modelling" or "habitat modeling" or "habitat distribution model" or "habitat distribution modelling" or "habitat distribution modeling" or "niche-based model" or "niche-based modelling" or "niche-based modeling" or "bioclimatic envelope" or "bioclimate envelope" or "climatic envelope" or "climate envelope". Omitted years contained no papers matching this term.

A crucial consideration that is often overlooked is exactly what component of a species' niche is being modelled (Soberón & Peterson 2005; Soberón 2007). Soberón & Peterson (2005) distinguish three broad categories of factors that determine the distributions of species: abiotic environmental factors, biotic factors concerning interactions among species, and factors that affect the ability of species to disperse to different areas (Figure 1.3). Areas that meet the abiotic conditions required by the species are part of the fundamental niche. Areas that meet these conditions and also contain an appropriate combination of interacting species make up the realized niche. Finally, those parts of the realized niche that can be accessed by the species in question constitute the actual distribution (Soberón & Peterson 2005).

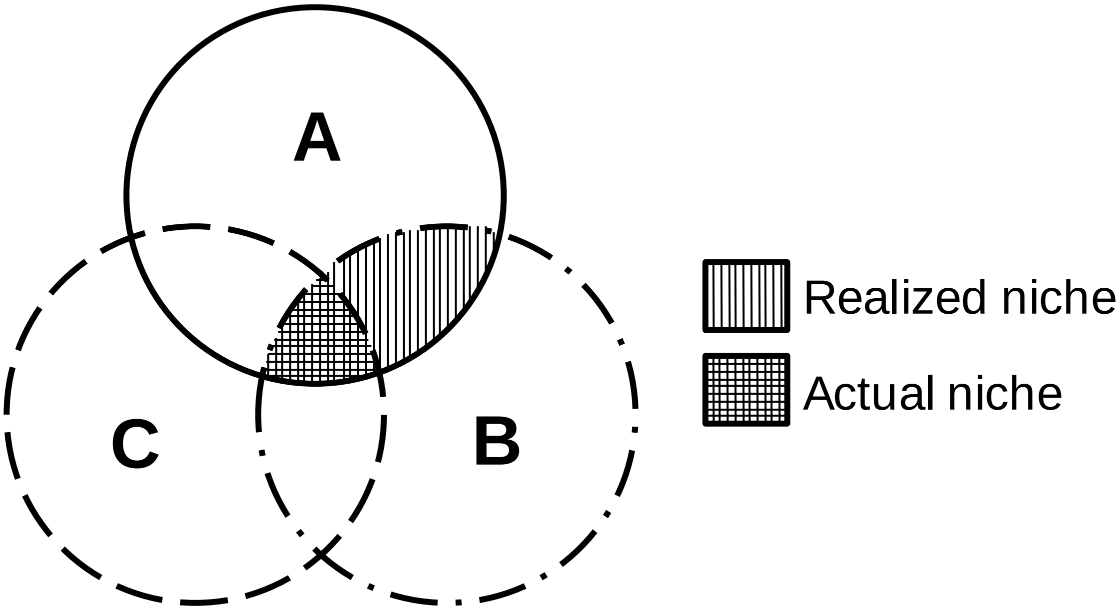


Figure 1.3 – The relationship between different components of species' niches. A represents the fundamental niche; B represents combinations of interacting species that allow the species of interest to persist; and C represents areas that the species is able to disperse to. Thus, the intersection of A and B constitutes the realized niche; and the intersection of A, B and C is the actual distribution. Modified from Soberón & Peterson (2005).

Several authors have argued that distribution models capture the realized niche, even if they only use abiotic variables in the models, because data on species occurrence used to build models describe actual (realized) distributions (Guisan & Zimmermann 2000; Austin 2002; Pearson & Dawson 2003; Araújo & Guisan 2006). On the other hand, Soberón & Peterson (2005) argue that, unless variables describing biotic interactions or dispersal limitation are included as explanatory variables, distribution models generally capture the fundamental niche. An exception to this rule occurs when biotic variables covary with abiotic variables, in which case the model may more closely approximate the realized distribution (Soberón & Peterson 2005). In my opinion, unless one can be absolutely sure that the variables used in the distribution models are direct drivers of species' distributions, then the model will more closely resemble the realized distribution than the fundamental distribution, because producing a model that explains observed occurrence well is not the same as identifying the important factors determining the niche (fundamental or realized). This issue has implications for trying to predict distributions outside the environmental conditions encountered during the building of distribution models; a model that captures the fundamental niche should be better able to extrapolate than a model that captures the realized niche of a species for a particular set of environmental conditions (Pearson & Dawson 2003). The challenges of extrapolating species distribution models outside the environmental conditions used to develop the models will be discussed in more detail later.

1.3.2 Choice of environmental variables

As we have seen, a great many factors may determine the distributions of species. The choice of environmental variables to include in distribution models impacts on the accuracy of those models (Parolo *et al.* 2008; Peterson & Nakazawa 2008), and using too many explanatory variables in distribution models will cause overfitting, where the model fits the species data very closely, at the expense of the ability to generalize (Chatfield 1995).

Independent variables used in species distribution models are of three different types (Austin & Meyers 1996; Austin 2002; Soberón 2007): resources required by a species, environmental conditions that have a direct effect on the ability of a species to persist in an area, or environmental conditions that have only an indirect effect on species through correlations with variables that have a direct effect. Models developed using resource variables or variables that have a direct effect on species are likely to capture better the underlying biology of species (Austin *et al.* 2006), and should make better predictions of distributions outside the environmental conditions encompassed by the data used to develop the models, than models developed using variables that have only an indirect effect on distributions (Austin & Meyers 1996; Austin 2007). The choice of independent variables for modelling is often driven by the availability of variables in a format suitable for modelling. As a result, many distribution-modelling exercises have considered only variables describing the abiotic environment, such as climate, edaphic factors and topography, or non-specific biotic variables, such as land cover, habitat and plant productivity. Many of the variables that can be obtained as maps covering entire study areas are those that have only an indirect effect on species (Austin 2007).

Very few studies have made *a priori* hypotheses regarding the determinants of species distributions, and then used these variables to model distributions. One exception was a study by Titeux *et al.* (2007), which modelled the distribution of the red-backed shrike *Lanius collurio* in Belgium using variables thought to have a direct influence on the species. Another (Anderson *et al.* 2009) compared three sets of variables in their ability to model the distribution of the hen harrier *Circus cyaneus* in Britain. Taking such a thorough and species-specific approach to modelling distributions will probably generate very good models. However, the aim is often to model the distributions of many species simultaneously. In this case, choosing directly relevant variables for each species in turn would probably be too time-consuming. Climate and habitat variables have repeatedly been shown to be very good correlates of species distributions (e.g. Guisan & Hofer 2003; Araújo *et al.* 2005a; Araújo *et al.* 2005b; Wintle *et al.* 2005; Elith *et al.* 2006; Guisan *et al.* 2006b, but see Anderson *et al.* 2009) and many have been hypothesized to have direct effects on species occurrence (Turner *et al.* 1987; Hawkins *et al.* 2003).

Therefore, it will often be desirable to build models using these readily-available variables, rather than developing a set of directly-relevant variables for each species.

1.3.3 Dispersal, neutrality and spatial autocorrelation

As we have seen earlier, dispersal limitation can play an important role in shaping species' distributions, causing species to be absent from areas that would otherwise be suitable (Pulliam 2000). Similarly, the existence of source-sink dynamics means that a species can be maintained outside suitable habitat by continual dispersal (Pulliam 2000). These processes will lead to spatial patterns in distributions (Segurado *et al.* 2006; Bahn *et al.* 2008), whereby sites close to areas occupied by a species are more likely to be occupied than more distant sites; this phenomenon is known as spatial autocorrelation, specifically positive spatial autocorrelation (Legendre 1993). Spatial autocorrelation is particularly likely to occur in studies that cover a large spatial scale (Lennon 2000). The existence of spatial autocorrelation in distributions means that records of occurrence used to develop distribution models may not be independent of one another; this decreases the effective sample size of statistical tests and models, and thus increases the Type I error rate (Legendre 1993). Some studies have used autologistic regression to account for spatial autocorrelation when modelling distributions (Osborne *et al.* 2001; Ferrier *et al.* 2002; Keitt *et al.* 2002; Lichstein *et al.* 2002; Segurado & Araújo 2004; Segurado *et al.* 2006; Dormann *et al.* 2007). This approach can only be used when the species data are collected in a regular grid and cannot easily be used for opportunistic records, such as those found in museum and natural history collections, although Syartinilia & Tsuyuki (2008) get around this problem by building an initial distribution model and then entering the output of this model into an autologistic model. A simpler method to account for spatial autocorrelation is to fit the geographical coordinates (longitude and latitude), with polynomials and interactions, as independent variables (Legendre 1993; Lobo *et al.* 2002; van Rensburg *et al.* 2002; Gutiérrez *et al.* 2005), although this appears to be less effective than the more complex methods (Diniz-Filho & Bini 2005).

Neutral theory hypothesizes that dispersal limitation is one of the primary drivers of distribution patterns and that climate variables should be unimportant (Hubbell 1997). If this were the case, then climate variables would correlate with species occurrence simply by capturing the spatial structure in distribution patterns and not because of any direct causal effect. Consistent with this, a number of studies have shown that models using spatial variables are nearly as accurate (Lobo *et al.* 2002; Bahn *et al.* 2006), and sometimes more accurate (Bahn & McGill 2007), than models using climate variables. However, these results could have come about because the spatial variables captured some aspect of the environment not included in the climate-based models (Lobo *et al.* 2002). An alternative test of the importance of climate variables is to generate null models by randomly rearranging species' distributions, disrupting the association with climate variables but maintaining their spatial structure (Beale *et al.* 2008). Using this approach, Beale *et al.* (2008) found that the real distributions of many species did not correlate with climate variables any better than the null distributions, consistent with the idea that climate-based distribution models simply capture the spatial structure in distributions. However, this study has been criticized on a number of methodological grounds by several authors (Araújo *et al.* 2009; Aspinall *et al.* 2009; Peterson *et al.* 2009).

It is almost impossible to infer causal relationships from correlative models, although the strength of the correlation with different variables may give us some idea of the underlying mechanisms (Lobo *et al.* 2002). For many conservation applications, where the aim is to provide an accurate representation of the distribution of species, it may not matter whether spatial variables act as a surrogate for environmental variables or vice versa. However, problems may arise when the models are used to predict outside the environmental conditions used to develop the model, if the variables used do not have a direct effect on species' distributions (Austin 2007). I return to this issue in Chapter 2.

1.3.4 Biotic interactions as determinants of species' distributions

Niche theory leads us to expect interactions among species, such as competition, predation, herbivory and parasitism, to play an important role in determining distributions. However, few studies have considered biotic interactions when developing species distribution models (Leathwick & Austin 2001; Anderson *et al.* 2002a; Anderson *et al.* 2002b; Gutiérrez *et al.* 2005; Araújo & Luoto 2007; Titeux *et al.* 2007). The inclusion of variables describing species interactions in species distribution models is the subject of Chapter 6.

Interactions with humans may also shape species' distributions, with different responses likely for different species. For instance, a number of studies have documented negative effects of human activity or disturbance on species (Gavashelishvili & Lukarevskiy 2008; Anderson *et al.* 2009; Ficetola & Padoa-Schioppa 2009), whereas Nyári *et al.* (2006) found that the distribution of the house crow *Corvus splendens* was positively related to an index of human impact.

1.3.5 Scale-dependency of distribution-environment relationships

The extent to which different factors determine species' distributions and patterns of species richness depends on the grain (resolution) and extent of study (Whittaker *et al.* 2001; Nogués-Bravo *et al.* 2008a); this in turn affects the accuracy of models developed using environmental variables at different resolutions (Seo *et al.* 2009). Field *et al.* (2009) conducted a meta-analysis of studies comparing the importance of different types of variable for explaining patterns of species richness. They found: first, that climate and energy-related variables generally had the most explanatory power, but that their importance was diminished at the finest resolutions and smallest extents of study; second, that variables describing interactions among species were most important in explaining species richness patterns at intermediate scales; and third, that the overall explanatory power of models increased with increasing resolution and extent (Field *et al.* 2009).

As with species richness patterns, determinants of the distributions of individual species probably vary in importance with scale. Mackey & Lindenmayer (2001) suggest that climate variables will be the most important drivers of species' distributions at broad scales, that topographical variables will be the primary drivers at intermediate scales, and that habitat and biotic interactions will drive distributions at the finest scales. They propose a hierarchical approach to modelling distributions and demonstrate that such an approach produces more accurate models for an Australian marsupial than models that do not consider scale (Mackey & Lindenmayer 2001). Incorporating fine-scale land-cover information into a broader-scale distribution model based on climate significantly improved its accuracy (Pearson *et al.* 2004). Climate variables modelling distribution (of the hen harrier) very well at a European scale, performed very poorly at the more local scale of Great Britain, where fine-scale habitat was a much better correlate (Anderson *et al.* 2009).

Variables describing relevant environmental features at very fine resolutions may be very hard to obtain. Although the importance of climate may diminish at small scales, a multitude of studies have shown that climate variables can be used successfully to explain species' distributions even at very fine scales. Nevertheless, the importance of land cover and habitat in shaping distributions is a point worth bearing in mind when designing models. Relatively detailed habitat data are available on a global scale (Hansen *et al.* 2000), and more accurate habitat classifications are available at regional and local scales in many parts of the world (e.g. Brown *et al.* 2002).

1.3.6 Evolution of ecological niches

The rate at which ecological niches evolve over time is an issue that has implications for several potential applications of species distribution models (Kozak *et al.* 2008). To address this issue, many studies have compared niches among closely-related species or subspecies, or have investigated niche shifts in single species over long time periods. The results of these studies have been mixed. Martínez-Meyer & Peterson (2006) developed distribution models for eight plant species in North America using data from the Last Glacial Maximum, approximately 20000 years ago, to predict distributions in the current day and vice versa, finding that the ability to predict from one time period to the other was high. Another study (Pearman *et al.* 2008b), using data for plants in Europe, showed that the ability to predict distributions between the mid-Holocene (approximately 6000 years ago) and the current day varied markedly among taxa. The authors highlight the fact that the species that showed the most accurate predictions across time periods were generally competitively-dominant species, suggesting that shifts in realized niches may have been responsible for the poor predictions for some taxa (Pearman *et al.* 2008a). Similarly, Martínez-Meyer *et al.* (2004b) found that the accuracy of distribution model predictions between the Last Glacial Maximum and the present day, for mammals in the United States, varied among species. In this case the least accurate predictions were for widespread species, possibly because the distributions of widespread species are determined more by biotic interactions than by climate (Martínez-Meyer *et al.* 2004a).

Studies comparing niches among closely-related taxa have also generated mixed conclusions. Distribution models for butterflies, mammals and birds in Mexico can predict the distributions of their sister species with a remarkable degree of accuracy (Peterson *et al.* 1999), and more closely-related plant species in Europe have more similar niches than would be expected by chance (Prinzing *et al.* 2001). Correlating ecological niche similarity with phylogenetic relatedness, there is a relatively high degree of conservatism in the New World blackbirds (Icteridae) in North America (Eaton *et al.* 2008). In contrast, other studies have provided less support for the existence of niche conservatism – several on diverse taxa (Losos *et al.* 2003; Peterson & Holt 2003; Rice *et al.* 2003; Graham *et al.* 2004b; Knouft *et al.* 2006; Evans *et al.* 2009) have shown considerable divergence in the niches of closely-related species or subspecies.

Overall, it appears that the strength of niche conservatism varies among taxa and in different parts of the world (Kozak *et al.* 2008). Certainly, conservatism of ecological niches is far from being universal (Losos 2008), although it will always be present at some phylogenetic scales (Wiens 2008). Niche conservatism has implications for attempts to use species distribution models to predict outside the environmental conditions encountered during development of the models, for example when predicting the impact of climate change on species' distributions or when predicting the extent of invasions by exotic species. Provided that direct determinants of species' distributions are used, niche conservatism would mean that models extrapolate well into new environmental conditions.

1.3.7 Variation among species in the strength of the distribution-environment relationship

Since there are a great many factors that can determine the distributions of different species, it may reasonably be expected that the distributions of certain species will be captured by climate-based models better than the distributions of others. Indeed, this has been shown to be the case for species from several taxonomic groups in different parts of the world (Elith *et al.* 2006). Many studies have investigated whether this variation in model accuracy can be attributed to characteristics of the species, such as niche breadth, range size, migratory behaviour and species detectability (Pearce *et al.* 2001; Hepinstall *et al.* 2002; Stockwell & Peterson 2002; Kadmon *et al.* 2003; Berg *et al.* 2004; Brotons *et al.* 2004; Segurado & Araújo 2004; Luoto *et al.* 2005; Seoane *et al.* 2005; Carrascal *et al.* 2006; Hernandez *et al.* 2006; Schwartz *et al.* 2006; McPherson & Jetz 2007; Murphy & Lovett-Doust 2007; Tsoar *et al.* 2007; Pöyry *et al.* 2008). I test patterns in distribution-model accuracy among species in Chapters 4 and 7. In order to be able to use distribution models for biodiversity conservation, it is very useful to know which species have distributions that are likely to be modelled accurately. For species with distributions that show poor relationships with environmental variables, it will be necessary to search for more relevant variables with which to model distributions, such as those describing biotic interactions or dispersal ability.

1.4 Applications of species distribution models

1.4.1 Conservation of species

One of the main potential applications of species distribution models is in making decisions regarding the conservation of particular, often threatened, species. One use of species distribution models, which can be of immediate benefit, is in guiding surveys for species. For example, Walther *et al.* (2007a) modelled the poorly-known wintering distribution of the threatened aquatic warbler (*Acrocephalus paludicola*) in sub-Saharan Africa, proposing that the model be used to direct surveys in order to increase knowledge about the species' distribution. Likewise, Guisan *et al.* (2006a) used distribution models for alpine sea holly (*Eryngium alpinum*) in Switzerland to guide field surveys, leading to the detection of seven new populations. Raxworthy *et al.* (2003) discovered seven new species of chamaeleon in Madagascar on the basis of their distribution models. This is probably one of the most powerful applications of species distribution models, driving an increase in our knowledge of species' ranges, knowledge which can be used to guide conservation decisions. Data from the new surveys can be used to build more accurate distribution models, which can in turn be used to direct further surveys, and so on (Guisan *et al.* 2006a).

Models can also be used to identify potential areas for species reintroductions (Rodríguez *et al.* 2007). For example, one study (Klar *et al.* 2008) modelled the distribution of European wildcats (*Felis silvestris*) in Germany. It was suggested that a suitable, but unoccupied, area could be used for reintroductions of the species (Klar *et al.* 2008). If distribution models are to be used in this way, it is crucial that the models are very accurate, since the outcome of potentially very expensive projects is at stake. Given that there are many uncertainties about the determinants of species' distributions, and consequently in models based on only a subset of these determinants, it is probably too soon to base important decisions solely on the outcome of species distribution models. On the other hand, where knowledge of species' ecologies and distributions is lacking, as is the case for the vast majority of taxa (especially invertebrates), models could provide a good starting point.

In the face of rapid habitat degradation, the conservation of species may depend on their inclusion in networks of protected areas. Many studies have used distribution models to assess the coverage of particular species by protected areas (e.g. Gaubert *et al.* 2006; Papeş & Gaubert 2007; Solano & Feria 2007; Thorn *et al.* 2009). These studies have often found that coverage is poor; in this case, the models can be used to propose additions and extensions to existing protected areas networks (Thorn *et al.* 2009).

Species distribution models can also be used to infer the causes for species decline. For example, Southgate *et al.* (2007) developed distribution models for the bilby (*Macrotis lagotis*) in Australia to assess different hypotheses for its decline. Nogués-Bravo *et al.* (2008b) used distribution models to investigate the extent to which the extinction of the woolly mammoth (*Mammuthus primigenius*) was caused by environmental change or by an increase in human hunting pressure, concluding that both factors may have played a role.

The use of species distribution models has been confined largely to the pages of academic journals and they have seen relatively little application in conservation decision-making. On the other hand, some studies using species distribution models have had a direct impact on policy-making (e.g. IPCC 2007). Conservation organizations such as the Royal Society for the Protection of Birds in Britain, the Darwin Initiative in Borneo, the Commonwealth Scientific and Research Organization in Australia, and the BioMAP Project in Egypt are beginning to use distribution models to support their work. A more immediate and direct application involved using Klar *et al.*'s (2008) models for the European wildcat to decide the location for a proposed golf-course development.

1.4.2 Modelling species richness patterns

Biogeographers have long sought to understand the drivers of species richness patterns. Many studies at widely differing scales and extents, and for many different taxonomic groups, have found that climate variables are very good correlates of species richness (Turner *et al.* 1987; Andrews & O'Brien 2000; Jetz & Rahbek 2002; van Rensburg *et al.* 2002; Algar *et al.* 2007; Buckley & Jetz 2007; Kivinen *et al.* 2007; Kuussaari *et al.* 2007; Menéndez *et al.* 2007; Qian 2007; Qian *et al.* 2007; Araújo *et al.* 2008; Schmidt *et al.* 2008; Schouten *et al.* 2009). In addition to contemporary climate, measures of climate stability over long periods of time and also climate seasonality have been shown to contribute to explaining richness patterns (Andrews & O'Brien 2000; Qian *et al.* 2007; Araújo *et al.* 2008). A meta-analysis of studies of species richness patterns found that climate variables were the strongest correlates of biodiversity in the vast majority of cases (Hawkins *et al.* 2003). A number of hypotheses have been proposed to explain why climate variables might determine species richness, including: 1) direct effects of available energy or habitat productivity on the number of individuals that an area can support and thus on species richness; 2) a balance between water availability and energy; 3) an effect of climate on the number of species able to tolerate the environmental conditions in an area; and 4) a positive effect of temperature on rates of speciation (Turner *et al.* 1987; Hawkins *et al.* 2003; Qian *et al.* 2007). Studies attempting to test these hypotheses have generally been correlative and thus have found it difficult to disentangle cause and effect; even where explicit predictions can be made, strong support for any one of the hypotheses has so far been lacking (Hawkins *et al.* 2003; Qian *et al.* 2007).

Variables other than those describing climate also have an effect on patterns of species diversity. At relatively small scales, habitat type and habitat diversity correlate well with species richness of various taxonomic groups (Kivinen *et al.* 2007; Kuussaari *et al.* 2007; Schouten *et al.* 2009). At a much broader scale, Jetz & Rahbek (2002) showed that the richness of sub-Saharan bird species increased with increasing habitat diversity.

Interactions among species may also be important in determining patterns of richness. For example, using structural equation modelling (SEM), it has been shown that the richness of butterfly species in Britain is directly influenced by the species richness of larval food plants; this effect was particularly strong for specialist species, whereas for generalist butterfly species there was a stronger correlation between climate and species richness (Menéndez *et al.* 2007). Conversely, Hawkins & Porter (2003) found that including the species richness of food plants in models of butterfly species richness for California offered little improvement in explanatory power over models fitting only climate variables.

Historical factors related to speciation and extinction rates, and to patterns of dispersal, may also help explain species richness. Differences in species richness among environmentally-similar regions in different parts of the world have sometimes been attributed tentatively to differences in speciation and extinction rates (Qian & Ricklefs 2000; Buckley & Jetz 2007), although the data available do not permit rigorous testing of this hypothesis (Currie *et al.* 2004).

Like the distributions of individual species, species richness patterns can show spatial autocorrelation, whereby the species richness values of cells near one another are more similar than expected by chance. Spatial autocorrelation may be exogenous, caused by spatial autocorrelation in the environmental variables that drive species richness patterns, or endogenous, caused by processes inherent to the species themselves, such as dispersal limitation (Currie 2007). Endogenous spatial autocorrelation can present problems for statistical analyses of patterns of species richness: using simulated species richness patterns, spatial autocorrelation can cause pseudo-replication and thus increase the chance of Type I errors (falsely rejecting the null hypothesis) in statistical tests and can bias the apparent relative importance of variables (Lennon 2000). When analyzing spatially autocorrelated patterns of mammal species richness in South America, the apparent importance of spatially autocorrelated environmental variables was inflated in models that did not account for spatial autocorrelation (Tognelli & Kelt 2004). On the other hand, parameter estimates of statistical models are sometimes unaffected by spatial autocorrelation (e.g. Hawkins *et al.* 2007).

Given that climate and habitat appear to drive both the distributions of individual species and patterns of species richness, it may be possible to combine species distribution models for a number of different taxa in order to model species richness. This has been successfully performed several times at small spatial scales for different taxonomic groups and in different environments (Gioia & Pigott 2000; Loiselle *et al.* 2003; García 2006; Pawar *et al.* 2007; Pineda & Lobo 2009; Raes *et al.* 2009), and once at a global scale for Viperid snakes (Terribile *et al.* 2009). Given that different species can show different responses to the environment, this approach may be better than simply correlating recorded species richness with environmental variables (Terribile *et al.* 2009).

An interesting possibility, and one that would have implications for conservation, is that of congruence in species richness patterns among taxonomic groups. Previous studies have generally found relatively high congruence in species richness patterns among plant and vertebrate-animal groups, both at more local spatial scales and at a global scale (Grenyer *et al.* 2006; Loyola *et al.* 2007; Qian 2007; Jetz *et al.* 2009). Furthermore, Thomson *et al.* (2007) found that richness patterns of indicator bird and butterfly species were good correlates of the overall richness patterns of these groups. Tests of congruence in species richness patterns among invertebrate taxa are very rare, although those of butterflies and plants can be very similar (Hawkins & Porter 2003), and Schouten *et al.* (2009) found good congruence in species richness patterns among several taxonomic groups, including grasshoppers, crickets, hoverflies and dragonflies. On the other hand, in some instances congruence in species richness patterns among groups is poor (e.g. Ryti 1992; Orme *et al.* 2005). Congruence among taxonomic groups in species richness patterns could come about through a direct effect of one group on the other, for example because plants provide food to herbivores or because a higher richness of plant species means greater structural complexity in the habitat leading to higher animal species richness (Kissling *et al.* 2008). However, global plant species richness correlates better with the species richness of animals from higher trophic levels and less well with the richness of herbivores, which would seem unlikely to be the case if plant richness had a direct effect on animal richness (Jetz *et al.* 2009). If species richness patterns are similar among different taxonomic groups, it may be possible to use richness patterns for a small number of taxa to determine which areas to conserve (Pinto *et al.* 2008), making the selection of these areas quicker and more efficient.

Previous assessments have suggested that the coverage of biodiversity by existing protected areas networks is generally poor. Several studies in different countries have shown that protected areas do not correspond well with areas of high species richness or high numbers of endemic species (García 2006; Pawar *et al.* 2007; Qian 2007; Traba *et al.* 2007; but see Lee *et al.* 2007). Furthermore, a global assessment of the efficiency of protected areas (Chape *et al.* 2005) suggested that existing protected areas have a very poor coverage of habitat diversity, used as a surrogate for species diversity. Models of species richness generated by combining species distribution models for many taxa can be used to assess the coverage of biodiversity by existing protected areas, and to suggest where new protected areas might be situated. For example, Pawar *et al.* (2007) modelled the distributions of reptiles and amphibians in the Himalayan and Indo-Burma biodiversity ‘hotspots’ (*sensu* Myers *et al.* 2000), combining them to estimate patterns of species richness; they then ran a reserve-selection algorithm to propose extensions to the existing protected areas network. One issue with this application of species distribution models is that different algorithms vary, resulting in very different networks of protected areas being selected (Loiselle *et al.* 2003).

1.4.3 Predicting future distributions

Species distribution models can be used to predict how the distributions of species will change in the future as a result of climate and land-use changes. A distribution model is built for the current time, using contemporary species occurrence and climate data. This model is then updated to reflect predicted changes in the climate or land use in the future. Many papers have used distribution models in this way, mostly at regional or global scales (e.g. Huntley 1995; Saetersdal *et al.* 1998; Iverson *et al.* 1999; Bakkenes *et al.* 2002; Berry *et al.* 2002; Peterson 2003; Miles *et al.* 2004; Thomas *et al.* 2004; Thuiller *et al.* 2005a; Levinsky *et al.* 2007; Hole *et al.* 2009; Randin *et al.* 2009), but sometimes at more local scales (Peterson *et al.* 2001; Peterson *et al.* 2002b; Randin *et al.* 2009). Most have considered only changes in the climate, but land-use changes will also have important effects on the distributions of species (Thuiller 2007), and very few have considered these (but see e.g. Peterson *et al.* 2006). The possibility of using species distribution models to predict how distributions will change in the future as a result of climate change is explored in Chapter 8.

1.4.4 Predicting the extent of species invasions

Models can be projected in space as well as in time, to predict distributions outside the area for which they were developed. Such projections can be used, for example, to predict where invasive species will be able to establish and survive outside their native ranges. A number of studies have used distribution models in this way, often finding that known invasions are predicted very successfully (Peterson & Vieglais 2001; Peterson & Robins 2003; Thuiller *et al.* 2005b; Herborg *et al.* 2007). On the other hand, in some cases the distributions of species in their invaded ranges are predicted very poorly by distribution models based on data from their native ranges (Randin *et al.* 2006; Broennimann *et al.* 2007). Model failure may be caused by differences in the fundamental or realized niches in the invaded range (Broennimann *et al.* 2007; Steiner *et al.* 2008). Differences in realized niches may result from species not yet having reached equilibrium with climate in the new range owing to dispersal limitation, from the species not having been in equilibrium with climate in its native range, or from changes in interactions among species (Thuiller *et al.* 2005b; Steiner *et al.* 2008).

In species invasions, suitability of climate is only one of several factors that determine invasion success. Propagule pressure, characteristics of the invading species, species composition of the invaded area and human influence can also be important (Thuiller *et al.* 2005b; Thuiller *et al.* 2006; Ficetola *et al.* 2007; Ficetola *et al.* 2009).

1.4.5 Addressing ecological and evolutionary questions

In addition to more applied problems, species distribution models can also be used to tackle more fundamental ecological or evolutionary issues. For example, they have been used to assess the extent to which climate drives distribution patterns compared to other factors, such as interactions among species (Araújo & Luoto 2007), dispersal limitation (Svenning *et al.* 2008) or habitat (see also Sections 1.3.2-1.3.4). Other studies have used distribution models to test whether niches are evolutionarily conserved by comparing modelled niches among closely-related species (Peterson *et al.* 1999; Eaton *et al.* 2008).

An idea that is receiving increasing attention is to use distribution models to test hypotheses about the phylogeographic or evolutionary history of species or populations. Phylogeography is the study of the historic patterns in the distributions of species and populations, and the processes driving these patterns. Phylogeographic studies often rely on genetic data to make inferences. However, many competing hypotheses are often generated. Some authors have recently proposed using species distribution models to support the hypotheses made by traditional phylogeography studies, by suggesting which putatively inhabited areas would have been suitable at the time (Richards *et al.* 2007; Kozak *et al.* 2008). Another possibility is to use species distribution models to infer mechanisms of speciation, i.e. whether populations are likely to have occurred in sympatry or allopatry at the time of speciation; this approach has already been used with Ecuadorian frogs (Graham *et al.* 2004b) and Madagascan geckos (Raxworthy *et al.* 2008b). One recent study used distribution models to test whether the ranges of two ibex species (*Capra nubiana* and *Capra walie*) in Africa are distinct, and thus, with the help of molecular analysis, whether the two taxa can be considered to be different species (Gebremedhin *et al.* 2009).

1.5 The value of museum data for species distribution models

There is a vast amount of data on the occurrence of species in museum and private collections, in herbaria, and in the literature (henceforth ‘museum data’). Several portals are now available on the internet to make museum data freely available to anyone with an interest in the distribution of species, including the National Biodiversity Network (NBN) Gateway for data on British species, and the Global Biodiversity Information Facility

(GBIF), which contains data from all over the world. At the time of writing, the NBN gateway contained 40,397,129 occurrence records and the GBIF database contained 177,448,319 records. Databases like these are an invaluable resource for conservation biologists and provide the means to develop distribution models for a vast number of species in many different parts of the world. However, there are two main limitations associated with museum data to be borne in mind when developing distribution models.

The first limitation of museum data is that the records can contain errors, either in the plotted locations or in the identification of species (Graham *et al.* 2004a). The potential for identification errors necessitates very careful checking of museum records by experts, and examination of the original museum specimens if possible (Graham *et al.* 2004a). The names of species must be updated to reflect currently-accepted taxonomies (Graham *et al.* 2004a). For some taxonomic groups, such as the mammals, there are websites available with complete and up-to-date information on taxonomy (e.g. Wilson & Reeder 2005a). For other groups, finding this information is more difficult.

In order to be used for distribution models, records must be assigned precise coordinates, a process known as georeferencing. Museum specimens are generally accompanied by descriptions of the location from which they were taken. A gazetteer is often used to match these descriptions with known localities to assign geographical coordinates. Errors can arise during georeferencing if the specimen description is matched to the wrong location and thus assigned incorrect coordinates (Graham *et al.* 2004a). This is particularly likely to occur when the descriptions accompanying the specimens and the locations in the gazetteer are given in different languages, especially when the languages employ different alphabets. For example, georeferencing many of the records gathered by Egypt's BioMAP Project (which will be used in many of the studies described in this thesis) involved interpreting location names transliterated into the Latin alphabet from Arabic. This can result in many different spellings for a single site. It is necessary to check very thoroughly for georeferencing errors in museum data, for example by checking for obviously outlying points (Williams *et al.* 2002).

The assigned coordinates of museum records are also subject to considerable uncertainty. Descriptions of locations accompanying museum specimens vary widely in their specificity, which translates into variable uncertainty in the assigned coordinates (Wieczorek *et al.* 2004). For example, the descriptions for Egyptian butterfly species associated with the museum specimens used by the BioMAP Project range from very precise (e.g. ‘St. Katherine’s Monastery’) to utterly vague (e.g. ‘Egypt’). Obviously, coordinates assigned to the latter will have a very high degree of uncertainty. Many descriptions of location describe an offset from a known locality, for example ‘6 km NW of St. Katherine’s. Uncertainty in the distance and direction of these offsets adds to the uncertainty in assigned coordinates (Wieczorek *et al.* 2004). Uncertainty can also arise from inaccuracies in the map used to georeference the records (Wieczorek *et al.* 2004). Finally, if museum specimens are accompanied by coordinates instead of a textual description, imprecision in the coordinates and uncertainty over the coordinate system used can generate uncertainty in the given coordinates (Wieczorek *et al.* 2004).

The usefulness of records for distribution modelling probably depends to some extent on the precision of the coordinates. A similar kind of model (the resource selection function) which assesses the strength of preference of a species for different habitat types, can be strongly affected by locational error in the species occurrence data (Visscher 2006), although the accuracy of distribution models may be relatively insensitive to moderate levels of imprecision because of spatial autocorrelation in the environmental variables, meaning that records with a small degree of imprecision still record very similar environmental conditions (Graham *et al.* 2008). The total uncertainty associated with a set of coordinates can be estimated using the point-radius method (Wieczorek *et al.* 2004).

The second limitation of museum data is bias in the scope of the records. Sampling of biodiversity is far from complete, with large gaps in our knowledge, especially in the tropics and in arid environments (Stockwell & Peters 1999; Anderson *et al.* 2002a; Soria-Auza & Kessler 2008). Species distribution models are designed to extrapolate from incomplete data and fill the gaps, but assume that the species data constitute a representative sample of the environments occupied. Museum specimens show three major types of bias: spatial, taxonomic and temporal (Soberón *et al.* 2000).

Several studies have demonstrated significant spatial bias in records from museums, collections and the literature. As mentioned before, sampling has been less intensive in the tropics and in arid environments, and much more intensive in temperate areas. Even within regions and countries, sampling has been spatially uneven (Peterson *et al.* 1998; Dennis & Hardy 1999; Dennis *et al.* 1999; Hijmans *et al.* 2000; Soberón *et al.* 2000). Sampling tends to be biased towards roads, rivers and cities (Hijmans *et al.* 2000; Soberón *et al.* 2000; Reddy & Dávalos 2003; Sánchez-Fernández *et al.* 2008), tends to be closer to the homes of the collectors (Dennis & Thomas 2000), and is generally more frequent inside protected areas than outside (Reddy & Dávalos 2003; Sánchez-Fernández *et al.* 2008) and at locations that are known to contain many species (Dennis & Thomas 2000; Sánchez-Fernández *et al.* 2008). Using simulated data, Sastre & Lobo (2009) showed that biasing surveying towards sites at which higher numbers of species have already been recorded has a strong adverse impact on the accuracy of recorded species assemblages.

Sampling of biodiversity has also been biased taxonomically. Plants and vertebrate animals, in particular mammals and birds, have been very well sampled. Most invertebrate groups are represented by very few records, given the number of species they contain (Figure 1.4). Within groups, sampling has been biased towards species that are more easily detected during surveys and of more interest to collectors (Hijmans *et al.* 2000; Soberón *et al.* 2000; Williams *et al.* 2002).

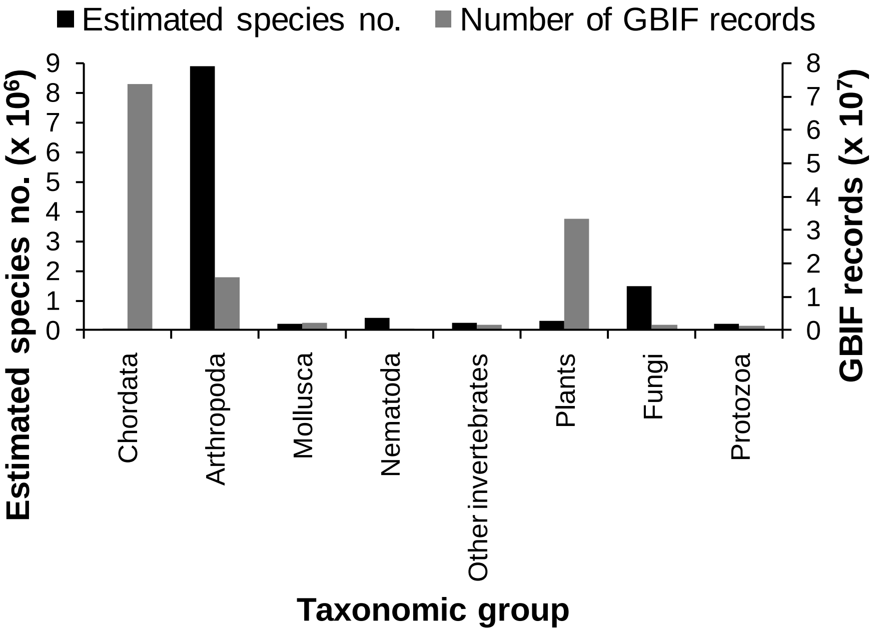


Figure 1.4 – numbers of records in the Global Biodiversity Information Facility (GBIF) database for several major taxonomic groups, compared to the estimated numbers of species in those groups, according to May (1997). The number of chordates is estimated to be approximately 50,000 (May, 1997), which is too few to be visible on the graph.

The intensity of the sampling of species in any one area also varies temporally because different collectors are active at different times (Peterson *et al.* 1998; Soberón *et al.* 2000).

For the purpose of modelling species' distributions, it is essential that species records are not systematically biased with respect to the environmental gradients of interest (Wintle *et al.* 2005). However, the biases described above can sometimes translate into environmental bias. For example, museum records for dung beetles (Scarabaeidae, Aphodidae and Geotrupidae) in Iberia do not cover the full range of environmental conditions they inhabit (Hortal *et al.* 2008). In contrast, other studies have found that museum data can be spatially biased without there being clear environmental bias (Austin & Meyers 1996; Kadmon *et al.* 2004).

It has been suggested that a third common limitation of museum data is a lack of records of species absence to complement records of species presence (Graham *et al.* 2004a). However, the fact that the majority of data describing the distributions of species consist only of records of presence has led to the development of several techniques for dealing with this issue. One solution is to take a random sample of grid cells with no presence records as ‘pseudo-absence’ data (Zaniewski *et al.* 2002). Alternatively, several distribution modelling techniques that need only records of presence have been developed recently, many of which have been shown to model distributions as accurately as models that require both presence and absence records (Elith *et al.* 2006).

1.6 Conclusions

My review of studies that have used distribution models suggests that the models are, on the whole, capable of providing a very accurate representation of the ranges of species. One must be careful of inferring causal relationships between species occurrence and environmental variables on the basis of distribution models. Nevertheless, the results of modelling exercises seem to correspond well with predictions made by niche theory. First, aspects of the abiotic environment, such as climate and habitat, seem to exert a strong influence on the potential distribution of species. Second, patterns of dispersal and interactions among species appear to have an important limiting effect on the distribution of species. Third, modelled niches are often very similar among species within single genera, and even within families, supporting the idea that niches show some degree of evolutionary conservatism.

Species distribution models have been applied in a great many studies and to address numerous issues, from applied conservation problems to more fundamental ecological and evolutionary topics. Applications that involve projecting the models outside the environmental conditions encompassed by the data used to develop them, such as predicting the impact of climate change or the extent of species invasions, are subject to a number of uncertainties. Attempts to validate the predictions made by these models have had mixed success.

Museums, collections and literature are potentially a very valuable source of data on the distributions of species. However, these data are prone to a number of errors and inaccuracies which must be addressed before they can be used to develop accurate distribution models. The quality of data on the occurrence of species should be assessed before any modelling exercise.

In the studies presented in this thesis, I assess the value of species distribution models as a tool for conservation ecology, focusing on several issues surrounding their use and several possible applications for which the models may be used. In Chapter 2, I introduce the distribution models and the general methods that will be used throughout the studies presented in the other chapters. In Chapter 3, I deal with a number of technical issues arising from the use of distribution models, exploring these issues using data for Egyptian butterflies and for simulated species in the real landscape of Egypt. In Chapter 4, I test whether the accuracy of distribution models varies among species, and whether this variation can be explained by characteristics of the species. Chapter 5 investigates whether species distribution models can be combined to produce models of species richness that can be used in conservation decision-making, and how these models compare with models made using species richness data. Chapter 6 compares the ability of two sets of variables to explain the distributions of species: environmental variables (climate and habitat) and variables describing the distributions of interacting species. In Chapter 7, I present a rare test of distribution models for Egyptian species by ground truthing, closer to an ideal test of the accuracy of distribution models, which also reveals some interesting patterns in accuracy among species. Finally, in Chapter 8 I test the ability of distribution models to predict how the distributions of species will change in the future as a result of environmental changes.

Chapter 2. General methods

2.1. Abstract

In this chapter, I introduce methods that will be used throughout the studies presented in this thesis. I describe: first, some of the most commonly-used techniques available for modelling the distributions of species; second, the environmental variables, for Egypt and for Britain, that will be used in my distribution models; third, the available data on the occurrence of species in Egypt and Britain, including an analysis of the quality and coverage of these data; fourth, the methods used to evaluate the accuracy of the distribution models, including a test of whether model accuracy measures are significantly better than would be expected by chance; and finally, a test of whether distribution models based on environmental variables are better than models based only on spatial variables. This final section attempts to deal with a recent controversy over the ability of environmental variables to tell us anything meaningful about the distributions of species.

2.2 Modelling techniques

There are a growing number of techniques available for modelling the distribution of species. A number of studies have compared the accuracy of these different techniques, the most comprehensive of which considered 16 of the most commonly used methods

(Elith *et al.* 2006). Here I provide a short overview of some of the more widely-used techniques, their merits and shortcomings, and their relative performance in previous comparisons.

2.2.1 Climate envelopes

Perhaps the simplest modelling techniques are the climate envelopes. These define an 'envelope' of suitable environmental conditions for a species by reference to the conditions at sites at which the species is known to occur (Figure 2.1). Climate envelopes use only records of species presence, and thus may be useful when information about species absence is not available (Elith *et al.* 2006).

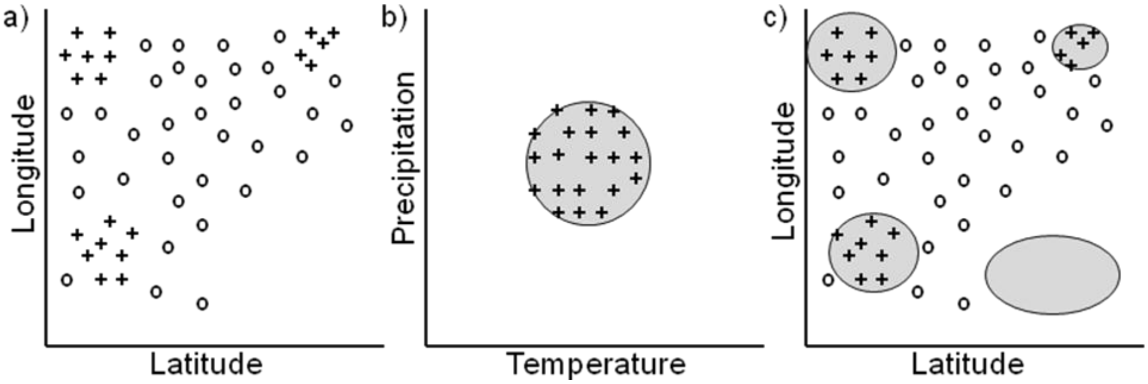


Figure 2.1 – The basic approach taken by climate envelope techniques for modelling the distribution of species: (a) a set of presence, and sometimes absence, records are collected and plotted in geographic space, for example using a geographic information system (GIS); (b) an 'envelope' of suitable conditions is defined around the presence points in environmental space; (c) the suitable conditions are projected back into geographic space to generate a predicted distribution. The environmental space is depicted in two dimensions here. Usually it would be a multidimensional space defined by many different environmental variables, but the principle is the same.

BIOCLIM (Nix 1986) is the most commonly used climate envelope model. In its simplest form it produces a binary prediction of presence and absence, but it can also produce a prediction of relative environmental suitability by using different proportions of the species occurrence data to define the climate envelope (Figure 2.2). In some studies, BIOCLIM has been reported to model the distributions of species reasonably well (Penman *et al.* 2005; Finch *et al.* 2006; Richardson *et al.* 2006). However, in comparisons of several techniques, BIOCLIM has emerged amongst the worst-performing (Elith 2002; Ferrier *et al.* 2002; Loiselle *et al.* 2003; Elith *et al.* 2006; Tsoar *et al.* 2007). It has a tendency to over-predict observed distributions (Elith 2002), particularly for more widespread species (Finch *et al.* 2006). This overprediction may be owing to the sensitivity of BIOCLIM to species records that are outliers in environmental space (Finch *et al.* 2006) or because interactions among climate variables are not considered (Carpenter *et al.* 1993). Most examples of BIOCLIM's poor performance have come from studies focusing on small areas. BIOCLIM may be useful for modelling the broad environmental limits to distributions over very large study areas.

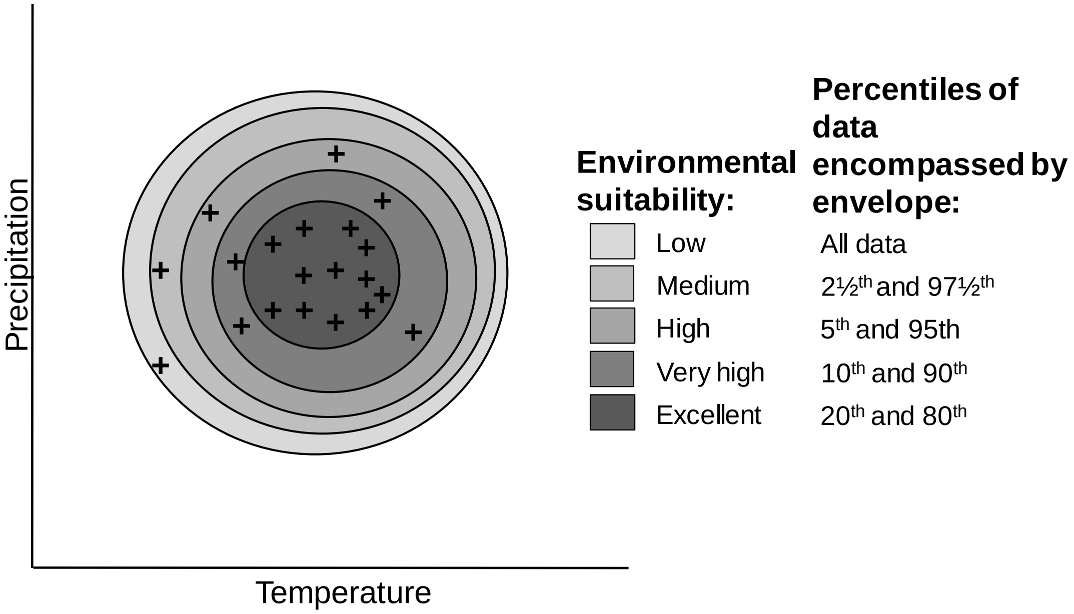


Figure 2.2 – The categories of suitability used in the implementation of BIOCLIM employed in the Diva-GIS software. Several envelopes are defined in environmental space around varying proportions of the species occurrence data (shown as the percentiles of the data that are included in the climate envelope), with smaller proportions corresponding to higher predicted suitability.

An alternative but related model, DOMAIN, estimates suitability based on the distance, in environmental space, to the most (environmentally) similar species presence record (Carpenter *et al.* 1993). The distance (d_{AB}) between the grid cell being considered (A) and the most similar grid cell containing a species record (B) is measured using the Gower metric, as follows:

$$d_{AB} = \frac{1}{p}\sum_{k=1}^{p}\frac{A_k - B_k}{range_k},$$

where p is the number of environmental variables, k is the environmental variable under consideration, A_k and B_k are the values of environmental variable k at grid cells A and B, and $range_k$ is the total range of variable k in the study area. Environmental suitability of a cell (R_{AB}) is calculated (Carpenter *et al.* 1993) as:

$$R_{AB} = 1 - d_{ab}.$$

DOMAIN has been shown to overcome some of the problems of over-prediction associated with BIOCLIM (Carpenter *et al.* 1993). In comparisons of modelling techniques its performance has generally been intermediate (Tsoar *et al.* 2007; Wisz *et al.* 2008) to poor (Elith *et al.* 2006), although relatively better than other techniques with very small numbers of presence records (Wisz *et al.* 2008).

2.2.2 Logistic regression

The second major category of modelling techniques comprises the traditional statistical approaches. *General* linear models, with which most ecologists are familiar, are not suitable for modelling species' distributions because they assume homogeneity of variance, a linear relationship between the response variable and the independent variables, and a normal distribution of errors (Ferrier *et al.* 2002). *Generalized* linear models (McCullagh & Nelder 1989), which I shall refer to as GLMs throughout this thesis, are an extension of general linear models, which allow for a variety of error distributions and relax the assumptions of linearity and of homogeneity of variance (Ferrier *et al.* 2002). They do this by using a link function to relate the response variable to the independent variables (McCullagh & Nelder 1989). To model species distributions using generalized linear models, species occurrence (presence and absence) records are fitted as the response variable and the environmental variables as independent variables. Models based on species presence and absence data have a binomial distribution of errors. Models fitting this error distribution are collectively known as logistic regression models. The link function in this case is the logit link:

$$x = \ln\left(\frac{p}{1-p}\right)\text{, or}$$

$$p = \frac{1}{1+e^{-x}}\text{,}$$

where p is the predicted response and x is the linear combination of independent variables (McCullagh & Nelder 1989).

GLMs have proven popular for modelling the distribution of species, in part because the relevant software is freely and readily available, but also because the output is easy to interpret with coefficients relating the occurrence of species to each of the environmental variables (Wintle *et al.* 2005). GLMs have generally performed very well in comparisons of different modelling techniques (Hirzel *et al.* 2001; Loiselle *et al.* 2003; Elith *et al.* 2006; Meynard & Quinn 2007; Wisz *et al.* 2008), although relatively poorly with very small sample sizes (Pearce & Ferrier 2000a; Walther *et al.* 2007a; Wisz *et al.* 2008, but see Stockwell & Peterson 2002).

Generalized additive models (GAMs) are an extension of GLMs that have also been used frequently for modelling species' distributions. In GAMs the data determine the relationships between the response variable and the environmental variables, although the complexity of these relationships can be constrained, whereas in GLMs the relationships (e.g. linear or quadratic) are specified by the user (Guisan *et al.* 2002). This means that no *a priori* hypotheses about the way that species respond to the environment are required, which allows GAMs to fit more complex relationships than GLMs (Guisan *et al.* 2002). GAMs have also performed very well in published studies, and often somewhat better than GLMs (Pearce & Ferrier 2000a; Ferrier *et al.* 2002; Moisen & Frescino 2002;

Zaniewski *et al.* 2002; Elith *et al.* 2006; Wisz *et al.* 2008), although they are even more sensitive to small sample sizes (Wisz *et al.* 2008). As with GLMs, the software is freely available and relatively easy to use, but the output is not easy to interpret (Wintle *et al.* 2005).

2.2.3 Maxent

Maxent is a machine-learning method based on the principle of maximum entropy, where the aim is to produce a prediction that is as close to uniform as possible with the constraint that the expected value of each environmental variable (the sum, across all grid cells, of the product of the probability of occurrence and the value of the environmental variable) must equal the empirical average (the mean value of the environmental variable at the presence points) (Phillips *et al.* 2004; Phillips *et al.* 2006). The risk of model overfitting (fitting the data very closely, at the expense of the ability to generalize; see Chapter 1) is reduced by employing a process known as regularization, which allows the expected value of each environmental variable to fall within a specified margin of the empirical average (Dudík *et al.* 2004). At each iteration, the algorithm adjusts the relationships between the environmental variables and the modelled probability of occurrence to increase the fit to the species data. The algorithm runs until the improvement in fit at each iteration falls below a specified threshold, or until a maximum number of iterations have been performed (Phillips *et al.* 2006). Maxent requires only species presence records, comparing these to a random background sample from all the grid cells in the study area (Phillips *et al.* 2004). Maxent can fit relationships of a number of different shapes between the environmental variables and species probability of occurrence: linear, quadratic, product (interactions between pairs of environmental variables), threshold (1 or 0 depending on whether it falls above or below a derived threshold), or hinge (similar to linear relationships, but constant below a threshold) (Phillips *et al.* 2006).

In comparisons of modelling techniques, Maxent has consistently been among the best-performing methods (Phillips *et al.* 2004; Elith *et al.* 2006; Phillips *et al.* 2006; Wisz *et al.* 2008), and appears to be relatively insensitive to decreases in the numbers of presence records used to build the models (Phillips *et al.* 2006; Pearson *et al.* 2007; Wisz *et al.* 2008).

2.2.4 GARP

Another machine-learning modelling technique that has seen widespread use is the Genetic Algorithm for Rule-set Prediction (GARP). GARP develops a set of if-then statements (‘rules’) that determines whether the species is predicted present or absent according to the environmental conditions of the grid cell in question (Stockwell & Noble 1992). Rules can be of three types: (1) envelope rules – presence or absence is predicted if the environmental variables fall within a certain range; (2) atomic rules – presence or absence is predicted for specific values of the environmental variables; and (3) logistic rules – presence or absence is predicted using a logistic regression function of the environmental variables (Stockwell & Peters 1999). GARP initially takes a random sample, with replacement, of 1250 species presence points and 1250 grid cells without presence records. These data are divided in half for model-building and internal model validation. A random set of rules is generated, and then these are modified by mutation (changes to the values of the environmental variables in the rules) and recombination (whole portions of rules are swapped). At each step the rules are tested against the internal validation data; rules that fit the data well are more likely to be retained (Stockwell & Peters 1999). The algorithm runs until improvement in accuracy falls below a certain threshold or until a maximum number of iterations have been performed. Since the starting set of rules is generated randomly, markedly different predictions can be made using exactly the same species and environmental data (Anderson *et al.* 2002a). One solution to this problem has been to develop a number of replicate models for each species, and then to sum these models to generate an index of predicted environmental suitability (Anderson *et al.* 2002a). However, Anderson *et al.* (2003) found that the accuracy of models for the same species was very variable and suggested that only the best models should be selected for the final prediction. Accurate models should predict as being present as many of the species records as possible, and should predict as being present an area that approximates the true range size of the species in question (Anderson *et al.* 2003). Anderson *et al.* (2003) propose identifying the 10 most-accurate models by selecting: 1) the 20 models that have the lowest numbers of presence locations predicted absent (omission error); and then 2) the ten of these models that have a proportion of background points predicted present (commission index) closest to the median value.

GARP has shown mixed performance in tests of its accuracy. Many studies have found that it models species' distributions very accurately (Peterson & Cohoon 1999; Peterson *et al.* 2002a; Loiselle *et al.* 2003; Peterson & Kluza 2003; Peterson & Robins 2003; Raxworthy *et al.* 2003; Papeş & Gaubert 2007). However, in comparisons of several techniques, GARP has generally been shown to perform relatively poorly (Elith *et al.* 2006; Pearson *et al.* 2007, but see Tsoar *et al.* 2007) and has a tendency to over-predict distributions (Peterson & Robins 2003). On the other hand, GARP has been shown to be relatively robust to small sample sizes (Solano & Feria 2007; Wisz *et al.* 2008), but perhaps less so than Maxent (Pearson *et al.* 2007).

2.2.5 Other techniques

In Chapter 3, I compare the accuracy of four commonly-used techniques, which had differing levels of accuracy in the study by Elith *et al.* (2006): Maxent, GLM, BIOCLIM and GARP. In the remaining chapters, I focus on just one model that has been shown several times to produce highly accurate models, namely Maxent. There are a great many other modelling techniques available, including regression trees, artificial neural networks and multivariate adaptive regression splines. However, because Maxent has been shown to produce highly accurate models, even with very small numbers of species records, I chose to focus on Maxent and not to consider any other techniques.

2.3 Environmental data

2.3.1 Environmental data for Egypt

The WorldClim dataset is a freely-available and widely-used set of climate variables with global coverage. The WorldClim climate maps were interpolated from temperature data recorded at 24542 weather stations, precipitation data recorded at 47554 weather stations and temperature range data recorded at 14835 weather stations (Figure 2.3), using a thin-plate smoothing spline (Hijmans *et al.* 2005). The interpolated maps were used to generate 19 bioclimatic variables (Table 2.1) (Hijmans *et al.* 2005). There were relatively few weather stations in Egypt and these were largely concentrated in the Nile Valley and Nile Delta (Figure 2.3, insets). Therefore it is important to note that there may be inaccuracies in the derived variables, particularly in remote desert areas far from the weather stations. Nevertheless, a number of studies have successfully used the WorldClim variables to model the distributions of species, including in tropical areas where the density of weather stations is very low (Hijmans & Graham 2006; Broennimann *et al.* 2007; Pearson *et al.* 2007; Peterson *et al.* 2007). The WorldClim dataset also includes a global elevation map, from which topography variables (slope and aspect) can be calculated.

Table 2.1 – Bioclimatic variables available in the WorldClim Version 1.4 dataset (see Hijmans *et al.* 2009 for full details). Names in parentheses correspond with the names used in the WorldClim dataset and are used in graphs later in this chapter.

Annual mean temperature (Bio1)
Mean diurnal temperature range (Bio2)
Isothermality (Bio3)
Temperature seasonality (Bio4)
Maximum temperature of the warmest month (Bio5)
Minimum temperature of the coldest month (Bio6)
Annual temperature range (Bio7)
Mean temperature of the wettest quarter (Bio8)
Mean temperature of the driest quarter (Bio9)
Mean temperature of the warmest quarter (Bio10)
Mean temperature of the coldest quarter (Bio11)
Annual precipitation (Bio12)
Precipitation of the wettest month (Bio13)
Precipitation of the driest month (Bio14)
Precipitation seasonality (Bio15)
Precipitation of the wettest quarter (Bio16)
Precipitation of the driest quarter (Bio17)
Precipitation of the warmest quarter (Bio18)
Precipitation of the coldest quarter (Bio19)

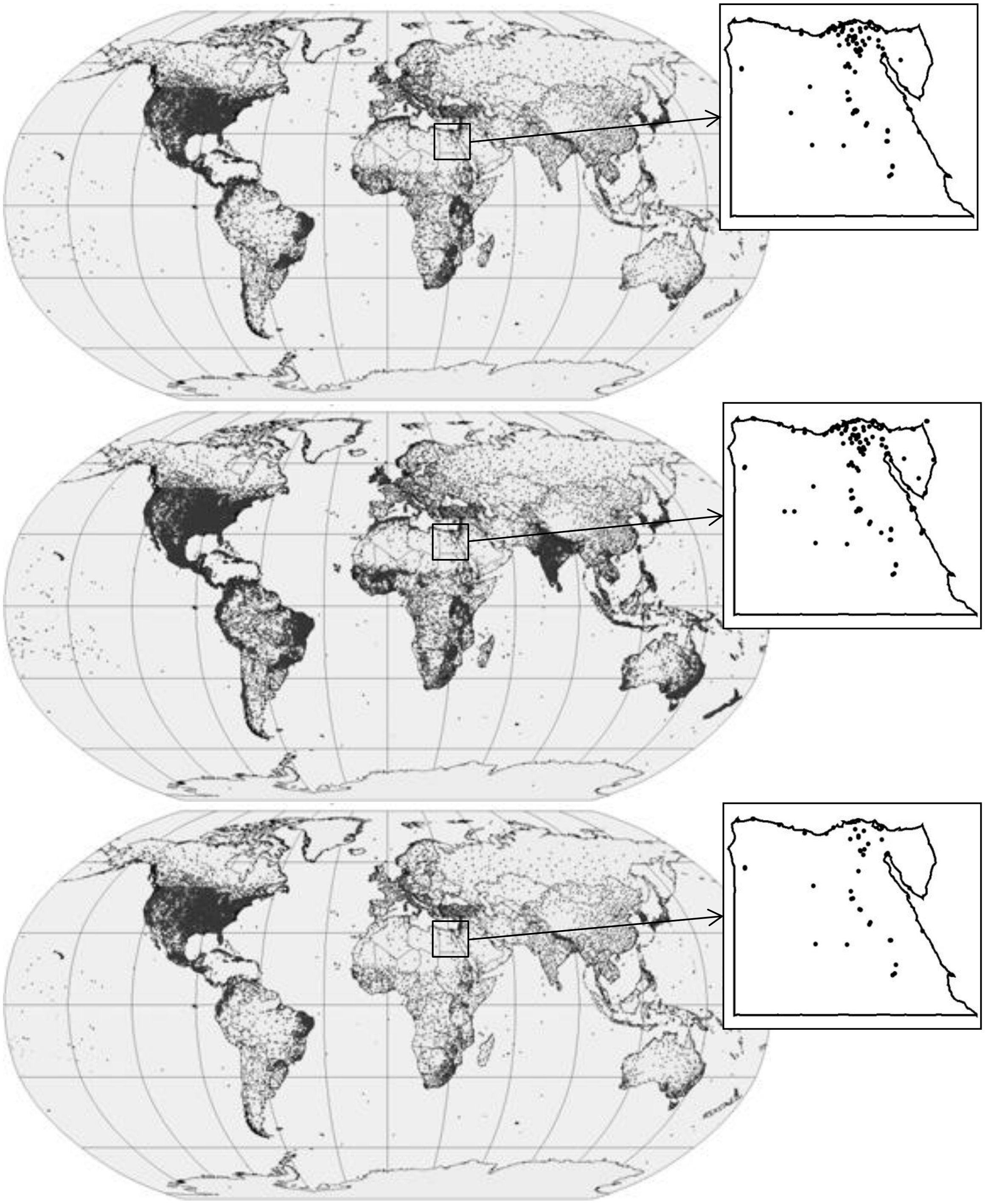


Figure 2.3 – Weather stations with: a) temperature; b) precipitation; and c) temperature range data that were used to generate the WorldClim bioclimate variables. Inset shows in Egypt.

Collinearity among environmental variables can result in relevant variables being excluded from distribution models, and unimportant variables being included (Guisan *et al.* 2002). The WorldClim climate variables show very high collinearity. Correlation coefficients (Spearman's rank) among variables at 2000 random locations in Egypt ranged from -0.89 to 0.996. One solution to this problem is to exclude randomly one out of each pair of variables that correlate strongly with each other (Loyn *et al.* 2001; Engler *et al.* 2004; Lütolf *et al.* 2006). However, there is a danger that variables with a direct effect on species' distributions will be excluded at the expense of variables that have only an indirect effect. A better approach is to perform principal components analysis (PCA) on the environmental variables to generate a set of uncorrelated factors (Manel *et al.* 1999a; Manel *et al.* 2001). I performed PCA on values of the 19 bioclimatic variables and the elevation variable from the WorldClim dataset for Egypt. At 30 arc-second resolution, Egypt contains over one million grid cells, too many data points to perform a PCA in the statistical package used (SPSS). Therefore, I performed ten replicate PCAs on 2000 random locations within the borders of Egypt. Mean eigenvectors and loadings across all ten replicate analyses were calculated. Four principal component axes with a mean eigenvector greater than one were retained. These axes collectively explained 86.5% of the variance in the climate variables (Figure 2.4). Mean loadings, which were highly consistent among replicate analyses (Figure 2.5), were used to generate new maps for each of these axes. High values of PC1 indicated warm and dry climatic conditions; high values of PC2 corresponded to areas that do not experience extremes of cold; PC3 increased with elevation and precipitation; and PC4 increased with decreasing precipitation seasonality, decreasing temperature in the driest quarter and decreasing isothermality (the ratio of daily temperature range to annual temperature range).

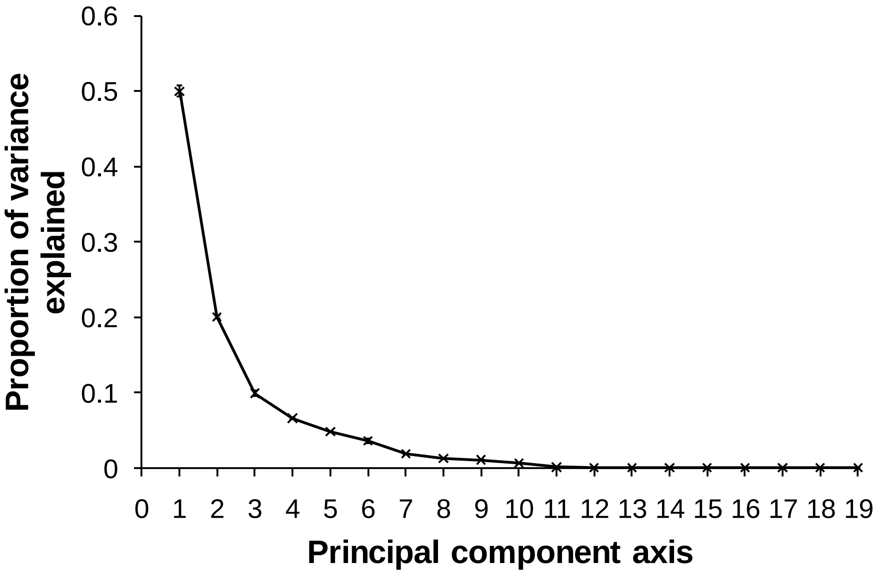


Figure 2.4 – proportion of variance explained by 19 principal component axes based on climate (temperature and precipitation) and elevation data for Egypt. Ten principal component analyses were performed, taking climate and elevation data at 2,000 random 30-arc-second grid cells for each. Mean (± SEM) proportion of variance explained across the ten analyses is shown here. The first four principal component axes, which had mean eigenvalues greater than one, were used in the distribution models.

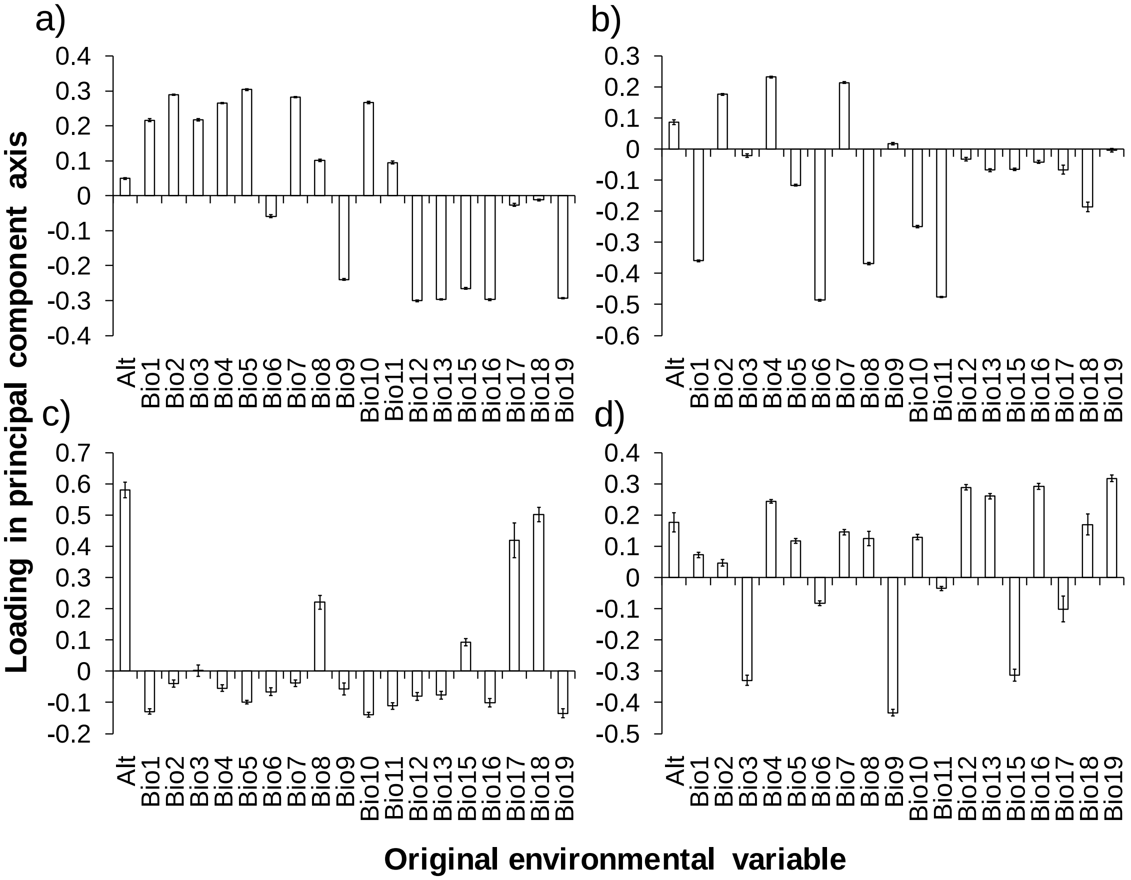


Figure 2.5 – For each of four principal component axes (a) PC1; b) PC2; c) PC3; d) PC4), mean loadings of each of the original environmental variables (± SEM), across 10 replicate principal components analyses. Each replicate analysis consisted of a principal components analysis on values of the environmental variables at 2000 points, randomly located within Egypt. Eigenvectors and loadings were averaged across the ten replicates. The four principal components axes shown are those that had mean eigenvectors greater than one. The mean loadings were used to generate new maps for these four axes.

In addition to the climate variables, I also used two habitat classifications for Egypt. The first was a global land cover classification derived using remotely-sensed data from the Advanced Very High Resolution Radiometer (AVHRR) (Hansen *et al.* 2000). Land cover was classified into 13 categories (needleleaf evergreen forest, broadleaf evergreen forest, needleleaf deciduous forest, broadleaf deciduous forest, mixed forest, woodland, wooded grassland, closed shrubland, open shrubland, grassland, cropland, bare ground and urban areas) using a decision tree. The second was a geological habitat classification, compiled by Dr. A. Hassan for the BioMAP project. Habitat was classified into one of 11 categories – sea, littoral coastal land, cultivated land, sand dune, wadis (dry desert valleys), areas of metamorphic rock, areas of igneous rock, gravels, serir sand sheets, sabkhas, and areas of sedimentary rock – using remote-sensing and extensive ground-truthing. The problem with including land cover variables in species distribution models is that human habitat modification often means that land cover changes rapidly with time. Since museum data often cover long periods of time, the habitat at a given location at the time of record collection may not match the habitat represented in land cover variables. Some authors have suggested developing distribution models using only climate variables, and then refining the models using a current habitat map and expert knowledge on the species' habitat requirements (Guisan *et al.* 2006a; Peterson *et al.* 2006; Papeş & Gaubert 2007). However, this approach would be very time-consuming for large numbers of species. The problem of temporal correspondence between species and habitat data is not relevant for the geological habitat map. Therefore, although models developed using the geological habitat map differed little in accuracy from models developed using the AVHRR land cover classification (see Chapter 3), the geological map was used in all studies presented in this thesis.

2.3.2 Environmental data for Britain

A wider variety of environmental variables are available for Britain, owing to greater recording effort. Furthermore, the data have been collected over a long time period allowing one to study temporal changes in the environment and resulting changes in the distribution of species.

The climate data for Britain were interpolated from values recorded at Met Office weather stations (Perry & Hollis 2006). Coverage by these weather stations was denser and more even than coverage by the WorldClim weather stations (Figure 2.6). I used 39 variables: monthly values of minimum temperature, maximum temperature and total precipitation; and annual values of growing degree days, consecutive dry days and growing season length. Values of these variables are available for 1914 onwards; I used data for 1968 to 2002.

Figure 2.6 – Location of the Met Office weather stations from which data were taken to generate the British climate variables, from Perry & Hollis (2006). Solid circles indicate stations that provided temperature data and open circles indicate stations that provided pressure data.

I took land cover data for Britain from the Institute of Terrestrial Ecology's Land Class and Land Cover maps. The Land Class map, part of the CORINE land class map for

Europe, was made by classifying each 100-m grid cell into one of 44 different land cover types (Table 2.2) based on remotely-sensed data for 1989 and 1990 from the Landsat satellites (Brown *et al.* 2002). The ten Land Cover maps report the percentages of each 1-km grid cell covered by each of ten aggregate land cover types (Table 2.2). A measure of land cover diversity was also used. This was developed by Stuart Ball of the Joint Nature Conservation Committee, by calculating the diversity of land cover types within 2 km of the centre of each 1-km target cell using the Shannon-Weiner diversity index.

Table 2.2 – 1) Categories used in the CORINE land-cover classification for Europe. Grid cells were assigned to the CORINE land-cover categories using remote sensing data, captured by the Landsat satellites in 1989 and 1990. 2) Aggregate land-cover types used to generate the Land Cover maps, which describe the percentage of each 1-km grid cell accounted for by different types of land use.

CORINE land cover types:
Continuous urban fabric
Discontinuous urban fabric
Industrial or commercial units
Road and rail networks and associated land
Port areas
Airports
Mineral extraction sites
Dump sites
Construction sites
Green urban areas
Sport and leisure facilities
Non-irrigated arable land
Permanently irrigated land
Rice fields
Vineyards
Fruit trees and berry plantations
Olive groves
Pastures
Annual crops associated with permanent crops
Complex cultivation patterns
Land principally occupied by agriculture, with significant areas of natural vegetation
Agro-forestry areas
Broad-leaved forest
Coniferous forest

Mixed forest
Natural grasslands
Moors and heathland
Sclerophyllous vegetation
Transitional woodland-shrub
Beaches, dunes, sands
Bare rocks
Sparsely vegetated areas
Burnt areas
Glaciers and perpetual snow
Inland marshes
Peat bogs
Salt marshes
Salines
Intertidal flats
Water courses
Water bodies
Coastal lagoons
Estuaries
Sea and ocean
Aggregate land cover types:
Broadleaved woodland
Conifer woodland
Arable farmland
Improved grassland
Semi-natural grassland
Montane
Built up
Standing water
Coastal
Sea

Topographic variables were also used in some of the distribution models for British species. These were based on the Ordnance Survey digital elevation model (DEM) at 50 m resolution (Ordnance Survey 2009). Specifically, I used elevation and slope; slope was calculated by Stuart Ball.

Finally, I used agriculture variables based on the Edina censuses (Anon. 2009b). These variables described total numbers of cattle and sheep, and the acreage of cereals grown. Censuses were taken in 1976, 1981, 1988, 1994, 1997 and 2004.

2.4 Species occurrence data

2.4.1 BioMAP data for Egypt

The BioMAP project in Egypt (see BioMAP 2009 for more details) spent three years collecting species occurrence records from natural history and museum collections, and from the literature. There are several limitations associated with data from these sources, discussed in Chapter 1. Therefore, an analysis of the quality of the data is crucial before distribution modelling exercises are undertaken.

One major problem with records from museums, natural history collections and literature sources is that they are often accompanied by very vague descriptions of their locality (Graham *et al.* 2004a). This results in very poor locational accuracy when the record is assigned geographical coordinates (a process referred to as 'georeferencing'). An additional problem in Egypt is that the transliteration of site names from Arabic into the Latin alphabet can yield many different spellings for the same site; this often makes it very difficult to identify the site to which a record refers. To aid the process of georeferencing, the BioMAP project developed a gazetteer of all sites from which species records were taken. As part of the development of this gazetteer, the locational accuracy of each site was calculated using the point-radius method (Wieczorek *et al.* 2004); records from excessively inaccurate sites were excluded from the database.

Another problem with museum data is environmental bias in the scope of the species records (Graham *et al.* 2004a; for a more detailed discussion, see Chapter 1). Therefore, I undertook a test of the environmental representativeness of the BioMAP data for butterflies, mammals, reptiles and amphibians. To do this, the distribution of the record localities along each of three main environmental gradients (elevation, mean annual temperature and total annual precipitation), and also along an index of human impact (Sanderson *et al.* 2002), were visually compared against the distribution of all grid cells in Egypt along the same gradients. The environmental representativeness of record localities was also tested quantitatively using an adaptation of the method used by Wintle *et al.* (2005). Four principal component axes, based on 11 temperature variables, 8 precipitation variables and 1 elevation variable (described in detail in Section 2.3.1), were each divided into four bins using Jenks' (1967) natural breaks. Combining these bins for all four principal component axes gave 256 possible combinations of categories (henceforth called 'areas of climatic space'). For each taxonomic group, I calculated the number of areas of climatic space that the surveyed localities represented. For comparison, I calculated the number of areas of climatic space represented by 100 sets of random points of the same number as surveyed localities, drawn from anywhere within Egypt's borders. To test the coverage of habitat types by surveyed sites, I used the geological habitat variable described in the previous section and tested departures from random sampling using a chi-squared test.

At the time of analysis, the BioMAP data for butterflies consisted of 1898 records for 59 species. These records were taken from museum specimens and the literature (Larsen 1990; Gilbert & Zalat 2007). The identification of all extant specimens was checked according to the latest taxonomic opinion. Most other specimens had been checked previously by Larsen (1990). Records were made between 1829 and 2006, although most were from the 20th Century (Figure 2.7). Geographical coverage was reasonable (Figure 2.8a). The lack of records in the Western Desert (see Figure 2.8e) was probably owing to the true absence of butterflies. On the other hand, the lack of records in the Qattara Depression probably represented under-sampling. Surveyed localities were clearly biased towards areas with a high human impact, i.e. areas near roads and human habitation (Figure 2.9a), but showed no obvious bias with respect to the main environmental gradients – elevation, temperature and precipitation (Figure 2.9b-d). Sites with butterfly records fell into 44 of 256 areas of climatic space, 84.1% of the number expected if the same number of sites were located completely at random. Sites were distributed non-randomly among habitat types ($\chi^2 = 1035$, d. f. = 9, $P < 0.001$). Littoral coastal areas, cultivated land, wadis (dry desert valleys), areas of metamorphic rock and areas of igneous rock were sampled more often than expected by chance. Sand dunes, gravels, serir sand sheets and areas of sedimentary rock were sampled less often than expected by chance. Sixty-three of 333 sites were located inside protected areas; protected areas cover 7.5% of Egypt’s land surface (see Figure 2.8d for a map of the protected areas).

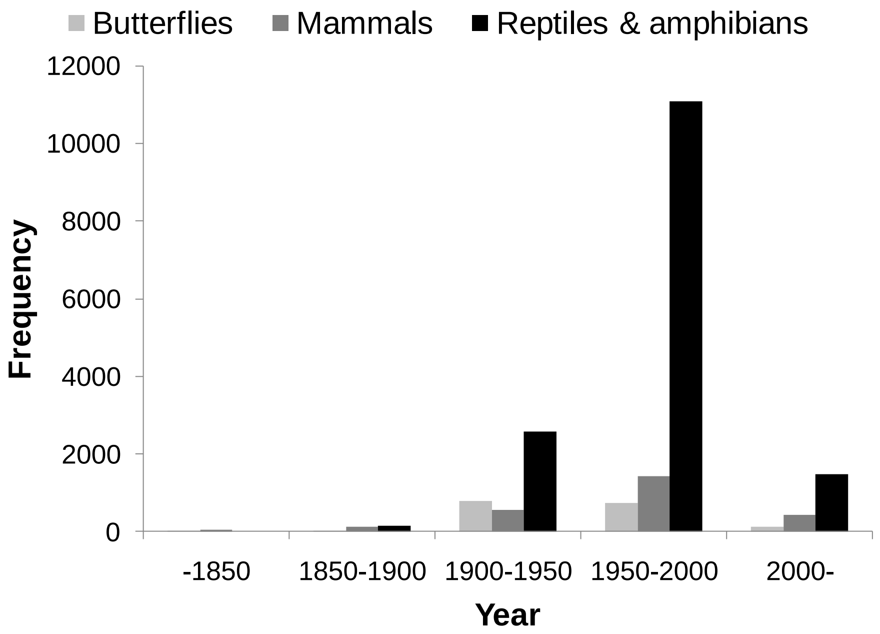
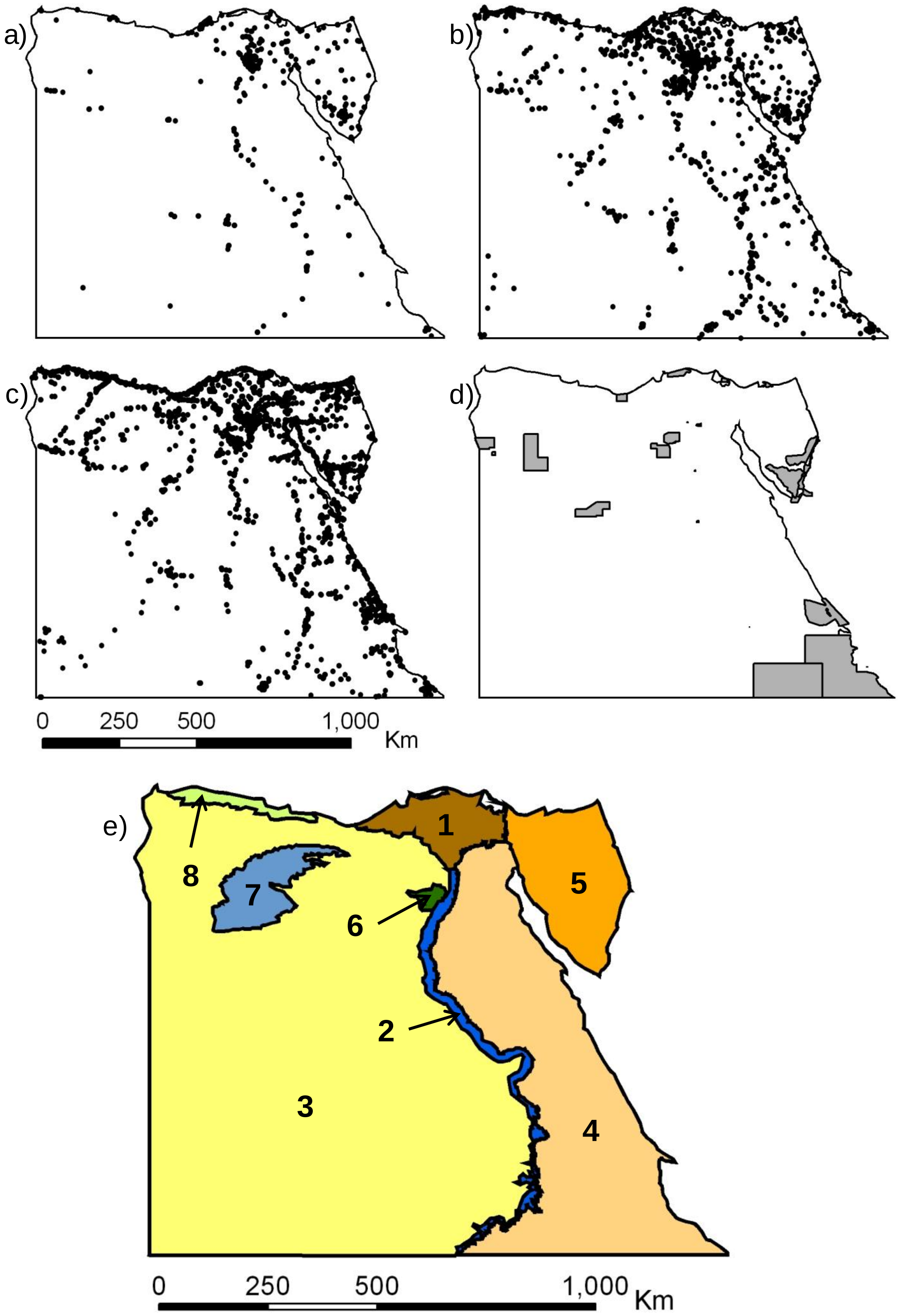


Figure 2.7 – Temporal distribution of butterfly, mammal, and reptile and amphibian records in Egypt's BioMAP database.


a)
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Km

Figure 2.8 – Sites in the BioMAP database with (a) butterfly records; (b) mammal records; and (c) reptile and amphibian records; (d) the location of Egypt's existing protected areas (see Egyptian Environmental Affairs Agency 2007 for more details); and (e) the approximate location of the main geographical areas of Egypt, which will be referred to throughout this thesis – (1) Nile Delta, (2) Nile Valley, (3) Western Desert, (4) Eastern Desert, (5) Sinai Peninsula, (6) Faiyum Oasis, (7) Qattara Depression, and (8) Mediterranean Coast.

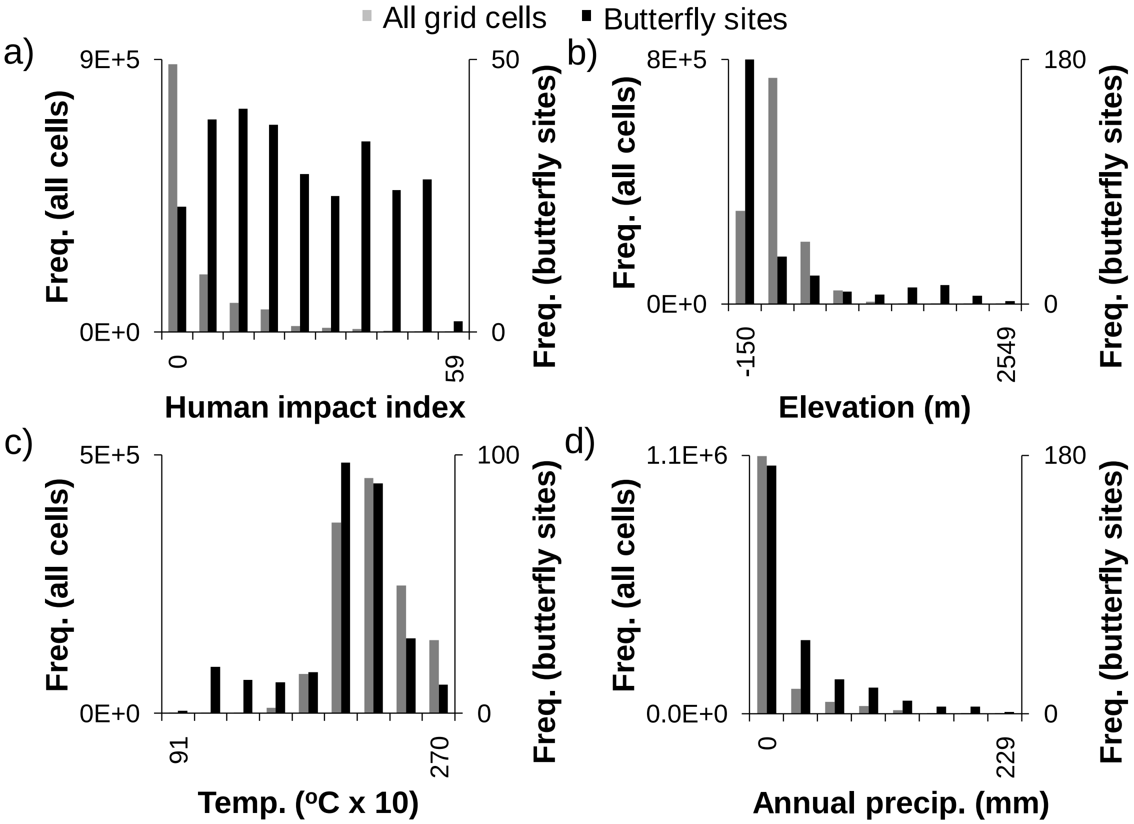

Figure 2.9 – Frequency distributions of all grid cells (grey bars) and sites with butterfly records (black bars) along four environmental gradients: a) human impact index; b) elevation; c) mean annual temperature; and d) total annual precipitation. The human impact index ranges from 0 to 64 and combines data on population density, proximity to roads, railroads and rivers, proximity to the coast, light pollution, location within cities, and human land cover (Sanderson *et al.* 2002). For details of the other environmental variables, see Section 2.3.1.

The mammal data consisted of 4718 records for 103 species, from museums and personal collections, and from the published literature. The identification of all species was checked according to the latest taxonomic opinion (Wilson & Reeder 2005b) by Dr. M. Bassiouny (Al Azhar University, Cairo). Records were made between the years 1580 and 2007, although most fell in the second half of the 20th Century (Figure 2.7).

Geographical coverage was very good, owing to systematic collecting in the period 1950-1980 (see Osborn & Helmy 1980) (Figure 2.8b). As with the butterfly records, there was a clear bias towards areas with higher human influence (Figure 2.10a) but little obvious bias in environmental space (Figure 2.10b-d). Sites with mammal records fell into 76 of 256 areas of climatic space, 107.5% of the number expected by chance. Sites with mammal records were distributed non-randomly among habitat types ($\chi^2 = 2248$, d.f. = 9, $P < 0.001$); littoral coastal areas, cultivated land, wadis, areas of metamorphic rock and areas of igneous rock were over-represented, and sand dunes, gravels, serir sand sheets and areas of sedimentary rock were under-represented. Two hundred of 1395 sites fell inside protected areas.

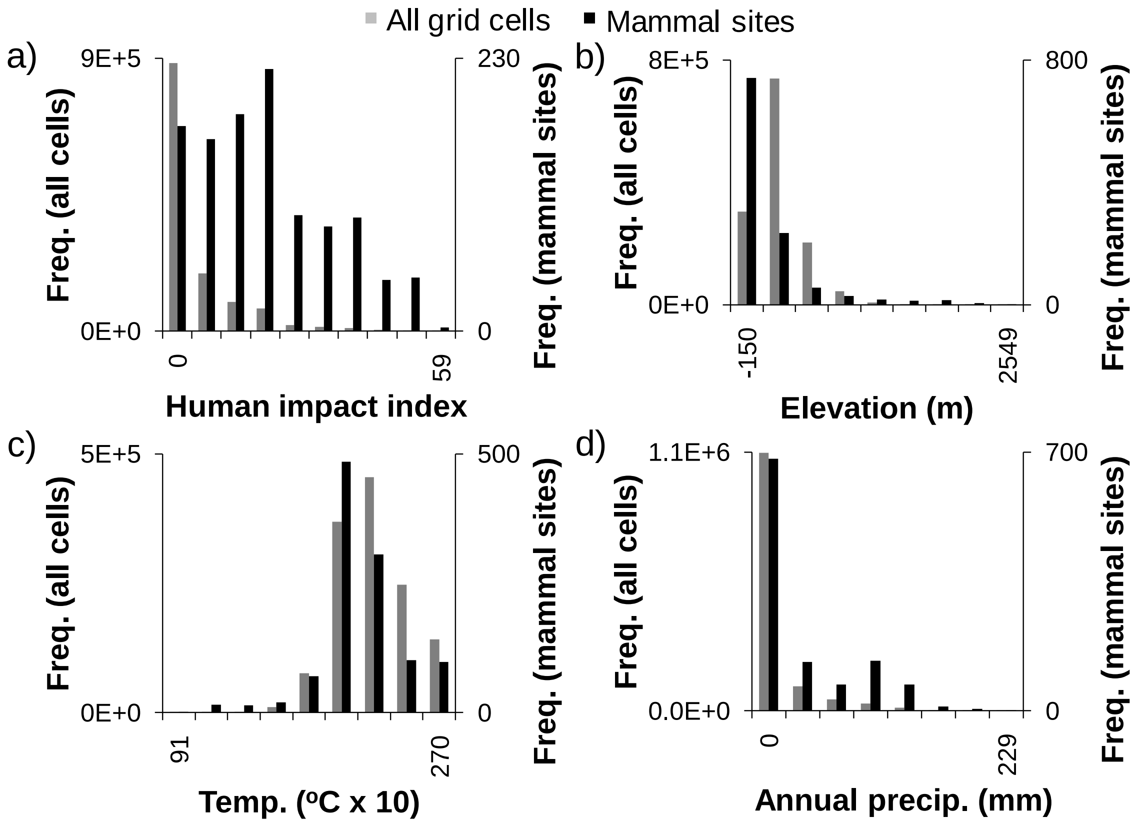

Figure 2.10 – Frequency distribution of all grid cells (grey bars) and sites with mammal records (black bars) along four environmental gradients: a) human impact index; b) elevation; c) mean annual temperature; and d) total annual precipitation. The human impact index ranges from 0 to 64 and combines data on population density, proximity to roads, railroads and rivers, proximity to the coast, light pollution, location within cities, and human land cover (Sanderson *et al.* 2002). For details of the other environmental variables, see Section 2.3.1.

The BioMAP database contained 16397 records for 147 reptile and amphibian species, from museum and personal collections, and from the literature. The identification of species was checked by Dr. Sherif Baha-El-Din (Cairo) according to current taxonomic opinion (Baha El Din 2006). Records were made between 1854 and 2007, with the vast majority made in the second half of the 20th Century (Figure 2.7). Geographical coverage was excellent, owing to extensive and systematic surveying in recent years by Dr. Sherif Baha-El-Din and Dr Mostafa Saleh (Figure 2.8c). Surveyed localities were biased towards areas with high human impact, but showed little environmental bias (Figure 2.11).

Surveyed localities fell into 77 of 256 areas of environmental space, 99.3% of the number expected if the sites were located at random. Surveyed sites were not distributed among habitat types as would be expected if they were randomly-distributed ($\chi^2 = 2495$, d.f. = 9, $P < 0.001$). Littoral coastal areas, cultivated land, wadis, areas of metamorphic rock and areas of igneous rock were sampled more often than expected by chance, while sand dunes, gravels, serir sand sheets and areas of sedimentary rock were sampled less often than expected. 457 of 2320 sites fell inside protected areas.

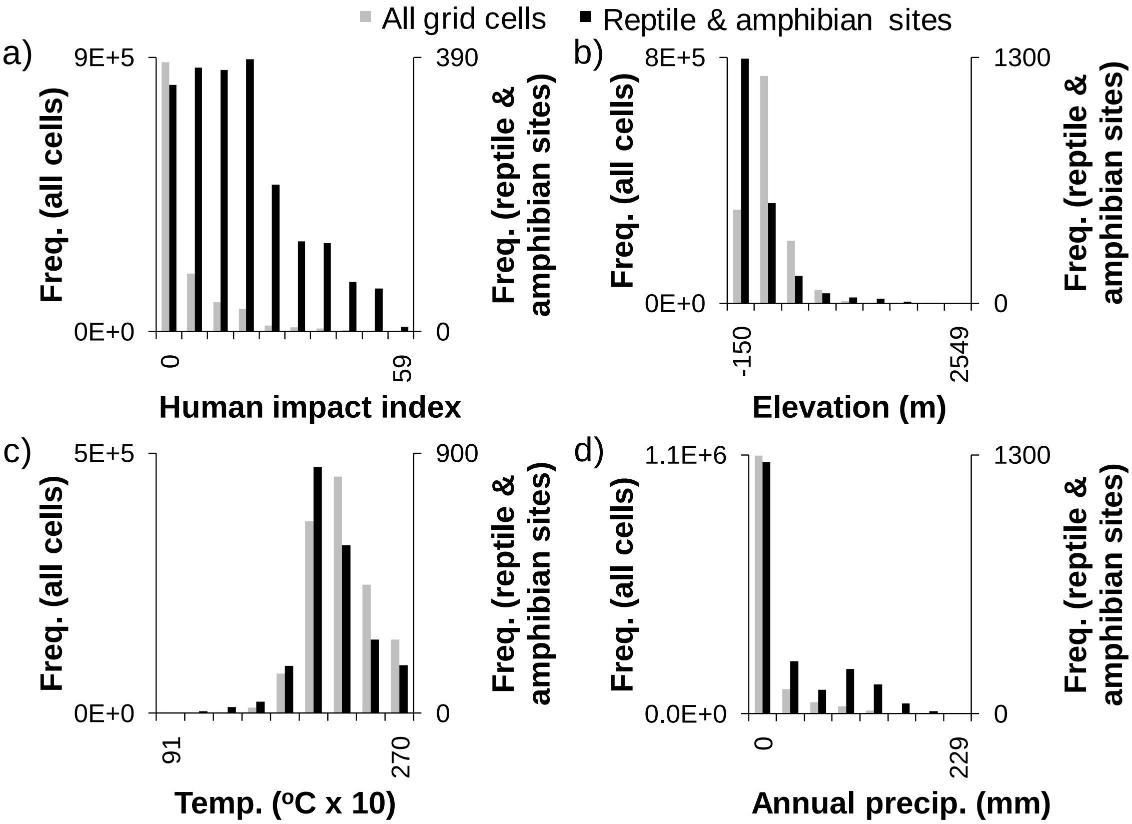

Figure 2.11 – Frequency distribution of all grid cells (grey bars) and sites with reptile and amphibian records (black bars) along four environmental gradients: a) human impact index; b) elevation; c) mean annual temperature; and d) total annual precipitation. The human impact index ranges from 0 to 64 and combines data on population density, proximity to roads, railroads and rivers, proximity to the coast, light pollution, location within cities, and human land cover (Sanderson *et al.* 2002). For details of the other environmental variables, see Section 2.3.1.

2.4.2 Species data for Britain

In Chapters 6 and 8, I model the distributions of species in Great Britain. Collecting of species records in Britain has been much more extensive than in Egypt and coverage, both geographical and environmental, is substantially better. Therefore, I shall not present a formal test of the quality of these data here.

In Chapter 6, I use data for butterflies, flowering plants, hoverflies, and hymenopterans from the National Biodiversity Network (NBN) gateway. The NBN gateway provides access to data from a large number of individuals and organisations (see Anon. 2009c for more details); a full list of contributors whose data I used is given in Appendix 2.1. Records for all of the taxonomic groups considered showed excellent geographic coverage (Figure 2.12). In total (at 10-km resolution), there were 3792 presence records for 15 butterfly species, 20907 records for 60 flowering plant species, 20140 records for 48 hoverfly species, and 27072 records for 93 hymenopteran species.

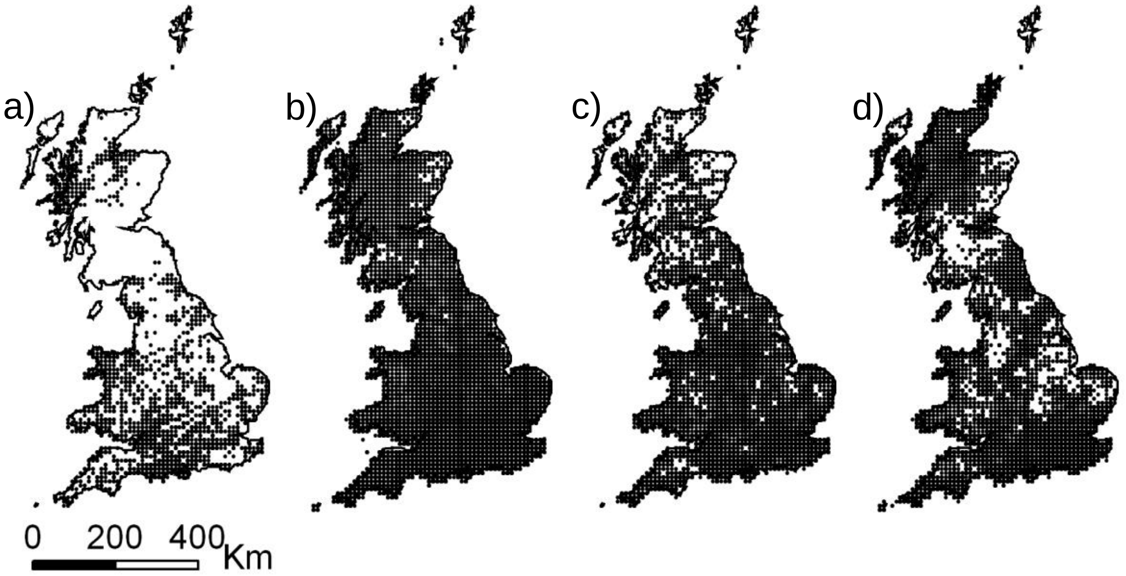

Figure 2.12 – Sites with presence records for: (a) 15 species of butterfly; (b) 60 species of flowering plant; (c) 48 species of hoverfly; and (d) 93 hymenopteran species, from the British National Biodiversity Network (NBN) gateway.

In Chapter 8, I use records for hoverfly and bird species. This chapter was concerned with temporal trends in distributions. Therefore, occurrence records were divided into discrete time periods. The data for hoverflies were taken from the Hoverfly Recording Scheme (see Ball 2009 for details). This dataset comprises 488550 records made between the years 1800 and 2006 by numerous volunteers. I used records made between 1972 and 2002, divided into the following time periods: 1972-1977, 1978-1982, 1983-1987, 1988-1992, 1993-1997, and 1998-2002. Records with a locational accuracy poorer than 1 km were excluded. The number of records was very large and generally increased over time (Table 2.3); geographical coverage was excellent in all six time periods (Figure 2.13). The bird data were taken from the two British Trust for Ornithology (BTO) breeding bird atlases (Sharrock 1976; Gibbons *et al.* 1993). These data were collected by volunteers during two extensive and systematic surveys of every 10-km square in the British Isles, and as a consequence they include reasonably reliable records of species absence as well as records of species presence.

Table 2.3 – Numbers of presence records (at 1-km resolution) from the Hoverfly Recording Scheme in each of six time periods, used to study temporal trends in the distributions of British hoverfly species (Ball 2009).

Time period	Number of presence records
1972-1977	7901
1978-1982	20927
1983-1987	62355
1988-1992	72323
1993-1997	59644
1998-2002	42215

Figure 2.13 – Geographical distribution of occurrence records for hoverfly species in Britain, taken from the Hoverfly Recording Scheme, in each of six time periods: a) 1972-1977; b) 1978-1982; c) 1983-1987; d) 1988-1992; e) 1993-1997; f) 1998-2002.

2.5 Evaluating model accuracy

2.5.1 Measures of model accuracy

The simplest measures of model accuracy are estimates of the proportions of species presence records correctly predicted by the model as being present (model sensitivity), the proportion of absence records correctly predicted by the model as being absent (model specificity), or the proportion of all records predicted correctly by the model (correct classification rate) (Fielding & Bell 1997). The problem with these measures is that they are sensitive to the relative proportions of presence and absence records used (the sample prevalence), with very high estimates of model accuracy possible by chance when there are highly unbalanced numbers of presences and absences. An alternative is the kappa statistic, which corrects the correct classification rate to account for the probability that the model will classify a record correctly by chance (Manel *et al.* 2001). The kappa statistic is calculated using the following formula:

$$\kappa = \left[\frac{(a+d) - (((a+c)(a+b) + (b+d)(c+d))/n)}{n - (((a+c)(a+b) + (b+d)(c+d))/n)} \right]$$

where *a* is the number of correctly predicted presence records, *b* is the number of incorrectly predicted presence records, *c* is the number of incorrectly predicted absence records, *d* is the number of correctly predicted absence records, and n is the total number of records.

Most models output a continuous prediction, either probability of occurrence or relative habitat suitability. All of the above measures of model accuracy thus require a threshold to be defined, to convert the continuous output into a binary prediction of presence or absence. Although objective measures exist for defining such thresholds (e.g. Pearson *et al.* 2004; Liu *et al.* 2005), there are measures of model accuracy that do not require a threshold to be set. Some authors (e.g. Engler *et al.* 2004; Pearson *et al.* 2004) have used the maximum value of kappa across all possible thresholds, but by far the most commonly-used measure of model accuracy, and one that I use throughout this thesis, is the AUC statistic. This is derived from a Receiver Operating Characteristic (ROC) curve, which is a plot of the proportion of presence records correctly predicted by the model (sensitivity) against the proportion of absence records incorrectly predicted (1 – specificity). The AUC statistic, which is simply the area under the ROC curve, measures the ability of models to discriminate presence records from absence records (Fielding & Bell 1997). A perfectly discriminating model would have an AUC value of 1, while a completely random model would have an AUC of 0.5 (Fielding & Bell 1997). Pearce & Ferrier (2000a) suggest that models with an AUC value greater than 0.7 are useful.

The AUC statistic has been criticized recently, because it is insensitive to the exact output values of the model, it places equal emphasis on correctly predicting presences and absences (particularly when pseudo-absence data are used instead of real absence data), it fails to consider spatial patterns of model accuracy, and it is sensitive to the proportion of the study area occupied by species (when pseudo-absences are used to evaluate models) (Lobo *et al.* 2008). This last issue is probably the most significant, and may have important implications when comparing model accuracy among species. For species with smaller ranges, given that environmental variables generally show strong positive spatial autocorrelation, randomly-placed pseudo-absences will have a greater chance of falling outside the environmental conditions inhabited by the species. Therefore, models for these species will have artificially high AUC scores (Lobo *et al.* 2008). Given these limitations, it is important to use alternative measures of model accuracy wherever possible, and particularly when making comparisons of model accuracy among species.

2.5.2 Testing whether distribution models are significantly better than random

If the species occurrence records used to develop distribution models are environmentally biased, then conventional estimates of model accuracy may be artificially elevated. An estimate of the extent to which this is a problem is to test whether the apparent accuracy of a distribution model (as measured by the AUC) is significantly better than random expectation, where the latter is generated by distributing the occurrence records randomly among sites sampled for a particular taxonomic group. For the Egyptian butterfly and mammal species, I followed this approach, as recommended by Raes & ter Steege (2007). To do this, for each species I created one real distribution model and 100 null models. Both the real and the null models were built with the same environmental variables: the geological habitat classification, and four principal component axes based on elevation and 19 bioclimatic variables from WorldClim Version 1.4 (see Section 2.3.1). The real models used the presence records for the target species, while the null models used the same number of presence records randomly selected from all sites recorded for the same taxonomic group as the target species. For each species, if the AUC value of the real model fell within the highest 10% of AUC values of the null models (one-tailed test), then the real distribution model was considered to be significantly better than random.

The results for butterfly species were mixed. Only 12/40 species had distribution models with AUC values significantly better than random (in the top 10% of AUC values achieved by the null models), although distribution models for 31/40 achieved AUC values higher than the mean AUC value of the null models (binomial probability = 0.0003). The distribution models for mammal species were much better. Distribution models for 47/63 species were significantly better than random, and 57/63 species had AUC values better than the mean of the null models (binomial probability <<0.001). Across species, the percentage of null models that outperformed the real distribution model was strongly negatively related to the AUC value of the real distribution model for both butterflies ($r_s = -0.965$, $N = 40$, $P < 0.001$) and mammals ($r_s = -0.865$, $N = 63$, $P < 0.001$). Most AUC values (of species models) that were greater than 0.85, were also significantly better than random.

Overall, these results suggest that the AUC statistic is a useful measure of the relative accuracy of distribution models. However, a higher threshold AUC value of 0.85 for distinguishing accurate distribution models may be more appropriate than a threshold of 0.7, especially if the models are to be used to make important conservation decisions.

2.6 Spatial autocorrelation in the distributions of species

The distributions of species almost always show positive spatial autocorrelation; i.e. a species is more likely to occur in a given grid cell if it also occurs in neighbouring grid cells (Legendre 1993). Such autocorrelation may be exogenous, caused by spatial autocorrelation in the environmental variables, or endogenous, caused by processes inherent to the species, such as dispersal patterns (Lichstein *et al.* 2002). Some authors have suggested that distribution models achieve good fit to species data simply because both species' distributions and the environment are spatially autocorrelated (Bahn & McGill 2007). In other words, spatial autocorrelation in distributions is entirely endogenous in origin, and distribution models using environmental variables capture this spatial structure only because the environment is autocorrelated as well. For example, models for bird species in North America fitting only spatial variables (i.e. longitude and latitude) were on average slightly better than models that fitted only environmental variables (Bahn & McGill 2007), and the fit of distribution models for real bird distributions in Europe were in most cases no better than the fit of null models for simulated distributions with the same spatial structure (Beale *et al.* 2008; but see Araújo *et al.* 2009; Aspinall *et al.* 2009; Peterson *et al.* 2009). A number of methods have been developed to account for spatial autocorrelation in distribution models (reviewed in Dormann *et al.* 2007; see also Section 1.3.3). Most methods only work properly if the species data consist of systematic presence and absence records in a regular grid. One approach that can be used with more opportunistic data is to fit the geographical coordinates (longitude and latitude) as explanatory variables (e.g. Bahn & McGill 2007). Unless spatial models are shown to be much better than environmental models, or vice versa, the confounding effects of environmental autocorrelation and autocorrelation in distributions (either endogenous or exogenous) will make it difficult to determine the extent to which species actually respond to the environment. Whatever the outcome, distribution models may still be useful within the study areas in which they were developed. However, the issue of whether distribution models capture any real biological signal will be crucial in attempts to extrapolate the models to predict distributions in other areas or time periods.

To compare the ability of environmental and spatial variables to fit the distributions of 40 Egyptian butterfly species and 63 Egyptian mammal species, I built two sets of generalized linear models with binomial errors. In the first, I used only environmental variables (habitat and four principal component axes based on elevation and climate, as above); linear and quadratic terms were fitted for the continuous variables. In the second set of models, only the following spatial variables were fitted: longitude, longitude^2, longitude^3, latitude, latitude^2, latitude^3, longitude x latitude, longitude^2 x latitude, and longitude x latitude^2. The deviances explained by each of the sets of models were compared.

For both butterflies (Wilcoxon matched-pairs test: $Z = 4.80$, $N = 40$, $P < 0.001$) and mammals ($Z = 2.83$, $N = 63$, $P = 0.005$), models fitting only environmental variables explained significantly more deviance in the species distribution data than models fitting only spatial variables. For butterflies, the environmental model explained more deviance than the spatial model for 33/40 species (binomial probability $\ll 0.001$). For mammals, the environmental model explained more deviance than the spatial model for 40/63 species (binomial probability = 0.02). These results generally support the use of environmental variables for modelling the distributions of species, at least in Egypt.

Chapter 3. Testing factors influencing distribution-model accuracy using data from real and simulated species

3.1 Abstract

In this chapter, I present a test of how data characteristics and the technical details of model-building affect the accuracy of species distribution models. Models were built for simulated species, allowing a test of model accuracy where the true distribution of species was known, and also for real species, enabling the models to be tested under more realistic ecological conditions. Using data for simulated species, I tested the effects of sample size, the choice of modelling technique, the complexity of species' response to the environment and the method of splitting the species records into model-building and model-evaluating datasets on model accuracy. Using the data for real species, I tested the effects of sample size, choice of modelling technique, choice of independent variables and species identity on the accuracy of models. I show that all the tested factors and many of the two-way interactions between them have significant effects on model accuracy. These results highlight the importance that choices made during the design of species distribution models have on the accuracy of the models produced, and thus make a significant contribution to the growing literature on species distribution models.

3.2 Introduction

The accuracy of species distribution models is often tested by assessing their ability to match the distributions of real species (e.g. Wintle *et al.* 2005; Elith *et al.* 2006). This approach has the disadvantage that the true distribution is not known, making it difficult to evaluate the predictions properly (Austin *et al.* 2006). An alternative is to simulate species distributions, making assumptions about how species occurrence is related to environmental conditions. Using simulated species distributions has the advantage that the distribution that the model is trying to fit is perfectly known (Hirzel *et al.* 2001). Only a few studies have used simulated data in this way (Hirzel *et al.* 2001; Hirzel & Guisan 2002; Moisen & Frescino 2002; Austin *et al.* 2006; Wintle & Bardos 2006; Meynard & Quinn 2007). In this study I test the accuracy of models using both the traditional approach with real species and the simulated species approach.

There are many different techniques available for modelling species distributions. A number of studies have compared the accuracy of different techniques using data for real species. In the most comprehensive of these studies, Elith *et al.* (2006) compared the ability of 16 techniques to model the distributions of species from several regions around the world, finding that some techniques were consistently better than others. Similar tests using simulated data have been much less frequent (Moisen & Frescino 2002; Meynard & Quinn 2007) and have generally supported the results of studies using data for real species. In this chapter, I focus on four techniques (Table 3.1) commonly used for modelling species distributions (e.g. Elith *et al.* 2006). The chosen techniques are only a small subset of the many that are available. Some of the other techniques were discussed in Chapter 2.

Table 3.1 – Comparison of the four model types used in this study, including their strengths, weaknesses and performance in previous studies.

Model	Advantages	Disadvantages	Relative accuracy
Maxent (Phillips *et al.* 2006)	Requires little technical skill.	Output parameters difficult to interpret.	Very good [2].
Generalized Linear Models (GLMs) (McCullagh & Nelder 1989)	Output easily interpretable parameters.	Require records of species presence and species absence. Require some statistical skill.	Very good [3].
BIOCLIM (Nix 1986)	Requires only records of species presence. Requires little technical skill.	Tends to over-predict actual distributions.	Generally poor [4].
Genetic Algorithm for Ruleset Process (GARP) (Stockwell & Noble 1992; Stockwell & Peters 1999)	Combines climate envelopes and regression-based statistics for greater flexibility.	Output parameters difficult to interpret. Tends to over-predict known distributions.	Mixed but generally very good [5].

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[2] (Elith 2002; Phillips *et al.* 2006)
[3] (Hirzel *et al.* 2001; Guisan *et al.* 2002; Moisen & Frescino 2002; Austin *et al.* 2006; Elith *et al.* 2006; Meynard & Quinn 2007)
[4] (Elith 2002; Elith *et al.* 2006; Tsoar *et al.* 2007)
[5] (Feria & Peterson 2002; Joseph & Stockwell 2002; Peterson *et al.* 2002; Anderson *et al.* 2003; Peterson & Robins 2003)

How best to evaluate the accuracy of species distribution models is an issue that has received considerable attention in the literature. The simplest approach, and one that has been used frequently in distribution-model studies, is to test the ability of models to predict the data that were used to build them (Fielding & Bell 1997). This is effectively a measure of the goodness-of-fit of the model. The main drawback of this approach is that models can fit the training data very closely without having any ecological meaning (model overfitting); this will lead to over-optimistic accuracy estimates (Chatfield 1995). An alternative is to split the species records randomly into model-training and model-evaluating datasets (Fielding & Bell 1997). However, if these datasets are drawn from the same original survey and the data in this survey are biased in environmental space, then the resulting model will also be biased and the accuracy measure will be inflated (Fielding & Bell 1997). Ideally, models should be tested using a completely independent and unbiased dataset (Chatfield 1995). Few studies have used this approach as it can be impractical, time-consuming and costly (Wintle *et al.* 2005, but see, e.g., Loyn *et al.* 2001; Elith 2002; Ferrier *et al.* 2002). I test models for Egyptian butterfly, mammal and reptile species using independently-collected survey data in Chapter 7. Some authors have experimented with building models using species records from one area, and then testing them against records from another area (Fielding & Haworth 1995; Özesmi & Mitsch 1997; Peterson & Shaw 2003; Randin *et al.* 2006; Heikkinen *et al.* 2007; Vanreusel *et al.* 2007; Syartinilia & Tsuyuki 2008). Accuracy estimates were generally much lower when the models were tested against data from the new as opposed to the original areas (but see Vanreusel *et al.* 2007). This could be because tests using geographically distinct data present a genuinely more rigorous assessment of model quality, or more likely because splitting the data in this way restricts the range of environmental conditions covered by the data used to build the model. Different methods for evaluating models have never been compared using simulated data.

For many species, especially those of most concern for conservation, recorded occurrences are few to very few in number. The sample size needed to build accurate distribution models is an issue that needs addressing. Several studies have investigated the effect of sample size on small numbers of different models or for small numbers of species. Pearce & Ferrier (2000a) reported a large increase in the accuracy of GLMs between sample sizes (i.e. presences + absences) of 50 and 250, with smaller increases thereafter; Maxent models with 50 to 100 presences are nearly as accurate as those with 1000 (Phillips *et al.* 2004); and GARP has been reported to predict distributions successfully with fewer than ten points (Peterson & Robins 2003) (but in this case 'success' was evaluated not using AUC, but by testing whether real presences fell into areas of predicted presence more often than expected by chance – testing a very different aspect of model performance). The issue of sample size has received little attention in studies using simulated species data (but see Hirzel & Guisan 2002; Meynard & Quinn 2007).

Many models assume that species will show simple linear or Gaussian (bell-shaped) responses to the environmental variables (Austin 2002). However, theory predicts that more complex responses to the environment will be common, for example through the effect of biotic interactions (Austin 2002). Therefore, the ability to handle complex responses may be very important for the accurate modelling of species' distributions. GLMs and Maxent models can be fitted using polynomial and interaction terms, but the complexity of the model is driven by the user (McCullagh & Nelder 1989; Phillips *et al.* 2006). GARP is more flexible, using a machine-learning approach to select the variables and the complexity of response that best predicts the data (Stockwell & Peters 1999); up to a point this may allow it to make more accurate distribution models when the species in question responds to its environment in a more complex fashion (Guisan *et al.* 2002), but ultimately the complexity of the response shape is constrained by the design of the software. Although increasing the complexity of models can capture the observed environmental responses of species more closely, it also increases the risk that the model will be overfitted (Chatfield 1995).

The choice of environmental variables used to build distribution models may also significantly affect their accuracy, an issue that has received little attention in the literature (but see Peterson & Nakazawa 2008). The most accurate models, and those that capture most closely the real ecological response of species, are built with variables that directly influence distributions (Austin 2002; Austin *et al.* 2006). However, such variables are rarely available in a suitable format and ecologists must often use variables that affect species' distributions indirectly. There are many different variables that can determine the distribution of a species (Hutchinson 1957), but using too many in a model will lead to overfitting. Furthermore, environmental variables are often very highly correlated with each other, which can lead to variables that do not have a causal effect on the distributions of species being selected by models (Guisan *et al.* 2002). One solution is to use only variables that show weak relationships with each other (Loyn *et al.* 2001; Engler *et al.* 2004; Lütolf *et al.* 2006). However, this requires variables to be selected subjectively and there is the danger that important variables will be excluded in favour of variables that have only an indirect effect on species. A better solution to the problem is to use principal components analysis to reduce the environmental variables to a set of uncorrelated variables (Manel *et al.* 1999a; Manel *et al.* 2001). This method has been used very little in species distribution modelling, despite its obvious benefits.

In this chapter, I test a number of factors that potentially could influence the accuracy of species distribution models using data for simulated species, and also for real butterfly species in Egypt. Using the simulated data, I test the effects of sample size, model type, complexity of species response to the environment, method of reserving test data, and interactions between these factors on the accuracy of models. Using data for real species, I test the effects of sample size, model type, choice of independent variables, and their interactions. Species distribution models are very powerful tools for conservation and ecology and understanding the factors that affect their accuracy is crucial for their successful application. Using simulated data allowed me to compare models with known distributions, while comparing models for real species introduced a degree of ecological realism that can be lacking in simulated data.

3.3 Methods

3.3.1 Simulated data

I simulated the distributions of three species within the real landscape of Egypt. These virtual species responded to three environmental variables taken from the WorldClim Version 1.4 dataset at a resolution of 30 arc seconds: elevation, annual mean temperature and annual precipitation (Hijmans *et al.* 2005). Maps of environmental suitability were created using the following basic function:

$$ES = \frac{1}{1+e^{-x}},$$

where *ES* is environmental suitability and *x* is a function describing the response of the species to the three environmental variables. This function *x* was varied to give three species with differing complexities of response to the environment (Table 3.2). Coefficients were chosen to give the maximum possible range of suitability values between 0 and 1 for each species. The responses of the simulated species to each of the environmental variables are given in Appendix 3.1. These responses were not intended to match those seen for real species, but rather to present the models with responses of varying degrees of complexity.

Table 3.2 – Functions used as the linear predictor (x) in a logistic regression equation ($1/(1+e^{-x})$) to generate environmental suitability maps for three simulated species with differing complexities of response to the three environmental variables: elevation (alt), annual mean temperature (temp), annual precipitation (prcp).

Response complexity	Linear predictor (x)
Linear	(0.01 x alt) – (0.01 x temp) – (0.1 x prcp)
Quadratic	(0.01 x alt) – (10^{-5} x alt^2) + (0.1 * temp) – (10^{-5} x $temp^2$) + (0.1 x prcp) – (10^{-3} x $prcp^2$) – 19.36
Cubic	(0.01 x alt) – (10^{-5} x alt^2) + (10^{-8} x alt^3) + (0.1 x temp) – (10^{-4} x $temp^2$) + (10^{-6} x $temp^3$) + (0.1 x prcp) – (10^{-3} x $prcp^2$) + (10^{-6} x $prcp^3$)

I generated a set of 4000 random points to serve as hypothetical sampling locations within the borders of Egypt using ArcMap 9.1. For each model, I assigned recorded presence or absence to these sites by generating a random number between 0 and 1 for each. If this number was less than the environmental suitability for the site then the species was deemed to be present. If the random number was greater, the species was deemed to be absent. This process added some noise to the relationships; noise would almost certainly be present in real ecological datasets.

Eight different model types were considered: Maxent (Phillips *et al.* 2006) with either linear features (1: Maxent L), linear and quadratic features (2: Maxent Q), linear, quadratic and product features (3: Maxent P), or threshold features only (4: Maxent T); a climate envelope model (5: BIOCLIM, Nix 1986); generalized linear models (McCullagh & Nelder 1989) with either linear terms (6: GLM L) or linear and quadratic terms (7: GLM Q); and the Genetic Algorithm for Rule-set Process (8: GARP) (Stockwell & Noble 1992). GLMs were fitted with binomial errors and the logit link. Variables were selected using the ‘step’ function (Venables & Ripley 2002) in R (R Development Core Team 2004), an automated backward stepwise function based on Akaike’s Information Criterion. For the GARP models, 100 replicates were made for each dataset. The best models were selected using an adaptation of the “best subsets” method (Anderson *et al.* 2003), as follows. For each replicate, I calculated omission (the percentage of grid cells containing presence records used to build the model that were incorrectly predicted by the model as absences) and commission (the percentage of all grid cells without a presence record that were predicted as containing the species). First, all model replicates with omission greater than 10% were removed. Second, if more than ten replicates remained, the mean commission of these remaining replicates was calculated and the ten with commission values closest to this mean were retained as the best subset. Otherwise, all the remaining replicates were retained. The number of replicates in the best subset that predicted a given grid cell as containing the species in question was used as a measure of predicted suitability.

Three methods were used to divide the data into model-building and model-evaluating partitions. First, the data were randomly divided in half; one half was used for both model building and model evaluation and the second half was discarded. Second, the data were randomly divided in half; one half was used for model building and the other was used for model evaluation. Third, the data were divided in half geographically by dividing Egypt into four quarters along 31^{o}E and 27.75^{o}N; data from the northeast and southwest quarters were used for model building and data from the northwest and southeast quarters were used for model evaluation. The land area was approximately equal in both pairs of quarters.

To test the effects of sample size on model accuracy, I randomly reduced the model-building datasets by 99%, 90%, 50% or 0% to give groups of datasets with means of 10, 103, 513 and 1027 presence records. The model-evaluation datasets were not reduced in size.

For each combination of response complexity, model type, test data type and sample size, I generated ten models, making overall a total of 2880 models. The ability of models to predict the model-evaluation dataset was tested using the AUC statistic (Fielding & Bell 1997), calculated using the trapezoid method (Pearce & Ferrier 2000b); full details are given in Chapter 2. For Maxent and GLM models, sensitivity (the proportion of presences from the evaluation dataset correctly predicted as being present) and commission (the proportion of absences incorrectly predicted as being present) were calculated at 100 thresholds spread evenly throughout the output range. For BIOCLIM models, I used one threshold for each predicted suitability category (unsuitable, low, medium, high, very high and excellent). For GARP models, I used the number of replicates in the best subset that predicted a pixel as being occupied as the thresholds.

Concerns have recently been voiced over the validity of the AUC statistic as a measure of model accuracy (Lobo *et al.* 2008). To test its consistency and to provide an alternative measure of model performance, I calculated a second accuracy statistic. Across a random sample of 2000 grid squares in Egypt, using Spearman's rank correlation I related environmental suitability as predicted by the models with 'true' environmental suitability calculated using the original response functions. The correlation coefficients were used as an estimate of model accuracy, henceforth referred to as 'correlation-with-truth' values. Since correlation-with-truth is derived from the known distribution of the simulated species, I would expect it to be a more reliable measure of model accuracy.

3.3.2 Butterfly data

To test the effects of model type, choice of independent variables and sample size on the accuracy of distribution models for real species, I selected three species from the BioMAP database of Egyptian butterflies. These species were chosen to provide as representative a sample of the Egyptian butterfly fauna as possible. *Colias croceus* is a non-endemic, generalist species that is both resident and migratory in Egypt (Gilbert & Zalat 2007). *Pseudophilotes sinaicus* is an endemic, resident species that specializes on just one host plant, the Sinai thyme *Thymus decussatus* (James *et al.* 2003; Gilbert & Zalat 2007). *Zizeeria karsandra* is a non-endemic, generalist species; populations in Egypt are entirely resident (Gilbert & Zalat 2007).

I compared the same eight model types as for the simulated data. The real species data contained no absence records. For the GLMs, which required absences as well as presences, I generated 2500 random pseudo-absences (Zaniewski *et al.* 2002) in grid cells that did not contain a presence record for a given species. As before, variables were selected for the GLMs using the 'step' function in R (Venables & Ripley 2002); for all other model types, I used exactly the same parameters and methods as for the simulated data.

Three sets of independent variables were tested for their effect on model accuracy. First, I used four principal components describing the 19 bioclimatic variables and elevation from the WorldClim 1.4 dataset (Hijmans *et al.* 2005); for details of the methods I used to generate these variables, see Chapter 2. Second, the full set of bioclimatic variables and elevation from WorldClim were used. Third, the four principal components were combined with a categorical variable describing land cover (Hansen *et al.* 2000). Land cover was classified into 13 categories (needleleaf evergreen forest, broadleaf evergreen forest, needleleaf deciduous forest, broadleaf deciduous forest, mixed forest, woodland, wooded grassland, closed shrubland, open shrubland, grassland, cropland, bare ground and urban areas) using a decision tree, based on data from the Advanced Very High Resolution Radiometer (Hansen *et al.* 2000). All variables had a resolution of 30 arc-seconds.

Ten separate models were built for each combination of species, model type and set of independent variables, a total of 720 models. For each of these, the occurrence records for the species in question were divided randomly in half for model building and model evaluation. This gave different numbers of presence records for each model, allowing a test of the effect of sample size on model accuracy.

3.3.3 Statistical analysis

For the simulated species, to test the agreement of the AUC statistic with the correlation-with-truth values, I correlated the two across all models. To test factors affecting the accuracy of distribution models, separate analyses were constructed with AUC values and correlation-with-truth values as the dependent variables respectively. The following factors were tested for their effect on model accuracy: model type, complexity of the response of simulated species to the environmental variables, test data type and number of presence records (grouped according to the average proportion by which the datasets were reduced). All two-way interactions were tested. Terms were removed in a backward stepwise procedure following the method of Crawley (2002) to obtain the 'minimum adequate model'. Two-way interactions were tested first, then removed to test the main effects. Post-hoc comparisons were carried out using Tukey's tests.

To investigate factors influencing the accuracy of models for the real butterfly species, a single analysis of covariance was constructed with AUC values as the dependent variable. Model type, set of independent variables used and species identity were considered as factors. Number of presence records was entered as a covariate. All two-way interactions were considered. Post-hoc comparisons were carried out using Tukey's tests.

3.4 Results

3.4.1 Simulated data

Across all models, the two measures of model accuracy agreed strongly ($r_s = 0.761$, $n = 2843$, $P < 0.001$).

Results of the analysis of factors affecting distribution model accuracy were the same whether AUC values or correlation-with-truth values were used to measure model accuracy. Therefore, I only present results using correlation-with-truth values here. All factors and their two-way interactions had a significant effect on model accuracy (Table 3.3). Overall, there was a significant difference in model accuracy among model types (Table 3.3). From most accurate to least accurate, models ranked as follows: GLM Q> GLM L> Maxent Q> Maxent P> Maxent L> Maxent T> GARP> BIOCLIM. Post-hoc tests showed that all pairwise comparisons were significant ($P < 0.05$). Unsurprisingly, models that fitted quadratic terms (GLM Q, Maxent Q and Maxent P) were relatively better for species that showed quadratic responses to the environment (Figure 3.1). The effect of model type on prediction accuracy also varied among test data types. Models that fitted more complex terms (Maxent P and Maxent T) performed relatively poorly when geographically-separated test data were used to evaluate the models (Figure 3.2). Finally, the effect of model type varied with sample size (number of presence records). With the smallest sample sizes, models fitting simpler terms (Maxent L, Maxent T and GLM L) performed the best, whereas with larger sample sizes - above 100 presence records - models fitting more complex terms (Maxent Q, Maxent P and GLM Q) performed better (Figure 3.3).

Table 3.3 - Results of an analysis of covariance testing the effects of model type, complexity of species' response to the environmental variables, type of data used to evaluate models and sample size on model accuracy, measured using correlation with truth values. Terms were removed in a backward stepwise fashion following the method of Crawley (2002). Two-way interactions were tested first and then removed in order to test the main effects.

Term	F	d.f.	P
Model Type	370	7, 2828	< 0.001
Response Complexity	753	2, 2828	< 0.001
Test Data Type	275	2, 2828	< 0.001
Number of Presence Records	553	3, 2828	< 0.001
Model x Complexity	40.7	14, 2763	< 0.001
Model x Test Data	30.4	14, 2763	< 0.001
Model x Presences	30.3	21, 2763	< 0.001
Complexity x Test Data	68.0	4, 2763	< 0.001
Complexity x Presences	23.6	6, 2763	< 0.001
Test Data x Presences	23.8	6, 2763	< 0.001

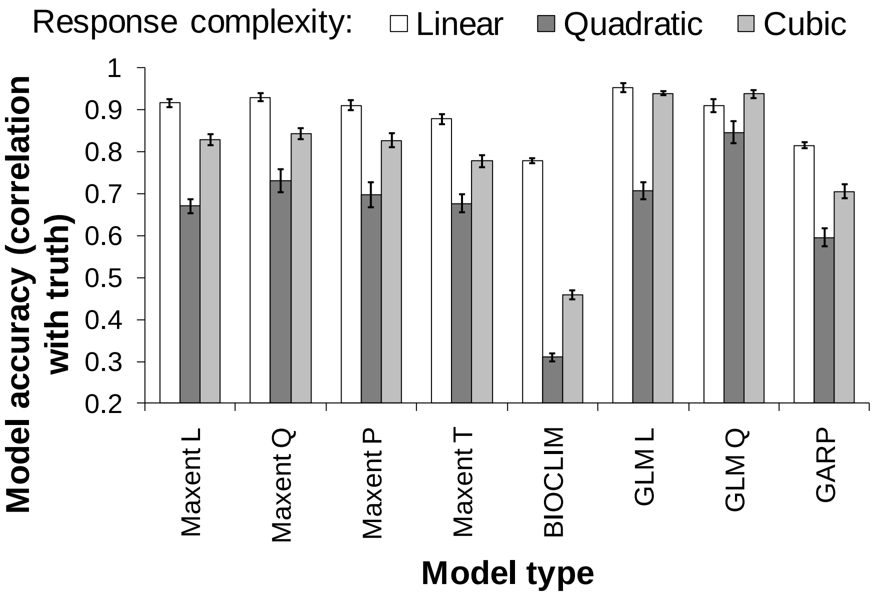

Figure 3.1 – Interaction between model type and the complexity of species' response to the environmental variables in determining the accuracy of distribution models, as measured using correlation with truth values.

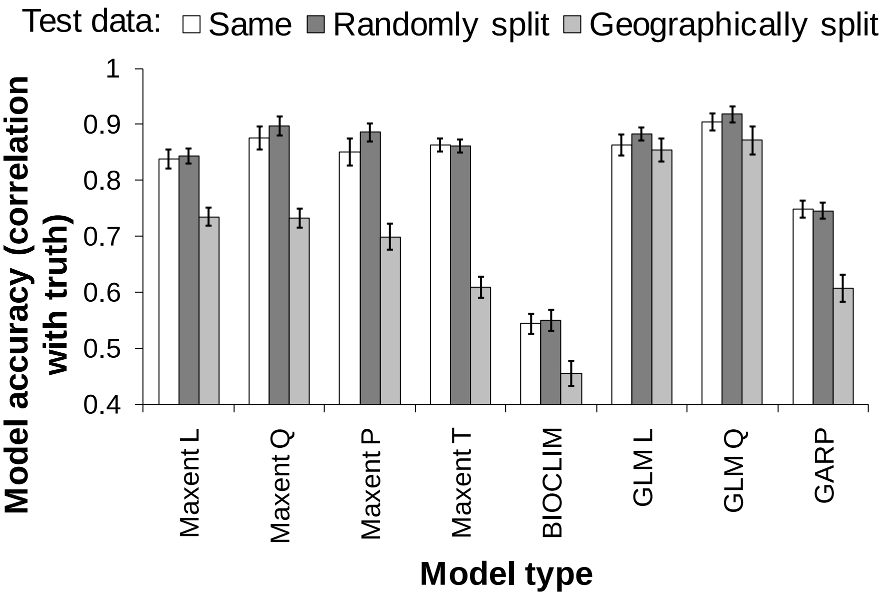

Figure 3.2 - Interaction between model type and test data type in determining the accuracy of distribution models, as measured using correlation with truth values.

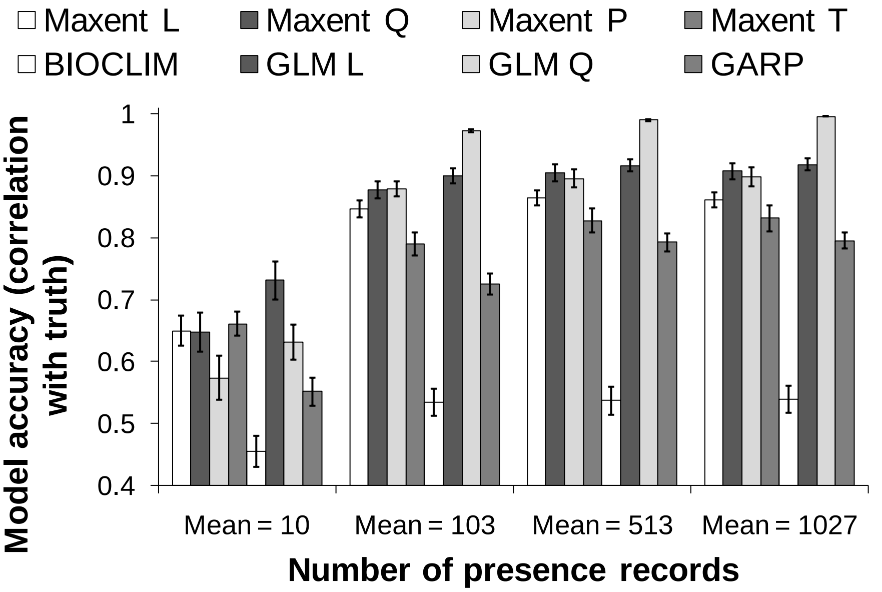

Figure 3.3 - Interaction between sample size and model type in determining the accuracy of distribution models, as measured using correlation with truth values.

Overall, model accuracy varied significantly among simulated species with different complexities of response to the environmental variables (Table 3.3). The simulated species with linear responses was modelled most accurately, followed by the species with cubic responses, and finally by the species with quadratic responses. Post-hoc comparisons showed that all pairwise comparisons were significant. The effect of response complexity interacted significantly with all other factors. Estimates of model accuracy were very low when the models were evaluated against geographically-separated test data for simulated species with quadratic responses and, to a lesser extent, cubic responses (Figure 3.4). The magnitude of differences among different response complexities reduced with larger sample sizes (Figure 3.5).

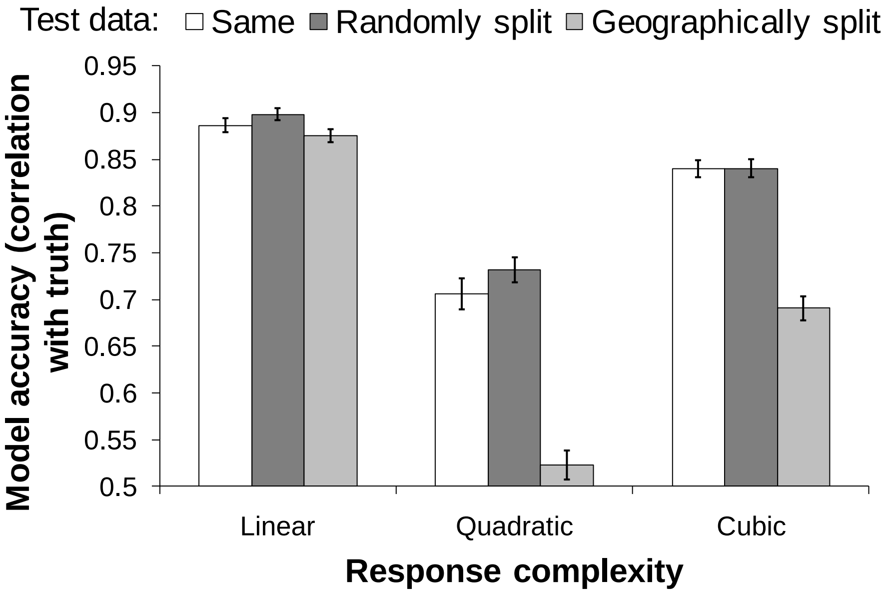

Figure 3.4 - Interaction between the complexity of species' response to the environmental variables and test data type in determining distribution model accuracy, as measured using correlation with truth values.

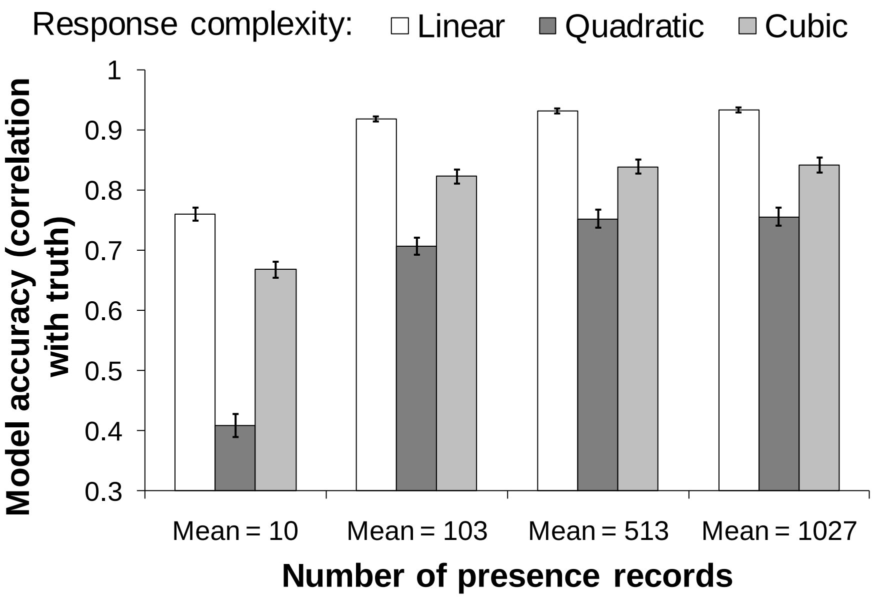

Figure 3.5 - Interaction between sample size and the complexity of species' response to the environmental variables in determining distribution model accuracy, as measured using correlation with truth values.

Test data type had a significant effect on estimates of model accuracy. Models that were evaluated against randomly-split test data had the highest estimates of model accuracy, followed by models evaluated against the data used to build them, and finally by models tested against geographically-split data. Post-hoc tests showed that all pairwise comparisons were significant. The effect of test data type interacted significantly with all other factors. The interactions with model type and response complexity have been described previously. The magnitude of the difference in model-accuracy estimates between geographically-split test data and other types of test data increased with increasing sample size (Figure 3.6).

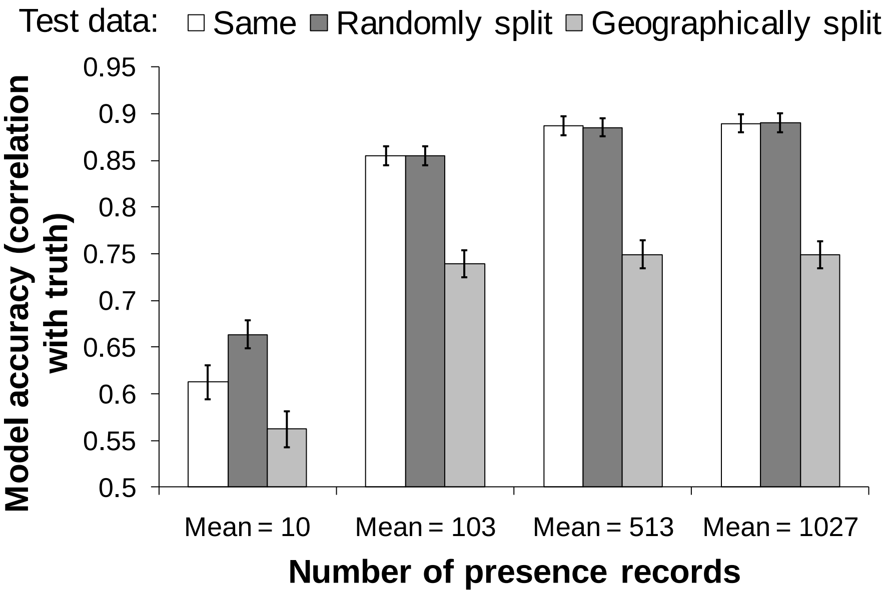

Figure 3.6 - Interaction between sample size and test data type in determining the accuracy of distribution models, measured using correlation with truth values.

3.4.2 Butterfly data

Sample size, model type, set of variables used and species identity all had a significant effect on the accuracy of butterfly distribution models (Table 3.4). Sample size (number of presences) had a small but significant positive effect on model accuracy (Figure 3.7). None of the other factors tested showed significant interactions with sample size.

Table 3.4 - Results of an analysis of covariance testing the effects of sample size (number of presences), model type, set of independent variables used and species identity on the accuracy of distribution model predictions for butterflies. Variables were removed in a backward stepwise fashion following the method of Crawley (2002). Two-way interactions were tested first, and then removed to test the main effects.

Term	F	d. f.	P
Number of Presence Records	7.21	1, 626	0.00744
Model Type	38.0	7, 626	< 0.001
Variables Fitted	11.0	2, 626	< 0.001
Species Identity	81.9	2, 626	< 0.001
Presences x Model	0.899	7, 587	0.507
Presences x Variables	1.58	2, 594	0.208
Presences x Species	0.300	2, 585	0.741
Model x Variables	14.5	13, 596	< 0.001
Model x Species	5.48	13, 596	< 0.001
Variables x Species	25.0	4, 596	< 0.001

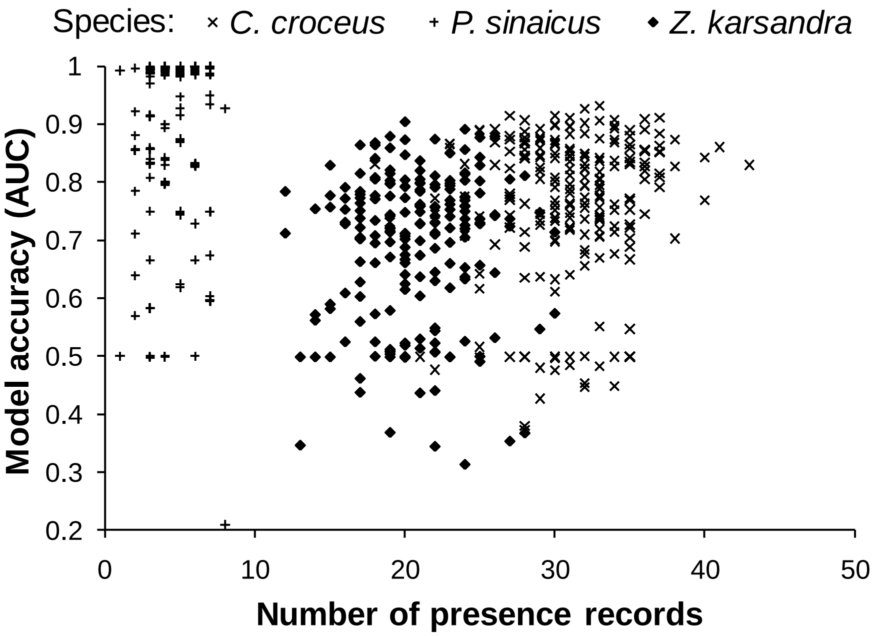

Figure 3.7 - The relationship between sample size (number of presence records) and the accuracy of distribution models for each of the three butterfly species considered, measured used the AUC statistic.

Model accuracy varied significantly among model types. This effect showed a significant interaction with choice of independent variables (Figure 3.8). Maxent and GARP models performed similarly well with all three sets of variables. The GLMs were much worse when fitted with the full set of climate variables than when fitted with principal components based on these variables. Conversely, BIOCLIM produced better models with the full set of variables than with the principal components. The effect of model type also interacted with species identity (Figure 3.9). The magnitude of differences in model accuracy among species was much greater for some model types (Maxent L, Maxent Q, BIOCLIM and both GLMs) and less for others (Maxent P, Maxent T and GARP).

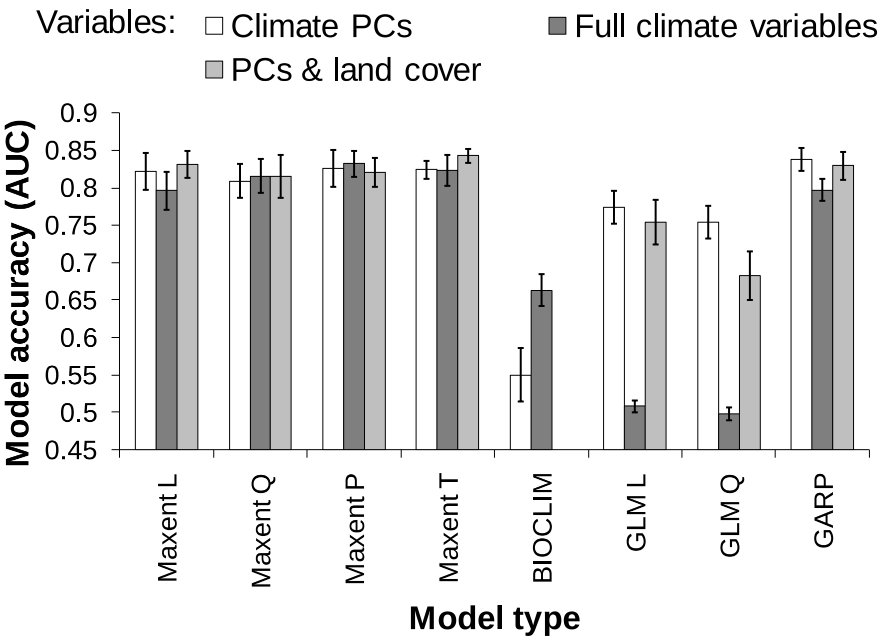

Figure 3.8 - Interaction between model type and set of independent variables used in determining the accuracy of butterfly distribution models, measured using the AUC statistic. BIOCLIM was unable to handle categorical variables so the land cover variable was not used for these models.

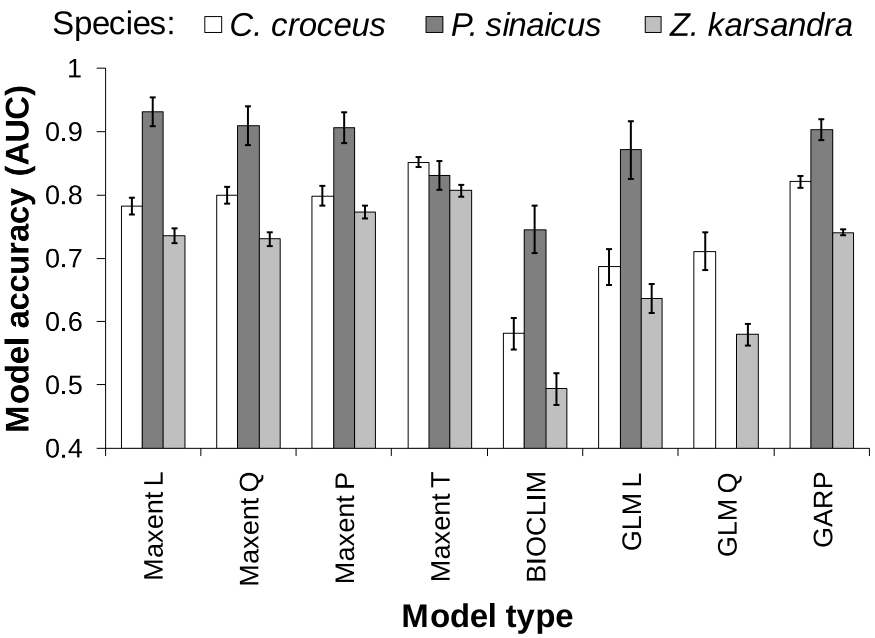

Figure 3.9 - Interaction between model type and species identity in determining the accuracy of species distribution models for three butterfly species, as measured using the AUC statistic.

Model accuracy differed significantly when different sets of independent variables were used to build the models. The highest accuracy was achieved by models that used land cover and the four principal components describing climate, followed by models that used the four principal components alone, and finally by models that used the full set of climatic variables (without land cover). Post-hoc tests revealed that all pairwise comparisons were significant. The effect of choice of independent variables on model accuracy showed a significant interaction with species identity (Figure 3.10). Including land cover markedly increased the accuracy of models for *Colias croceus* and, to a lesser extent, *Zizeeria karsandra*. For *Pseudophilotes sinaicus*, climate alone produced the best models, with the principal component variables yielding higher accuracy than the full set of climate variables.

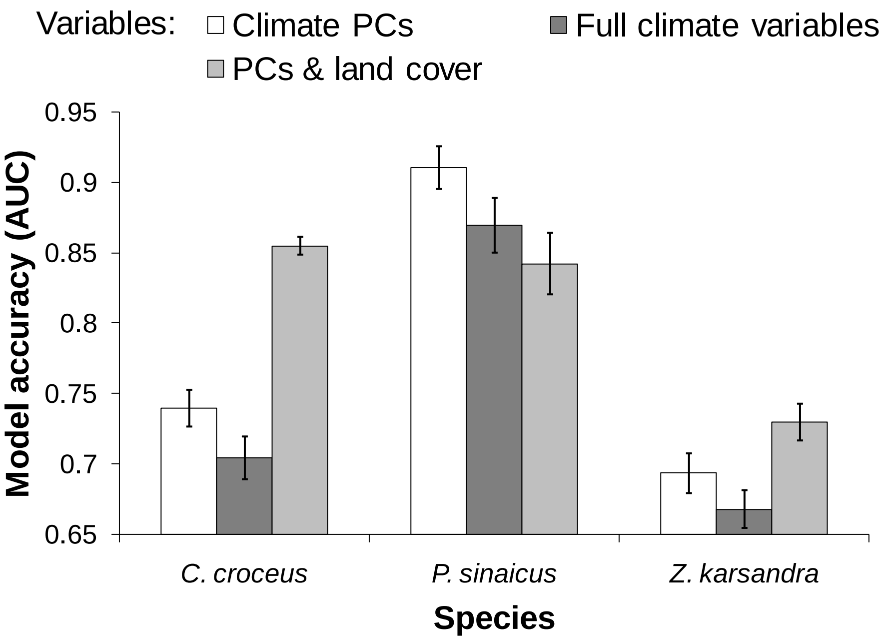

Figure 3.10 - Interaction between species identity and choice of independent variables in determining the accuracy of distribution models for real species, as measured using the AUC statistic.

3.5 Discussion

Overall, the models used were able to capture simulated and real species distributions with a high degree of accuracy. They were first tested using data for simulated species. Since the 'true' distribution for these species was known, this enabled a more rigorous test of model performance. However, simulating distributions required assumptions to be made about the way that species respond to their environment and this necessarily meant simplifying reality. Therefore, I also tested the models using data for real species. In both cases, across all treatments, the models performed very well. Nevertheless, I identified a number of factors that had a strong effect on model accuracy.

The results supported the use of the AUC statistic as a measure of model accuracy. This statistic has come under increasing criticism recently (Austin 2007; Lobo *et al.* 2008). However, the agreement between the predicted and the true distributions was, at least for simulated species, estimated very well by the AUC. It is important to note that the data for simulated species used both to build and evaluate the predictions contained real presence and real absence records. One of the major concerns over the use of the AUC statistic is that it may be inflated when the evaluation data contain absence records from outside the environmental space within which the presence records fall, a situation particularly likely to occur when pseudo-absence records are used (Lobo *et al.* 2008). A more rigorous test of the AUC statistic using simulated data under a variety of conditions likely to be encountered in real modelling exercises would be timely.

My results support previous studies (e.g. Elith *et al.* 2006) in showing a significant effect of choice of modelling technique on the accuracy of distribution predictions. Maxent has previously been shown to perform very well compared with other modelling techniques (Phillips *et al.* 2004; Elith *et al.* 2006; Phillips *et al.* 2006). In this study, it produced very accurate predictions both for simulated and real species. Maxent models are quick and relatively straightforward to build, making them a good choice for most modelling exercises. GLMs also performed very well with simulated data, but performed relatively poorly with data from real species. This result is probably a reflection of the automated variable selection technique used with the GLMs. Simulated species responded to just three environmental variables, and models for these species were fitted with the same three variables. Real species, on the other hand, respond to a wide variety of variables. The models for real species were fitted with 21 environmental variables, which probably included some of the determinants of the distributions as well as some other irrelevant variables. Automated variable-selection methods have been shown to be prone to exclude relevant variables and include irrelevant ones (Derksen & Keselman 1992; Wintle *et al.* 2005). The poor performance of GLMs with real species may therefore have been because the wrong variables were selected for the final models. This is further supported by my finding that GLMs fitting the full set of environmental variables, where the variable-selection routine was forced to choose among many inter-correlated variables, were much less accurate than GLMs fitting the principal components based on these climate variables. The lower accuracy of GLMs with real species data may also have been because I included a categorical variable describing land cover. Stockwell & Peterson (2002) found that GLMs did not handle categorical variables very well. Another possible reason for the poor performance of GLMs is overfitting, where the model fits the data used to build it very closely at the expense of the ability to generalise (Chatfield 1995). Real ecological data are very noisy, making overfitting more likely (Ginzburg & Jensen 2004). By comparison, the simulated data were simple and contained relatively little noise. Maxent includes a process called regularization that reduces the chance that the model will overfit the data (Dudík *et al.* 2004).

BIOCLIM is among the most accessible of the available techniques and is still widely used to model distributions (e.g. Penman *et al.* 2005; Richardson *et al.* 2006). However, at least at the small scale of this study, BIOCLIM appears to be among the least accurate modelling techniques. Other comparisons of modelling techniques have also found it to be among the poorest at modelling distributions (e.g. Elith *et al.* 2006; Tsoar *et al.* 2007). One might expect better results with Gaussian (bell-shaped) responses to environmental gradients, where species points fall within an envelope of suitable conditions. However, BIOCLIM models of the distribution of the simulated species with these types of responses were very poor. In previous studies, GARP has been shown to predict the distributions of real species very well (Feria & Peterson 2002; Peterson *et al.* 2002b; Peterson *et al.* 2002c), although Elith *et al.* (2006) found it to perform relatively poorly. In this study, GARP models were highly accurate for real species but were among the least accurate predictions for simulated species. This may be because simulated and real species differed in the complexity with which they responded to the environmental variables. It has been suggested that real species will show complex responses to the environment (Austin 2002). The flexibility of the GARP algorithm allows it to fit more complex relationships to the data than other model types do (Guisan *et al.* 2002; Sánchez-Flores 2007). On the other hand, Maxent and GLM models for real species produced accurate predictions fitting only linear and quadratic terms.

The results for simulated species showed that the distributions of species with quadratic responses were modelled less accurately than the distributions of species with either linear or cubic responses. The quadratic responses were roughly bell-shaped and consequently the least linear of the three functions. The cubic simulation, on the other hand, gave sigmoidal responses to the environmental variables, which could be approximated reasonably well by linear relationships. Unsurprisingly, Maxent and GLM models that fitted quadratic terms performed relatively better with quadratic simulations than those fitting only linear terms. GARP also performed reasonably well with quadratic data. Several different types of relationships between species occurrences and the environment (including logistic regression and envelopes) are considered in GARP models, which may allow it to fit more complex relationships (Guisan *et al.* 2002). I did not simulate species with more complex skewed or bimodal responses. Creating simulated species with more realistic responses to the environment is a possibility that deserves further attention.

It is important to know the sample size needed to produce accurate models. In my simulations, all model types achieved nearly maximum AUC values and correlation-with-truth coefficients by the second group of sample sizes, which had a minimum of 68 presences. Conversely, the most accurately modelled real butterfly species was the one that had the fewest records. Ecological characteristics of species may determine how accurately their distributions can be modelled (e.g. Hernandez *et al.* 2006), a topic that will be dealt with in Chapter 4. Within species, there was a positive effect of sample size on distribution model accuracy. Taken together, these results suggest that, for a given species, more complete sampling results in better distribution models. However, among species this effect is masked by differences unrelated to sample size.

It has been suggested by several authors that evaluating models using the training data will lead to over-optimistic measures of model performance (e.g. Chatfield 1995; Fielding & Bell 1997). This suggestion was not supported by the results for simulated species. However, I did not incorporate any of the biases that are commonly seen in real species data. Where such biases exist, testing the models using independent data from new surveys may be more important. Some authors have suggested that testing models with spatially-isolated test data could give more informative measures of model performance (Fielding & Haworth 1995; Özesmi & Mitsch 1997; Peterson & Shaw 2003; Randin *et al.* 2006; Heikkinen *et al.* 2007; Vanreusel *et al.* 2007; Syartinilia & Tsuyuki 2008). My results do not support this idea: lower AUC scores and correlation-with-truth coefficients suggest that models trained using data not covering the entire range of environmental conditions were less accurate than models trained using a complete dataset.

Using too many independent variables to build models can result in overfitting of the data (Chatfield 1995). Furthermore, environmental variables are often highly correlated with each other. Including correlated variables in models can result in important variables being missed in favour of variables that do not have a direct effect on the distribution of a species (Guisan *et al.* 2002). As an alternative, I generated a small set of uncorrelated independent variables using principal components analysis. GLMs made using these principal component variables were significantly better than GLMs made using the full set of climatic variables. However, there was no improvement in Maxent and GARP models using the principal component variables, suggesting that these techniques are more robust to overfitting. BIOCLIM models were better when the full set of variables was used probably owing to the envelope method that it uses; using too few predictors will result in overprediction.

The effect of including a categorical variable describing land cover on the accuracy of butterfly distribution models varied according to the species in question. For the Sinai baton blue *Pseudophilotes sinaicus*, including land cover did not significantly improve the model predictions. This species is restricted to a very small range in a single habitat type in the high mountains of the Sinai, and the bioclimatic variables were probably sufficient to explain its distribution. On the other hand, models for the dark grass blue *Zizeeria karsandra* were improved slightly and models for the clouded yellow *Colias croceus* were improved dramatically by considering land cover. Butterflies rely on plants for food. Thus although *Colias croceus* and *Zizeeria karsandra* are relatively generalist in their preference for host plants, both feeding on a wide variety of legumes (Gilbert & Zalat 2007), it is not surprising that land cover was such a good correlate of their distributions. The importance of habitat and land cover for butterfly species is well established (Araújo & Luoto 2007; Kivinen *et al.* 2007; Kuussaari *et al.* 2007; Menéndez *et al.* 2007).

Species distribution models have great potential as tools in conservation ecology and they are already being used to guide efforts to preserve biodiversity. Therefore, it is crucial that we refine their predictions to produce the most accurate representation of reality. This study has highlighted some important considerations for the development of accurate species distribution models. I have shown that several factors, and critically their interactions, have substantial effects on the accuracy of models. Real species are likely to show more complex relationships with their environments than I used here for simulated species, and will almost certainly be affected by other factors (such as interactions with other species and dispersal limitation), which makes such issues even more important. Simulating species data allows us to address questions about model performance that would be impossible for real species, and together with empirical studies will advance our understanding of the value of models of species distributions.

Chapter 4. The effect of characteristics of species on the accuracy of distribution models for Egyptian butterfly species[6]

4.1 Abstract

The accuracy of distribution models has been shown to vary markedly among species. This variation may be explained by ecological characteristics of the species. In this chapter, I test the effect of five characteristics (local range size, global range size, migratory behaviour, host-plant specialization and niche breadth) of Egyptian butterfly species on the accuracy of distribution models, the first such comparison for butterflies in an arid environment. Unlike most previous studies, I perform independent contrasts to control for species relatedness. I show that range size, both globally and locally has a negative effect on model accuracy. The other three characteristics tested did not have a significant effect on model accuracy. The results reveal important differences among species in the way that their distributions respond to the environment and have relevance for attempts to model accurately the distribution of different species.

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[6] A modified version of this chapter was published in *Biodiversity & Conservation*

4.2 Introduction

Many studies have compared the accuracy of models made by different species distribution modelling techniques, often finding that many techniques perform similarly well (Elith *et al.* 2006; Hernandez *et al.* 2006; Phillips *et al.* 2006). In fact, there may be more variation in model accuracy among species than among modelling techniques (Berg *et al.* 2004; Elith *et al.* 2006). As a result, whether the characteristics of species affect the accuracy of distribution models is a question receiving increasing attention in the literature. This is an issue of great interest to ecologists because it suggests that species differ fundamentally in the way that their distributions are determined by the environment, with important implications for niche theory.

The breadth of a species' niche has often been considered when trying to explain differences in model accuracy among species. Species with narrow, well-defined niches seem to be better modelled than those with broader niches (Boone & Krohn 1999; Pearce *et al.* 2001; Kadmon *et al.* 2003; Berg *et al.* 2004) and models for specialist species are generally more accurate than models for generalists (Hepinstall *et al.* 2002; Segurado & Araújo 2004; Elith *et al.* 2006). This is probably because species with narrow niches generally have better-defined climate and habitat requirements, which are easier to model (Kadmon *et al.* 2003). The breadth of a species' niche relative to the environmental conditions found in the study area as a whole may influence model accuracy more than niche breadth *per se* (Seoane *et al.* 2005; Hernandez *et al.* 2006). More marginal species (i.e. those that have niches furthest from the average conditions of the study area) are modelled more accurately than less marginal species, probably for similar reasons (Luoto *et al.* 2005; Seoane *et al.* 2005; Carrascal *et al.* 2006; Hernandez *et al.* 2006). One would expect therefore that the accuracy of species distribution models will decrease with increasing niche breadth.

Models for species with narrow distributions in geographical space are more accurate than models for species with larger distributions (Stockwell & Peterson 2002; Brotons *et al.* 2004; Segurado & Araújo 2004; Hernandez *et al.* 2006). This may be related to the effect of niche breadth, with smaller range size being associated with better-defined habitat requirements (Brotons *et al.* 2004; Hernandez *et al.* 2006). Alternatively, populations of species with larger ranges can show local adaptation to different environmental conditions, decreasing the accuracy of models that consider all populations together (Stockwell & Peterson 2002; Brotons *et al.* 2004; Murphy & Lovett-Doust 2007). McPherson & Jetz (2007) found that endemic species were modelled more accurately than non-endemic species; this effect may be related to the effects of local range size and niche breadth, or maybe because the environmental gradients inhabited are incompletely sampled in the case of non-endemics. Overall, I expect species with smaller range sizes, both on local and regional scales, to be modelled more accurately than species with larger ranges. Tests of the effect of range size on model accuracy may be confounded by statistical artefacts. The AUC statistic is a common measure of the accuracy of species distribution models and has been used in many of the studies reviewed here. However, it may be biased in favour of species with narrow ranges when only data on species presence are available, and thus when pseudo-absence data are used for modelling (Lobo *et al.* 2008) (see Chapter 2).

Only a few studies have considered the effect of migratory behaviour on the accuracy of distribution models. All such studies have focused on birds, with most finding that models for migratory species were poorer than those for non-migratory ones (Pearce *et al.* 2001; McPherson & Jetz 2007), probably because the distributions of migratory species are determined by environmental conditions at very specific times of the year and often by conditions outside the modelled area (McPherson & Jetz 2007). Conversely, Stockwell & Peterson (2002) found no difference in model accuracy between migratory and non-migratory species, and Mitchell *et al.* (2001) found that models for migratory bird species were better than models for resident species. No previous study has compared model accuracy between migratory and non-migratory butterfly species, but as with birds I expect distribution models to be more accurate for residents than migrants. However, more mobile (as assessed by experts) butterfly species in Finland were better modelled than less mobile species (Pöyry *et al.* 2008), probably because they can expand their ranges into uninhabited areas more easily, and hence occupy a greater proportion of the suitable habitat than less mobile species (but see Pearce *et al.* 2001).

There is evidence that both sample size and prevalence (the relative number of presence and absence records) affect the accuracy of distribution models (Manel *et al.* 1999a; Stockwell & Peterson 2002; Luoto *et al.* 2005; Seoane *et al.* 2005). Therefore, it is important to control for these factors when comparing model accuracy among species (Karl *et al.* 2002; Huntley *et al.* 2004; McPherson *et al.* 2004). Reported effects of prevalence on model accuracy have been mixed, including both positive and negative relationships (Brotons *et al.* 2004; Luoto *et al.* 2005), but I expect model accuracy to increase with sample size.

Some authors have demonstrated evolutionary conservatism of ecological niches among closely-related (sister) species (Peterson *et al.* 1999). Furthermore, there may be substantial phylogenetic heritability in many of the characteristics of species that are used to explain differences in model accuracy among species, particularly range size (Jablonski

1987; Hunt *et al.* 2005; Beck *et al.* 2006, but see Quinn *et al.* 1998; Webb & Gaston 2003; Lester *et al.* 2007). However, to date, only one study has controlled for phylogeny when investigating differences in distribution-model accuracy among species (Pöyry *et al.* 2008). In this case, incorporating phylogeny did not affect the results, but this may not be true for other taxonomic groups, regions and characteristics.

In this study, I test the effect of five characteristics of species (local range size, global range size, migratory behaviour, host-plant specialization and habitat tolerance) on the accuracy of distribution models for butterflies in Egypt, controlling for the potentially confounding effects of sample size and prevalence on model accuracy. Two separate measures of model accuracy were used, to minimize the impact of statistical artefacts on my conclusions. I control for the influence of species relatedness using independent contrasts.

4.3 Methods

For this study, I used the BioMAP occurrence data for butterfly species recorded in Egypt. I used five environmental variables as predictors: four principal components based on bioclimatic variables from the WorldClim Version 1.4 dataset (Hijmans *et al.* 2005), and the land cover variable derived from AVHRR data (Hansen *et al.* 2000). For full details of the environmental variables, see Chapter 2. All variables were used at their original resolution of 30 arc seconds (approximately 1 km).

Models were built with Maxent Version 2.3 (Phillips *et al.* 2006). I generated ten distribution models for each of 40 species with at least eight occurrence records, with half the records used for model building and half for model evaluation.

The models were initially evaluated using the AUC statistic (Fielding & Bell 1997), using the reserved presence records and 2,500 pseudo-absence records, randomly selected from cells that lacked a presence record. The AUC statistic may be sensitive to the extent of the study area and the proportion of this area that the species inhabits (Lobo *et al.* 2008). As an additional evaluation of model performance, I fitted a generalized linear model with binomial errors, using the same presences and pseudo-absences as the binary dependent variable, and the model-predicted probability of occurrence at these sites as a single independent variable. The deviance explained by this model was used as a second measure of model accuracy. If the relationship between model-predicted probability and species occurrence was negative, then a value of zero was assigned. AUC values and deviances explained were averaged across the ten model runs for each species.

I considered six characteristics of species that might affect the accuracy of distribution models: 1) the mean number of presence records used to build the models; 2) whether the species is a migrant, partial migrant or resident in Egypt; 3) whether the species is a specialist or generalist in terms of the host plants it uses; 4) the inhabited range size within Egypt; 5) its global range size (endemic, near-endemic, restricted-range, narrowly distributed or widespread); and 6) its habitat tolerance. Information about migratory behaviour was taken directly from Gilbert & Zalat (2007). Species were defined as specialists if their known host plants are confined to one genus, and as generalists otherwise, according to Gilbert & Zalat (2007). Maxent produces a cumulative predicted probability of occurrence for each model between 0 and 100. The mean proportion of grid cells, across the ten model runs for each species, with a predicted value of greater than 50 was used as an index of range size within Egypt. Global range size followed the classifications used in Gilbert & Zalat (2007). The breadth of a species' habitat tolerance was estimated as the number of land cover categories into which recorded species occurrences fell.

The results of cross-species comparisons may be confounded by an effect of species relatedness on their niches and on the species characteristics considered. To control for this I calculated independent contrasts for both measures of model accuracy and all six characteristics of species (Harvey & Pagel 1991). One ecological characteristic (migratory behaviour) had more than two categories; in this case I generated a binary variable for each category. A phylogenetic topology was generated based on published studies (Pieridae: Pollock *et al.* 1998; Braby *et al.* 2006; Lycaenidae: Pierce *et al.* 2002; Pech *et al.* 2004; Nymphalidae: Brower 2000; Wahlberg *et al.* 2003; Freitas & Brown 2004; all groups: García-Barros 2000; Wahlberg *et al.* 2005). In the absence of data describing branch lengths, all branches were assigned a length of one, assuming punctuational evolution (Bro-Jorgensen 2007). I inserted small branches of length 0.0001 into polytomous clades. The phylogenetic tree was constructed in TreeView 1.6.6 (Page 1996) and modified using Mesquite 1.12 (Maddison & Maddison 2007). The independent contrasts were calculated using Compare Version 4.6b (Martins 2004).

4.3.1 Statistical Analysis

I arc-sine transformed AUC values to meet assumptions of normality. The effects of species characteristics on model accuracy were assessed using two analyses of covariance, using AUC values and the deviances explained by the models as the dependent variable in each case. Migratory behaviour, host-plant specialism, global range size, and habitat tolerance were considered as factors. Number of presence records and range size within

Egypt were considered as covariates. Preliminary analyses suggested that two-way interactions did not have a significant effect on model accuracy, so these were excluded from the final analyses.

I used a model selection method based on the approach recommended by Burnham & Anderson (2002) to select relevant variables. First, I built a global model with all six terms, and candidate models with every combination of terms. AIC scores were extracted for each model and the difference between a model's AIC value and the lowest value of all models (the AIC difference, Δ_i) was calculated. The relative ability of each model to explain variation in model accuracy ('model weight', w_i) was calculated using the following formula (Burnham & Anderson 2002):

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\frac{1}{2}\Delta_r\right)}$$

where Δ_i is the AIC difference of the model in question, R is the total number of models, and Δ_rs are the AIC differences of all models. The relative importance of each variable was assessed by summing the weights of all candidate models containing it (Burnham & Anderson 2002), hereafter referred to as the 'sum of AIC weights'. To test the effect of including species with very small numbers of presence records on the conclusions drawn, I repeated the same analyses considering only the 22 species with more than 20 unique presence records.

Relationships among independent contrasts for model accuracy measures and species characteristics were analysed using Pearson's correlation tests.

All statistical tests were carried out in SPSS Version 15.0 (SPSS Inc., Chicago, USA) and R Version 2.6.1 (R Development Core Team 2004).

4.4 Results

Models were generally accurate, attaining a mean AUC value of 0.83 ± 0.015 (n = 40) and explained a mean percentage deviance in species occurrence of 24.5 ± 2.65. Predicted range size within Egypt had a strong negative effect on model performance, using both AUC values (sum of AIC weights = 0.977; Table 4.1; Figure 4.1) and deviances explained by the models (sum of AIC weights > 0.999; Table 4.2; Figure 4.2) as measures of model accuracy. World range also had a strong negative effect on model accuracy, measured using both AUC values (sum of AIC weights = 0.916; Table 4.1; Figure 4.3) and the deviance explained by the models (sum of AIC weights = 0.983; Table 4.2; Figure 4.4). World range and range within Egypt did not correlate significantly with one another (Spearman rank correlation: $r_s = 0.120$, $n = 40$, $P > 0.05$). There was little support for an effect on model accuracy of the number of presence records used to build models (sum of AIC weights = 0.408 and 0.373, for AUC values and deviances explained by models respectively), migratory behaviour (sum of AIC weights = 0.421 and 0.220), host-plant specificity (sum of AIC weights = 0.345 and 0.290) or habitat tolerance (sum of AIC weights = 0.110 and 0.047). Considering only species for which models were developed with more than 10 unique presence records, on average, did not qualitatively alter the results, although migratory behaviour appeared to be a more important determinant of model accuracy in these analyses (see Appendix 4.1).

Table 4.1 – Results of a set of analyses of covariance testing the effect of species characteristics on the accuracy of species distribution models for 40 Egyptian butterfly species, measured using the AUC statistic. Characteristics tested were: the number of presence records used to build the distribution models (P), migratory behaviour (M), host-plant specificity (S), predicted range size in Egypt (R), world range size (W) and habitat tolerance (H). Candidate models were built with every possible combination of terms. These models were compared using the approach recommended by Burnham & Anderson (2002), by calculating AIC values for each model, the difference between the AIC for a model and the minimum AIC for all models (Δ_i), and model weights based on these values. I only present the best models ($\Delta_i < 4$) here.

Model	Deviance explained	AIC	AIC difference (Δ_i)	Model weight (w_i)
R + W	42.6	-35.69	0	0.181
P + M + R + W	49.63	-34.91	0.78	0.122
P + R + W	44.07	-34.74	0.95	0.112
M + R + W	46.79	-34.73	0.96	0.112
S + R + W	44.02	-34.7	0.99	0.110
M + S + R + W	47.67	-33.39	2.3	0.057
P + S + R + W	44.9	-33.33	2.36	0.056
P + M + S + R + W	49.82	-33.07	2.62	0.049

Table 4.2 - Results of a set of analyses of covariance testing the effect of species characteristics on the accuracy of species distribution models for 40 Egyptian butterfly species, measured as the deviance explained by the distribution models. Where the relationship between model predicted probability and species occurrence was negative, a deviance explained of zero was applied. Characteristics tested were: the number of presence records used to build the distribution models (P), migratory behaviour (M), host-plant specificity (S), predicted range size in Egypt (R), world range size (W) and habitat tolerance (H). Candidate models were built with every possible combination of terms. Models were compared using the approach recommended by Burnham & Anderson (2002), by calculating AIC values for each model, the difference between the AIC for a model and the minimum AIC for all models (Δ_i), and model weights based on these values. I only present the best models ($\Delta_i < 4$) here.

Model	Deviance explained	AIC	AIC difference (Δ_i)	Model weight (w_i)
R + W	62.03	313.6	0	0.344
P + R + W	62.74	314.8	1.2	0.189
S + R + W	62.13	315.4	1.8	0.14
M + R + W	63.16	316.4	2.8	0.085
P + S + R + W	62.75	316.8	3.2	0.069
P + M + R + W	64.31	317.1	3.5	0.06

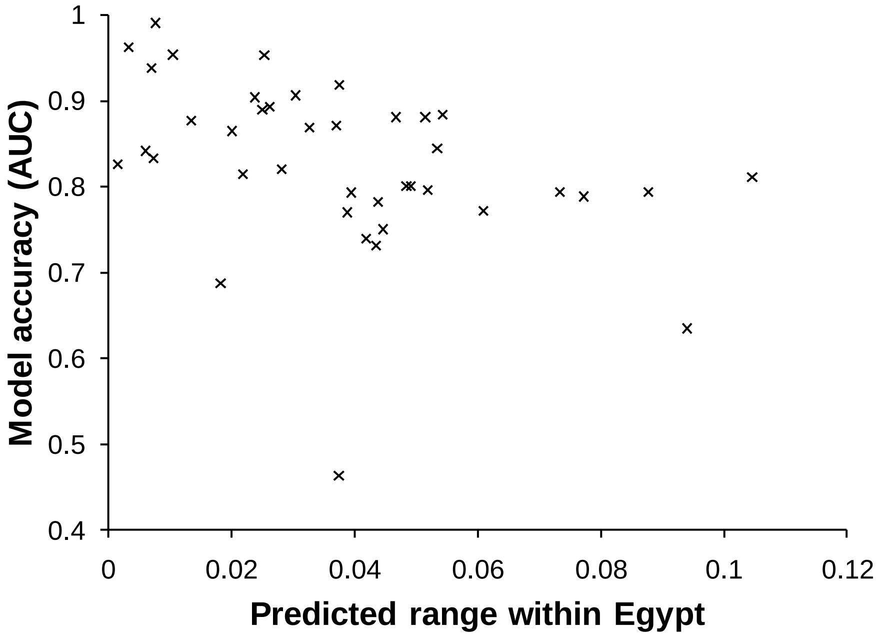

Figure 4.1 – Effect of predicted range size within Egypt on the accuracy of species distribution models for 40 Egyptian butterfly species, measured using the AUC statistic.

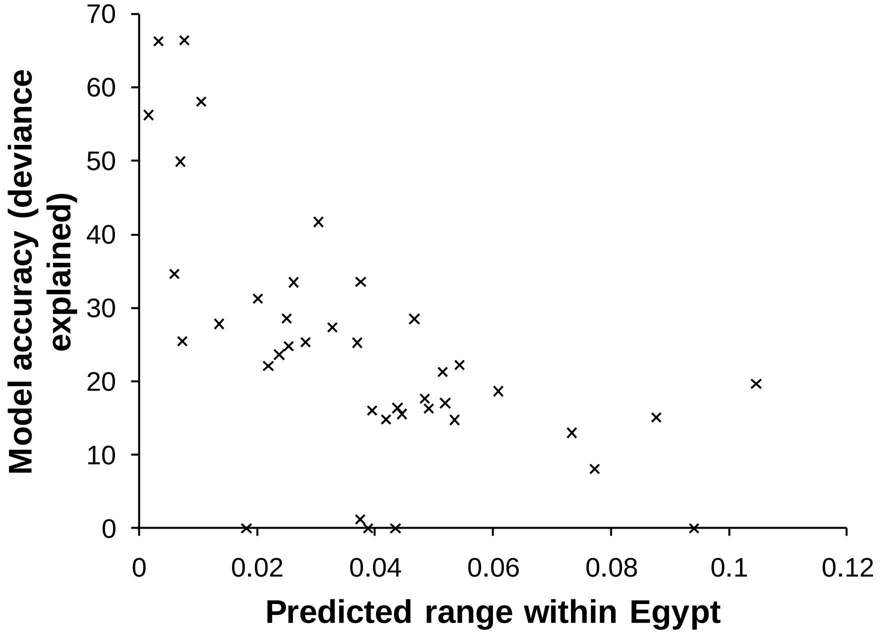

Figure 4.2 – Effect of predicted range size within Egypt on the accuracy of species distribution models for 40 species of Egyptian butterflies, measured using the deviance in species occurrence explained by the model predicted probability of occurrence. When the relationship between model predicted probability and species occurrence was negative, a value of zero deviance explained was assigned.

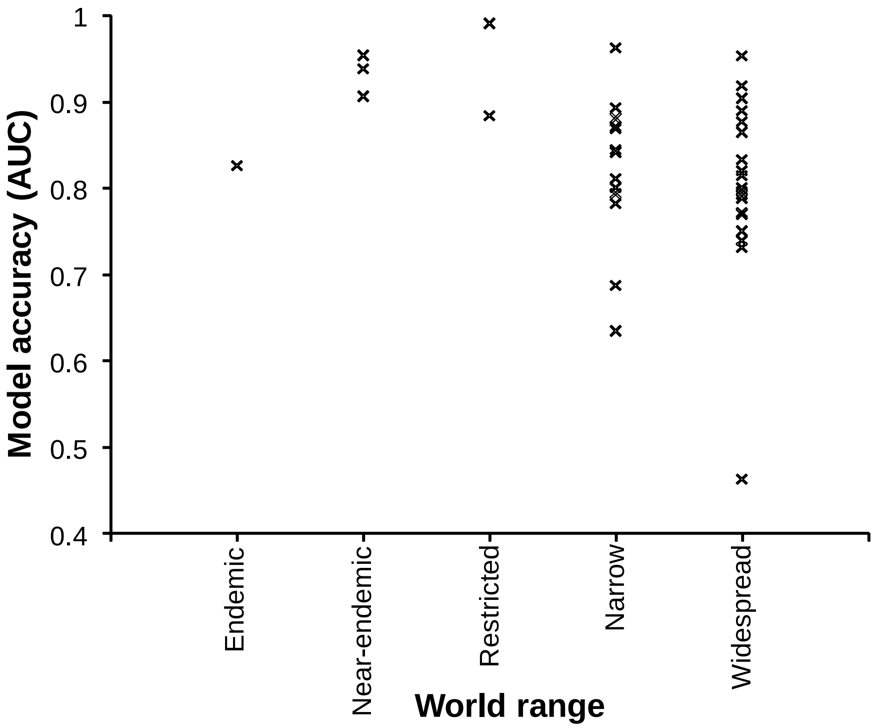

Figure 4.3 – Effect of global range size on the accuracy of species distribution models for 40 Egyptian butterfly species, measured using the AUC statistic.

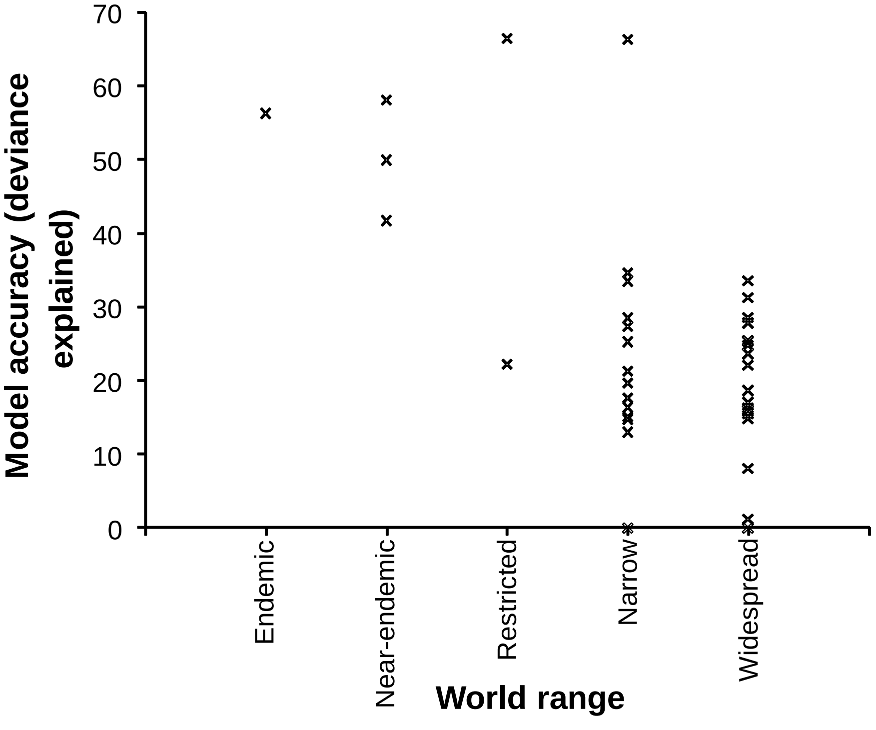

Figure 4.4 – Effect of global range size on the accuracy of species distribution models for 40 species of Egyptian butterflies, measured using the deviance in species occurrence explained by the model predicted probability of occurrence. When the relationship between model predicted probability and species occurrence was negative, a value of zero deviance explained was assigned.

When species relatedness was accounted for using independent contrasts, world range still showed a significant negative relationship with model accuracy, estimated using both AUC (Pearson's correlation coefficient: r = -0.323, n = 39, P = 0.045; Figure 4.5) and deviance explained by the models (r = -0.478, n = 39, P = 0.002; Figure 4.6). In this case, world range was treated as a covariate. Predicted range within Egypt showed a significant negative relationship with deviance explained by the models (r = -0.394, n = 39, P = 0.013; Figure 4.7), but not with average AUC score (r = -0.110, n = 39, P = 0.506; Figure 4.8). All other characteristics tested did not have a significant effect on model accuracy after accounting for the relatedness of species (-0.241 ≤ r ≤ 0.172, n = 39, P > 0.05).

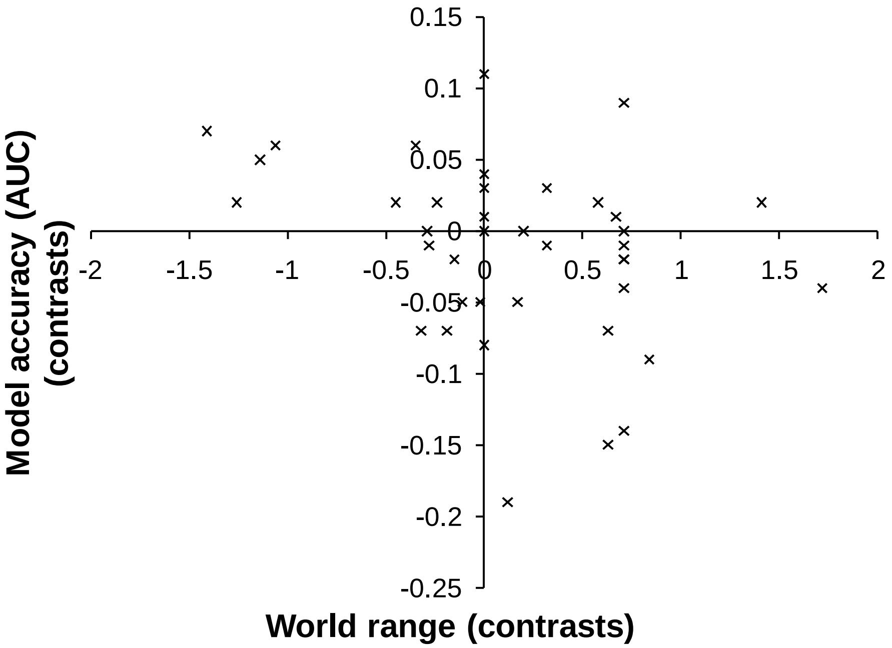

Figure 4.5 - Effect of global range size on the accuracy of species distribution models for 40 Egyptian butterfly species, measured using the AUC statistic. Species relatedness was controlled for by calculating independent contrasts (Harvey & Pagel 1991).

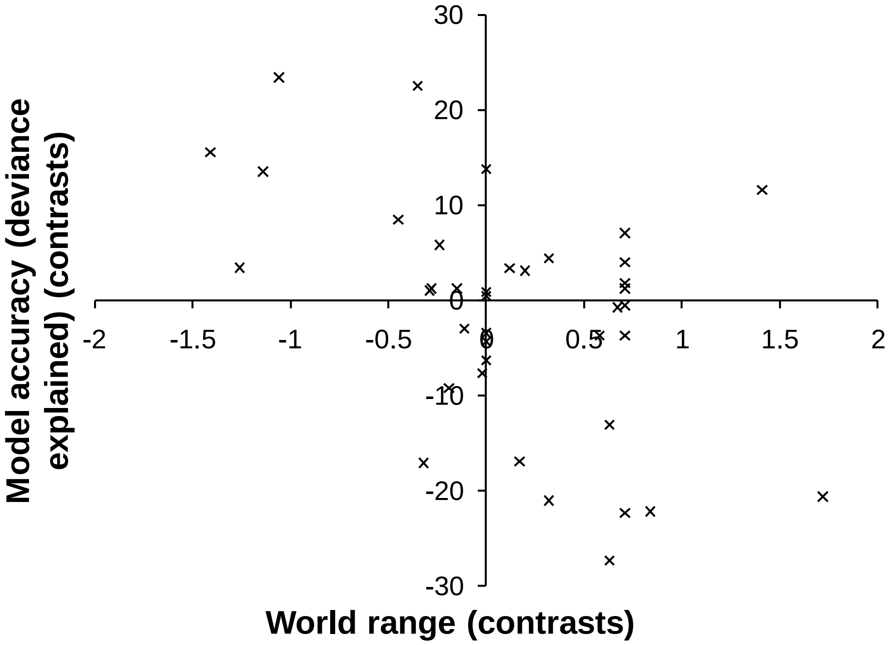

Figure 4.6 - Effect of global range size on the accuracy of species distribution models for 40 species of Egyptian butterflies, measured using the deviance in species occurrence explained by the model predicted probability of occurrence. Species relatedness was controlled for by calculating independent contrasts (Harvey & Pagel 1991).

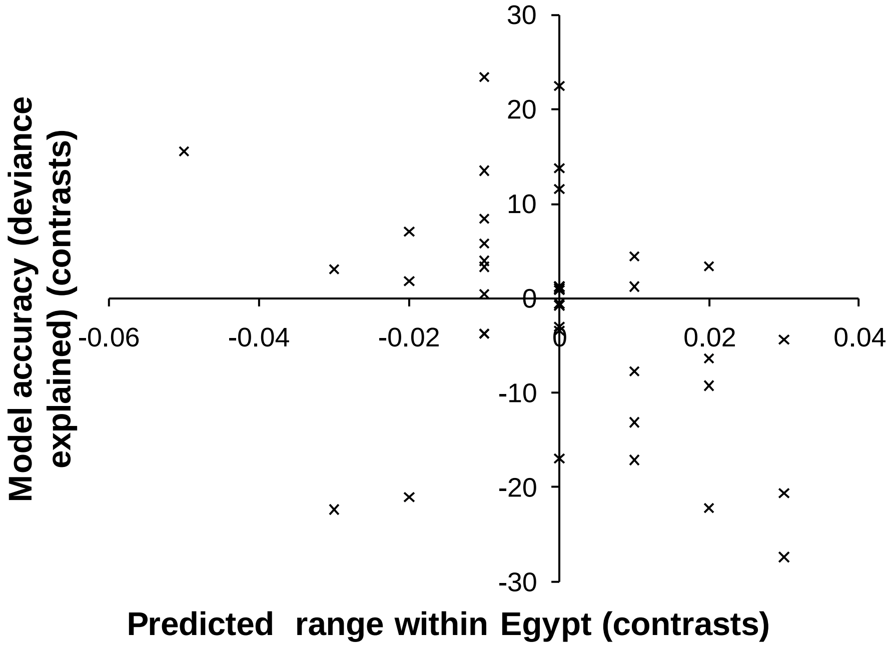

Figure 4.7 - Effect of predicted range size within Egypt on the accuracy of species distribution models for 40 species of Egyptian butterflies, measured using the deviance in species occurrence explained by the model predicted probability of occurrence. Species relatedness was controlled for by calculating independent contrasts (Harvey & Pagel 1991).

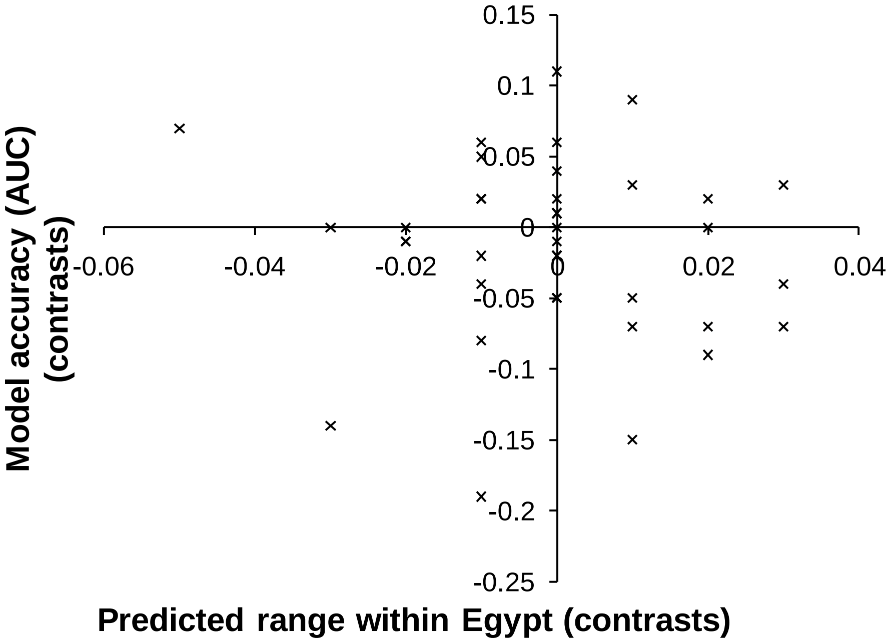

Figure 4.8 - Effect of predicted range size within Egypt on the accuracy of species distribution models for 40 Egyptian butterfly species, measured using the AUC statistic. Species relatedness was controlled for by calculating independent contrasts (Harvey & Pagel 1991).

4.5 Discussion

My results confirm that characteristics of species can be significantly related to model accuracy, although the factors considered explained a relatively small proportion of the variation in accuracy measures. Of the six characteristics that I tested, two had consistent effects on model performance. Disentangling causal mechanisms for patterns such as these is difficult because range size shows relationships with abundance and occupancy (Gaston *et al.* 2000; Hurlbert & White 2007; Figueiredo & Grelle 2009), and also with characteristics of species, such as dispersal ability and niche breadth (Beck & Kitching 2007; Lester *et al.* 2007). However, my results are consistent with hypothesized relationships between range size and the accuracy of distribution models.

Species with large local range sizes had less accurate models than those with small range sizes. This is consistent with the results of other studies (Stockwell & Peterson 2002; Brotons *et al.* 2004; Segurado & Araújo 2004; Hernandez *et al.* 2006). Species with small ranges included both desert species and those inhabiting the Nile Valley and Delta. Thus, the effect of range size was apparently not an artefact caused by certain habitats containing better-modelled species. Some authors have suggested that species with smaller ranges have more specific habitat requirements, making them easier to model (Brotons *et al.* 2004; Hernandez *et al.* 2006). However, contrary to the findings of other studies (Boone & Krohn 1999; Pearce *et al.* 2001; Kadmon *et al.* 2003; Berg *et al.* 2004), I found no evidence of an effect of habitat tolerance on the accuracy of species distribution models. A similar study to my own, comparing model accuracy among butterfly species in a temperate environment (Pöyry *et al.* 2008), also found no effect of niche breadth. Therefore, it would seem that other characteristics of butterfly species are more important in determining the accuracy of butterfly distribution models than habitat tolerance or niche breadth, or that the aspects of niche breadth that determine model accuracy were not captured by the measures used.

It has been suggested that the AUC statistic may be biased in favour of species that occupy a small proportion of the study area (Lobo *et al.* 2008), which may explain the existence of negative relationships between range size and model accuracy. However in my study, the effect of range size was the same for two independent measures of model accuracy, suggesting that the relationship was not an artefact associated with use of the AUC statistic. The use of pseudo-absences generally may affect measures of model accuracy, biasing estimated accuracy in favour of species that occupy small ranges within the study area (VanDerWal *et al.* 2009a). Nevertheless, global range size and local range size correlated with each other only weakly in this study and I found a strong effect of both global and local range size on model accuracy. While the effect of local range size may be affected by statistical artefacts, the effect of global range size should not.

Species with larger ranges may be modelled less accurately because the study area contains populations that show different responses to the environment (Stockwell & Peterson 2002; Brotons *et al.* 2004; Murphy & Lovett-Doust 2007). Although some studies suggest that niches are highly evolutionarily conserved (Peterson *et al.* 1999), others have found that organisms can adapt their niches very rapidly in certain situations (Knouft *et al.* 2006). The existence of different populations of the same species that respond differently to the environment is certainly possible in my study; at least two butterfly species (*Carcharodus stauderi* and *Spialia doris*) are known to be represented by two sub-species in Egypt (Gilbert & Zalat 2007). Furthermore, the Nile river, Suez canal and the mountains of the Eastern and Sinai deserts almost certainly present significant dispersal barriers for some species, causing isolation of populations. Modelling techniques such as geographically-weighted regression and varying-coefficient modelling can be used to capture varying responses to the environment across the range of widespread species (Kupfer & Farris 2007; Osborne *et al.* 2007).

Global range size also had a strong effect on the accuracy of my models. Predictions for endemic, near-endemic and restricted-range species were better than those for more widespread species. This has been shown before for birds (McPherson & Jetz 2007), but never for insects. It has been suggested that endemic species are modelled more accurately because the environmental gradients that they inhabit have been completely sampled, whereas only part of the total inhabited environmental space is sampled for non-endemics (McPherson & Jetz 2007). Alternatively, the effect of global range may be brought about by similar mechanisms to the effect of local range size, i.e. larger-ranged species having locally-adapted populations (e.g. Stockwell & Peterson 2002) or having broader habitat requirements, which are more difficult to model (e.g. Hernandez *et al.* 2006).

Previous studies have suggested that the distributions of specialist species are better modelled than those of generalist species (Hepinstall *et al.* 2002; Segurado & Araújo 2004; Elith *et al.* 2006). Mine is the first study to test for this effect in butterflies, and I find little evidence that specialists and generalists differ in the accuracy of their distribution models. Butterflies are dependent on certain plant species as host plants, and the distribution of these plants can strongly affect the distribution of the butterflies (Araújo & Luoto 2007, but see Quinn *et al.* 1998). Therefore it may be the identity, rather than the number, of host plants that affects the accuracy of butterfly distribution models. If the distribution of a butterfly's host plant is largely determined by climate and habitat, then we might expect that a model for the butterfly based on climate and habitat variables will be more accurate than if the host-plant's distribution is determined by other factors.

Few studies have considered the effect of migratory behaviour on the accuracy of species distribution models and these have focused on bird species, generally finding that migrant species are modelled less accurately than resident species (Pearce *et al.* 2001; McPherson & Jetz 2007). If anything, partial migrants had the least accurate models in this study. One possible explanation is that the distributions of both residents and migrants are strongly determined by environmental variables, but that each responds slightly differently to those variables. If partially-migratory species consist of separate populations of migrants and residents, then their distribution models will be less accurate than species that are entirely migratory or entirely resident and respond consistently to the environmental variables. Given the weak trend suggested in my data, more work is needed to explore this phenomenon further.

Several authors have reported a significant effect of sample size on model accuracy (Pearce & Ferrier 2000b; Stockwell & Peterson 2002; Phillips *et al.* 2004; Hernandez *et al.* 2006), although this effect has been shown to vary among modelling techniques. In this study I used Maxent to build models, and found no relationship between sample size and model performance. This supports the results of other studies that have shown that Maxent is generally robust to variation in sample size, and that it produces accurate predictions even with very small samples (Hernandez *et al.* 2008). Most studies of the effects of sample size on model performance (Pearce & Ferrier 2000b; Stockwell & Peterson 2002; Phillips *et al.* 2004; Hernandez *et al.* 2006) have experimentally altered sample sizes for one species. I tested the effect of the available sample size across many species. It may be that the completeness of sampling with respect to the environmental gradients rather than sample size alone is most important in determining model accuracy (see Chapter 3), although Kadmon *et al.* (2003) found, surprisingly, that distribution-model accuracy decreased with the completeness of sampling with respect to climatic gradients.

It is important to account for the effect of species relatedness in comparisons of models across species; otherwise, false conclusions might be drawn regarding the effect of some species characteristics on model accuracy, as is the case in other comparative studies (e.g. Harvey & Pagel 1991). Although accounting for species relatedness had no effect on the conclusions of this study, species distributions, and also some of the species characteristics tested, are known to be evolutionarily conserved (Jablonski 1987; Peterson *et al.* 1999; Hunt *et al.* 2005).

The results have important consequences, both for species distribution modelling itself and for conservation biology and ecology more generally. Fundamentally, they reveal important differences among species in the way that their occurrence is related to the environment. From a more applied perspective, it is important to understand why models for different species perform differently before using them to make conservation decisions. This is the first test of differences in accuracy among distribution models of butterflies in an arid environment. The results are generally consistent with those of similar studies of butterflies in other parts of the world, although I present the first test of the effects of migratory behavior and host-plant specialism on the accuracy of models for butterfly species. It is important to note that the factors that determine species distributions vary according to the scale of analysis (Whittaker *et al.* 2001; see Chapter 1), and thus the characteristics of species that affect distribution-model accuracy may also differ. Although there was substantial variation among species in model accuracy, accurate models were produced for many species, confirming the value of such models in conservation ecology.

Chapter 5. Modelling patterns of species richness using species distribution models[7]

5.1 Abstract

There is a long history in ecology of trying to understand why there are more species in some areas than in others. A great many studies have investigated whether aspects of the environment can explain patterns of species richness, mostly by correlating recorded values of species richness with environmental variables. An alternative is to sum species distribution models for a number of species in order to estimate species richness. In this chapter, I compared estimates of species richness, for Egyptian butterflies and mammals, made by summing distribution models for individual species with estimates made by modelling species richness directly. Estimates of species richness from both methods correlated positively with each other and with observed species richness. Protected areas had higher species richness (both predicted and observed) than unprotected areas. My results suggest that climate-based models of species richness could provide a rapid method for selecting potential areas for protection and thus have important implications for biodiversity conservation.

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[7] A modified version of this chapter was published in *Journal of Biogeography*

5.2 Introduction

In order to conserve biodiversity most effectively, it is important to select objectively areas of the world to protect (Pressey *et al.* 1993). Species richness is commonly used as a measure of diversity to prioritise areas for conservation (Pressey *et al.* 1993). However, knowledge of spatial patterns of species richness is limited, especially in the tropics (Anderson *et al.* 2003; Soria-Auza & Kessler 2008) and in arid regions (Stockwell & Peters 1999). Some authors have experimented with combining distribution models for individual species in order to estimate species richness. For example, García (2006) modelled the distributions of 267 reptile and amphibian species in Mexico and summed the resulting predictions to make a map of species richness. Pineda & Lobo (2009) did the same for amphibians in Mexico, finding that modelled species richness correlated with observed species richness reasonably well. When large numbers of species are involved, this approach may be time-consuming (Gioia & Pigott 2000); an alternative is to model species richness directly. There have been many attempts to find climatic and habitat-related correlates of species richness patterns (e.g. Kivinen *et al.* 2006; Levinsky *et al.* 2007). However, only one study so far has explicitly compared summed distribution predictions with models of species richness *per se* (Terribile *et al.* 2009), although Gioia & Pigott (2000) used both approaches. Such a comparison will be very useful for conservation biologists attempting to understand spatial patterns of biodiversity, because both approaches may be useful in different circumstances. Combining species distribution models may enable us to capture the individualistic responses of species to their environment (Terribile *et al.* 2009), whereas models of species richness itself will be useful when species identity is unknown.

Many studies have investigated patterns of species richness, often finding climate variables to be good correlates of observed patterns (e.g. Hawkins *et al.* 2003). Arid environments are under-studied in this respect (but see van Rensburg *et al.* 2002; Schmidt *et al.* 2008). The mechanistic explanation for these relationships remains a matter of debate, and the conclusions of any study of patterns of species richness are strongly affected by the spatial scale at which they are conducted (Field *et al.* 2009). Using data for three taxonomic groups in North America, Currie *et al.* (2004) explored three hypotheses for climate-based patterns in species richness: ambient energy, the climatic tolerance of species and speciation rates (see Chapter 1). They did not find unequivocal support for any of these hypotheses in the literature. At broad scales, historical factors (Qian & Ricklefs 2000) and the distribution of resources (Araújo & Luoto 2007) can play important roles in determining species richness. At finer scales, competition (Anderson *et al.* 2002a), metapopulation dynamics (Hanski 1991) and human disturbance (Uehara-Prado *et al.* 2007; Ficetola & Padoa-Schioppa 2009) have also been shown to exert a significant influence on species richness.

Several studies have shown that butterfly and mammal species richness correlate with climate and habitat variables in temperate and tropical regions (Turner *et al.* 1987; Nogués-Bravo & Araújo 2006; Algar *et al.* 2007; Kivinen *et al.* 2007; Kuussaari *et al.* 2007; Levinsky *et al.* 2007). However, to date very few studies have investigated correlates of mammal and butterfly species richness in an arid environment (but for mammals see Andrews & O'Brien 2000).

In this chapter I investigate patterns of species richness in Egypt’s butterfly and mammal fauna. Egypt has two endemic and two near-endemic butterfly species, and also three endemic subspecies (Larsen 1990). The mammal fauna includes four endemic and ten near-endemic species (Osborn & Helmy 1980). My study had three objectives. First, I sought to identify environmental correlates of species richness at a local scale. Second, I asked whether estimates of the species richness of Egyptian butterflies and mammals derived from models of species richness had a good match with estimates made by summing individual models of the distribution of species, and whether both these estimates matched observed patterns of species richness.

One application of models of species richness is in assessing the effectiveness of protected areas. Global estimates of the effectiveness of protected areas generally suggest poor coverage of biodiversity (Chape *et al.* 2005). Country-level studies have often found species richness to be no higher in protected areas than in unprotected areas (e.g. Pawar *et al.* 2007; Traba *et al.* 2007; but see e.g. Lee *et al.* 2007).

Egypt has 27 current or proposed protected areas, covering a total of 11% of its land surface (see Egyptian Environmental Affairs Agency 2007). All these have been gazetted since 1983, mostly at the recommendation of scientists familiar with Egypt's biodiversity. Because of this, one may expect them to show good coverage of biodiversity. My third objective was to test whether protected areas in Egypt have higher species richness than unprotected areas.

5.3 Methods

5.3.1 Species and climate data

Species occurrence data for this study were taken from the BioMAP database and consisted of 1898 records for 59 butterfly species and 4718 records for 103 mammal species (see Chapter 2 for full details).

Climatic and elevation variables were taken from the WorldClim Version 1.4 dataset at a resolution of 30 arc seconds (approximately 1 km) (Hijmans *et al.* 2005). I also used the new Egyptian geological habitat map (hereafter referred to as simply “habitat”) (Dr. A. Hassan 2007, unpublished data). In preliminary analyses I experimented with topographical predictors (slope and aspect). However, these variables did not significantly improve model accuracy and were excluded from the final analyses. For more details about the environmental variables, see Chapter 2.

5.3.2 Modelling species richness

I modelled the species richness of butterflies and mammals separately, using two methods. First, I summed predictions of the distribution of individual species, using a resolution of 30 arc seconds (approximately 1 km). I made initial distribution models for the 40 butterfly species and 68 mammal species with at least eight records of occurrence, using Maxent Version 2.3 (Phillips *et al.* 2006). I used the 19 climatic variables, elevation and habitat as predictor variables. Linear and quadratic terms were fitted for continuous variables. I used default values for all parameters (a regularization value of 1, a convergence threshold of 0.00001, a maximum of 500 iterations and a sample of 10000 points to characterize the background environment). Ten initial models were made for each species. For each model, the species data were randomly divided into half for developing the model and half for evaluating it. The accuracy of each model was assessed using the "area under the receiver operating characteristic curve" (AUC) statistic (see Chapter 2 for details), as calculated within the Maxent procedure. Following the recommendations of Pearce & Ferrier (2000a) for interpreting AUC values, I eliminated five butterfly species and seven mammal species with mean AUC values of less than 0.7. This left 35 butterfly species, including one of the two endemic species and both near-endemic species, and 61 mammal species, including three of the four endemic species and five out of ten near-endemic species.

A single final model was then made for each of the remaining species, again at a resolution of 30 arc-seconds, using the same modelling protocol; for these models, all presence records were used because the objective was not to assess model accuracy but to develop the most accurate model for each species using all of the available data. The output of statistical models varies among species according to the relative numbers of presences and absences in the species data (prevalence) (Manel *et al.* 2001). Therefore, simply summing the output of individual distribution models may bias estimates of species richness in favour of taxa with many records. It is better to convert the model output into a binary prediction of presence or absence around a threshold value. Many methods have been proposed for choosing appropriate thresholds (Pearson *et al.* 2004; Liu *et al.* 2005). For datasets consisting only of presences, Pearson *et al.* (2004) recommended using a threshold that maximises sensitivity (the percentage of presences correctly predicted as being present at a given threshold). Here I used a threshold that resulted in predictions with a sensitivity of 95%. Once the models had been converted to binary predictions of presence or absence, they were summed across all species to give an estimate of species richness.

The second method of modelling species richness was to model observed species richness values directly. This part of the study was concerned with the total number of species recorded in each cell rather than individual records of species. Therefore, I used a resolution of 0.5^{o} because at the finer resolution used for the distribution models most cells had a recorded species richness of zero. Observed species richness was calculated from the original survey data in Diva-GIS 5.2 (Hijmans 2009). A species was considered present in a cell if it had been recorded at least once. Species richness was modelled using generalized linear models (GLMs) with the same independent variables as in the species distribution models. The variables were resampled to the coarser resolution using bilinear interpolation. In bilinear interpolation, the values of the four nearest grid cells to the target cell are averaged after being weighted according to their distance to the target cell. Fitting too many independent variables in GLMs may result in overfitting and the selection of variables not directly relevant in the final model (Wintle *et al.* 2005). To avoid these problems, I performed principal components analysis (PCA) on the 19 climatic variables and elevation across all 406 of the 0.5^{o} cells. Components with an eigenvalue greater than one were retained as new predictor variables. In the GLMs, linear and quadratic terms were fitted for each of these components. Overfitting should not have been an issue with the Maxent models (see Chapter 3). I constructed two separate models of species richness. Following an inspection of the residuals of a *general* linear model and consideration of dispersion, the most appropriate family of GLM was chosen for each model. In the first, I fitted recorded species richness values of all 406 of the 0.5^{o} grid cells in the study area. I used a generalized linear model (GLM) with negative binomial errors (NB-GLM) and the log link (Crawley 2002; Venables & Ripley 2002). For the second model, since some cells with a recorded richness of zero may occur simply because they have not been sampled and the results could be biased by the inclusion of false zero values, I fitted the species richness values of 0.5° cells with at least one record of the taxonomic group in question – 100 cells for butterflies and 196 cells for mammals. A GLM with Poisson errors (P-GLM) and the log link (McCullagh & Nelder 1989) was used.

5.3.3 Statistical analysis

The agreement between fitted values of species richness generated using the different methods was tested using Spearman's rank correlation tests. For comparison, the species richness prediction generated by summing individual distribution models was resampled from its original resolution of 30 arc seconds to a resolution of 0.5^{o} using bilinear interpolation. Thus, all tests compared species richness across all 362 of the 0.5^{o} grid cells with an estimate of species richness by all three models. These comparisons included cells with no species records; these cells were assumed to have a species richness of zero. I also repeated the same correlation tests using only cells that had at least one record of a species in the taxonomic group being considered.

I tested whether Egypt's protected areas network represented butterfly and mammal species richness well by comparing estimated (using the distribution model-sum method) and observed species richness inside and outside protected areas at 2000 points, randomly situated in 1 km cells throughout the study area. These points were generated using Hawth's analysis tools for ArcMap 9.1 (see Beyer 2004). I also compared both estimated and observed richness of endemic and near-endemic species inside and outside protected areas. For this comparison, I grouped mammals and butterflies because the number of endemic species was small.

The P-GLMs and NB-GLMs were built using the glm (Poisson errors) and glm.nb (negative binomial errors) packages in R 2.6.1 (R Development Core Team 2004). For both, a backward stepwise selection procedure was used to remove terms that did not significantly improve the deviance explained, until a minimum adequate model was obtained. All other analyses were carried out using SPSS 15.0 (SPSS Inc., Chicago, USA). The comparison of actual and predicted species richness inside and outside protected areas was undertaken using a Mann-Whitney U test.

5.4 Results

A map of Egypt's protected areas and the sites that were sampled for mammals and butterflies is given in Figure 5.1. The final distribution models (those using all the species occurrence data) achieved AUC values between 0.863 and 0.999 (mean = 0.936 ± 0.0072) for butterfly species and between 0.831 and 0.999 (mean = 0.944 ± 0.0054) for mammal species. The relative contribution of habitat, elevation and the 19 climatic variables to the final distribution models of butterflies and mammals is shown in Figure 5.2 and full details of the contributions of variables in the models for each species are given in Appendix 5.1. Habitat and elevation were important in explaining the distributions of both butterflies and mammals. Among the climatic predictors, temperature-related variables explained butterfly distributions better than precipitation-related variables, while for mammals, annual and maximum precipitation variables also correlated well with species occurrence.

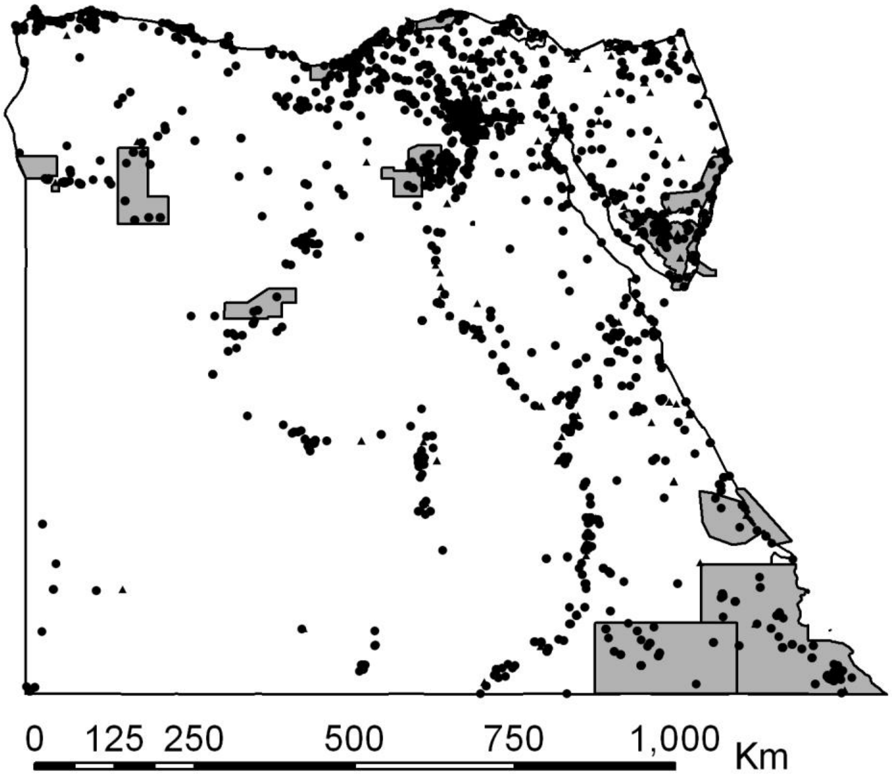

Figure 5.1 – Sites where mammals (circles) and butterflies (triangles) were sampled, and the location of Egypt's protected areas (grey shading).

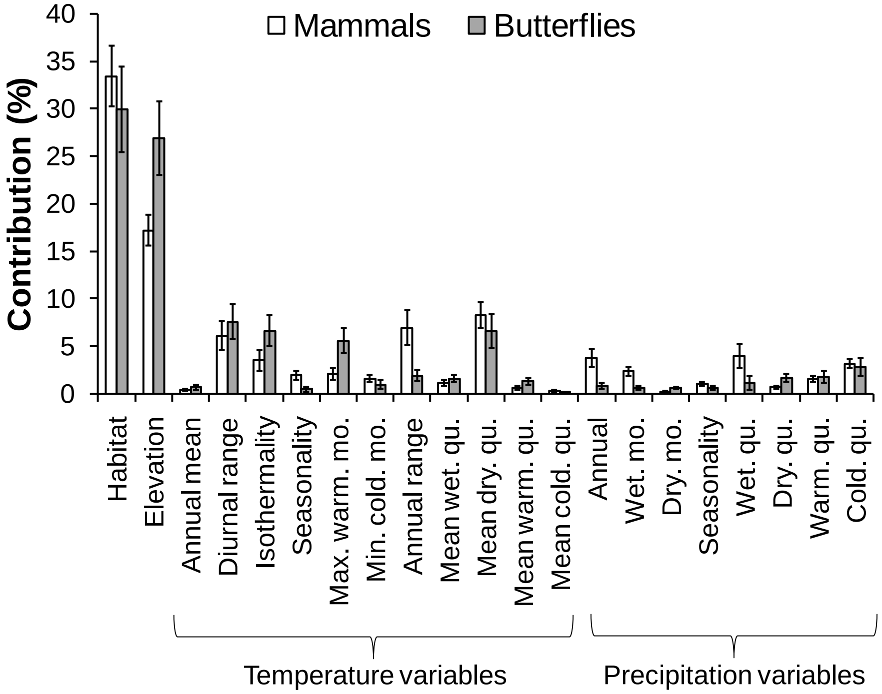

Figure 5.2 - Mean contribution (%) of each of the environmental variables to the Maxent species distribution models, averaged across all species. Max. = maximum, min. = minimum, qu. = quarter, mo. = month, warm. = warmest, cold. = coldest, wet. = wettest, dry. = driest. A full breakdown of the contribution for each individual species is given in Appendix 5.1.

The predictions of species richness made using the first method (summing distribution models for individual species) are mapped in Figures 5.3 and 5.4. The models of species richness generated using this method correlated positively and significantly with observed species richness (Table 5.1; Figure 5.5a).

Table 5.1 - Correlations among fitted values of each of the three models of species richness of butterflies (B) and mammals (M) in Egypt, and correlations between these fitted values and observed species richness. The three models of species richness were: (1) summed distributions – distribution models were built for each species at 30 arc second resolution using Maxent, then summed to estimate species richness; (2) NB-GLM – species richness values of all 0.5° cells were fitted using a generalized linear model (GLM) with negative binomial errors; 3) P-GLM – species richness values of sampled cells were fitted using a GLM with Poisson errors. Correlations were calculated both for all cells, and for sampled cells only. Species richness values cannot be considered independent in the presence of spatial autocorrelation; the effective sample size is reduced in the presence of such non-independence. The minimum sample sizes at which the reported correlation coefficients would remain significant (at $\alpha = 0.05$) are given in brackets after the correlation coefficient.

Correlation	Cells	Taxon	r_s	n	P
Observed and summed distributions	All	B	0.456 (15)	362	< 0.001
		M	0.595 (10)	362	< 0.001
	Sampled	B	0.343 (25)	88	0.001
		M	0.534 (12)	171	< 0.001
Observed and NB-GLM	All	B	0.319 (28)	362	< 0.001
		M	0.553 (11)	362	< 0.001
	Sampled	B	0.296 (32)	88	0.005
		M	0.334 (26)	171	< 0.001
Observed and P-GLM	All	B	0.232 (52)	362	< 0.001
		M	0.414 (17)	362	< 0.001
	Sampled	B	0.392 (19)	88	< 0.001
		M	0.388 (20)	171	< 0.001
Summed distributions and NB-GLM	All	B	0.529 (12)	362	< 0.001
		M	0.762 (7)	362	< 0.001
	Sampled	B	0.508 (12)	88	< 0.001
		M	0.620 (9)	171	< 0.001
Summed distributions and P-GLM	All	B	0.455 (15)	362	< 0.001
		M	0.633 (9)	362	< 0.001
	Sampled	B	0.308 (30)	88	0.004
		M	0.575 (10)	171	< 0.001
NB-GLM and P-GLM	All	B	0.891 (6)	362	< 0.001
		M	0.802 (7)	362	< 0.001
	Sampled	B	0.692 (8)	88	< 0.001
		M	0.760 (7)	171	< 0.001

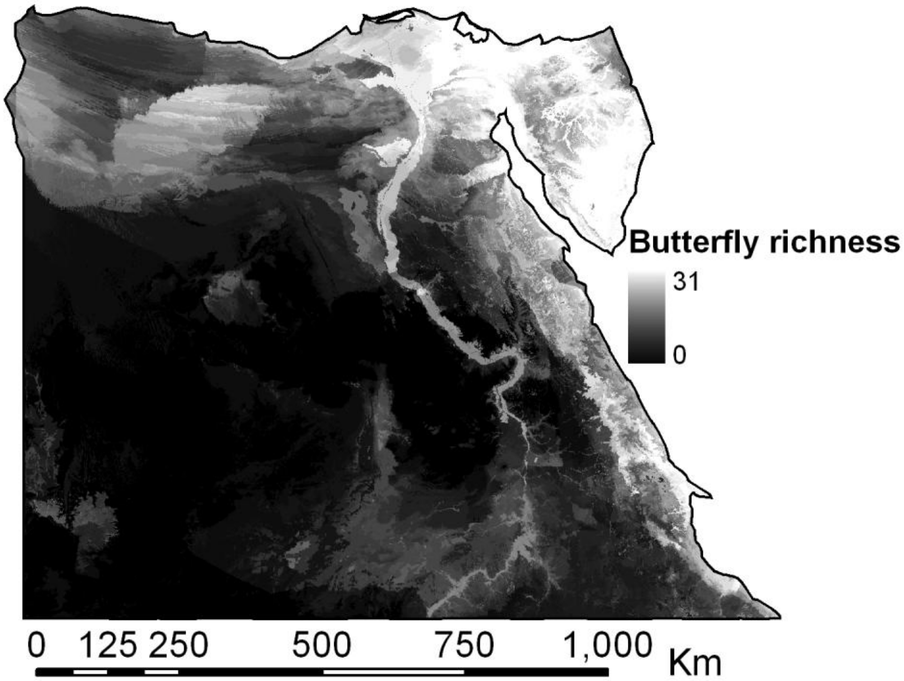

Figure 5.3 – Map of predicted butterfly species richness generated by summing individual predictions of the distributions of species. Lighter tones indicate high predicted species richness and darker tones indicate lower species richness. The distribution predictions were made using Maxent.

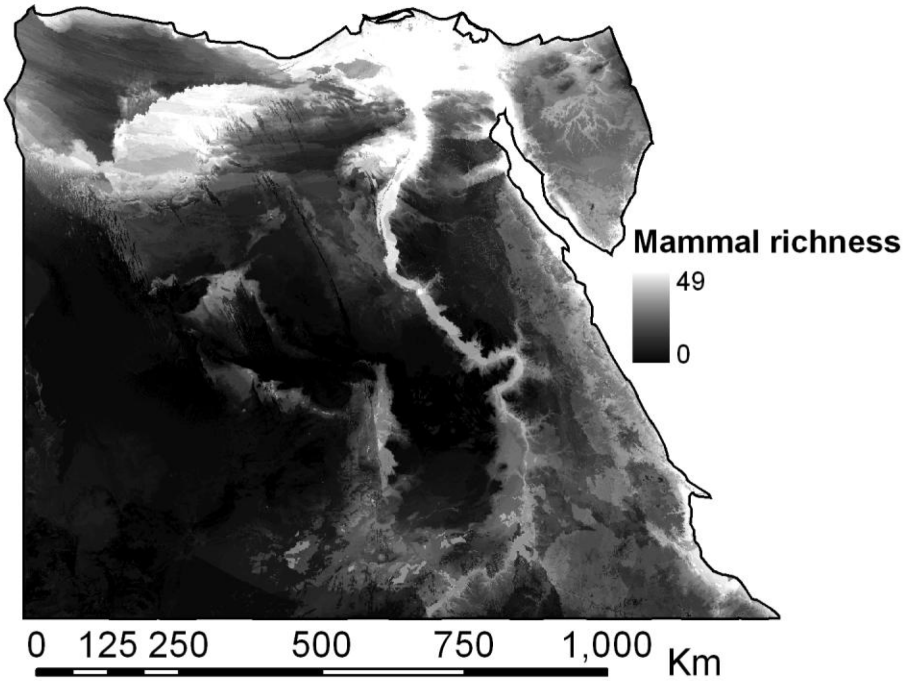

Figure 5.4 – Map of predicted mammal species richness generated by summing individual predictions of the distributions of species. Lighter tones indicate high predicted species richness and darker tones indicate lower species richness. The distribution predictions were made using Maxent.

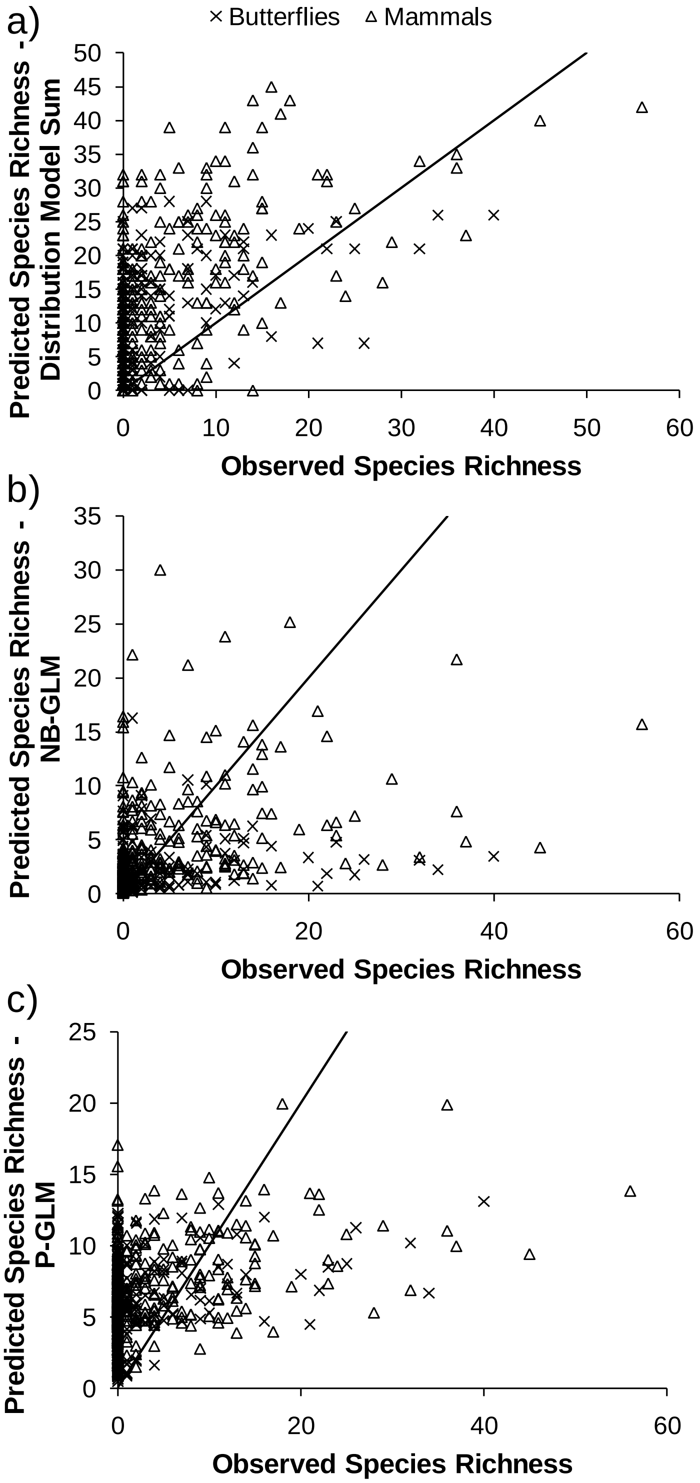

Figure 5.5 - Correlations between observed species richness and modelled species richness, estimated using each of three methods: a) models of the distribution of each species, produced using Maxent, were summed; b) recorded species richness values of all grid cells were modelled using a generalized linear model with negative binomial errors; c) recorded species richness values of sampled grid cells were modelled using a generalized linear model with Poisson errors. The lines represent y=x, for information.

The second method of estimating spatial patterns of species richness was to model species richness values directly. For this analysis, it was necessary to perform principal components analysis (PCA) on the environmental variables to avoid overfitting of the GLMs. The PCA of the 19 climatic variables and elevation produced four components with eigenvalues greater than 1.0, and which collectively explained 86.8 % of the variance in the original environmental variables (Figure 5.6). All original climate variables were represented in at least one of the extracted components (Table 5.2). The first principal component increased with increasing maximum temperature and decreasing precipitation annually and at the wettest times of year. The second component increased with increasing annual temperature and increasing temperature during cooler periods of the year. The third component described increasing elevation, decreasing annual temperature and increasing precipitation at drier times of the year. The fourth component increased with decreasing temperature during dry periods, increasing precipitation (annually and during cold times of the year), and decreasing minimum precipitation (Table 5.2).

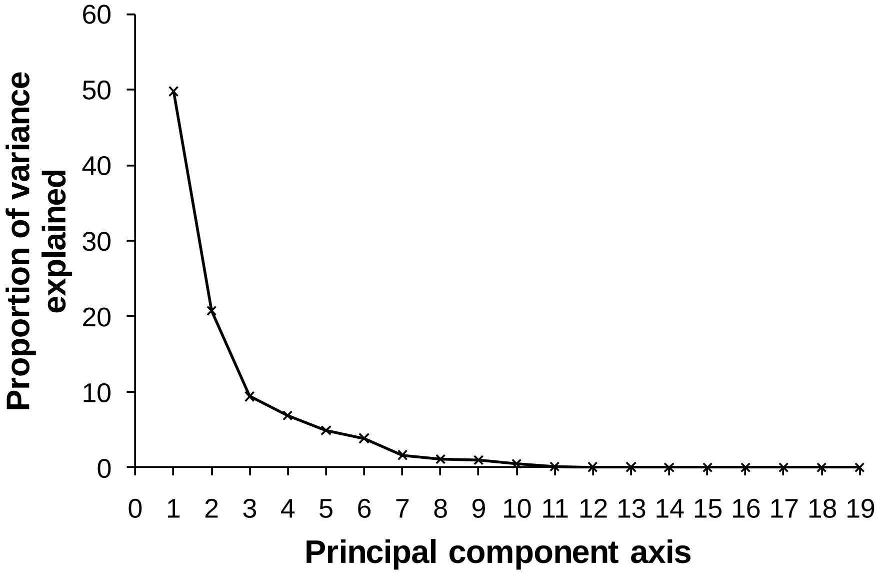

Figure 5.6 – Proportion of variance explained by principal component axes based on 19 bioclimatic variables and an elevation variable for Egypt. The principal components analysis was performed using values for all 0.5° grid cells in Egypt. The first four axes, which has eigenvalues greater than one, were used in the analysis of species richness patterns.

Table 5.2 – Loadings of the 19 climatic variables and altitude in the principal components analysis across the 406 0.5^{o} cells in Egypt. The four components (PC1-4) with mean eigenvalues greater than 1 are shown. The five highest loadings for each principal component are displayed in bold.

Variable	**PC1**	**PC2**	**PC3**	**PC4**
Altitude	0.020	-0.037	**0.472**	0.143
Annual Mean Temperature	0.070	**0.178**	**-0.108**	0.087
Mean Diurnal Temperature Range	0.093	-0.093	-0.040	0.029
Isothermality	0.069	0.004	-0.071	**-0.270**
Temperature Seasonality	0.086	**-0.122**	-0.013	0.185
Max Temperature of Warmest Month	**0.099**	0.048	-0.078	0.113
Min Temperature of Coldest Month	-0.023	**0.240**	-0.066	-0.033
Annual Temperature Range	0.091	-0.112	-0.019	0.107
Mean Temperature of Wettest Quarter	0.034	**0.196**	**0.158**	0.137
Mean Temperature of Driest Quarter	-0.083	0.006	-0.032	**-0.344**
Mean Temperature of Warmest Quarter	0.088	0.119	-0.107	0.128
Mean Temperature of Coldest Quarter	0.028	**0.238**	-0.108	0.002
Annual Precipitation	**-0.097**	0.001	-0.055	0.257
Precipitation of Wettest Month	**-0.096**	0.019	-0.059	0.233
Precipitation Seasonality	-0.089	0.040	0.049	-0.228
Precipitation of Wettest Quarter	**-0.096**	0.005	-0.071	**0.262**
Precipitation of Driest Quarter	-0.008	0.070	**0.281**	**-0.303**
Precipitation of Warmest Quarter	0.002	0.089	**0.399**	0.205
Precipitation of Coldest Quarter	**-0.094**	-0.014	-0.084	**0.277**

The models fitting species richness values for all 406 of the 0.5° cells (NB-GLM), which included cells with a recorded species richness of zero, explained 16.3% of the deviance in the species richness of butterfly species and 21.3% of the deviance in mammal species richness. For butterflies, only the linear term of PC1 (describing mainly precipitation but also maximum temperature) and habitat had a significant effect on species richness (Table 5.3). For mammals, habitat, the quadratic term of PC1, and both linear and quadratic terms of PC2 (describing several temperature-related variables) and PC4 (describing variables related to extremes of temperature and rainfall) had a significant effect on species richness (Table 5.3). Estimated species richness according to the NB-GLMs correlated significantly and positively with observed species richness (Table 5.1; Figure 5.5b).

Table 5.3 - Results of generalized linear models with negative binomial errors, fitting the observed species richness of all 0.5^o grid squares as the dependent variable, with habitat and four bioclimatic principal component axes (linear and quadratic terms) as independent variables. Significant terms are shown in bold.

Term	Coefficient	d.f.	LR statistic	P
Butterflies:				
Intercept	0.410			
PC1	**-0.664**	**1**	**17.3**	**< 0.001**
$(PC1)^2$	NA	1	0.975	0.324
PC2	NA	1	0.545	0.460
$(PC2)^2$	NA	1	2.41	0.121
PC3	NA	1	-0.124	> 0.999
$(PC3)^2$	NA	1	-1.79	> 0.999
PC4	NA	1	-3.14	> 0.999
$(PC4)^2$	NA	1	3.44	0.064
Habitat	**NA**	**9**	**19.1**	**0.025**
Mammals:				
Intercept	1.33			
PC1	NA	1	0.854	0.355
$(PC1)^2$	**0.776**	**1**	**57.1**	**< 0.001**
PC2	**0.580**	**1**	**17.3**	**< 0.001**
$(PC2)^2$	**-0.175**	**1**	**5.74**	**0.017**
PC3	NA	1	0.0297	0.863
$(PC3)^2$	NA	1	1.20	0.273
PC4	**-1.17**	**1**	**55.5**	**< 0.001**
$(PC4)^2$	**-0.286**	**1**	**11.3**	**< 0.001**
Habitat	**NA**	**9**	**22.0**	**0.009**

The models fitting species richness values only for 0.5° cells with at least one species record (P-GLM) explained 19.1% of the deviance in butterfly species richness and 18.3% of the deviance in mammal richness. For butterflies, both terms of PC1 and PC4, the quadratic term of PC3 (high values of which indicate high elevation areas with rainfall all year round) and habitat were all significantly related to species richness (Table 5.4). For mammals, both terms of PC1, the quadratic terms of PC2 and PC4, the linear term of PC3 and habitat were significant correlates of species richness (Table 5.4). Species richness estimates from these models also correlated significantly and positively with observed species richness (Table 5.1; Figure 5.5c). Across all 0.5° grid cells, the estimates made using the three different modelling methods (summing individual distribution predictions and both models of species richness values) correlated significantly with each other (Table 5.1; Figure 5.7).

Table 5.4 - Results of generalized linear models with Poisson errors, fitting the observed species richness of sampled 0.5° grid cells only (i.e. excluding zero values), with habitat and four bioclimatic principal component axes (linear and quadratic terms) as independent variables. Significant terms are shown in bold.

Term	Coefficient	d.f.	Deviance explained	P
Butterflies:				
Intercept			Null = 717.8	
PC1	**-0.339**	**1**	**25.4**	**< 0.001**
$(PC1)^2$	**-0.147**	**1**	**14.8**	**< 0.001**
PC2	NA	1	0.100	0.750
$(PC2)^2$	NA	1	0.470	0.490
PC3	NA	1	0.350	0.550
$(PC3)^2$	**-0.079**	**1**	**17.7**	**< 0.001**
PC4	NA	1	0.110	0.740
$(PC4)^2$	**0.090**	**1**	**9.66**	**0.002**
Habitat	**NA**	**9**	**92.21**	**< 0.001**
Mammals:				
Intercept	2.08		Null = 1408	
PC1	**-0.276**	**1**	**112**	**< 0.001**
$(PC1)^2$	NA	1	3.29	0.070
PC2	NA	1	0.590	0.440
$(PC2)^2$	NA	1	1.58	0.210
PC3	**-0.288**	**1**	**94.3**	**< 0.001**
$(PC3)^2$	NA	1	2.83	0.090
PC4	**-0.085**	**1**	**10.1**	**0.001**
$(PC4)^2$	NA	1	0.760	0.380
Habitat	**NA**	**9**	**65.2**	**< 0.001**

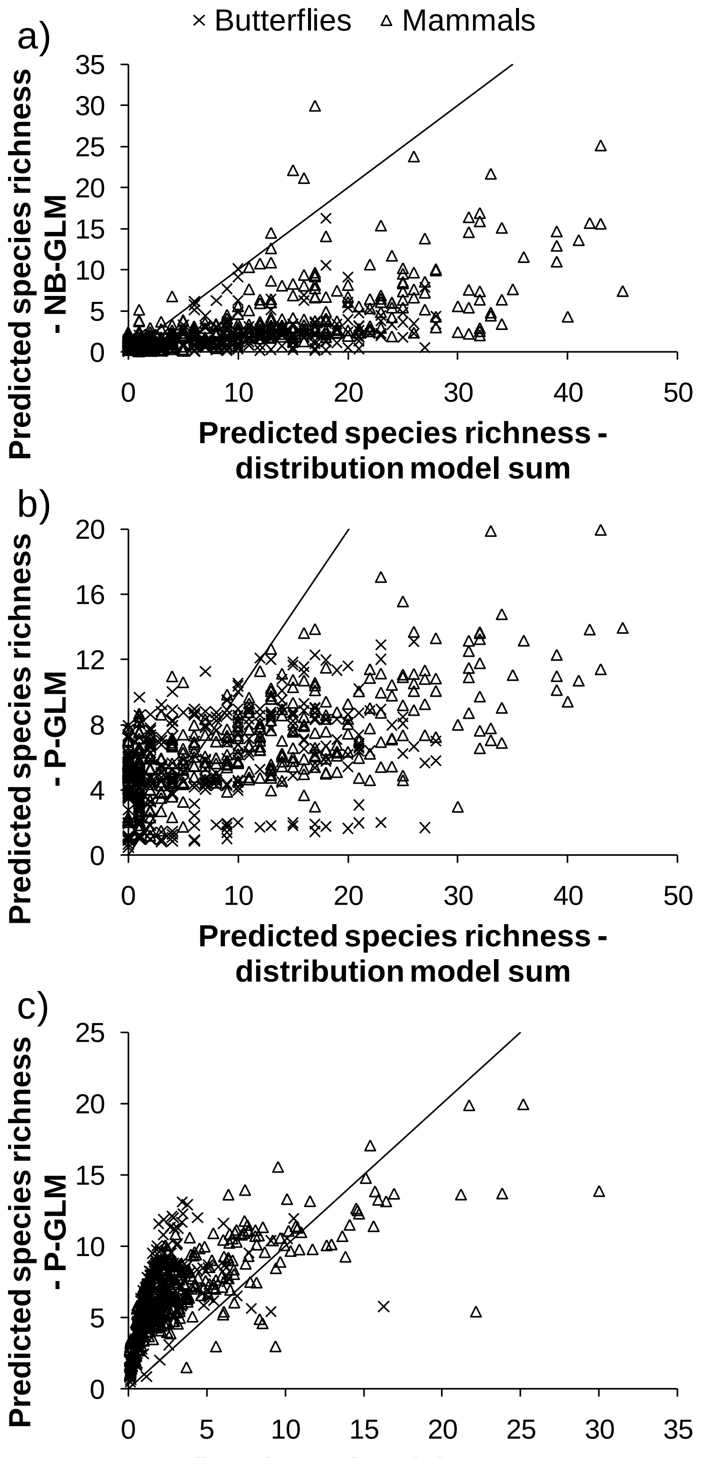

Figure 5.7 - Correlations among the different models used to model species richness patterns: a) between the sum of individual species distribution models and the generalized linear model of species richness values of all grid cells (NB-GLM); b) between the sum of individual species distribution models and the generalized linear model of species richness values of sampled cells (P-GLM); c) between the NB-GLM and P-GLM models of species richness values. The lines represent y=x, for information.

Observed mammal and butterfly species richness values correlated significantly with each other in cells where at least one butterfly species and one mammal species had been recorded ($r_s = 0.615$, $n = 97$, $P < 0.001$). Predicted species richness (estimated using the distribution model-sum method) also correlated strongly and significantly between butterflies and mammals ($r_s = 0.920$, $n = 362$, $P < 0.001$).

Across a random sample of 2000 1-km grid cells, predicted species richness, estimated by summing individual modelled species distributions, of both butterflies (Mann-Whitney test: $U = 76100$, $n = 1995$, $P < 0.001$) and mammals ($U = 70300$, $n = 1995$, $P < 0.001$) was significantly higher inside protected areas than outside (Figure 5.8a). Observed species richness was also significantly higher inside protected areas than outside for both butterflies ($U = 111000$, $n = 1995$, $P = 0.016$) and mammals ($U = 80700$, $n = 1995$, $P < 0.001$) (Figure 5.8b). Predicted ($U = 105000$, $n = 1963$, $P = 0.028$) and observed ($U = 102000$, $n = 1963$, $P = 0.001$) richness of endemic and near-endemic species (mammals and butterflies combined) was significantly higher inside protected areas than outside.

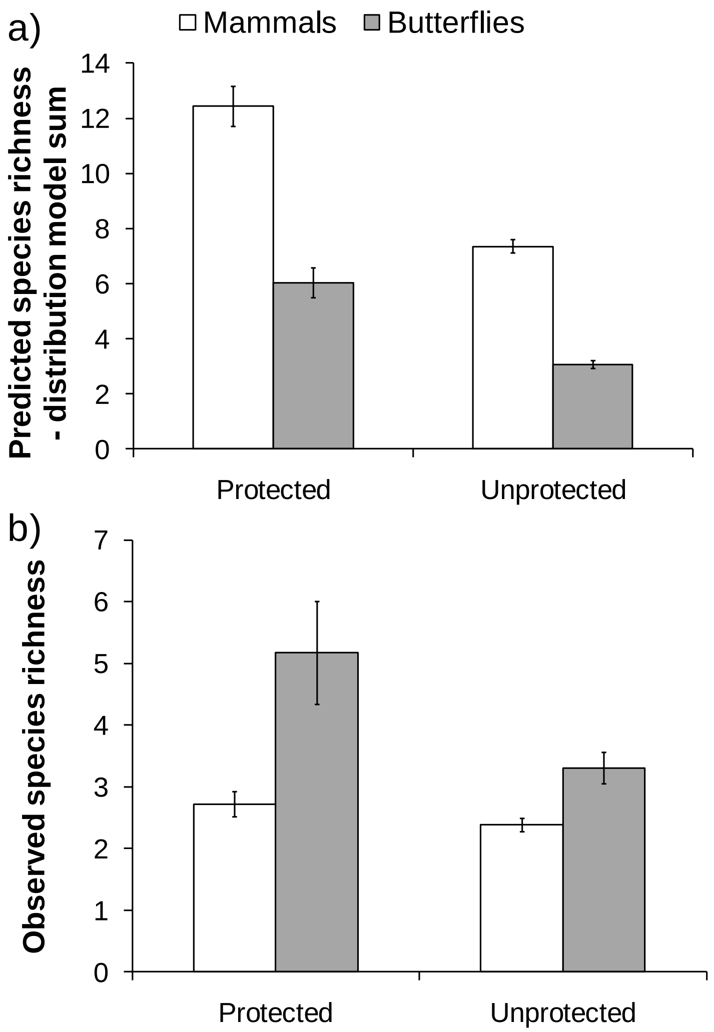

Figure 5.8 - a) Comparison of predicted species richness (mean ± SEM), estimated by summing individual species distribution models, between protected areas and unprotected areas; b) Comparison of observed species richness (mean ± SEM) between protected areas and unprotected areas.

5.5 Discussion

I found significant relationships between species occurrence, species richness and the climate and habitat variables that I used. This finding is consistent with previous studies of butterflies and mammals, where climate and habitat have been identified as good correlates of richness, both at continental and local scales (e.g. Nogués-Bravo & Araújo 2006; Algar *et al.* 2007; Kivinen *et al.* 2007; Levinsky *et al.* 2007; Schouten *et al.* 2009).

The association with habitat may reflect the effect of variation in plant communities on animal species distributions. Butterflies and herbivorous mammals are directly dependent on plants for food and the availability of host plants has been shown to correlate with the occurrence of individual species (Araújo & Luoto 2007) and with species richness (Menéndez *et al.* 2007). Other species may rely on certain vegetation types indirectly, for example through the availability of herbivorous prey. Temperature variables appeared to have a particularly strong effect on butterfly species, although causality cannot be inferred from correlative models. Similar relationships have been noted before (Turner *et al.* 1987) and could be brought about by direct effects of temperature on thermoregulation, or indirectly through climate-driven variation in habitat diversity or plant productivity.

Many other factors, in addition to climate, can affect species richness, such as competition (Anderson *et al.* 2002a), metapopulation dynamics (Hanski 1991), human disturbance (Uehara-Prado *et al.* 2007) and other environmental variables, such as soil type (Kuussaari *et al.* 2007), although some of these factors are likely to play a role in determining species richness only at larger spatial scales than were studied here (Whittaker *et al.* 2001). Given all these non-climatic determinants of species richness patterns, it is not surprising that only a relatively low proportion of the variation in species richness was explained by the models, and that the correlations between modelled and observed species richness were only moderately strong. Some progress is being made towards including factors other than climatic ones in species distribution models (e.g. Araújo & Luoto 2007) and this must remain a priority for improving the accuracy of the models. However, the need to identify areas to conserve is urgent and we cannot wait to act until the most accurate models possible have been developed for every species.

Climate-based models matched observed distributions well and are quick and easy to build for a large number of species.

Another reason for the relatively low explanatory power of the models may be that species inventories in sampled cells were incomplete. This seems likely, given that it may be necessary to visit a site many times before absence can be inferred with confidence (MacKenzie *et al.* 2002). In the case of the NB-GLMs, the inclusion of cells with no records of species presence may have introduced false absences to the models. This is especially likely for the butterfly models, because surveying was less extensive. Ground-truthing may help to assess the extent to which mismatches between modelled and observed species richness are due to incomplete inventories or to errors in the models, although imperfect species detectability may make this difficult in practice (see Chapter 7).

Across all grid cells in the study area, the three methods of modelling richness produced models that showed positive correlations with observed species richness and with each other, suggesting that they could all be used to predict the species richness of unknown areas from limited data on the distributions of species, an application that would be of great value to conservation. Summing the individual distribution models produced the best estimates of species richness, while the NB-GLMs, which included grid cells with a recorded species richness of zero, produced the models that correlated most weakly with observed species richness. Species occurrence and richness data often contain many absences or zero values, especially datasets for small or cryptic species with a low probability of detection (MacKenzie *et al.* 2002). This can bias the parameter estimates of statistical models (Martin *et al.* 2005). The weaker correlations between observed species richness and species richness estimated using the NB-GLMs may be caused by the inclusion of false absences. This conclusion is further supported by the observation that the NB-GLMs produced much lower estimates of species richness than the other two methods (see Figure 5.5). The weaker correlation between observed and modelled species richness for butterflies than mammals may also have been caused by false absences. The mammal data covered a much larger proportion of both geographic and environmental space than the butterfly data, suggesting that recorded species richness values of zero were more reliable in the mammal data. This trend was seen even for the richness models generated by summing the Maxent distribution models. This would be concerning, given that Maxent is designed to be used with datasets containing only presences (Phillips *et al.* 2006) and is a possibility that deserves further attention.

Some previous work has indicated good spatial agreement among different groups in their species richness both at regional scales (Grenyer *et al.* 2006; Qian 2007; Jetz *et al.* 2009) and at more local scales (Hawkins & Porter 2003; Loyola *et al.* 2007; Schouten *et al.* 2009), although it has been shown that the strength of this relationship varies among taxonomic groups and that the relationship is weaker for rare and threatened species (Grenyer *et al.* 2006). The results of this study show that, at least at a local scale within a single country, butterfly and mammal diversity correlate strongly and positively. One might expect good congruence among taxonomic groups in an environment like Egypt's where most species are strongly limited by steep climatic gradients.

In contrast to the findings for many other countries and taxonomic groups (e.g. Chefaoui *et al.* 2005; Evans *et al.* 2006; Pawar *et al.* 2007; Traba *et al.* 2007), Egypt's protected areas network seems to be effective in representing butterfly and mammal diversity. In many parts of the world, protected areas have historically included land that has relatively little commercial value; such areas do not necessarily represent the best choice in terms of conserving biodiversity (Margules & Pressey 2000). The land in most parts of Egypt is of relatively low economic value. The protected areas network is relatively new and the areas were chosen with the aid of knowledge about the country's biodiversity. Given such knowledge, and the ability to overcome conflicting interests over land use, it seems that good coverage of biodiversity can be achieved. On the other hand, large areas of the Nile valley and delta were predicted to have relatively high butterfly diversity but are not yet protected, suggesting that although great progress has been made towards protecting species rich areas, more could still be done. The Nile valley contains land of high economic value and setting aside areas to be protected may present a greater challenge. It is important to note that species richness is only one measure of the importance of conserving different areas. Some authors have suggested using taxonomic uniqueness (e.g. Kershaw *et al.* 1995), complementarity (Margules & Pressey 2000) or threat (Wilson *et al.* 2007) instead. Many of Egypt's endemic and near-endemic mammal and butterfly species were included in the models, and the richness of endemic and near-endemic species was higher inside protected areas than outside, but a more comprehensive assessment of the protected areas should consider a number of different criteria.

In summary, I have shown that seemingly accurate estimates of species richness can be made using relatively small datasets, allowing us to predict the species richness of sites that have not been surveyed. The three predictions were largely similar, although the model based on individual distribution models produced the most consistently accurate results. A similar comparison of the same three models in different regions and for different species would be useful in establishing the general reliability of the approach. Models based on species richness itself, rather than individual species distributions, may be useful when species identity is unknown, for example when using species richness estimators. The results are important for conservation, given the urgency with which we must identify areas that need to be protected, although similar comparisons of species richness models for more taxonomic groups and for a broader geographical region would be useful.

Chapter 6. The effect of interspecific interactions on the distribution of species

6.1 Abstract

Niche theory suggests that interactions among species should be important in determining the extent to which species' potential distributions are realized. Several studies have used species distribution models to test whether the ranges of interacting species are related to one another, focusing mostly on competitive interactions, or on interactions between herbivores and their food-plants. In this chapter, I test whether the accuracy of distribution models for focal species is improved by including the distributions of interacting species as explanatory variables. I focus on two interactions in Britain: the interaction between butterflies and their larval food-plants and the interaction between hoverfly mimics and their hymenopteran model species. For butterflies and bumblebee-mimicking hoverflies, interacting species were good correlates of the distributions of the target species. For wasp-mimicking hoverflies, interacting species did not make a significant contribution to the distribution models, probably because the interacting species are very widespread in Britain. Overall, the results are consistent with predictions made by niche theory about the importance of interactions among species in determining distributions. However, the distribution of control species often showed as good (or nearly as good) a correlation with focal species' occurrence as the distributions of interacting species, suggesting that the distributions of non-focal species (interacting or non-interacting) may be acting as surrogates for environmental conditions, without necessarily having a direct effect on the distributions of the focal species. The results have important implications for modelling the distribution of species. This issue is particularly relevant for attempts to model the potential impact of climate change, since interactions among species that affect their distributions will almost certainly affect the way that species respond to future climate change.

6.2 Introduction

Interactions among species are an important component of ecological niche theory (Hutchinson 1957; Pulliam 2000), being hypothesized to have a significant effect on the distribution of species. While this has been shown on small scales by experiments in the laboratory and in the field (Connell 1961; Davis *et al.* 1998), demonstrating experimentally that distributions on a broad scale are influenced by interactions would be almost impossible. An alternative to experimental tests is to use species distribution models to test whether the occurrence of one species is related to the occurrence of interacting species.

It has long been known that interspecific competition can play an important role in shaping the distributions of species (e.g. Hutchinson 1957; Tilman 1976). Competition has often been considered in studies trying to incorporate interactions among species into distribution models. For example, Anderson *et al.* (2002a,b) modelled the distributions of two species of spiny pocket mouse (*Heteromys spp.*) in North America and by comparing the two models made inferences about competitive interactions between the two species. Another study (Leathwick & Austin 2001) showed that the accuracy of distribution models for 12 tree species in New Zealand was improved by adding the density of competing *Nothofagus* trees. Similarly, Ritchie *et al.* (2009) showed that including the distributions of competitors improved distribution models for marsupials in northern Australia.

Many herbivores, especially insects, show very tight associations with particular food-plants (Ehrlich & Raven 1964). Therefore, the distribution of herbivore species may be constrained by the distribution of their host plants. For example, the accuracy of distribution models for the relatively specialist clouded apollo butterfly (*Parnassius mnemosyne*) was increased by including variables describing the distribution of its larval host plants (Araújo & Luoto 2007). On the other hand, the distributions of larval host plants were not good correlates of the distribution of the more generalist silver-studded blue butterfly *Plebejus argus*, but the distributions of a mutualistic ant species were (Gutiérrez *et al.* 2005).

Batesian mimics are harmless prey species that have evolved to resemble in some way defended (model) prey species, in order to gain protection against predation (Bates 1862; Ruxton *et al.* 2004). In order for the mimic to be protected, its potential predators must be exposed to the defended model. In the absence of the model species, the conspicuous mimic is predicted to suffer higher-than-expected rates of attack by predators (Pfennig *et al.* 2007; Prudic & Oliver 2008), and in fact predators do attack mimics more frequently at sites where the model species is absent (Pfennig *et al.* 2001; Pfennig *et al.* 2007). Therefore, conspicuous mimics are likely to be at a selective disadvantage in areas where their models are not present, and the distribution of a mimic species is expected to overlap the distribution of its models. For the remainder of this chapter, I shall refer to a mimic's model species as 'target' species, to avoid confusion with statistical 'models'.

In this study, I investigate the effect that two types of interactions among species have on distributions: the interaction between butterflies and their host plants, and the interaction between hoverfly mimics and their target species. To assess the extent to which interactions among species are important correlates of species' occurrence, I compare the accuracy of distribution models developed using climate variables, the distributions of interacting species, and the distributions of control species. I also compare the relative strength of the correlation between species occurrence and these different variable groups. Previous studies have tested the effect of food-plant occurrence on the distributions of single butterfly species (Gutiérrez *et al.* 2005; Araujo & Luoto 2007), with mixed results. Mine is the first to test for such an effect across several butterfly taxa. The extent to which the distributions of mimic species correlate with the distributions of their target species has never been considered before. In examining the different factors that correlate with the distributions of species, this study sheds some light on determinants of the ecological niche of species and has important implications for attempts to model the distributions of species.

6.3 Methods

Distribution models were built for three groups of focal species in Britain: 1) butterflies; 2) hoverflies that mimic bumblebees; and 3) hoverflies that mimic wasps. Three different types of independent variables were fitted in different combinations to the models for each species: environmental variables, variables describing the modelled distributions of interacting species, and variables describing the modelled distributions of control species. For the butterflies, the interacting species were larval food plants (Table 6.1) and the control species were other higher-plant species. For the bumblebee-mimicking hoverflies, the interacting species were the target bumblebees (see Table 6.1) and the control species were separately either other bumblebee species or other hymenopteran species. For the wasp-mimics, the interacting species were wasp target species (all *Vespula spp.* and *Dolichovespula spp.* present in Britain) and the control species were other hymenopteran species.

Table 6.1 – Focal species, for which distribution models were made and the species that interact with them. Only interacting species for which accurate distribution models were produced are listed here. For butterflies, the interacting species were the larval host plants, as listed in Asher *et al.* (2001). For bumblebee-mimicking hoverflies, the interacting species were target bumblebees (Francis Gilbert, pers. comm.). Taxonomies followed those used in Asher *et al.* (2001) for butterflies and their host-plants, in Stubbs & Falk (2002) for hoverflies, and in Prys-Jones & Corbet (1991) for bumblebees.

Focal species	Interacting species
Butterflies:	
Lysandra bellargus	*Hippocrepis comosa*
Aricia agestis	*Erodium cicutarium*
Lysandra coridon	*Hippocrepis comosa*
Callophrys rubi	*Genista tinctoria*
Quercusia quercus	*Quercus ilex* *Quercus cerris*
Plebeius argus	*Hippocrepis comosa*
Satyrium w-album	*Ulmus minor*
Erynnis tages	*Hippocrepis comosa*
Thymelicus acteon	*Brachypodium pinnatum*
Hipparchia semele	*Agrostis curtisii*
Argynnis adippe	*Viola hirta*
Melanargia galathea	*Brachypodium pinnatum*
Lasiommata megera	*Brachypodium pinnatum*
Papilio machaon	*Peucedanum palustre*
Gonepteryx rhamni	*Rhamnus catharticus* *Frangula alnus*

Bumblebee-mimicking hoverflies:	
Arctophila superbiens	*Bombus muscorum*
	Bombus pascorum
	Bombus humilis
	Bombus subterraneus
	Bombus distinguendus
Blera fallax	*Bombus pomorum*
	Bombus lapidarius
	Bombus ruderarius
	Bombus rupestris
Cheilosia chrysocoma	*Bombus muscorum*
	Bombus pascorum
	Bombus humilis
	Bombus subterraneus
	Bombus distinguendus
Criorhina floccosa	*Bombus muscorum*
	Bombus pascorum
	Bombus humilis
	Bombus subterraneus
	Bombus distinguendus
Eriozona syrphoides	*Bombus pomorum*
	Bombus lapidarius
	Bombus ruderarius
	Bombus rupestris
	Bombus monticola
Leucozona lucorum	*Bombus pomorum*
	Bombus lapidarius
	Bombus ruderarius
	Bombus rupestris
	Bombus monticola
Pocota personata	*Bombus lucorum*
	Bombus jonellus
	Bombus terrestris
	Bombus hortorum
	Bombus sorooensis
	Bombus bohemicus
	Bombus barbutellus
	Bombus ruderatus
	Bombus sylvestris
	Bombus vestalis
	Bombus hypnorum

The species data for target species, interacting species and controls were downloaded from the National Biodiversity Network (NBN) gateway (for details, see Chapter 2). Occurrence data were downloaded for: 48 hoverfly species that are thought to mimic either bumblebees or wasps, 24 bumblebee species (*Bombus spp.* and *Psithyrus spp.*), nine wasp species (*Vespula spp.* and *Dolichovespula spp.*), 60 other hymenopteran species, 52 butterfly species, and 60 plant species, including all known larval food plants of British butterfly species. The control species were chosen for being reasonably well-sampled in Britain. A list of the providers that contributed the data that I used is given in Appendix 2.1. All species data were mapped at 10-km resolution. A cell was considered occupied by a given species if it contained at least one presence record.

Gridded climate variables were interpolated from recorded values at Met Office weather stations (Perry & Hollis 2006; see Chapter 2). Averages of 39 variables (monthly values of minimum and maximum temperature, monthly values of total precipitation, and annual values of growing degree days, growing season length and consecutive dry days) over all years between 1971 and 2000 were used. To eliminate collinearity among variables and to reduce the chance of overfitting the distribution models, principal components analysis was performed on the 1971-2000 averages of the climate variables. Three principal component axes with eigenvalues greater than 1.0 were retained and used as explanatory variables in the distribution models. In addition to the climate variables, I also used two variables describing land cover. The first was the Institute of Terrestrial Ecology’s land cover classification (Brown *et al.* 2002). The second was a measure of land cover diversity, developed by Stuart Ball of the Joint Nature Conservation Committee by calculating the diversity of land cover categories present within a 2-km radius of the centre of a given grid cell using the Shannon-Weiner diversity index. For full details of the environmental variables used, see Chapter 2. To develop variables describing the distributions of interacting species and control species (non-focal species), I modelled the distributions of these species using Maxent Version 3.1.0. Only the environmental variables were used as independent variables in these models. Linear and quadratic terms were fitted for each of the continuous variables. Default values were used for all parameters: a regularization value of 1, a maximum of 500 iterations, a convergence threshold of 0.00001 and a maximum of 10000 random background grid cells (Phillips *et al.* 2006). Model accuracy was assessed using the AUC statistic (see Chapter 2), as calculated within the Maxent algorithm. Models with an AUC value greater than 0.7 were considered useful (but see Section 2.5.2) and were retained to be used as independent variables in the distribution models for target species. In some cases, especially for the butterflies because models for some of the host plants were very poor, this meant that interacting species were not considered in the models for target species. This may have weakened the observed improvement in model accuracy of including interacting species. The model outputs consisted of modelled probabilities of occurrence. These probabilities were used directly in the distribution models for target species.

Distribution models for the focal species were also developed using Maxent Version 3.1.0, with the same settings as before. In addition to the environmental variables as explanatory variables in these models, I also used the variables describing the distributions of interacting species and control species. The following combinations of variables were used: 1) environmental variables only; 2) interacting species only; 3) control species only; 4) environmental variables and interacting species; 5) environmental variables and control species; 6) all variables together. Control species were of the same number as interacting species, and were randomly selected from the sets of well-sampled species described above. For bumblebee-mimicking hoverflies, non-target bumblebee species and non-bumblebee hymenopteran species were fitted separately as control species. For each species and each combination of independent variables, 100 replicate model runs were made. In each run the data were randomly divided in half, with 50% of the data used to train the model and 50% used to evaluate it. A different set of randomly-chosen control species was used in each model run. Model accuracy was measured using the AUC statistic, as calculated within the Maxent algorithm. For the models fitting all variables together, the relative importance of each variable was extracted from the Maxent output and averaged across all variables in each group (i.e. environmental variables, distributions of interacting species, and distributions of control species).

I tested whether there was a significant difference in model accuracy among models fitting the different combinations of variable types (excluding models fitting all variables together) using repeated-measures (across species) analyses of variance (ANOVAs), if assumptions of normality were met, or Friedman tests otherwise. In all analyses, each species was treated as an independent replicate. For each combination of explanatory variables, distribution-model accuracy was averaged across the 100 replicate distribution-model runs. For the repeated-measures ANOVAs, violations of the assumption of sphericity (assessed using Mauchly's test) were accounted for using the Greenhouse-Geisser correction. Paired-samples t-tests (for normally-distributed data) and Wilcoxon matched-pairs tests (for data that were not normally-distributed) were used to perform planned comparisons between pairs of variable combinations (comparisons 1-6 in Table 6.2). For the bumblebee mimics, models fitting bumblebee control species and models fitting other hymenopteran control species were analysed separately.

Table 6.2 – Predicted outcomes of planned comparisons of model accuracy between pairs of variable types. First, model accuracy (AUC) was compared between models fitting six different combinations of variable types (comparisons 1-6). Second, I compared the percentage contribution of the three variable types to models fitting all variables simultaneously (comparisons 1-3). Pairwise comparisons were made using paired-samples t-tests, if assumptions of normality were met, or Wilcoxon matched-pairs tests otherwise.

1. Environmental variables > interacting species' distributions
2. Environmental variables > control species' distributions
3. Interacting species' distributions > control species' distributions
4. Environmental variables and interacting species' distributions > environmental variables
5. Environmental variables and control species' distributions > environmental variables
6. Environmental variables and interacting species' distributions > environmental variables and control species' distributions

I tested whether there were significant differences among variable types in their percentage contribution to the distribution models fitting all variables ('full models') simultaneously using repeated-measures ANOVAs or Friedman tests, according to whether assumptions of normality were met. Paired-samples t-tests and Wilcoxon matched-paired tests were used to perform planned comparisons between pairs of variable types (comparisons 1-3 in Table 6.1). For the bumblebee mimics, variables describing the distributions of bumblebee control species and variables describing the distributions of other hymenopteran control species were treated separately.

6.4 Results

6.4.1 Butterflies

Distribution models for butterflies were reasonably accurate, regardless of which set of explanatory variables was used (Table 6.3). However, the choice of variable types had a significant effect on the accuracy of distribution models (repeated-measures ANOVA:

$F_{1.484,\ 20.781} = 17.22$, $P < 0.001$; Figure 6.1). As expected, models fitting only climate variables were more accurate than models fitting only variables describing the distributions of plant species (paired-samples t-tests: climate vs. larval food plants – t = 3.76, d.f. = 14, P = 0.001; climate vs. control plant species – t = 5.98, d.f. = 14, P < 0.001). However, contrary to expectations, models fitting only the distributions of their food plants were not significantly more accurate than models fitting only the distributions of control species as predictors (t = 0.28, d.f. = 14, P = 0.786). Models fitting both climate variables and larval food plant distributions, and models fitting both climate variables and control plant species' distributions, were significantly more accurate than models fitting only climate variables (t = 2.59, d.f. = 14, P = 0.011 and t = 1.80, d.f. = 14, P = 0.046 respectively). However, the addition of food plant distributions to the climate variables did not improve model accuracy significantly more than adding control plant distributions to the climate variables (t = 0.65, d.f. = 14, P = 0.525).

Table 6.3 – Average accuracy of distribution models, for 15 butterfly species, fitting different sets of explanatory variables. Climate variables were interpolated from Met Office weather stations (Perry & Hollis 2006; see Chapter 2). Interacting species were larval host plants. Control species were plant species not identified as larval host plants, randomly chosen from 60 plant species that have been well sampled in Britain.

Explanatory variables	Mean model accuracy (AUC)
Climate	0.789
Interacting species	0.721
Control species	0.725
Climate & interacting species	0.791
Climate & control species	0.790

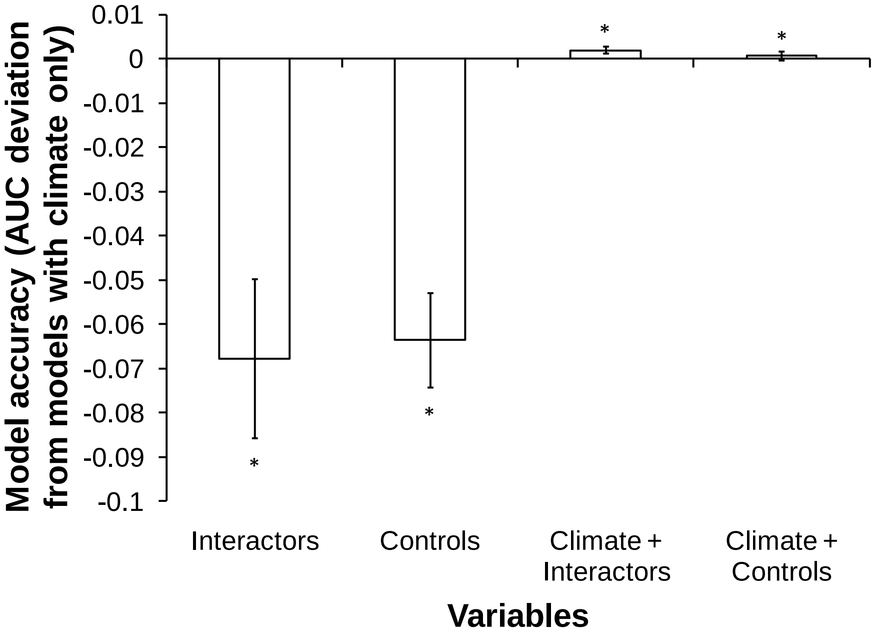

Figure 6.1 – For 15 British butterfly species, the difference in model accuracy between distribution models fitted with only climate variables and distribution models fitted with other sets of variables. Variable types used were: climate variables (‘climate’), variables describing the modelled distribution of interacting species, in this case larval food plants (‘interactors’), and variables describing the modelled distribution of control flowering plant species (‘controls’). *s above or below the bars indicate that the accuracy of models developed using the variables in question was significantly different, in the direction hypothesized, from models developed using only climate variables.

Variables describing the distributions of larval food plants made the greatest percentage contribution to the full models for butterflies, followed by variables describing the distributions of control plant species, followed finally by climate variables. The difference in the percentage contribution of different variable types was marginally non-significant (Friedman’s test: $\chi^2 = 4.13$, N = 15, P = 0.064; Figure 6.2).

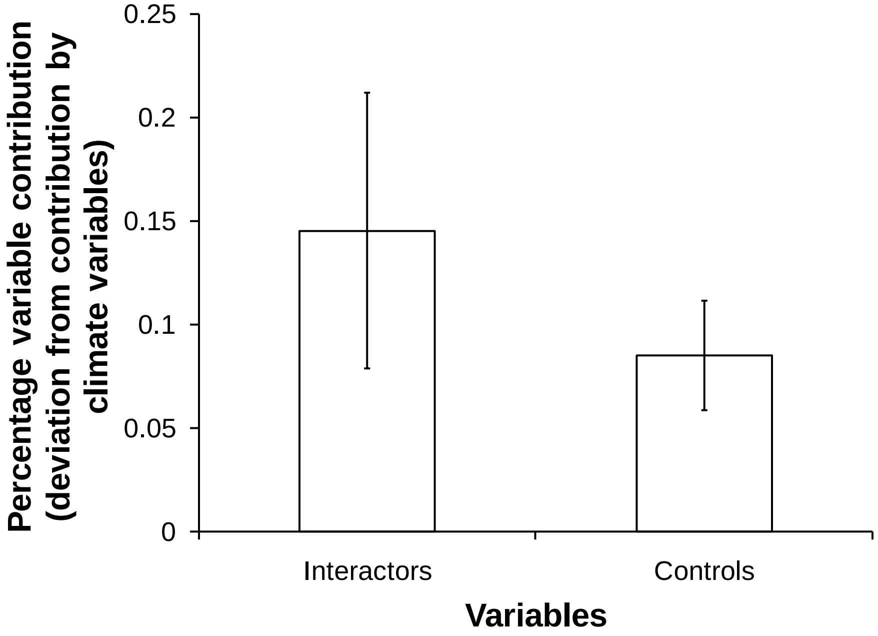

Figure 6.2 – For 15 British butterfly species, the difference in percentage contribution, between climate variables and other variable types, to distribution models fitting all variable types simultaneously. Variable types used were: climate, modelled distributions of larval food plant species (‘interactors’) and random plant species (‘controls’).

6.4.2 Bumblebee mimics

Distribution models for hoverfly mimics of bumblebees were all reasonably accurate (Table 6.4). The accuracy of distribution models for these species also varied significantly among different variable types (Friedman’s test: $\chi^2 = 14.02$, N = 7, P = 0.015; Figure 6.3). Models fitting only climate variables were significantly more accurate than models fitting only the distributions of non-target bumblebee species as predictors (Wilcoxon matched-pairs test: Z = 2.37, N = 7, P = 0.009). All other comparisons of accuracy among models fitting single groups of variables were not significant (Z < 1.18, N = 7, P > 0.05), but the models fitting the different variable types were ranked as expected (climate > interacting species > control species). Models fitting climate variables and the distributions of target species were significantly more accurate than models fitting only climate variables (Z =

1.69, N = 7, P = 0.046). In contrast, the addition of the distributions of either bumblebee control species or hymenopteran control species to the climate variables did not significantly improve model accuracy (Z < 0.85, N = 7, P > 0.05). Models fitting both climate variables and target species' distributions were more accurate than models fitting climate variables and control species' distributions, but not significantly so (bumblebee controls: Z = 1.52, N = 7, P = 0.064; hymenopteran controls: Z = 1.18, N = 7, P = 0.119).

Table 6.4 – Average accuracy of distribution models, for 7 hoverfly species that mimic bumblebee species, fitting different sets of explanatory variables. Climate variables were interpolated from Met Office weather stations (Perry & Hollis 2006; see Chapter 2). Interacting species were the hoverflies' target bumblebee species. Control species were either non-target bumblebee species or other hymenopteran species, randomly chosen from 60 hymenopteran species that have been well sampled in Britain.

Explanatory variables	Mean model accuracy (AUC)
Climate	0.729
Interacting species	0.722
Control species	0.714
Climate & interacting species	0.738
Climate & control species	0.733

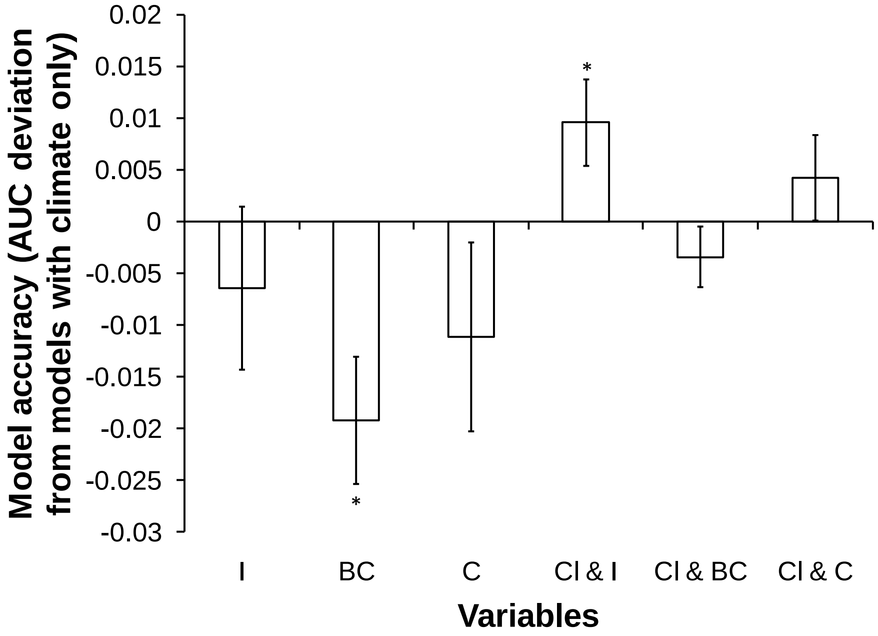

Figure 6.3 – For seven British hoverfly species that mimic bumblebees, the difference in model accuracy between distribution models fitted with only climate variables and distribution models fitted with other sets of variables. Variable types used variously in combination were: climate variables (Cl), variables describing the modelled distribution of interacting species, in this case target bumblebee species (I), variables describing the modelled distributions of control bumblebee species (BC), and variables describing the modelled distributions of control hymenopteran species (C). *s above or below the bars indicate that the accuracy of models developed using the variables in question was significantly different, in the direction hypothesized, from models developed using only climate variables.

For bumblebee mimics, the percentage contribution to the full distribution models of climate variables, variables describing the distributions of target species and variables describing the distributions of control species were not significantly different from one another (repeated-measures ANOVA: $F_{1.587, 9.524} = 0.68$, $P = 0.499$; Figure 6.4).

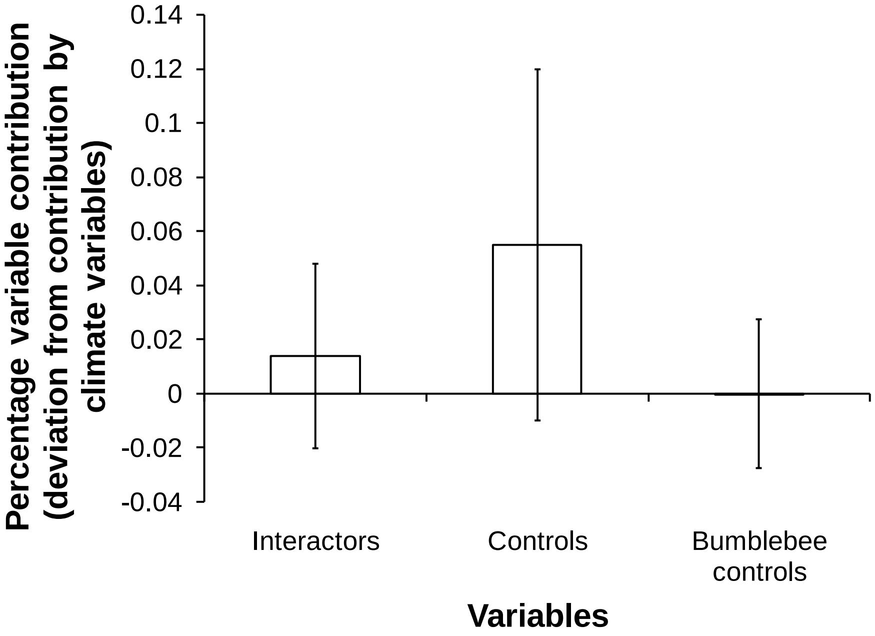

Figure 6.4 – For seven British hoverfly species that mimic bumblebee species, the difference in percentage contribution to distribution models between climate variables and other variable types: modelled distributions of the mimic's bumblebee targets ('interactors'), control bumblebee species ('bumblebee controls') and control hymenopteran species ('controls').

6.4.3 Wasp mimics

Distribution models for hoverflies that mimic wasp species were generally accurate (Table 6.5). The choice of predictor variables had a significant effect on the accuracy of the resulting distribution models (repeated-measures ANOVA: $F_{1.453,\ 58.115} = 9.01$, $P < 0.001$; Figure 6.5). Models fitting only climate variables were significantly more accurate than distribution models fitting only variables describing the distributions of target species (paired-samples t-tests: model species – t = 2.63, d.f. = 40, P = 0.006) and marginally non-significantly more accurate than distribution models fitting only variables describing the distributions of control species (t = 1.59, d.f. = 40, P = 0.060). Adding the distributions of both interacting species and control species to climate variables significantly improved distribution model accuracy (interacting species: t = 2.14, d.f. =

40, P = 0.019; control species: t = 2.39, d.f. = 40, P = 0.011). However, there was no significant difference in accuracy between distribution models fitting climate variables and the distributions of the mimic's target species, and distribution models fitting climate variables and the distributions of control species (t = 0.26, d.f. = 40, P = 0.797).

Table 6.5 – Average accuracy of distribution models, for 41 hoverfly species that mimic wasp species, fitting different sets of explanatory variables. Climate variables were interpolated from Met Office weather stations (Perry & Hollis 2006; see Chapter 2). Interacting species were the hoverflies' target wasp species. Control species were hymenopteran species, randomly chosen from 60 species that have been well sampled in Britain.

Explanatory variables	Mean model accuracy (AUC)
Climate	0.719
Interacting species	0.703
Control species	0.714
Climate & interacting species	0.723
Climate & control species	0.723

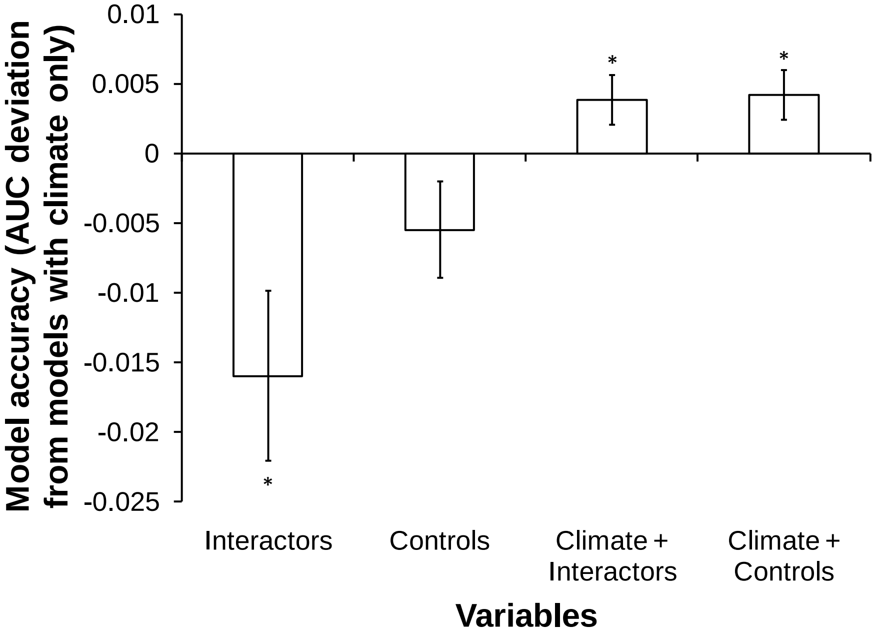

Figure 6.5 – For 41 British hoverfly species that mimic wasp species, the difference in model accuracy between distribution models fitted with only climate variables and distribution models fitted with other sets of variables. Variable types used variously in combination were: climate variables ('climate'), variables describing the modelled distributions of interacting species, in this case target wasp species ('interactors'), and variables describing the modelled distributions of control hymenopteran species ('controls'). *s above or below the bars indicate that the accuracy of models developed using the variables in question was significantly different, in the direction hypothesized, from models developed using only climate variables.

Variables describing the distribution of control species made the greatest percentage contribution to the full distribution models for wasp mimics, followed by variables describing the distributions of target species, followed finally by climate variables; these differences were marginally non-significant (repeated-measures ANOVA: $F_{1.102, 44.086} = 2.16$, $P = 0.074$; Figure 6.6).

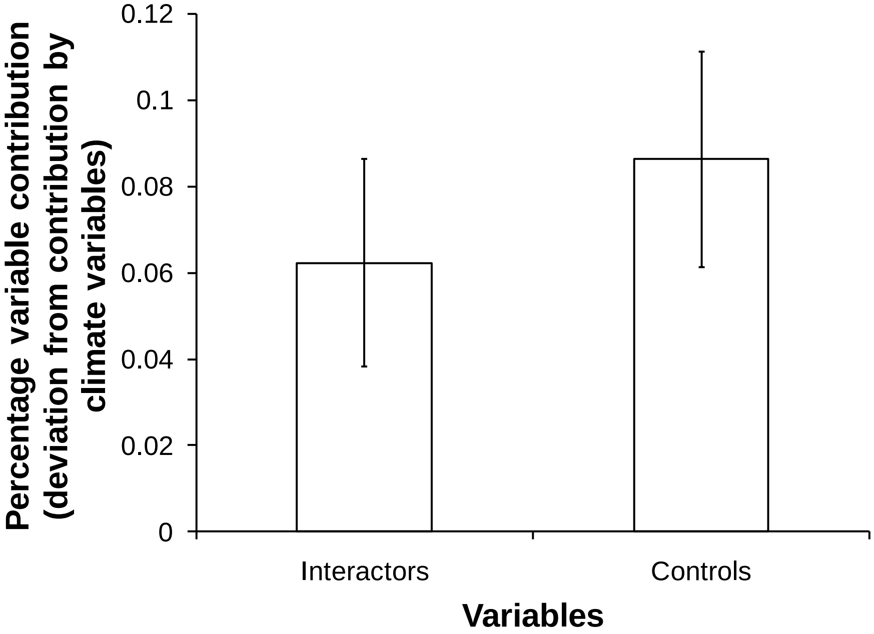

Figure 6.6 – For 41 British hoverfly species that mimic wasps, the difference in percentage contribution, between climate variables and other variable types, to distribution models fitting all variable types simultaneously. Variable types used were: climate, modelled distributions of the mimic's target wasp species ('interactors') and control hymenopteran species ('controls').

6.5 Discussion

Overall, the results provided some support for the idea that interactions among species can result in associations between their distributions. However, the effect was small and was not consistent among all of the groups of species tested.

I show that distribution models for several British butterfly species are significantly improved by adding variables describing the distributions of known food plants. However, a similar improvement was seen when the distributions of control flowering plant species were added to the models. Furthermore, models fitting only variables describing food-plant distributions were no more accurate than models fitting only the distributions of control plant species. This may have been because the distributions of plant species act as surrogates for some aspect of habitat or climate not represented by the environmental variables used (Austin 2002). Alternatively, the small improvement in model accuracy with the addition of host-plant distributions may have been because we did not consider host plants with inaccurate distribution models. For some butterfly species, the main host plants were omitted (R. J. Wilson, pers. comm.). Repeating this exercise at a broader, for example European, scale should allow accurate distribution models for the omitted plant species to be developed; including these plants in models for the butterfly species at this scale might increase their accuracy more than was observed in this study.

In any case, other studies that have incorporated the distributions of other species as explanatory variables in distribution models (e.g. Leathwick & Austin 2001; Araújo & Luoto 2007; Ritchie *et al.* 2009) only considered interacting species and did not use control species for comparison. On the basis of such a test, it is impossible to say whether the associations came about through direct effects of the interactions between species. On the other hand, in this study, the distributions of food plant species made a greater contribution to the distribution models than the distributions of random plant species or climate variables, suggesting that butterfly distributions do correlate, at least to some extent, with the availability of food.

It is reasonable to expect the distributions of mimics to be influenced by the distributions of their target species, since a mimic should only be afforded protection from predators in areas where the unpalatable model is also present (Prudic & Oliver 2008). However, the broad-scale effect of the occurrence of target species on the distribution of their mimics has never been tested before. My results for bumblebee-mimicking hoverflies provide some support for a correlation between the distributions of mimics and their target species. Distribution models fitting both climate variables and target species' distributions were significantly more accurate than models fitting climate variables alone, or climate variables and control species' distributions. Furthermore, distribution models fitting the distributions of target species alone were more accurate than models fitting the distributions of control species alone, although less accurate than models fitting only climate variables. Variation in the accuracy of the distribution models was small and there were no obvious differences in the percentage contribution of different variables to the models, probably owing to low statistical power caused by small numbers of bumblebee mimics.

In contrast, the results for wasp-mimicking hoverflies provided no support for the hypothesis that the occurrence of target species has a significant effect on the distribution of their mimics. The accuracy of climate-only distribution models was improved by adding either the distributions of the wasp target species or the distributions of control species, and distribution models fitting the distributions of control species alone were more accurate than models fitting the distributions of a mimic's target species alone. Furthermore, variables describing the distributions of control species made a greater percentage contribution to the distribution models than variables describing the distributions of wasp target species. This may be because most wasp species are distributed very widely throughout Britain and thus their occurrence can exert little influence over the distributions of their mimics. Alternatively, it may be because wasp-mimicking hoverflies are, on average, more generalist in their target species than bumblebee-mimicking hoverflies (Gilbert 2005). The addition of variables describing the distributions of control hymenopteran species may have improved the accuracy of the hoverfly distribution models by capturing some aspect of the environment not represented by the climate and habitat variables used (Austin 2002). Alternatively the spatial structure in the distributions of the control species may have helped to capture some of the spatial structure in the distributions of the hoverfly species (see also Bahn & McGill 2007).

The existence of tight associations between different species, either directly-interacting or non-interacting species, raises the possibility that the distributions of certain species could be used as surrogates for the distributions of other species (Caro & O'Doherty 1999). Given that knowledge about some taxa is very limited, this would be of great value for conservation. However, tests of the effectiveness of surrogacy in conservation planning have provided mixed results (van Jaarsveld *et al.* 1998; Thomson *et al.* 2007; Pinto *et al.* 2008; Franco *et al.* 2009). The correlation between the distributions of species in this study was relatively low: models using only climate as explanatory variables were almost always better than models using only the distributions of other species as explanatory variables. Therefore, the species used here would be relatively poor surrogates for each other and, where the necessary data are available, gaps in our knowledge about the distribution of species would be better filled by developing climate-based distribution models rather than by using surrogate species.

The relative importance of different aspects of the environment in determining the distributions of species will depend on the resolution of analysis and on the extent of the study area considered (Whittaker *et al.* 2001). The effect on distributions of interactions among species may be greater at different spatial extents and resolutions than those studied here. However, in a global meta-analysis, interactions among species had the strongest effect on species richness patterns at intermediate (10-500 km^2) resolutions (Field *et al*., 2009), encompassing the 100-km^2 resolution that I used here. On the other hand, effects of scale or resolution may help explain why interactions had no discernible effect on the distributions of wasp mimics in my study.

Interspecific competition has received a great deal of attention from ecologists for many years and has been shown many times to have an effect on the distribution of species and on the composition of ecological communities (e.g. Tilman 1976). Considering the distributions of competitor species has been shown to increase the accuracy of distribution models (Leathwick & Austin 2001; Anderson *et al.* 2002a; Anderson *et al.* 2002b; Ritchie *et al.* 2009). On the other hand, identifying specific competitive interactions can be very difficult compared with the very tight associations between butterflies and their food plants, and between mimics and their models. Moreover, the association between the distributions of interacting species is likely to be stronger for more specific interactions than for more diffuse interactions (e.g. Gutiérrez *et al.* 2005; Araújo & Luoto 2007).

The effect on the accuracy of distribution models of considering interactions among species was generally very small; highly accurate models were generated for most species using only climate and habitat variables. This further supports the use of climate-based distribution models in conservation and ecology. Identifying relevant interspecific interactions may be very difficult for the majority of species, particularly in poorly-studied parts of the world. Nevertheless, including interactions, where possible, can improve the accuracy of distribution models. Small differences between climate-only models and models including interactions may be exaggerated if the models are projected onto different time periods (for example when predicting the potential impact of climate change) or onto different geographical areas (such as when predicting the extent of species’ invasions) (Araújo & Luoto 2007). Therefore, incorporating interactions among species into models must be a priority in the future.

Chapter 7. Testing the accuracy of species distribution models using new species occurrence data collected during a field survey[8]

7.1 Abstract

Species distribution models are generally evaluated against a subset of the species records used to develop them. However, this can lead to artificially inflated estimates of model accuracy, especially when the species records are biased. A better approach is to evaluate the distribution models against completely independent records. However, this approach is rarely used owing to the large amount of time and money required to obtain such data. In this chapter, I use independent records from a new survey to validate distribution models for Egyptian butterfly, reptile, amphibian and mammal species. The accuracy of the distribution models was estimated using: 1) the traditional approach of partitioning the species records, half for model development and half for model evaluation; and 2) using new records of species occurrence collected during a survey of 21 previously unvisited sites in diverse habitat types. I tested whether variation in model accuracy among species could be explained by species detectability, range size, the number of records used to develop the distribution models, and body size. Estimates of accuracy derived using the new species records correlated positively with estimates generated

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[8] A modified version of this chapter is soon to be published in *Oikos*

using the traditional data-partitioning approach, but were on average 22% lower. Model accuracy was negatively related to range size and number of records used to build the models, and positively related to the body size of butterflies. There was no clear relationship between species detectability and model accuracy. Overall, the field data generally validated the species distribution models but revealed important differences among species in the accuracy of models.

7.2 Introduction

There is a vast amount of data on the distributions of species in museums, natural history collections and in the literature (Graham *et al.* 2004a). However, there are several limitations associated with data from these sources, which can affect their usefulness for distribution modelling. First, records are often accompanied by a very vague description of the locality from which they were taken. This translates into poor locational accuracy when the record is georeferenced (i.e. when it is assigned geographical coordinates – Graham *et al.* 2004a; Section 1.5). Errors in the locations of species records may have a negative impact on the accuracy of distribution models based on them (Visscher 2006, but see Graham *et al.* 2008). Second, museum data are often biased. Such bias could be: 1) spatial – towards areas to which it is easy for scientists to gain access, or towards areas that are biologically interesting; 2) temporal – towards time periods when collecting was more frequent; or 3) taxonomic – towards species that are easy to detect or of more interest to the collectors (Hijmans *et al.* 2000). Soberón *et al.* (2000) evaluated a large database of North American butterflies, finding that sampled sites were located significantly closer to roads than expected by chance, that only a few species were well recorded, and that sampling was temporally biased. Reddy & Dávalos (2003) conducted a similar test on a database of bird records from sub-Saharan Africa: records were significantly closer to roads, rivers and cities than expected by chance, and samples were biased towards protected areas. If these effects cause the records to be biased towards certain climate or habitat types, then distribution models based on them may be inaccurate (Wintle *et al.* 2005).

The third major problem with data from museums and literature sources is that there are rarely data documenting places where the species is known not to exist (absence records) (Graham *et al.* 2004a). There are modelling techniques designed to be used with datasets that consist only of presence records, such as climate envelope approaches and techniques that model the presences with reference to the background environmental conditions (Wintle *et al.* 2005). However, several of the most popular modelling approaches, such as generalized linear models (GLMs) and generalized additive models (GAMs), can only be used with both presence and absence data. A commonly-used solution to this problem is to generate 'pseudo-absence' data (Ferrier & Watson 1997). Several methods have been proposed to do this, the simplest being to take a random sample of grid squares that lack presence records (Ferrier & Watson 1997). One obvious problem with using pseudo-absence data is that some absences are likely to be found in areas that are suitable for, and even inhabited by, the species (Graham *et al.* 2004a). Of course, actual records of species absence may also prove to be erroneous. Many species are very difficult to detect and it can take many visits to a site before absence can be inferred with any degree of confidence (Kéry 2002; MacKenzie *et al.* 2002). Given accurate species records from a well-designed survey, models built with only presence records have been shown to perform as well as models built with both presences and absences (Wintle *et al.* 2005) and may present the safest option when there is uncertainty over the reliability of absence data.

Data from museums, private collections and from the literature are too valuable a source of data to ignore for distribution modelling studies. For tropical areas, these are often the only available data (Stockwell & Peters 1999; Anderson *et al.* 2003). However, given the potential biases and inaccuracies associated with them, it is particularly important to test the accuracy of distribution models based on them. The simplest way to assess the accuracy of a model is to test its ability to predict correctly the data used to develop it in the first place (Fielding & Bell 1997). This is effectively a measure of goodness-of-fit of the model. The main drawback of this approach is that a model can fit the data used to build it very well without having the ability to generalize (a phenomenon known as overfitting), and this method of model evaluation tends to lead to over-optimistic measures of model accuracy (Chatfield 1995). A better approach is to partition the data in some way, building the model with part of the dataset and evaluating it against the remainder (Fielding & Bell 1997). This is the approach taken by most studies (e.g. Hernandez *et al.* 2008; Franklin *et al.* 2009). If species records are scarce, there are statistical methods, such as jack-knifing and cross-validation, which can partition the data sequentially allowing the models to be evaluated against independent data without wasting any that could be used for model building (Fielding & Bell 1997; Manel *et al.* 1999b; Ferrier *et al.* 2002; Pearson *et al.* 2007). A problem with all data-partitioning approaches is that if the same bias in the species data is present in all partitions, then the model may be biased and the estimate of model accuracy inflated (Chatfield 1995). Ideally models should be evaluated using new, independent data on species occurrence

(Chatfield 1995). With the wide availability of global positioning systems (GPS), these new records can be assigned geographical coordinates on collection, eliminating the problem of locational errors. Few studies have used independent data to validate models because collecting such data can be impractical, time-consuming and costly (Wintle *et al.* 2005; but see Loyn *et al.* 2001; Pearce *et al.* 2001; Elith 2002; Ferrier *et al.* 2002; Elith *et al.* 2006).

Even if one is confident of a lack of bias in the data, different kinds of species may be more or less suited to the model-building process. There have been attempts to assess differences among species in the accuracy of their distribution models (Kadmon *et al.* 2003; Berg *et al.* 2004; Seoane *et al.* 2005; Hernandez *et al.* 2006; see also Chapter 4). These studies have often found that species that are more narrowly distributed produce more accurate distribution models, possibly because small-ranged species have better-defined habitat requirements and tend to inhabit a greater proportion of the suitable environment, or because in species with larger ranges populations show local adaptation to the environment in different areas (Stockwell & Peterson 2002; Brotons *et al.* 2004; Segurado & Araújo 2004; Hernandez *et al.* 2006). On the other hand, effects of range size could be a statistical artefact. The species datasets used for most studies contain only presence records. Therefore, measures of model accuracy are normally calculated using pseudo-absence data. If pseudo-absence data are drawn randomly from throughout the study area, then species with smaller range sizes will have artificially higher estimates of model accuracy because, assuming that variation in the environment is spatially autocorrelated, many pseudo-absences will fall in areas of environmental space distant from occupied areas (Lobo *et al.* 2008). Using new survey data with real species absence records to evaluate the models makes it possible to disentangle real effects of range size on model accuracy from statistical artefacts.

Species that are easier to detect are likely to have more complete occurrence data. This may result in more accurate distribution models for these species (Seoane *et al.* 2005), although this has rarely been tested. In butterflies, larger-bodied species are probably easier to detect during surveys, and Pöyry *et al.* (2008) showed that models for butterfly species with a larger wingspan were more accurate than models for smaller species. On the other hand, larger-bodied butterflies may be more accurately modelled because they are more mobile and thus able to occupy a greater proportion of areas with suitable climate and habitat (Pöyry *et al.* 2008). Modelling the detectability of species using presence and absence data from a new survey (MacKenzie *et al.* 2002) allows the relationship between species detectability and model accuracy to be tested more explicitly.

In this chapter, I modelled the distributions of Egyptian butterfly, mammal, reptile and amphibian species using records from museums, collections and the literature, presenting a rare test of their accuracy using new, independently-collected survey data as well as a test using the more traditional data-partitioning method. It was not possible to collect new species records systematically or randomly in the time available because of the remoteness and inaccessibility of many parts of Egypt, but the records were completely independent of the data used to build the models, were designed to be representative of as many habitat types as possible given the constraints imposed by the logistics of sampling in a remote and hostile environment, and were georeferenced using a GPS and so had negligible locational error. I used the new survey data, which comprise both presence and absence records, to test whether a negative effect of species range size on model accuracy persists in the absence of statistical artefacts. I also tested whether model accuracy is related to species detectability and body size (of butterflies).

7.3 Methods

Distribution models were developed for Egyptian butterfly, mammal, reptile and amphibian species using Maxent Version 3.1.0 (Phillips *et al.* 2006). The species data for developing the models were taken from the BioMAP database (see Chapter 2 for more details). The number of records available for each species ranged from 10 to 412 (Median = 58).

The environmental variables used in the models consisted of climate, elevation and habitat variables. The 19 climate variables and the elevation variable were taken from the WorldClim Version 1.4 dataset (Hijmans *et al.* 2005; see Chapter 2). The habitat variable used was a geological habitat classification with 11 categories (sea, littoral coastal land, cultivated land, sand dune, wadi, metamorphic rock, igneous rock, gravel, serir sand sheet, sabkha and sedimentary rock). This map was compiled using satellite imagery, and was verified by extensive ground-truthing (Dr. A. Hassan 2007, unpublished data; see Chapter 2).

To create a second set of species data (hereafter referred to as the independent species records) with which to evaluate the distribution models, a small team of field assistants and I conducted a survey of butterflies, mammals, reptiles and amphibians in Egypt in the summers (May – July) of 2007 and 2008. The reptile, amphibian and mammal species surveyed are active throughout the summer months, and the flight periods of all of the butterfly species surveyed encompassed the whole period of sampling. The new records were *not* used to develop distribution models, only to evaluate them.

The new data were biased towards roads. The terrain in Egypt makes it almost impossible to sample completely randomly, with many areas situated hundreds of kilometres from the nearest road. I minimized bias in environmental space as much as possible by selecting sites that covered: (1) as large a geographical area as possible; and (2) as many different habitat types as possible, defined using a geological habitat map (Dr. A. Hassan 2007, unpublished data) and a vegetation land cover map, derived using data from the Advanced Very High Resolution Radiometer (AVHRR) (Hansen *et al.* 2000). At each site we performed four 1-km walking transects at different times of day (early morning, late morning, late afternoon, evening), paced to take approximately an hour and a half each. At the same time, some members of the expedition actively searched for species in the area surrounding the start-point of the transect. Transects were located such that they sampled all the major micro-habitat types present at each site, including small water-bodies. A species was recorded as being present if it was observed at least once, and absent otherwise. Twenty-one sites were surveyed in this way (Figure 7.1; Appendix 7.1). In addition to records from the fully-surveyed sites, we also included incidental observations of species from 13 other localities (Figure 7.1; Appendix 7.1). Data from the incidental sites consisted of records of species presence only, because I did not carry out replicate transects at these sites and thus could not infer species absence. Almost all new sites were situated at least 1 km from sites with records in the original dataset (Figure 7.1). All fully-surveyed sites were at least three kilometres from the nearest other site, and all but four were at least ten kilometres from the nearest other site. Including locations with incidental records, distances among sites were sometimes much smaller; four sites were less than one kilometre from the nearest other site and 15 sites were less than ten kilometres from the nearest site. Butterflies were sampled by visual searching and sweep netting, reptiles and amphibians by visual scans and active searches, and mammals mainly by checking for tracks and signs, although sightings of species were also noted. Sixty species were recorded in total, 34 of which were recorded at least twice: 20 reptiles and amphibians, ten butterflies and four mammals (Appendix 7.1).

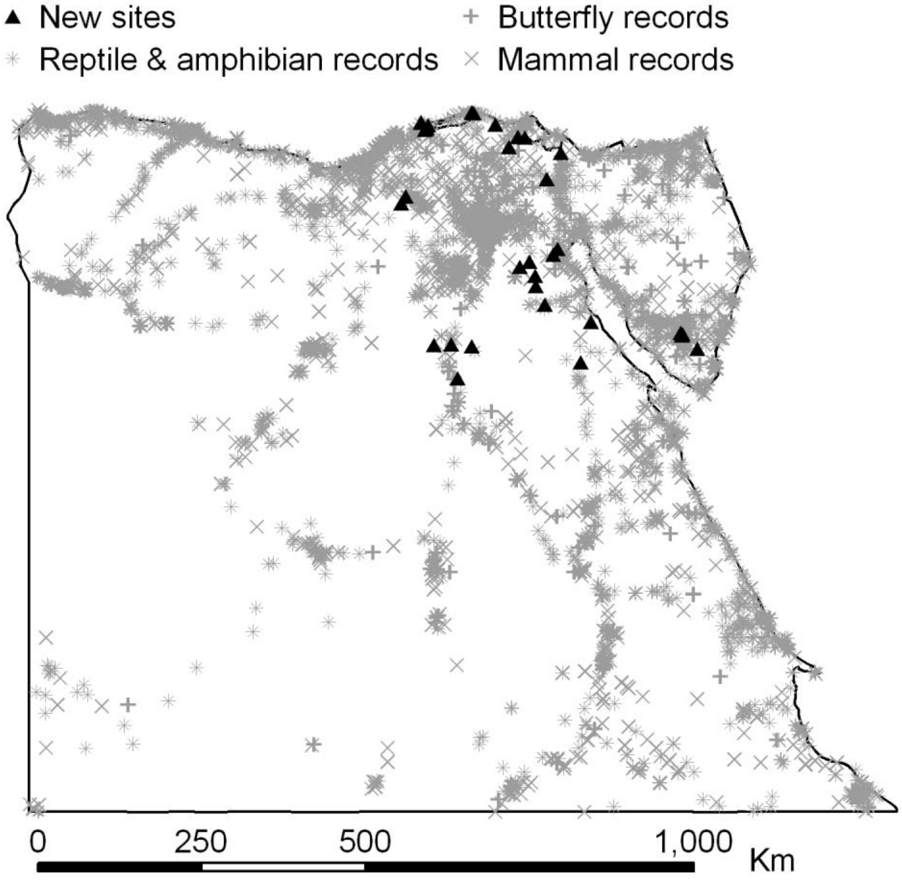

Figure 7.1 – Sites with reptile, amphibian, butterfly and mammal records in the BioMAP database (grey crosses and asterisks), and sites that were sampled during the new survey (black triangles).

Imperfect detectability of species is likely to have an impact on the reliability of data describing species absence from surveys such as mine (Kéry 2002; MacKenzie *et al.*

2002). I modelled the detectability of species in the new survey data, following MacKenzie *et al.* (2002). The four transects undertaken at each site were treated as independent visits (n_1, n_2, n_3, and n_4). The likelihood (L) of obtaining a particular pattern of occurrence for a species across all four transects at all fully-surveyed sites is:

$$L = \left[\psi^{n.} \prod_{t=1}^{t=4} p^{n_t} \left(1 - p\right)^{n. - n_t} \right] \times \left[\psi \prod_{t=1}^{t=4} \left(1 - p\right) + \left(1 - \psi\right) \right]^{N - n.} ,$$

where ψ is the probability that a species occurs at a given site, p is the probability that the species is detected during one transect given that it occurs at the site, t is the transect number, $n.$ is the number of sites where the species was recorded in at least one transect, and N is the total number of sites visited (MacKenzie *et al.* 2002). The parameters p and ψ were estimated using a maximum likelihood approach with the package ‘mle’ in R (R Development Core Team 2004). Upper and lower bounds of 0.0001 and 0.9999 were set for p and ψ respectively. The model has been shown to be reasonably accurate with sample sizes as small as those encountered here (Wintle *et al.* 2004). The model assumes that occurrence and detection probabilities are constant across sites, which is almost certainly not true. The modelled probabilities should therefore be considered rough estimates to gauge the reliability of the occurrence data and not as accurate estimates of the probabilities of detection and occurrence.

The distribution models were evaluated using three different sets of data. First, using partitioned data, whereby the original species records were divided randomly before modelling – half for model building and half for model evaluation. Models were evaluated using the reserved presence records and 2,500 pseudo-absences (Ferrier & Watson 1997), drawn randomly from cells that lacked a record of the species in question. Second, using the independent species presence records and 2,500 pseudo-absences, generated as before. Third, using the independent presence *and* absence records. Model accuracy was measured using the AUC statistic (Fielding & Bell 1997). Estimated accuracy according to AUC values was compared among the three approaches. I correlated estimates of accuracy made by partitioning the original species records with estimates made using the independent presence and absence records, to test whether models were ranked similarly. To provide an alternative measure of accuracy to the AUC statistic, the models were also tested against the independent presence and absence records using the slope of the relationship between model predicted probability and species occurrence (presence or absence), fitted using a generalized linear model with binomial errors (McCullagh & Nelder 1989).

I tested a number of factors that might explain variation in model accuracy (measured using the independent presence and absence records) among species: (1) estimated species detectability (2) range size in Egypt; (3) number of presence records used to build the models; and (4) taxonomic group (mammals, butterflies, or reptiles and amphibians). The proportion of Egypt's land area predicted by the distribution models to be occupied was used as an index of range size. To calculate this, I converted the continuous prediction of probability of occurrence into a binary prediction of presence or absence, by assigning a threshold probability of occurrence to the model for each species. The threshold was set such that 95% of the presence records used to build a model were predicted correctly as being present (Pearson *et al.* 2004).

The effect of estimated species detectability on distribution-model accuracy was tested by a simple correlation test, because detectability could not be estimated for all species (i.e. for species that were not recorded during the walking transects). I also correlated butterfly wingspans (wing-tip to wing-tip; Gilbert & Zalat 2007) with model accuracy and with detectability. It has been suggested that larger butterflies should be more detectable during surveys than small butterflies (Pöyry *et al.* 2008). The remaining factors were tested using generalized linear models with normal errors. AUC values were entered as the dependent variable, taxonomic group as a factor, and predicted range size and number of presence records used to develop the model as covariates. I used a model selection method based on the approach recommended by Burnham & Anderson (2002). I built a global model with all terms, and candidate models with every combination of terms. AIC scores were extracted for each model and the difference between a model's AIC value and the lowest value of all models (the AIC difference, Δ_i) was calculated. Model weight was calculated using the following formula (Burnham & Anderson 2002):

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\frac{1}{2}\Delta_r\right)}$$

where Δ_i is the AIC difference of the model in question and Δ_rs are the AIC differences of the other models. The relative importance of each variable was assessed by summing the AIC weights of all candidate models containing it (Burnham & Anderson 2002), hereafter referred to as the 'sum of AIC weights'.

7. 4 Results

Estimates of the probability of detecting a species in a single transect (*p*) ranged from less than 0.001 to approximately 0.75 (Table 7.1). For butterflies, the migratory species *Vanessa atalanta* and *Vanessa cardui*, and the skipper *Pelopidas thrax* had low probabilities of detection, but most species were relatively easily detected. Mammals generally had much lower probabilities of detection than butterflies; the gazelle *Gazella dorcas* was an exception because its presence could be reliably ascertained by tracks and faeces. Reptiles and amphibians were highly variable in their estimated detectability. The snakes and the chamaeleon *Chamaeleo africanus* had very low probabilities of detection, while the lizards, skinks and amphibians generally had higher probabilities. Estimates of the probability of site occupancy (ψ), which is equivalent to the proportion of sites predicted to be occupied, were consistent with estimates of range size derived from the species distribution models (Spearman's rank correlation test: $r_s = 0.453$, $n = 23$, $P = 0.03$).

Table 7.1 - Estimated probabilities of occurrence (ψ), and detection given occurrence (p), for species recorded in the walking transects at the fully-surveyed sites. Each transect was treated as an independent sampling event. Ψ and p were estimated using a maximum likelihood approach (MacKenzie *et al.* 2002), assuming that both probabilities are constant across sites.

Species	ψ	p
Reptiles and amphibians:		
Acanthodactylus boskianus	0.466	0.508
Acanthodactylus scutellatus	0.429	0.112
Cerastes cerastes	0.413	0.019
Chamaeleo africanus	0.413	0.019
Malpolon monspessulanus	0.420	< 0.001
Mesalina guttulata	0.413	0.019
Natrix tessellata	0.413	0.019
Ptychadena mascareniensis	0.471	0.208
Rana bedriagae	0.413	0.019
Sphenops sepsoides	0.512	0.361
Trapelus mutabilis	0.408	0.039
Butterflies:		
Colias croceus	0.461	0.247
Danaus chrysippus	0.521	0.438
Lampides boeticus	0.625	0.750
Leptotes pirithous	0.476	0.190
Pelopidas thrax	0.450	0.108
Pieris rapae	0.440	0.238
Pontia glauconome	0.474	0.294
Vanessa atalanta	0.420	< 0.001
Vanessa cardui	0.427	< 0.001
Zizeeria karsandra	0.500	0.300
Mammals:		
Capra nubiana	0.420	< 0.001
Gazella dorcas	0.406	0.296
Lepus capensis	0.460	0.159

Model accuracy estimates made by partitioning the original species records into model-building and model-evaluation datasets were high and significantly better than random (one sample t-test: t = 22.0, d.f. = 33, P < 0.001). AUC values ranged from 0.666 to 0.975, with an average of 0.845 ± 0.016. Accuracy estimates made using the independent presence records (i.e. records from the new survey) and pseudo-absences were also high and significantly better than random (t = 16.7, d.f. = 33, P < 0.001). AUC values ranged from 0.485 to 1.000, with an average of 0.875 ± 0.022. Finally, accuracy estimates generated using the independent presences *and* absences were reasonably high and significantly better than random ($t = 4.03$, d.f. = 33, $P < 0.001$), although lower than estimates made using pseudo-absences. AUC values ranged from 0.219 to 1.000, with an average of 0.655 ± 0.039 (for examples of the distribution models, see Figure 7.2). Testing the accuracy of models against the independent records using the slope of the relationship between model predicted probability of occurrence and observed occurrence (presence or absence) also showed the models to be reasonably accurate. The relationships were positive for 26/34 species (binomial probability < 0.002), although only nine were significantly positive (GLM: $P < 0.05$). Slope coefficients ranged from -5.67 to 22.13; the average coefficient was significantly greater than zero (one sample t-test: $t = 3.16$, d.f. = 32, $P = 0.003$). Estimates of accuracy made by partitioning the original presence records correlated significantly and positively with estimates made using the independent records (Spearman's rank correlation: $r_s = 0.544$, $n = 34$, $P = 0.001$; Figure 7.3).

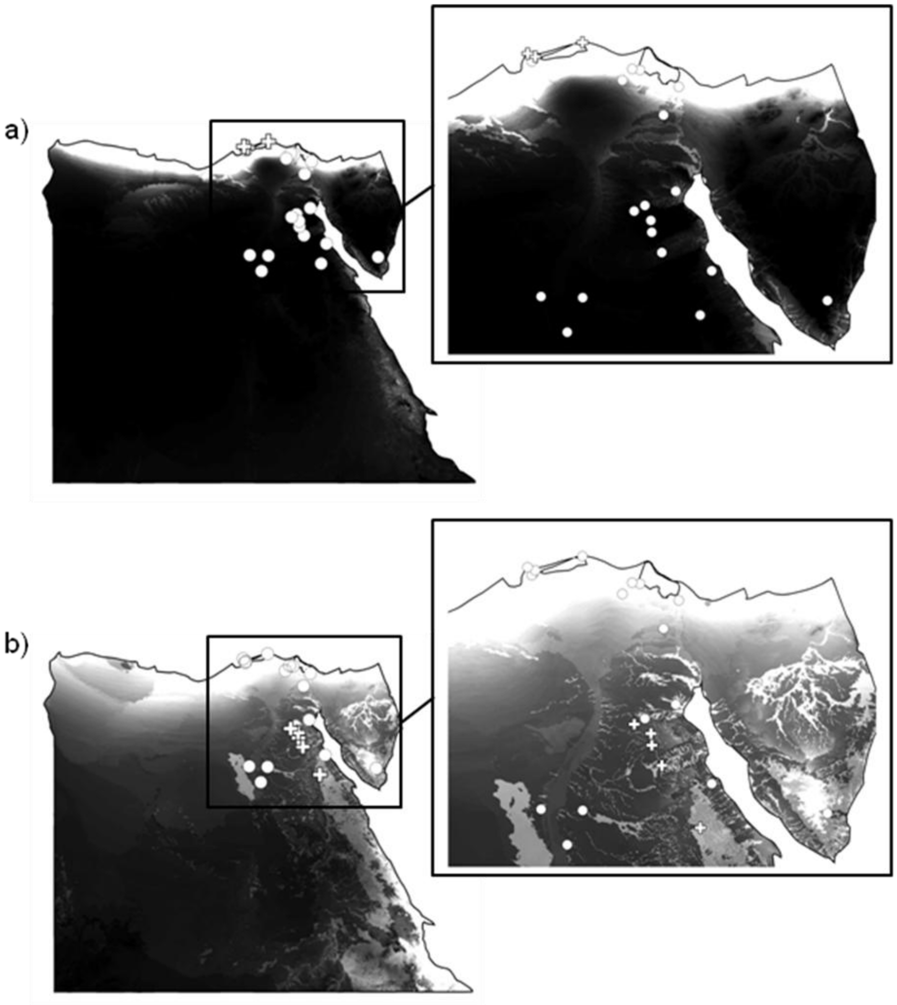

Figure 7.2 – Predicted distributions and independent occurrence records for two species: (a) the Montpellier snake *Malpolon monspessulanus,* which had the most accurate distribution model; and (b) the cape hare *Lepus capensis*, which had the least accurate distribution model. Distribution models were built with Maxent Version 3.1.0 using records from the BioMAP database and variables describing climate and habitat. Light shading indicates areas with a high probability of occurrence, while dark shading indicates a low probability of occurrence. The independent occurrence records (+ = presence; O = absence) were collected during a new field survey of 21 sites in the summers (May – July) of 2007 and 2008; these records were used to evaluate the distribution models.

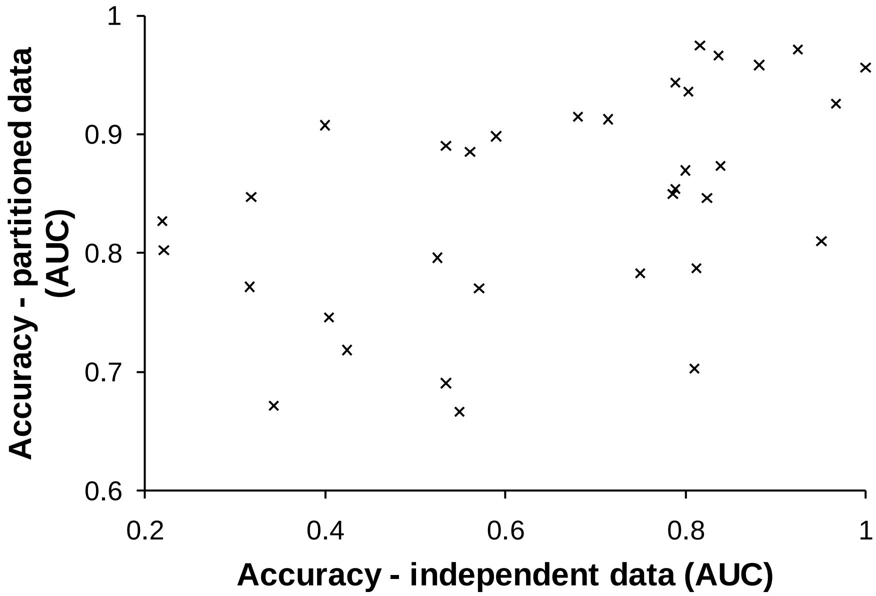

Figure 7.3 – The relationship, for 34 species of Egyptian mammal, butterfly, reptile and amphibian species, between distribution-model accuracy estimated using independent species presence and absence records, and distribution-model accuracy estimated by partitioning the original data, half for model building and half for model evaluation. Accuracy was estimated using the AUC statistic (Fielding & Bell 1997).

Model accuracy showed no clear relationship with estimated species detectability (Spearman's rank correlation: $r_s = -0.294$, n = 25, P = 0.154). However, for butterfly species, wingspan correlated positively with model accuracy (Pearson's correlation coefficient: r = 0.652, n = 10, P = 0.041; Figure 7.4). Butterfly wingspan did not correlate with detectability (Pearson's correlation coefficient: r = -0.151, N = 10, P = 0.677). Model accuracy was negatively related to the predicted range size of species within Egypt (GLM: sum of AIC weights = 0.952; Table 7.2; Figure 7.5a). Surprisingly, there was also a strong negative effect of the number of species presence records used to build the models on the accuracy of predictions (sum of AIC weights = 0.991; Table 7.2; Figure 7.5b). There was little support for an effect of taxonomic group on the accuracy of distribution models (sum of AIC weights = 0.172; Table 7.2).

Table 7.2 – Results from a set of general linear models testing factors affecting variation in the accuracy of species distribution models among species. Factors tested were predicted range size in Egypt (R), number of presence records used to build the models (S), and taxonomic group (T). Candidate models were built with every combination of terms. These models were compared using AIC and the difference between the AIC of a model and the minimum AIC of all models. Model weights were calculated following Burnham & Anderson (2002).

Model	Deviance in AUC values explained	AIC	AIC difference (Δ_i)	Model weight (w_i)
R+S	48.34	-20.41	0	0.804
R+S+T	49.05	-16.9	3.51	0.139
S+T	40.63	-13.68	6.73	0.0278
S	31.96	-13.04	7.37	0.0202
R+T	34.53	-10.35	10.06	0.00526
R	24.6	-9.55	10.86	0.00353
T	3.71	0.756	21.17	2.04×10^{-5}

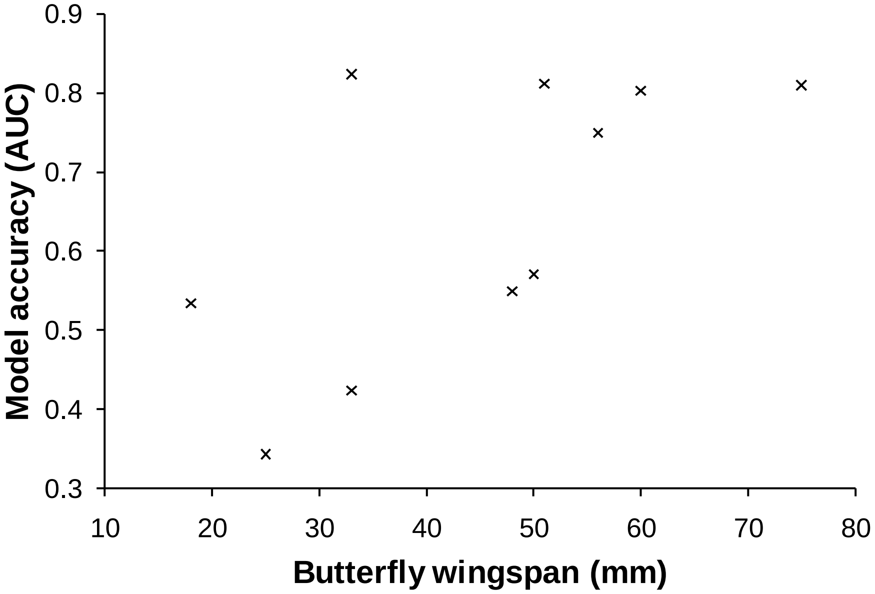

Figure 7.4 – Relationship between the wingspan (wing-tip to wing-tip; Gilbert & Zalat 2007) of ten Egyptian butterfly species and the accuracy of distribution models, assessed using independent species records from a new field survey. Model accuracy was measured with the AUC statistic (Fielding & Bell 1997).

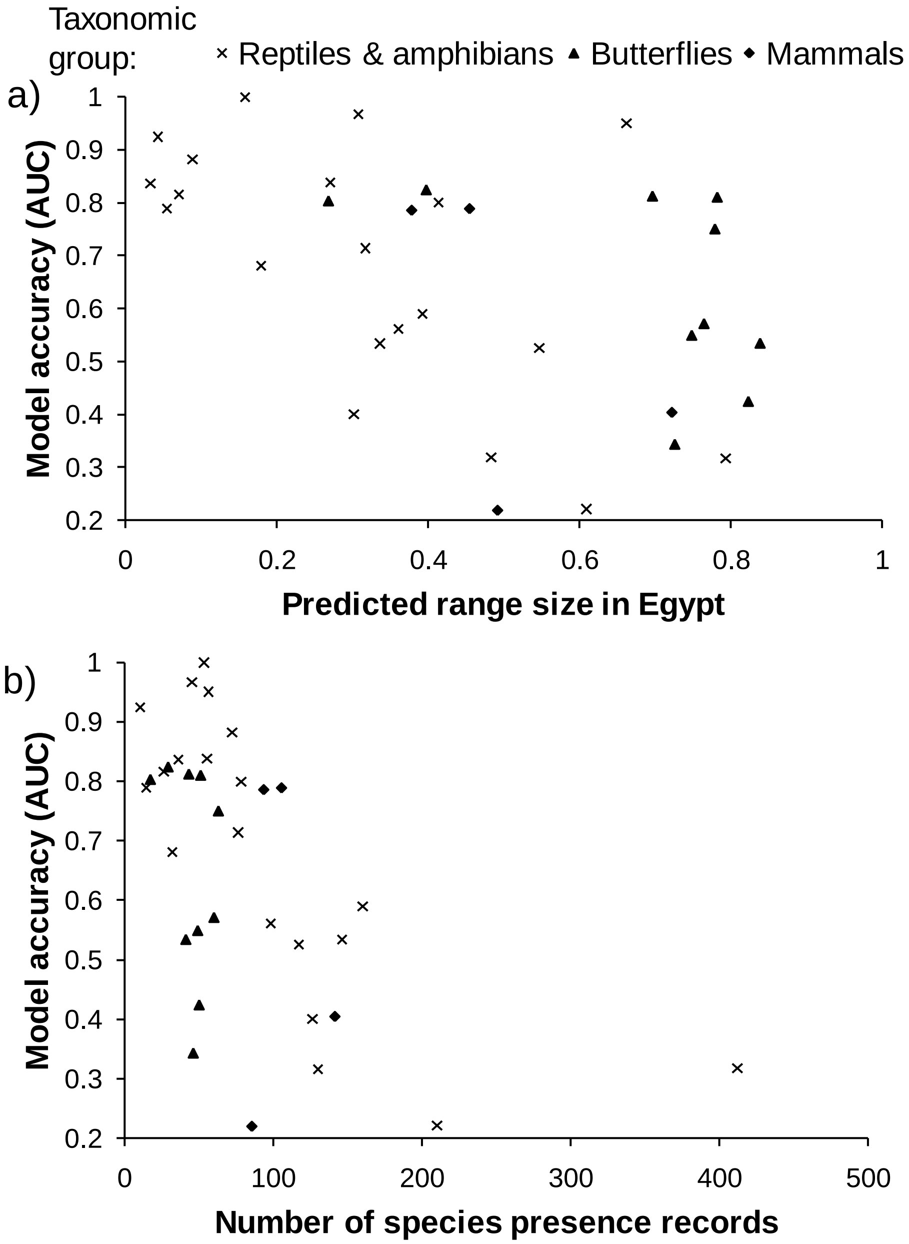

Figure 7.5 – For 34 species of Egyptian reptiles, amphibians, butterflies and mammals: (a) the relationship between range size, estimated as the proportion of grid cells in Egypt predicted occupied, and the accuracy of distribution models estimated using independent species records from a new field survey; (b) the relationship between the number of presence records used to build the distribution model and model accuracy, estimated using independent species records. Model accuracy was measured using the AUC statistic (Fielding & Bell 1997).

7. 5 Discussion

Overall, the distribution models built in this study were shown to be significantly better than random when tested against independent data collected by surveying a diverse range of habitats in Egypt. This strongly suggests that data from museums, natural history collections and the literature can be used to make useful predictions about species' ranges. Several studies have reached a similar conclusion (Peterson *et al.* 2002a; Raxworthy *et al.* 2003), but it is rare that models are tested against independent evaluation data (but see Loyn *et al.* 2001; Mitchell *et al.* 2001; Pearce *et al.* 2001; Elith 2002; Ferrier *et al.* 2002). I am only aware of one study that has used independent data to test the accuracy of distribution models developed using museum data (Feria & Peterson 2002). Uncertainties and biases will be more prevalent in models built using museum and literature records (Graham *et al.* 2004a), making evaluation with independent data more important. Some authors have experimented with using species records from separate geographical areas (Peterson & Shaw 2003; Randin *et al.* 2006; Heikkinen *et al.* 2007) or time periods (Raxworthy *et al.* 2003) as independent records to evaluate models. However, predictions extrapolated outside the environmental conditions encompassed by the data that were used to develop the model may be inaccurate in the new areas even if they are accurate in the area for which they were built. The best approach is to collect new, independent data inside the study area for which the models were developed, reducing bias as much as possible, particularly bias in environmental space (Wintle *et al.* 2005).

The reliability of data on species absence probably depends on the relative detectability of the taxa in question (MacKenzie *et al.* 2002). There was substantial variation in estimated detection probability among species in the new survey. The results of the maximum likelihood model were consistent with our expectations. First, the predicted proportion of sites occupied correlated positively with predicted range size according to the distribution models. Second, detection probabilities were very low for elusive species and for rare migrants, and higher for conspicuous and more abundant species, including some of the lizards and most of the butterflies. The accuracy of species distribution models did not appear to be affected by detection probability, suggesting that, even in small-scale surveys with relatively few visits to each site, imperfect detection of species may not be a major problem. On the other hand, the accuracy of distribution models for butterfly species was positively correlated with body size, which has been used as a surrogate for detectability (Pöyry *et al.* 2008). In my study, butterfly wingspan was not obviosuly related to detectability.

It is possible that my maximum likelihood-based estimates of detection probability were inaccurate; for instance, one of the major assumptions of the maximum likelihood model that I used is that occurrence and detection probabilities are constant across sites (MacKenzie *et al.* 2002), which is very unlikely to be true. However, very abundant and easily detectable species, such as the long-tailed blue butterfly *Lampides boeticus* and Bosc's lizard *Acanthodactylus boskianus*, had high detection probabilities and inaccurate distribution models, whereas species that are difficult to detect, such as Montpellier's snake *Malpolon monspessulanus*, had low estimated detectability but very accurate distribution models. An alternative explanation for the relationship between butterfly wingspan and distribution-model accuracy is that larger butterflies are more mobile and able to reach a greater proportion of suitable habitat, giving a closer correlation between environmental variables and occurrence (Pöyry *et al.* 2008), although the effect of body size on butterfly mobility is contentious (Cowley *et al.* 2001).

Estimates of model accuracy made using the data-partitioning approach were relatively consistent with estimates made using the new survey data. This suggests that a data-partitioning approach can give us a good idea about the relative accuracy of models and can be used to compare model accuracy among species. Accuracy estimates made using the partitioned species records and pseudo-absences, and also with independent presence records and pseudo-absences, were much higher than estimates made using both independent presence and independent absence records. This is consistent with a previous suggestion that overly-optimistic estimates of model accuracy can be generated using pseudo-absence data (Lobo *et al.* 2008), but it should be borne in mind that the small numbers of independent records may partly explain the low measures of accuracy using independent data. Nevertheless, I recommend further comparisons of model accuracy using pseudo-absences and real absences, and caution against using data partitioning as the sole method for evaluating distribution models, especially if the models are to be used for conservation decision-making. The accepted threshold of 0.7 above which models are considered to be good (e.g. Pearce & Ferrier 2000a) may place undeserved confidence in poor predictions.

Some of the variation in model accuracy was explained by range size. Species with larger ranges within Egypt were modelled less accurately than species with smaller ranges. A negative effect of range size on the accuracy of species distribution models has been reported before (Stockwell & Peterson 2002; Brotons *et al.* 2004; Segurado & Araújo 2004; Hernandez *et al.* 2006), but most of these studies have used real presence data with pseudo-absence data. In this case, the apparent effect of range size could be a statistical artefact owing to pseudo-absences being more distant in environmental space from the presence records for species with smaller range sizes, yielding artificially high

AUC values (Lobo *et al.* 2008). My results show that the distributions of species with smaller ranges are modelled more accurately when the potential for statistical artefacts is removed. This could be because narrowly-distributed species have more specific climate and habitat requirements than more widespread species (Brotons *et al.* 2004; Hernandez *et al.* 2006). Alternatively, separate populations of widespread species may show local adaptation to the environmental conditions in different parts of the study area (Stockwell & Peterson 2002; Brotons *et al.* 2004); although two of the butterfly species have more than one subspecies in Egypt (*Carcharodus stauderi* and *Spialia doris*; Gilbert & Zalat 2007), these distinctions were not considered in this study.

Surprisingly, we found a significant negative effect of the number of species records used to build models on the accuracy of model predictions. Most previous studies have found the relationship between sample size and model accuracy, if present, to be positive (Pearce & Ferrier 2000a; Phillips *et al.* 2004). Several studies have shown that species with more specific habitat requirements are modelled more accurately than habitat generalists (Kadmon *et al.* 2003; Hernandez *et al.* 2006). It is probable that some aspect of this was captured by sample size but not by the measure of range size that I used. For example, habitat specialists may be easier to model because they have very specific requirements, but may be restricted to particular microhabitats or resources and thus have been detected less frequently in the past.

Ideally data used to evaluate the accuracy of distribution models should be completely independent of the data used to build the models and free from any bias (Chatfield 1995), but given limited time and resources this may not be possible (Wintle *et al.* 2005). Although my new species records contained some bias (for example, towards locations near roads), I reduced environmental bias by selecting sites that covered as broad a range of climate and habitat types as possible. This approach is better than simple data partitioning, because bias has been reduced and because locational error in the records has been eliminated. Moreover, it is more practicable than a truly random survey, especially for less accessible areas such as Egypt.

In conclusion, my results support the use of species distribution models in ecology. Models for many species in three very different taxonomic groups were shown to be accurate using completely independent species occurrence data. However, there was considerable variation across species in the accuracy of distribution models. Distribution models have great potential as tools for conservation, but it is crucial that their predictions are first evaluated thoroughly. Currently, using completely independent data to evaluate model predictions is a rare practice, not surprising given that conducting new surveys can be time-consuming and very expensive (Wintle *et al.* 2005). However, I show that even small field surveys can be used to test model accuracy and can highlight patterns in the accuracy of models.

Chapter 8. Testing the ability of species distribution models to predict changes in the distribution of species as a result of climate change

8. 1 Abstract

The impact of climate change on biodiversity is a crucial issue in conservation. Species distribution models are being used increasingly to predict how species ranges will shift with changing climate. Evaluating the accuracy of these predictions is difficult because the changes have not yet occurred. One possible approach is to test the ability of models to predict changes that have happened in the past. In this chapter, I use data on climate and on the distribution of hoverfly and bird species in Britain for the last thirty years. These data were divided into discrete time periods and models were then built using data from each time period to predict the distribution of species in every other time period, either assuming that changes in the climate caused changes in distributions (change models) or assuming that distributions did not change as a result of climate change (control models). I tested models against nationwide occurrence data and single-site abundance data. Models assuming no change in distributions in response to climate change predicted past and future distributions and abundances better than models that incorporated changes in the climate. This result was highly consistent across taxa for both hoverflies and birds. Marked northward shifts in distributions over time were predicted by the models, but not matched by the data. The results suggest that species are not yet responding to climate change in ways predictable by simple climate-based models, and thus have very important implications.

8.2 Introduction

Climate change is one of the most serious threats facing biodiversity today (Thuiller 2007). There is growing evidence for an effect of climate change on the distribution (Parmesan & Yohe 2003; Devictor *et al.* 2008; Raxworthy *et al.* 2008a), phenology (Parmesan & Yohe 2003; Willis *et al.* 2008) and population dynamics (Green *et al.* 2008; Willis *et al.* 2008) of species, and on the composition of ecological communities (González-Megías *et al.* 2008). Increasingly, species distribution models have been used to predict the impact that climate change will have on species ranges in the future, on the basis of projections of future environmental conditions (Miles *et al.* 2004; Thomas *et al.* 2004; Araújo *et al.* 2005a; Hole *et al.* 2009).

The accuracy of model predictions is generally evaluated by comparing models with data on the current distribution of species, before projecting into the future. However, there are at least five kinds of uncertainties associated with the use of distribution models to project into the future (Pearson & Dawson 2003) which are ignored when evaluated this way. First, predictions of changes in the environment are unlikely to be entirely accurate and there may be variability in the predictions made by different models of climate change (Reilly *et al.* 2001; Beaumont *et al.* 2008). Second, species distribution models are correlative; therefore the predictor variables used may not directly influence the distributions of species (Pearson & Dawson 2003) and may not correlate with the distribution of the same species in the future. Third, the realised distributions of species may be determined to a large extent by interactions with other species (Pearson & Dawson 2003; Hampe 2004; Pearson & Dawson 2004; Guisan & Thuiller 2005). Including variables describing interactions among species has been shown to alter dramatically predictions of future distributions made by correlative models (Araújo & Luoto 2007; Schweiger *et al.* 2008). Furthermore, experimental tests have shown that interactions among species can have a large effect on how species respond to climate change (Davis *et al.* 1998; Post & Pedersen 2008; Harmon *et al.* 2009). Fourth, models often assume that species can disperse to new suitable habitat as fast as is necessary to keep up with changes in the environment (Pearson & Dawson 2003; Hampe 2004; Pearson & Dawson 2004), although some studies do include different dispersal-ability scenarios (e.g. Peterson *et al.* 2001; Peterson *et al.* 2002b; Peterson 2003; Miles *et al.* 2004; Thomas *et al.* 2004; Thuiller *et al.* 2005a; Levinsky *et al.* 2007) or use dispersal models to simulate how ranges might shift given dispersal limitation (Iverson *et al.* 1999; Dullinger *et al.* 2004; Miles *et al.* 2004; Keith *et al.* 2008; Engler & Guisan 2009; Engler *et al.* 2009). Modelling changes in the distributions of three butterfly species in Britain, Willis *et al.* (2009) went a step further, using only a dispersal model and ignoring climate changes altogether, assuming that species were lagging behind climate change and thus limited only by habitat availability and their ability to disperse. These purely dispersal-based models showed a remarkably good fit to recent observed changes in the distributions of the species (Willis *et al.* 2009). Studies of both plants and animals have shown considerable differences among taxa in the extent to which they are at equilibrium with the climate (Svenning & Skov 2004). Dispersal limitation may lead to considerable differences between predicted and observed distributions after climate change (Best *et al.* 2007; Devictor *et al.* 2008; Mustin *et al.* 2009). Fifth, species may adapt to the changing environment rather than shifting their distributions (Pearson & Dawson 2003; Hampe 2004; Pearson & Dawson 2004; Skelly *et al.* 2007). Although some evidence suggests that niches are conserved over evolutionary time (Peterson *et al.* 1999), other authors have suggested that species could adapt rapidly to changing climates (Knouft *et al.* 2006). Studying how plant species were affected by climate changes in the past, Davis & Shaw (2001) concluded that responses included both range shifts and adaptation. Some species have shown adaptive responses to recent climate change (Charmantier *et al.* 2008). On the other hand, future climate change may be too fast to allow species to adapt to the new conditions (Davis & Shaw 2001; Davis *et al.* 2005; Skelly *et al.* 2007; Visser 2008).

A better test of the ability of models to predict the impact of climate change on future distributions is to predict changes that have already happened. However, there have been very few such tests. One study (Walther *et al.* 2007b) modelled the distribution of the Chinese windmill palm (*Trachycarpus fortunei* Hook.) in its native range in Southeast Asia, then applied this model to Europe for two separate time periods in the recent past; the actual distribution of the palm coincided closely with the model predictions. Another (Araújo *et al.* 2005a) showed that predicted changes in the distributions of British bird species matched changes that had already occurred moderately well. Araújo *et al.* (2005b) showed that these predictions were improved by taking a consensus of several different models, although in this case the accuracy of models was assessed as the concordance between observed and predicted range shifts across the whole study area, rather than being assessed in a spatially explicit fashion. On the other hand, changes in the distribution of the map butterfly (*Araschnia levana*) in Finland between 1961-95 and

2000-04 were predicted relatively poorly (Mitikka *et al.* 2008), and recent temporal changes in bird community structure and composition in North America were predicted very poorly by models based on spatial associations with climate variables (La Sorte *et al.* 2009). Finally, predictions from distribution models about trends in climatic suitability for bird species, both in Britain and throughout Europe, match recent observed population trends (Green *et al.* 2008; Gregory *et al.* 2009). As with the study by Araújo *et al.* (2005b), these studies averaged predicted trends across the whole study area and did not test the ability of models to make spatially explicit predictions. There have also been attempts to predict changes in species distributions associated with changes in the climate over very much longer (geological) time periods (e.g. Martínez-Meyer *et al.* 2004a; Martínez-Meyer & Peterson 2006; Pearman *et al.* 2008b). An alternative method for testing the accuracy of models predicting changes in the distribution of species would be to test the transferability of models in space (Araújo & Rahbek 2006). Projecting distribution models in space will incur some of the uncertainties associated with predicting distributions in different time periods, including dispersal limitation, adaptation and changes in interactions among species.

In this chapter, I provide the first comparison between the accuracy of models predicting contemporary distributions, those that incorporate known changes in the climate to predict past and future distributions, and models that predict past and future distributions assuming no effect of climate change on species distributions. I divide data for Britain into discrete time periods to document changes in the distribution and abundance of hoverflies and birds (see Appendix 8.1 for a full list of species), and in the climate, over the last 40 years. Models are tested against two independent datasets, the presence/absence of species across the whole study area of Great Britain, and the abundances of species from a single site for each taxonomic group. The abundance data allow me to make a rare test of the ability of occurrence-based models to predict species abundance, an interesting and potentially very important but neglected aspect of predictive distribution modelling (He & Gaston 2007). I also compare observed with predicted latitudinal shifts in hoverfly distributions over the last 40 years in response to known climate changes.

8.3 Methods

Nationwide occurrence data (U.K. excluding Northern Ireland) for 255 hoverfly species were taken from the Hoverfly Recording Scheme (Ball 2009), selecting those data collected since 1972. These records were mapped at a resolution of 1 km and records with less accurate locations excluded. If a grid cell contained at least one record for a given species, then it was defined as occupied. The hoverfly occurrence data consisted only of presence records; species absence was not assumed for grid cells with no records. For each time period, I excluded species that had fewer than thirty records. Much larger numbers of presence records were available for many species (Table 8.1). Constant-effort abundance data for the hoverfly species were collected using a single Malaise trap in a suburban garden on the outskirts of Leicester by Dr. Jennifer Owen ($52^o38'$N $1^o05'$E) between 1972 and 2001. The Malaise trap was set up continuously from March to October each year, and emptied every week (see Owen 1991). Annual total catches for each species were then averaged across years in each of six time periods (1972-1977; 1978-1982; 1983-1987; 1988-1992; 1993-1997; 1998-2002), chosen to give adequate sample sizes in each period (see Table 8.1).

Table 8.1 Minimum, maximum and median numbers of presence records available for modelling hoverfly and bird species in each of the time periods used. Numbers refer to the numbers of grid cells with at least one presence record, at a resolution of 1 km for hoverflies and 10 km for birds. There were a total of 236416 grid cells at 1-km resolution and 2234 cells at 10-km resolution.

Time Period	Number of Presence Records		
	Minimum	Maximum	Median
Hoverflies:			
1972-1977	31	290	76
1978-1982	30	725	104
1983-1987	32	2344	167
1988-1992	32	2897	198.5
1993-1997	34	4723	167
1998-2002	30	6178	220.5
Birds:			
1968-1971	1037	2223	2045.5
1988-1991	730	2190	1824

Occurrence data for thirty-two woodland bird species were taken from the BTO breeding bird atlases for the years 1968-72 (Sharrock 1976) and 1988-91 (Gibbons *et al.* 1993); they therefore represent two discrete snapshots in time rather than the continuous sampling of the hoverflies. These data had a resolution of 10 km. Cells with no record of a given species were assumed to be unoccupied, so the data consisted of both presences and absences. There were large numbers of presence records for most species (Table 8.1). The abundance data for birds were collected as part of the BTO Constant Effort Sites scheme (Anon. 2009a), at Treswell Wood in north Nottinghamshire (53°18’N 0°52’W). For each year, I summed the number of unique individuals of each species caught weekly in mist nets between April and July (for details, see Peach *et al.* 1995). Annual abundances were then averaged across years in each of eight time periods (1968-1971; 1972-1975; 1976-1979; 1980-1983; 1984-1987; 1988-1991; 1992-1995; 1996-1999), selected to coincide with the time periods covered by the two atlases.

I used two sets of environmental variables to construct the distribution models. The first set consisted only of climate variables. The Climate data consisted of gridded values of 39 climate variables (annual growing degree days, annual consecutive dry days, annual growing season length, monthly maximum temperatures, monthly minimum temperatures and monthly precipitation) interpolated from data recorded at Met Office weather stations (Perry & Hollis 2006; see Chapter 2). Annual values for each variable were averaged across years in each of the time periods. Using 39 variables in species distribution models presents a significant risk of overfitting, particularly for species with small numbers of records (Wintle *et al.* 2005). To avoid this problem, I reduced the number of climate variables used in the models for both taxonomic groups. For birds, I performed separate principal components analyses on the climate variables for each of the two time periods for which atlas data were available. In both cases, three principal components with eigenvalues greater than 1.0 were extracted. These components collectively explained 90.8% and 95.0% of variance in the climate variables for the first and second time periods respectively. All original variables were represented in at least one of the extracted components. For hoverflies, logistical constraints caused by the finer resolution of analysis meant that a Principal Components Analysis was not practical. Instead, I selected five climate variables known to influence animal distributions and used in previous attempts to predict the impact of climate change (Berry *et al.* 2002; Araújo *et al.* 2005a; Araújo *et al.* 2005b; Walther *et al.* 2007b): minimum temperature of the coldest month, maximum temperature of the warmest month, average annual precipitation, average summer (July-September) precipitation and growing degree days.

The second set of environmental variables, in addition to the climate variables described above, also included topography, land cover and agriculture variables. Although topography and land cover are known to correlate with the occurrence of both hoverflies (Keil *et al.* 2008) and birds (Rahbek *et al.* 2007), the use of these variables in biogeography studies, particularly those investigating responses to climate change, is controversial because they may affect the distributions of species only indirectly (Körner 2007; Ruggiero & Hawkins 2008). Furthermore, land cover data for Britain were only available for a single point in time, so we were unable to include changes in land cover in our models. Therefore, in this chapter I present the results based on models using only climate variables. The results based on the models with the additional variables are presented in Appendix 8.2. The only effect of including topography, land cover and land use was to increase the overall accuracy of the models without affecting the pattern of the results: the main result of my study was the same regardless of which set of variables I used.

Predicted distributions for hoverfly species, at a resolution of 1 km, were generated using two types of model: generalized linear models (GLMs) (McCullagh & Nelder 1989) and Maxent (Phillips *et al.* 2006). Predictions for birds, at a resolution of 10 km, were made using only GLMs because the very high prevalence of many species presented problems for the Maxent algorithm. In all models, linear, quadratic and first-order interaction terms were fitted for each of the climate variables. I also fitted a set of models using only linear terms: the overall results were the same, but average model accuracy was lower, so these models were not considered further.

GLMs were built in R (R Development Core Team 2004). An automatic backward stepwise selection routine (the ‘step’ function in R) was used to select simplified models that represented the best trade-off between deviance explained and model complexity, according to the Akaike Information Criterion (AIC) (Venables & Ripley 2002). GLMs require records of both species presence and species absence, but the hoverfly data contained only records of presences. To generate a set of ‘pseudo-absences’ (Zaniewski *et al.* 2002) for use in GLMs, I randomly selected 2500 of those grid squares that had been well sampled but that contained no record of a given species. Well-sampled squares for each species were identified (by Stuart Ball of the JNCC) as follows: 1) cumulative numbers of records each week were calculated using all records of a given species; 2) the weeks in which 2.5% and 97.5% of all observations were made were defined as the start and end dates of the flight period; 3) the proportion of all visits within the flight period on which a species was detected was used as an estimate of the probability that a species would be seen if it was present; 4) a binomial probability distribution was used to estimate the number of times that a site would have to be visited before absence could be inferred with 95% confidence; 5) sites that had been visited at least this number of times were considered well-sampled for a given species. The standard method of selecting pseudo-absence records is to take a random sample of all grid cells with no record of a species in. My approach of selecting a set of well-surveyed cells should result in much more reliable absence data.

Maxent models were built using Version 3.2.9 of the software (Phillips *et al.* 2006). Maxent randomly samples 10,000 grid cells to characterize the background environmental conditions of the study area and does not require absence data (Phillips *et al.* 2006). Models were built using default parameters: a regularization value of 1, a maximum of 500 iterations, a convergence threshold of 0.00001 and a maximum of 10000 random background grid cells (Phillips *et al.* 2006).

Initial models were made for each species using the data from each time period separately; their fit was evaluated against the data used to create them using AUC (see below). I then treated these initial models in two ways: 1) for *change* models, they were projected to other time periods by applying the coefficients to the altered climatic data of each time period. The generated predictions were then tested against the real data for the relevant time period, thus assessing their ability to predict (past and future) distributions incorporating climate changes. 2) for *control* models, predictions from the initial models were applied unchanged to other time periods, thus testing their ability to predict (past and future) distributions without accounting for climate changes.

All models were evaluated against two separate sets of data. First, I tested them against nationwide occurrence data, using the AUC statistic as a measure of model accuracy (see Chapter 2 for details). The use of the AUC statistic has been criticised recently, principally because it is affected by the proportion of the study area occupied by a given species (Lobo *et al.* 2008). In my study this limitation is not important, because I was comparing the ability of two types of model (change and control models) to predict identical sets of species records, covering an identical proportion of the study area. Furthermore, I also provide a completely independent test of model accuracy, against the single-site abundance data (see below). Model evaluation for hoverflies used records of species presence with 2500 pseudo-absences, randomly selected from well-sampled sites (see above). Model evaluation for birds used real presence and real absence records, insofar as unoccupied cells can be considered to be genuine absences.

A second and completely independent dataset against which I evaluated the models consisted of abundances from single constant-effort monitoring sites. The relationship, across all species within each time period, between the predicted probability of occurrence according to the models and recorded abundance, was tested using GLMs with negative binomial errors. Model fit was measured using the percentage deviance explained by the regression line. Change and control models were also compared using the slope of this line.

For each combination of the time period for which the model was built and the time period onto which the model was projected, I compared the AUC scores of the change and control models using a paired(by species)-sample t-test. To test the accuracy of the models in predicting average range shifts, I compared observed range shifts with those predicted by the change models. To estimate predicted latitudinal shifts of hoverfly species I calculated, for every species, the mean latitude of all grid cells with a model-predicted probability greater than 0.5. For each time period onto which the models were projected, these latitude centroids were averaged across all species. This was repeated for models using data from each of the time periods. To produce a comparable estimate of observed latitudinal shifts, I averaged the latitude of all occurrence records for each species in each time period. These observed latitude centroids were also averaged across all species. To account for recording bias, I corrected the observed centroids according to the mean latitude of all visited sites in a given time period. A similar comparison could not be made for birds, because observed distributions were available only for two time periods.

8.4 Results

The fits of the initial models to the data used to create them were at the very least adequate (hoverflies, AUC > 0.6), to very good (birds, AUC > 0.85) (Figure 8.1). When tested using the independent data of other time periods, the change models were significantly (paired-samples t-tests: $P < 0.05$) less accurate than the control models in

17/32 comparisons, and were never significantly more accurate than control models (binomial probability << 0.001) (Figure 8.1). In other words, models which assumed no effect at all of climate change on species distributions were better than those that included information on known changes in climate. For hoverflies, where both modelling methods were used, the same pattern was seen using either method (Maxent and GLMs): I have chosen to present only the results obtained using Maxent.

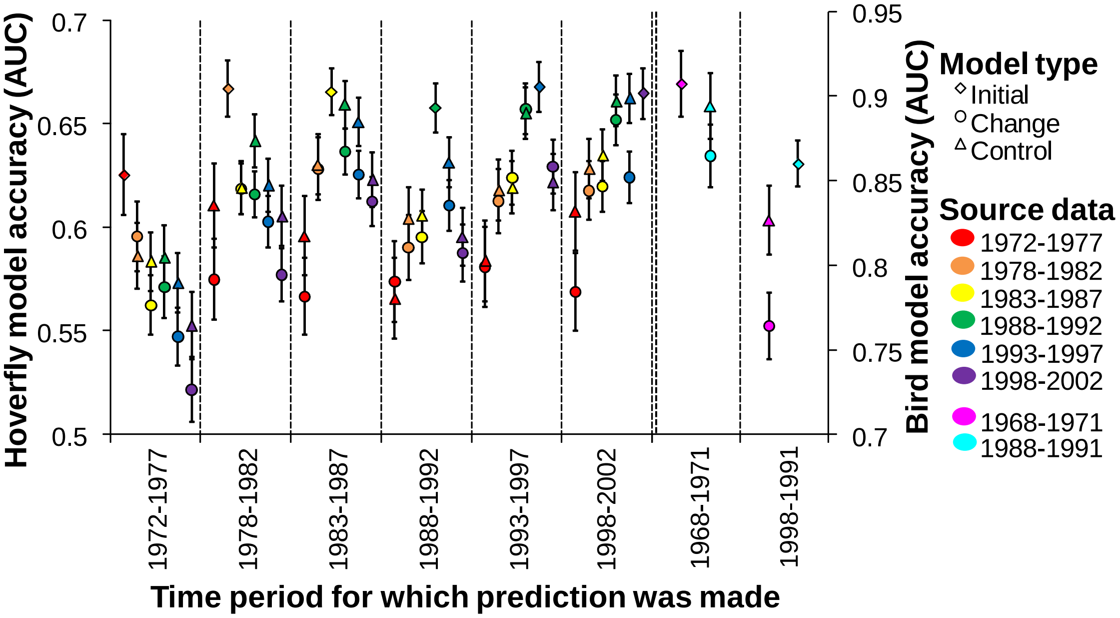

Figure 8.1 – Mean accuracy (AUC +/- SEM) of distribution-model predictions for 255 British hoverflies and 32 birds in different time periods. Models for hoverflies and birds are separated by a double line. Separate models were built using observed occurrence data (source data) from each of six (hoverflies) or two (birds) different periods. Predictions were generated from each of these models for each time period, and these predictions were tested against the source data (initial models) or against observed occurrence data from future and/or past periods. Change model predictions for past/future periods were generated using known changes in climate; control models assumed no change in distributions as a result climate change.

Very similar results were obtained when model predictions were tested against the abundance time-series. The initial models predicted contemporary abundances very well (Figure 8.2; Table 8.2). All relationships between observed abundance and predicted probability of occurrence were positive, and 4/7 were significantly positive (GLMs: P <

0.05). When change models were used, these relationships were weaker. Although 35/43 relationships were positive (binomial probability < 0.001), only 16/43 were significantly positive, and 4/43 were significantly negative. Control models were better: 37/43 relationships were positive ($p << 0.001$), 29/43 were significantly positive, and none was significantly negative. The fit of the relationship was generally better for the control predictions than for the change predictions (Figure 8.2; Table 8.2): the slope of the relationship between predicted probability of occurrence and observed abundance was more positive for control models than for change models in 32/43 cases (paired-samples t-test: $t = 4.09$, d.f. = 42, $P < 0.001$; Fig. 2); when the relationship was positive for both change models and control models, the deviance in observed abundance explained was greater for control models than for change models in 20/34 cases (paired-samples t-test: $t = 1.92$, d.f. = 33, $p = 0.064$; Table 2). It is important to note that because I tested every combination of time periods (source vs. predicted), these data are not truly independent. However, it is clear that the control models were generally better then change models in predicting abundance.

Table 8.2 - The ability of the predicted probability of occurrence from species distribution models (SDMs) to predict abundance at a single site (a suburban garden on the outskirts of Leicester for hoverflies, and Treswell Wood in Nottinghamshire for birds). Tests involved generalized linear models with negative binomial errors, using across-species data. SDMs were of three types: 1) *initial* (highlighted in grey) – SDMs were built using data from the same time period for which they were used to predict; 2) *change* – models created using data for one time period were applied to other time periods with the relevant climate data for those times; and 3) *control* –models created using data for one time period were applied unchanged to other time periods, i.e. *not* using the relevant climate data, and hence assuming that the distributions of species did not respond to climate change. Models that predict distributions in the past are presented in grey text. Models that predict the future are presented in black text. "+" and "-" symbols indicate the direction of the relationship (magnitudes plotted in Fig. 2). Model fit was measured by the percentage of the deviance explained by the models (% dev). The poorer fit of hoverfly models created using data from 1972-77 and 1978-1982 is likely to be due to the lower number of records for those years (see Table 8.1).

Source data time period	Period for which the prediction was made	Change models		Control models	
		Slope	% dev	Slope	% dev
Hoverflies:					
1972-1977	1972-1977			+	1.23
	1978-1982	-	17.37	-	0.42
	1983-1987	-	23.48	+	0.44
	1988-1992	-	14.56	-	0.02
	1993-1997	-	2.92	+	0.19
	1998-2002	-	11.59	-	0.05
1978-1982	1972-1977	+	16.14	+	0.02
	1978-1982			+	1.64
	1983-1987	+	17.89	-	0.03
	1988-1992	+	7.57	+	0.29
	1993-1997	+	11.90	-	0.11
	1998-2002	+	9.46	+	0.02
1983-1987	1972-1977	+	7.76	+	23.42
	1978-1982	+	6.95	+	24.63
	1983-1987			+	22.74
	1988-1992	+	11.15	+	12.94
	1993-1997	+	12.71	+	14.85
	1998-2002	+	10.40	+	9.97
1988-1992	1972-1977	+	15.19	+	14.72
	1978-1982	+	4.91	+	19.39
	1983-1987	+	1.05	+	18.04
	1988-1992			+	10.56
	1993-1997	+	6.90	+	11.54
	1998-2002	+	2.71	+	7.27
1993-1997	1972-1977	+	2.99	+	26.42
	1978-1982	+	3.69	+	15.84
	1983-1987	+	10.34	+	18.94
	1988-1992	+	9.58	+	14.67
	1993-1997			+	16.521
	1998-2002	+	20.85	+	11.45

1998-2002	1972-1977	+	9.11	+	6.25
	1978-1982	-	1.28	+	6.05
	1983-1987	-	3.23	+	7.10
	1988-1992	+	2.42	+	2.20
	1993-1997	+	0.23	+	3.59
	1998-2002			+	1.38
Birds:					
1968-1971	1972-1975	+	20.25	+	21.70
	1976-1979	+	30.28	+	28.23
	1980-1983	+	39.61	+	35.94
	1984-1987	+	10.38	+	11.44
	1988-1991	+	14.08	+	15.28
	1992-1995	+	17.37	+	15.94
	1996-1999	+	13.17	+	9.25
1988-1991	1972-1975	+	21.61	+	23.77
	1976-1979	+	26.89	+	24.98
	1980-1983	+	37.77	+	43.46
	1984-1987	+	23.53	+	26.79
	1988-1991			+	19.53
	1992-1995	+	18.13	+	19.61
	1996-1999	+	23.37	+	22.39

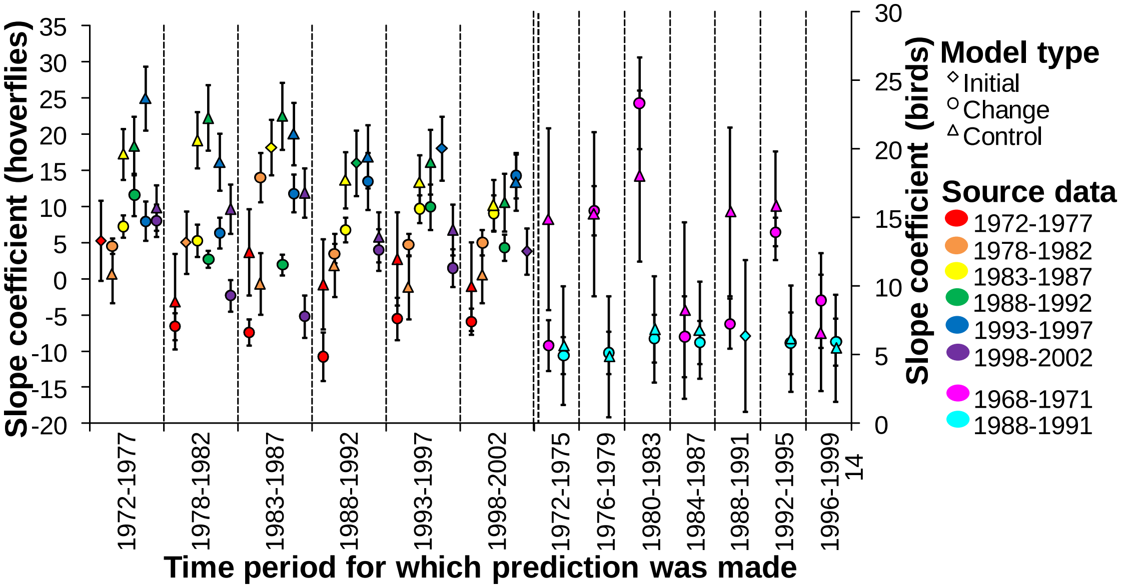

Figure 8.2 – Estimates of the strength of the relationship (slope coefficients ± SEM) between the predicted probability of occurrence, from distribution models for British hoverflies and birds, and observed abundance at locations in central England (hoverflies: Leicester; birds: Treswell Wood, Nottinghamshire) during six (hoverflies) or seven (birds) different time periods. Models for hoverflies and birds are separated by a double line. Predictions come from models built using source data from the time period in which the relationship is tested (initial models), or are projections from models built with source data from a different time period. Projections were generated using known changes in climate (change models), or assuming no change in the climate (control models).

Predicted latitudinal range shifts matched observed shifts poorly. With the exception of models developed using data from the first time period (where there were substantially fewer data), models projected forward from the time period for which they were built generally predicted northward shifts in the distributions of species. There was little evidence for these shifts in observed distributions (Figure 8.3).

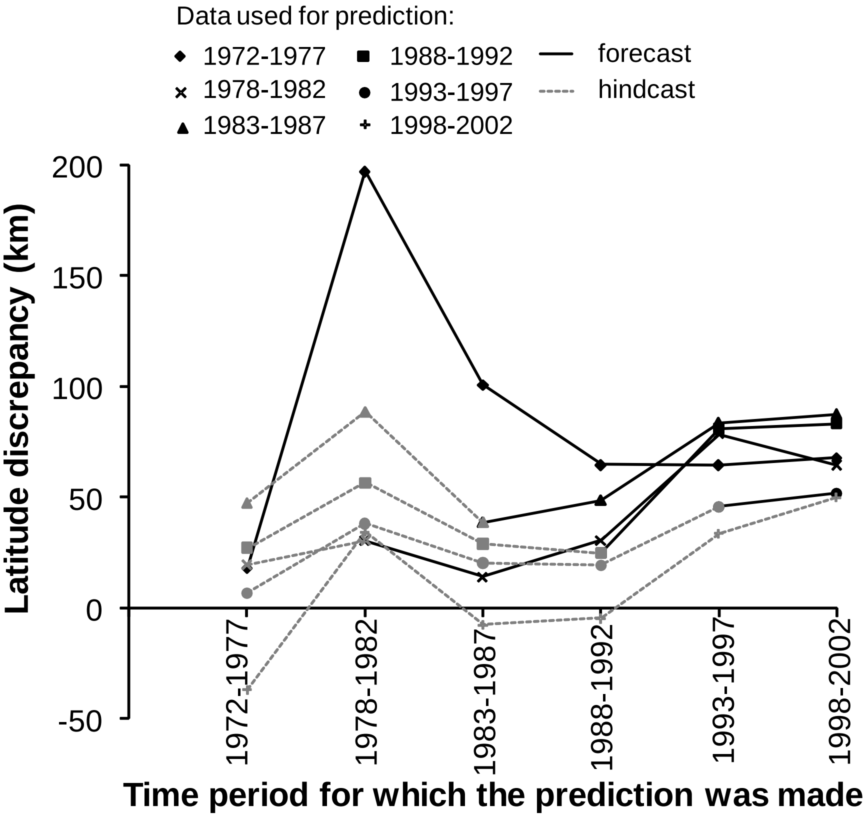

Figure 8.3 – The discrepancy between the latitude of the predicted and observed range centroids (latitude discrepancy = predicted centroid – observed centroid). Notice that the predicted latitude is nearly always further north than the observed range (i.e. the discrepancy is positive). Each line corresponds to models built using data from one source time period. Centroids were averaged across species in each time period. Black points and lines represent models that predict the future and grey points and lines represent models that predict the past, relative to the source time period from which the data were taken to build the models. Observed centroids were corrected according to the mean latitude of visited sites, to account for latitudinal sampling bias.

8.5 Discussion

The use of models such as mine to predict likely changes in species distributions with climate change has given rise to alarming estimates of extinction rates and to predictions of dramatic shifts in the distribution of species (Berry *et al.* 2002; Thomas *et al.* 2004; Huntley *et al.* 2007). In this context, it is disturbing to discover that the accuracy of such predictions can be worse that those made assuming no changes in distributions as a result of climate change, even when uncertainty regarding how the climate will change is absent.

The poor performance of my change models may have several explanations. The most obvious possibility is that species may not track changes in the climate if they are unable to disperse quickly enough or if there are barriers to dispersal along potential migration routes (Saetersdal *et al.* 1998; Best *et al.* 2007; Devictor *et al.* 2008; Mustin *et al.* 2009). My models generally predicted marked northward shifts in the distributions of species over time, shifts that were not apparent in the occurrence records from the original databases (Figure 8.3). A possible alternative is that changes in species interactions under climate change will affect the way that the distributions of species are related to climatic and other environmental variables (Pearson & Dawson 2003; Araújo & Luoto 2007; Post & Pedersen 2008; Schweiger *et al.* 2008).

The fact that distributions in past and future time periods were better predicted by control models than by those that attempted to account for changes in the climate is consistent with the idea that there is a time lag between changes in the environment and changes in species. Alternatively or additionally, species may have adapted to the new conditions. There is some evidence to suggest that rapid adaptive responses are possible in response to climate change (Knouft *et al.* 2006). However, it seems unlikely that such responses would appear in such a diverse range of taxa over as small a time scale as that considered here (approximately thirty generations in most of the hoverfly species) (Visser 2008). On the other hand, phenotypic plasticity in relevant traits may allow very rapid responses to climate change, as has been shown for example for great tits (*Parus major*) in Wytham Woods in Britain (Charmantier *et al.* 2008).

The poor performance of my change models may have been because they were built using data that did not cover the entire range of environmental conditions occupied by the species worldwide; this has been shown to decrease the ability of models to predict distributions under new environmental conditions (Thuiller *et al.* 2004b). However, this seems unlikely because initial models predicted contemporary distributions well and the results were consistent across a large number of species with very different range sizes. Modelling the distributions of species at broad geographical scales has its own problems; local populations or subspecies can show different responses to the environment, making models of the complete range of a species less accurate (Stockwell & Peterson 2002). Furthermore, modelling climate change impacts at fine resolution and at more local scales can capture fine-scaled responses to micro-climate variation that would be not be apparent in models at a coarser resolution and at larger scales (Randin *et al.* 2009). Time-series data comparable with those I used are not currently available on a continental scale, but in the future it may be possible to test the applicability of my findings at a larger scale.

It has been predicted that changes in population trends would be evident before shifts in the distributions of species (Iverson *et al.* 1999). Recent studies of bird species in Britain, and in Europe as a whole, show that trends in predicted climate suitability correlate with population trends (Green *et al.* 2008; Gregory *et al.* 2009). However, if this were the case in my study, I would expect to see stronger relationships between predicted probabilities of occurrence by change models and recorded abundances. In reality, the abundance of bird species was better predicted by the control models. I considered only the more common British birds, which may explain why my results differ from those of a study (Green *et al.* 2008) concentrating on rare species, but my results were also consistent across 255 hoverfly taxa including both rare and common species.

A brief inspection of both the nationwide distribution data and single-site abundance data shows that there have been changes over time in both birds and hoverflies. It is possible that these are driven by environmental changes other than climate change, such as changes in habitat. Models that included habitat, agriculture and topography variables were more accurate than those that included only climate variables (see Appendix 8.2), suggesting that non-climatic variables are important determinants of the distributions of species. However, I did not have data on changes in land cover or land use, and so was unable to include these variables in the projected models. Future developments of models predicting how species distributions will change in the future should focus on predicting how land use will change and incorporating this into the predictions.

The failure of the change models may have been owing to my choice of modelling technique (Thuiller 2003; Thuiller *et al.* 2004a; Pearson *et al.* 2006) or predictor variables (Peterson & Nakazawa 2008). Previous studies have shown that using consensus models, which take an average of several different model types or of models including different variables, reduces some of the uncertainty in predictions of the effect of climate change on the distributions of species (Araújo *et al.* 2005b; Araújo & New 2007; Dormann *et al.* 2008). However, the techniques and variables chosen in this study are commonly used in attempts to forecast the effects of climate change on biodiversity (Berry *et al.* 2002; Araújo *et al.* 2005a; Walther *et al.* 2007b). In comparisons of different modelling techniques both Maxent and GLMs have been shown to perform very well (e.g. Elith *et al.* 2006). Nevertheless, the use of consensus models is an approach that deserves further testing with data such as mine.

Despite the failure of models incorporating changes in the climate to predict changes in species distributions in our study, contemporary distributions were predicted very well, supporting the use of these models in conservation ecology. The possibility of predicting species abundance from patterns of occurrence has received some theoretical attention in the literature (He & Gaston 2007). I have shown here for the first time that species distribution models based on occurrence data are usually able to predict abundance at single sites with remarkable accuracy. This was especially true for the bird data.

Many species have already been shown to be responding to recent climate change. However, it is clear that, in the short term, these changes cannot be reliably predicted by species distribution models. Species may respond to climate change, but my results suggest that, at least at present, this response is not predictable using the available methods. There is clearly an urgent need for further tests and development of models of climate-driven distribution shifts before they can be used with confidence to make important conservation decisions.

Chapter 9. Final Discussion

9.1 Discussion

9.1.1 Choosing the right methods

A very large number of studies have used species distribution models and, for the most part, have found that current ranges are modelled very accurately (e.g. Wintle *et al.* 2005; Elith *et al.* 2006; Tsoar *et al.* 2007). The results of the studies presented in this thesis support this conclusion. Models of the current distributions of Egyptian and British species were almost always very accurate. Nevertheless, I showed important patterns in the accuracy of the models, which reveal something about the ecology of the species concerned and which also have relevance for attempts to use the models for conservation purposes.

Despite the generally very good performance of distribution models, the methods used to develop them can have a large effect on their accuracy. There are a number of techniques available for modelling distributions (described in Chapter 2). Several studies have shown that model accuracy varies consistently among these techniques (Elith *et al.* 2006; Tsoar *et al.* 2007; Wisz *et al.* 2008). In Chapter 3, I tested the ability of several techniques to model the distributions of real Egyptian species and of simulated species. Consistent with the results of earlier studies, certain techniques (particularly Maxent and generalized linear models) produced more accurate models than others (such as the bioclimatic envelope models).

The quantity of data on the distribution of species available may also have an effect on the accuracy of distribution models (Pearce & Ferrier 2000a; Phillips *et al.* 2004; Wisz *et al.* 2008). In Chapter 3, I show that distribution models for simulated species were more accurate when developed using a greater number of occurrence records. However, the effect of sample size on the accuracy of distribution models for real Egyptian species was less clear. Across several different modelling techniques (Chapter 3), sample size had a small but significant positive effect on the accuracy of the models. However, when only a single technique (Maxent) was used (Chapters 4 and 7), there was no obvious effect of the number of occurrence records on model accuracy. This supports previous suggestions that Maxent is reasonably robust to variation in sample size (Phillips *et al.* 2004; Wisz *et al.* 2008). It seems likely that the intensity of sampling is more important than the absolute number of occurrence records in determining the accuracy of models.

9.1.2 Evaluating the accuracy of distribution models

There has been much discussion about the best way to evaluate the accuracy of distribution models. Of course, the most appropriate method for testing model accuracy, and also what is considered an 'accurate' model, will depend on the aim of the model. A model that is able to explain the distribution of a species within a study area of interest may be useful for conservation purposes, even if it does not capture directly the ecology underlying the distribution. On the other hand, if the purpose of the model is predictive, for example to predict the effect of climate change or how a species might be distributed if it invaded a new area, or if the purpose of the model is to infer something about the ecology of the species in question, then the criteria for defining an ‘accurate’ model will be much more specific.

The simplest method of evaluating the accuracy of distribution models is to test them against the data used to develop them (Fielding & Bell 1997). This has the advantage that all of the available data on the distribution of species can be used in developing the model. However, it has been suggested that estimates of accuracy made in this way may be inflated because the model can fit the data very well without capturing well the distribution of the species in the study area as a whole (Chatfield 1995). There was no evidence that this was the case for models of the distribution of simulated species (Chapter 3), but this may have been because the simulated data contained none of the biases commonly seen in species distribution data which may cause model accuracy measures to be over-optimistic. Therefore, caution is necessary in using this approach to evaluate distribution-model accuracy.

An alternative approach to model evaluation is to divide the species records, using some of the records for developing the model and the remainder of the records for evaluating the model (Fielding & Bell 1997). This is the most commonly-used approach and the one that I use throughout most of the studies described here. However, if there are biases in the records of species occurrence, then estimates of model accuracy made this way may also be over-optimistic (Fielding & Bell 1997).

The best way to evaluate the accuracy of distribution models is to use occurrence records completely independent of those used to develop the models, if such data are available (Chatfield 1995). Some authors have suggested dividing the study area geographically and using records from some areas to develop models and records from other areas to evaluate them (Fielding & Haworth 1995; Özesmi & Mitsch 1997; Peterson

& Shaw 2003; Randin *et al.* 2006; Heikkinen *et al.* 2007; Vanreusel *et al.* 2007; Syartinilia & Tsuyuki 2008). However, this approach tests the ability of models to predict distributions outside the environmental conditions used to develop the models, and not the ability to explain distributions within the area of interest. Therefore, this approach will only be desirable if the aim of the models is predictive rather than explanatory. Furthermore, a test of different evaluation methods using data for simulated species (Chapter 3) suggested that restricting the environmental conditions encompassed by the species records used to develop the distribution models, by dividing the records into different geographical areas, leads to very inaccurate models. In many cases, it is better to use model-training data and independent evaluation data from the same geographical area. Owing to constraints of time and money on the collection of independent sets of species records, only a few studies have used this approach (Loyn *et al.* 2001; Pearce *et al.* 2001; Elith 2002; Ferrier *et al.* 2002; Elith *et al.* 2006). In Chapter 7, I use data from a field survey to test distribution models for Egyptian butterfly, reptile, amphibian and mammal species. Although I could not sample completely randomly, the new records were almost entirely independent of the records used to develop the models, were chosen to represent as many different habitats as possible, and covered a large portion of Egypt's land area. Therefore, these records probably gave reasonably good coverage of the main climate gradients. Model accuracy estimated using these new data was lower than that estimated by dividing the original records, but the models still appeared to explain distributions well.

Most studies have focused on the ability of distribution models to explain patterns of presence and absence. However, the abundance of species at a site may be a better indicator of its status. An interesting possibility is that the probability of species occurrence, estimated by distribution models, may correlate with local abundance, as shown previously by VanDerWal *et al.* (2009b). In Chapter 8, I show that this is the case for hoverflies and birds and Britain. Given that abundance is probably related to the probability that a species will persist in an area (Araújo & Williams 2000; Araújo *et al.* 2002), this result has important implications for conservation.

9.1.3 Climate and habitat as determinants of distributions

Niche theory leads us to expect that climate and habitat should be important determinants of the potential distribution of species (Pulliam 2000). Indeed, a great many published studies using species distribution models have shown that climate and habitat correlate very well with the distributions of species (Guisan & Hofer 2003; Wintle *et al.* 2005; Elith *et al.* 2006; Guisan *et al.* 2006a). The results of my studies support this: the distributions of British hoverflies, birds and butterflies, and of Egyptian butterflies, reptiles, amphibians and mammals correlate very well with variables describing climate and habitat. However, other factors may also be important.

How the potential distribution of a species relates to its actual distribution depends on a number of additional factors. For example, dispersal limitation may prevent a species from filling all of its potential distribution, while the existence of source-sink dynamics may enable populations of a species to persist outside the potential distribution (Pulliam 2000). This can result in spatial patterns in the distribution of species that are independent of spatial patterns in the environmental variables determining distributions (termed endogenous spatial autocorrelation). Species distribution models have been used to show the importance of dispersal limitation in determining realized distributions, for example by comparing areas of suitable climate and habitat with areas that are actually occupied (Munguía *et al.* 2008). To improve the accuracy of distribution models, endogenous spatial autocorrelation can be captured either by including the geographical coordinates as explanatory variables in the models or by using more sophisticated spatial modelling approaches (Legendre 1993; Bahn *et al.* 2006; Bahn & McGill 2007). Some authors have shown that distributions can be modelled better using just geographical coordinates than just climate variables as explanatory variables (Bahn & McGill 2007). In Chapter 2, I show that the converse is true for Egyptian species. This suggests that, at least for Egypt, there is some signal of the environment in the distributions of species that is independent of spatial structure. In such an arid environment, abiotic conditions are perhaps likely to play a relatively greater role in determining the distributions of species than in other environments (see also the discussion on the relative importance of abiotic and biotic factors in shaping species' distributions in MacArthur 1972)

Interactions among species may alter how the potential distribution of species is realized (Hutchinson 1957). A large part of the study of ecology is concerned with the way that species interact with each other, and how this affects patterns of distribution and abundance (Tilman 1976). The accuracy of models of the distribution of species has been shown to be improved by including the distributions of interacting species as explanatory variables (e.g. Araújo & Luoto, 2007). In Chapter 6, I show that two types of interaction among species (the interaction between herbivores and their food-plants and the interaction between mimics and their models) cause associations among their distributions and that the accuracy of distribution models can be improved by considering these interactions.

Models that best capture the real drivers of distributions will be more useful and more generalizable than models that explain distributions using variables that have only an indirect effect on the distribution of species (Austin *et al.* 2006). Thus, there should be greater effort to include important factors other than climate and habitat in distribution models in the future.

9.1.4 Variation among species in the distribution-environment correlation

The ecological characteristics of species can affect the extent to which their distributions are determined by the environment, and thus the accuracy of distribution models based on variables describing the environment. Several studies have tested whether the accuracy of distribution models is related to characteristics of species, generally finding that resident species, with smaller ranges and more specific habitat requirements are better modelled than migratory species, species with larger ranges and species that can tolerate more diverse environmental conditions (e.g. Kadmon *et al.* 2003; Berg *et al.* 2004; Brotons *et al.* 2004; Segurado & Araújo 2004; Hernandez *et al.* 2006; McPherson & Jetz 2007). In Chapter 4, I show that both local and global range sizes of butterflies are significantly associated with the accuracy of models of their distribution, in accordance with the findings of previous studies.

Most previous studies of the effect of the range size of species on the accuracy of distribution models have used records of species presence with random ‘pseudo-absence’ data. Pseudo-absences for smaller-ranged species will, on average, be environmentally less similar to the presence records than pseudo-absences for larger-ranged species by chance. Thus, estimates of model accuracy will be artificially higher for these species. To test whether there is a genuine effect of range size on the accuracy of distribution models, model accuracy should be assessed using real records of species absence. This is the approach that I took in Chapter 7. Using the records of species presence and absence collected during the new field survey, I showed that the negative effect of range size on the accuracy of species distribution models is valid, even after the possibility of statistical artefacts has been minimized. The distributions of wider-ranged species must be determined, to some extent, by factors other than climate and habitat, such as dispersal ability or interactions with other species.

In Chapter 7, I also showed that the accuracy of distribution models for butterflies is positively related to wingspan. This effect was not owing to larger butterflies being more easy to detect in the field, but may be because larger butterflies are more mobile and thus able to disperse and occupy a greater proportion of environmentally-suitable areas (Pöyry *et al.* 2008).

9.1.5 The value of distribution models for conservation

Given the high accuracy of distribution models, they can be very valuable tools for biodiversity conservation. Global sampling of biodiversity is far from complete and there are large gaps in our knowledge in large parts of the world and for many taxa (Stockwell & Peters 1999; Soberón *et al.* 2000; Anderson *et al.* 2002a; Williams *et al.* 2002; Soria-Auza & Kessler 2008). Species distribution models offer the means to fill some of these gaps.

One useful application is in directing future surveys for species. A number of studies have used distribution models as a basis for searching for new populations of species, often with very great success (Raxworthy *et al.* 2003; Guisan *et al.* 2006a). The field surveys that I conducted in Egypt, described in Chapter 7, extended sampling of butterflies, reptiles, amphibians and mammals into the mountains of the Eastern Desert, an area that has been sampled relatively little in the past. These surveys yielded the first record of the red admiral butterfly (*Vanessa atalanta*) in Egypt in over ten years.

Distribution models can be combined to produce a model of species richness (García 2006; Pineda & Lobo 2009; Raes *et al.* 2009; Terribile *et al.* 2009). Given that different species may respond differently to the environment, this may provide a better model of species richness than simply relating species richness values to environmental variables directly (Terribile *et al.* 2009). In Chapter 5, I combine distribution models for Egyptian butterfly and mammal species in order to estimate species richness. Estimated values of species richness correlated positively with observed species richness, suggesting that the approach is valid. I used the model of species richness to show that Egypt's protected areas network is effective in representing butterfly and mammal diversity.

Distribution models are often projected outside the environmental conditions encountered during model development, for example to predict the impact that future environmental change will have on the distribution of species (Miles *et al.* 2004; Thomas *et al.* 2004; Araújo *et al.* 2005a; Hole *et al.* 2009), or to predict the extent of species invasions (Peterson & Robins 2003; Thuiller *et al.* 2005b; Herborg *et al.* 2007). Projecting models into new areas or time periods is associated with several uncertainties. First, species may adapt to the new conditions and thus respond differently to the environmental variables (Broennimann *et al.* 2007; Charmantier *et al.* 2008). Second, interactions among species may be different in the new areas or time periods (Araújo & Luoto 2007; Schweiger *et al.* 2008). Third, species may not be able to disperse to new suitable areas

(Best *et al.* 2007; Devictor *et al.* 2008; Mustin *et al.* 2009). In Chapter 8, I show that predictions about temporal changes in the distribution of species made by climate- and habitat-based models match observed changes very poorly. Making accurate predictions about distributions in different areas or time periods will require incorporating into the models factors other than climate that are known to have an effect on the distribution of species.

9.1.6 The importance of controls when comparing distribution models

In Chapters 6 and 8, I compare different approaches for modelling distributions. In the first case, I test the effect of including the distributions of interacting species as explanatory variables in the distribution models. In the second case, I compare models for predicting future distributions of species, either incorporating changes in the environment or assuming that environmental changes have no effect on distributions. In both studies, the importance of including controls is revealed. Without the controls, misleading conclusions may have been reached. In Chapter 6, one might conclude that the proposed interactions among species are important drivers of distributions. However, in some cases the distributions of control species showed as strong an association with the focal species as did the interacting species. In Chapter 8, one might conclude that models incorporating the effects of environmental change produce a reasonably accurate prediction of distributions in the future, whereas the control models (those that assumed no effect of environmental change on species' distributions) were actually more accurate. Previous studies investigating both of these issues have not considered controls in their comparisons. This is an important oversight and one that should be rectified in the future.

9.2 Conclusions

In summary, species distribution models can provide us with valuable information about where species are likely to be found. As well as being important tools for conservation, they can help determine which aspects of a species' environment are important in determining its distribution, and thus advance our understanding of ecological niches. It is important to remember, however, that the models are correlative: variables that show a good association with the occurrence of species do not necessarily determine distributions directly. This distinction is particularly important when distribution models are applied outside the study area, or to predict temporal changes in distributions. An obvious alternative is mechanistic distribution modelling, but the main problem with this approach is that we do not have enough information to parameterize mechanistic models for most species (Guisan & Zimmermann 2000). For most species, correlative models are the best way to make inferences about the distribution of species, but there are obvious ways that we can improve these models in order to make more educated inferences. Future research needs to focus on identifying the variables that have a direct effect on the occurrence of species, in order that more accurate and more generalizable models can be made. Experimental studies on the drivers of distribution patterns will have an important part to play in this process. On the other hand, conserving biodiversity is an urgent problem. With due respect to their limitations, distribution models can provide invaluable information to fill some of the gaps in our existing knowledge about spatial patterns of biodiversity.

Chapter 10. Appendices

10.1 Appendix 2.1

Table 10.1 – Contributors of data to the National Biodiversity Network (NBN) Gateway of Britain whose data I used in Chapter 6.

Bees, Wasps and Ants Recording Society
Botanical Society of the British Isles
Bristol Regional Environmental Records Centre
Countryside Council for Wales
Dorset Environmental Records Centre
Dr Francis Rose Field Notebook Project
EcoRecord
Environment and Heritage Service
Exploring Your Environment Project
Highland Biological Recording Group
Hoverfly Recording Scheme
Joint Nature Conservation Committee
Lothian Wildlife Information Centre
National Trust
National Trust for Scotland
Natural England
North Ayrshire Countryside Ranger Service
North East Scotland Biological Records Centre
Pond Conservation
Royal Horticultural Society
Scottish Borders Biological Records Centre
Scottish Natural Heritage
Shropshire Environmental Data Network
South East Wales Biodiversity Records Centre
Staffordshire Ecological Record
Thames Valley Environmental Records Centre
Tullie House Museum
Wildlife & Conservation, Division Dept. of Agriculture, Fisheries & Forestry, Isle of Man Government

10. 2 Appendix 3.1

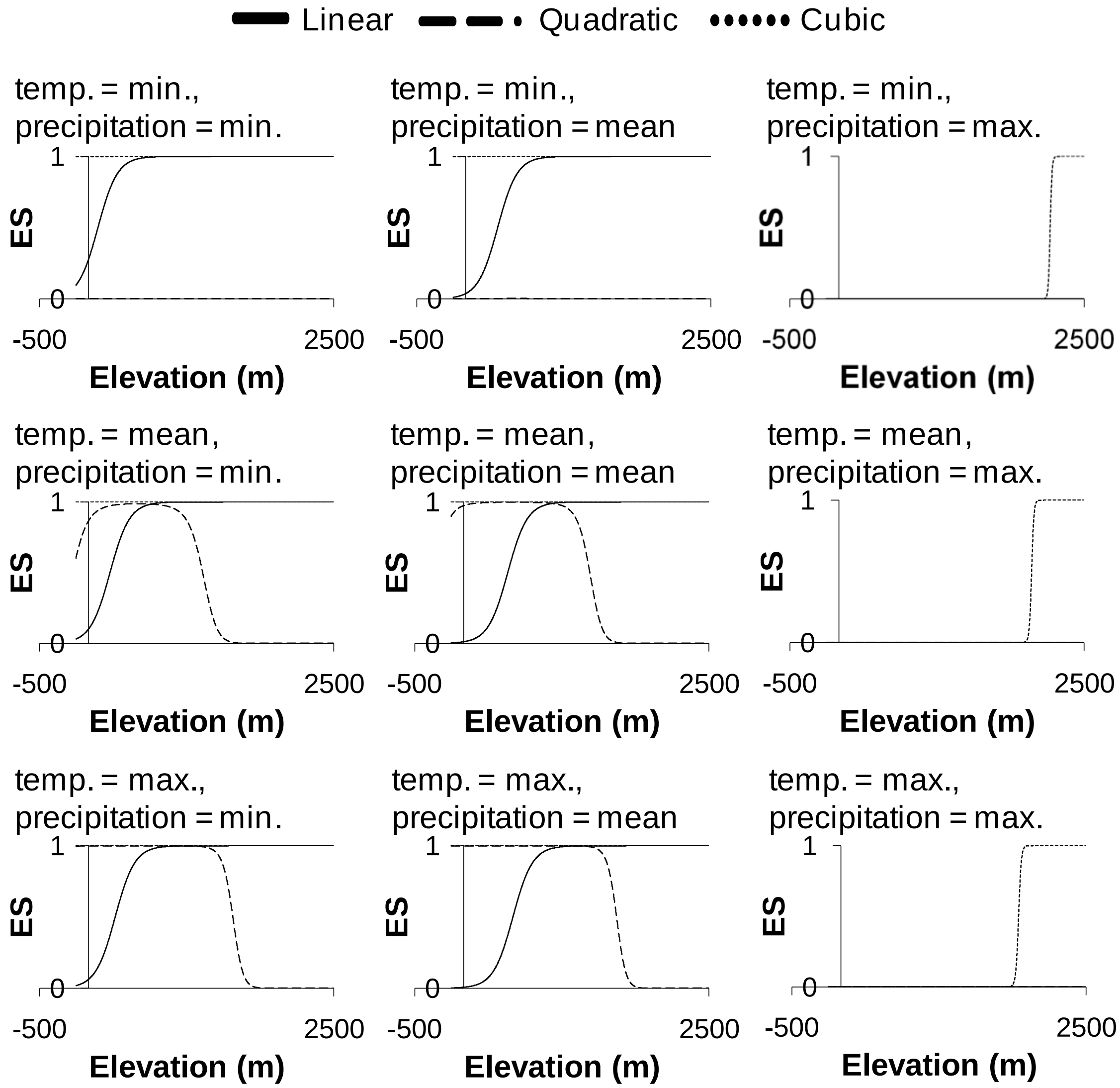

Figure 10.1 – Response of the three simulated species used in Chapter 3 to varying elevation. Environmental suitability (ES) was a logistic function of three environmental variables: elevation, temperature (temp.), and precipitation. The functions for the three species had differing complexities: 1) linear terms only ('linear'); 2) linear and quadratic terms ('quadratic'); and 3) linear, quadratic and cubic terms ('cubic'). The nine graphs correspond to each combination of minimum, mean and maximum temperature, and minimum, mean and maximum precipitation.

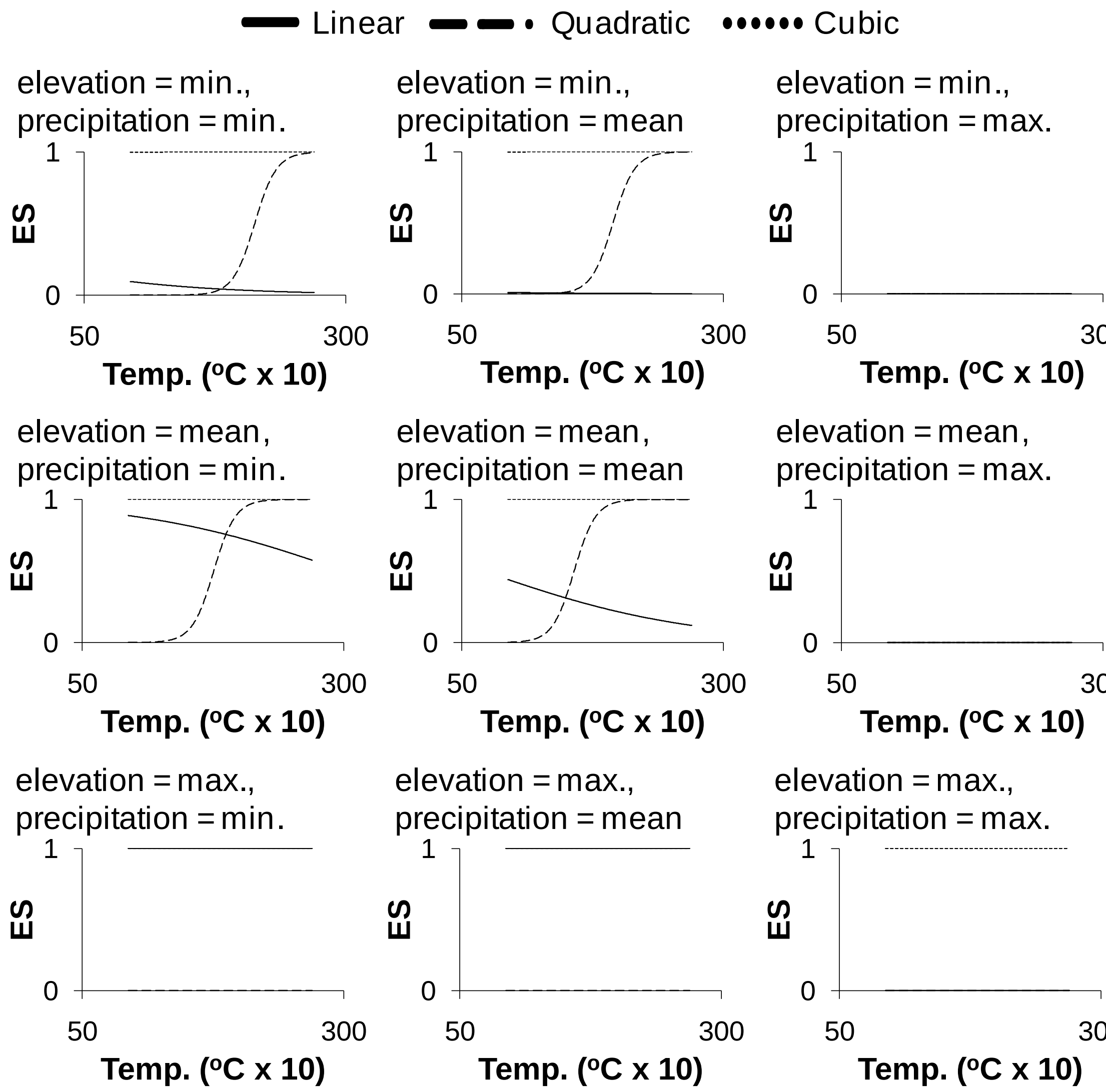

Figure 10.2 – Response of the three simulated species used in Chapter 3 to varying temperature (temp.). Environmental suitability (ES) was a logistic function of three environmental variables: elevation, temperature, and precipitation. The functions for the three species had differing complexities: 1) linear terms only ('linear'); 2) linear and quadratic terms ('quadratic'); and 3) linear, quadratic and cubic terms ('cubic'). The nine graphs correspond to each combination of minimum, mean and maximum elevation, and minimum, mean and maximum precipitation.

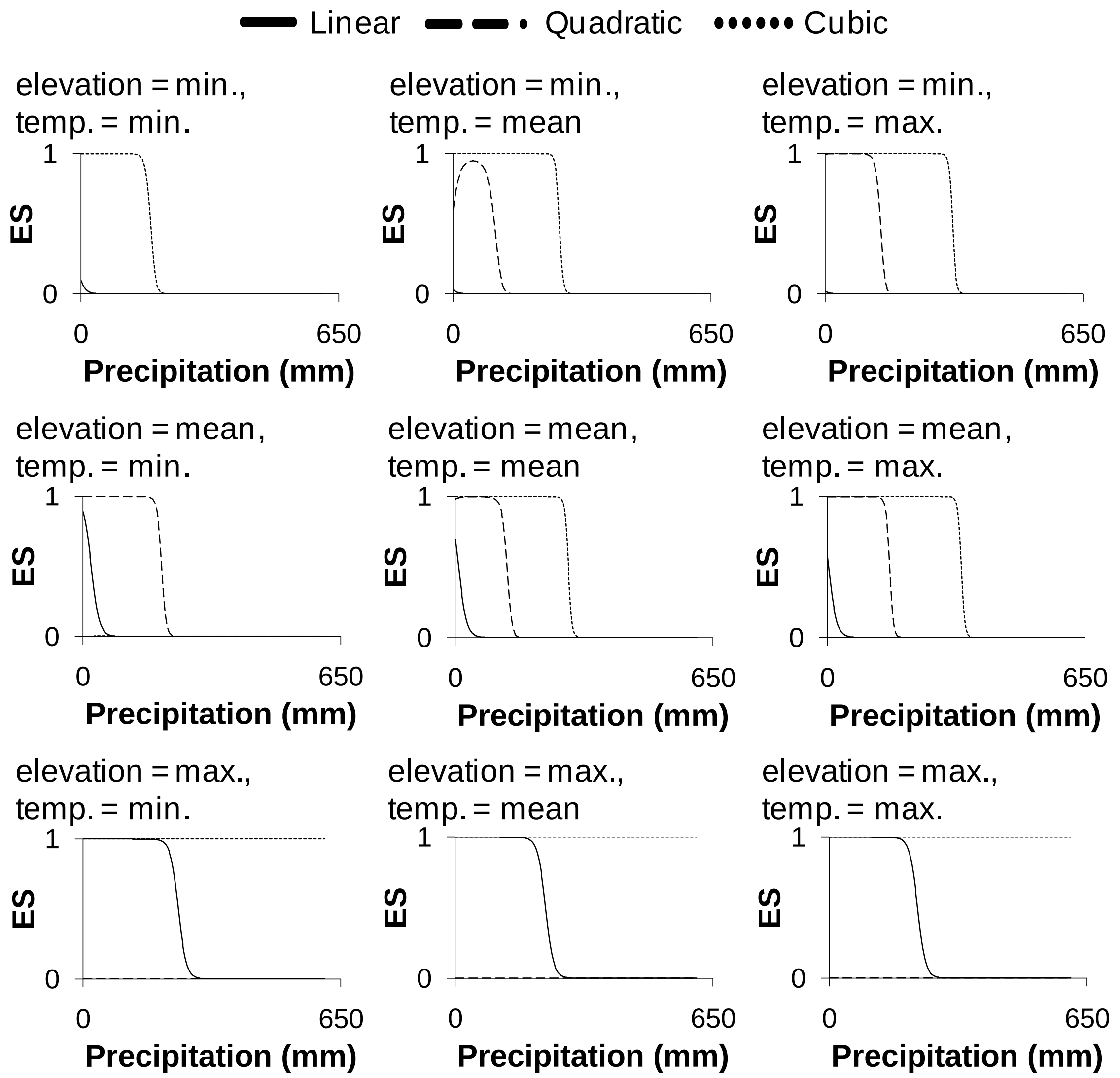

Figure 10.3 – Response of the three simulated species used in Chapter 3 to varying precipitation. Environmental suitability (ES) was a logistic function of three environmental variables: elevation, temperature (temp.), and precipitation. The functions for the three species had differing complexities: 1) linear terms only ('linear'); 2) linear and quadratic terms ('quadratic'); and 3) linear, quadratic and cubic terms ('cubic'). The nine graphs correspond to each combination of minimum, mean and maximum elevation, and minimum, mean and maximum temperature.

10.3 Appendix 4.1

Table 10.2 – Results of a set of analyses of covariance testing the effect of species characteristics on the accuracy of species distribution models for 22 well-sampled (>10 records, on average, used for modelling) Egyptian butterfly species, measured using the AUC statistic. Characteristics tested were: the number of presence records used to build the distribution models (P), migratory behaviour (M), host-plant specificity (S), predicted range size in Egypt (R), world range size (W) and habitat tolerance (H). Candidate models were built with every possible combination of terms. These models were compared using the approach recommended by Burnham & Anderson (2002), by calculating AIC values for each model, the difference between the AIC for a model and the minimum AIC for all models (Δ_i), and model weights based on these values. I only present the best models ($\Delta_i < 4$) here. The sum of the weights of all models containing a characteristic was used as a measure of the relative importance of that characteristic in determining model accuracy (Burnham & Anderson 2002); the summed weights were as follows: P = 0.703, M = 0.987, S = 0.607, R = 0.597, W = 0.980, H = 0.759.

Model	**Deviance explained**	**AIC**	**AIC difference (Δ_i)**	**Model weight (w_i)**
P + M + S + R + W + H	78.54	-49.24	0	0.197
P + M + W + H	73.68	-48.76	0.48	0.155
P + M + S + W + H	75.89	-48.69	0.55	0.150
P + M + R + W + H	75.05	-47.93	1.31	0.102
M + S + R + W	63.52	-47.57	1.67	0.085
P + M + S + R + W	65.89	-47.06	2.18	0.066
M + S + R + W + H	73.36	-46.49	2.75	0.050
M + S + W + H	70.14	-45.98	3.26	0.039
M + W + H	67.21	-45.92	3.32	0.037
M + R + W	56.81	-45.86	3.38	0.036

Table 10.3 – Results of a set of analyses of covariance testing the effect of species characteristics on the accuracy of species distribution models for 22 well-sampled (>10 records, on average, used for modelling) Egyptian butterfly species, measured as the deviance explained by the distribution models. Where the relationship between model predicted probability and species occurrence was negative, a deviance explained of zero was applied. Characteristics tested were: the number of presence records used to build the distribution models (P), migratory behaviour (M), host-plant specificity (S), predicted range size in Egypt (R), world range size (W) and habitat tolerance (H). Candidate models were built with every possible combination of terms. These models were compared using the approach recommended by Burnham & Anderson (2002), by calculating AIC values for each model, the difference between the AIC for a model and the minimum AIC for all models (Δ_i), and model weights based on these values. I only present the best models ($\Delta_i < 4$) here. The sum of the weights of all models containing a characteristic was used as a measure of the relative importance of that characteristic in determining model accuracy (Burnham & Anderson 2002); the summed weights were as follows: P = 0.309, M = 0.428, S = 0.335, R = 0.715, W = 0.219, H = 0.082.

Model	**Deviance explained**	**AIC**	**AIC difference (Δ_i)**	**Model weight (w_i)**
R	16.50	153	0	0.169
M + R	25.96	154.3	1.3	0.088
P + R	17.89	154.6	1.6	0.076
S + R	17.32	154.8	1.8	0.069
M	16.26	155	2	0.062
R + W	21.46	155.6	2.6	0.046
S	4.47	156	3	0.038
M + S + R	26.41	156.2	3.2	0.034
P + M + R	25.98	156.3	3.3	0.032
P + S + R	18.85	156.4	3.4	0.031
M + S	18.7	156.4	3.4	0.031
M + R + W	31.62	156.6	3.6	0.028
P + M	17.39	156.8	3.8	0.025

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Table 10.4 – Number of presence records used to build the Maxent distribution models and contribution (%) of each of the 19 climatic variables, altitude and habitat to the models for each of the species. A key to the variables used is given at the bottom of the table. Taxonomies followed those used in Gilbert & Zalat (2007) for butterflies, Gilbert *et al.* (2008) for mammals, and Baha El Din (2006) for reptiles and amphibians.

Species	**Number of presence records**	**% contribution by variable:**																				
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
Butterflies:																						
Agrodiaetus loewii	28	46	0	26	1	0	0	0	2	3	1	2	0	0	5	0	0	0	0	0	5	8
Apharitis acamas	15	59	0	13	0	1	10	0	6	1	2	1	0	1	1	0	0	1	0	2	1	3
Azanus jesous	8	1	8	24	32	0	0	0	1	1	0	0	0	0	1	0	0	0	0	7	0	25
Azanus ubaldus	18	0	0	2	1	0	0	1	14	0	6	0	0	0	0	1	0	0	3	0	30	44
Borbo borbonica	19	1	0	0	0	0	0	3	0	0	5	0	0	0	0	0	0	24	6	0	6	56
Carcharodus alceae	14	55	0	1	13	0	13	0	3	1	0	3	0	0	0	0	0	0	0	0	0	10
Carcharodus stauderi	16	40	1	2	22	0	15	0	0	1	0	3	0	3	0	1	1	0	0	0	0	11
Colias croceus	60	30	0	6	0	0	5	0	13	2	3	2	0	0	0	0	0	0	1	0	2	35
Colotis fausta	23	53	1	26	5	0	0	0	4	0	0	0	0	0	0	1	0	0	0	1	6	3
Danaus chrysippus	51	18	0	0	0	0	1	0	0	0	6	0	0	0	4	1	1	0	3	0	0	66
Deudorix livia	51	3	0	0	0	0	0	0	0	0	3	0	0	0	0	1	0	0	2	0	4	84
Euchloe aegyptiaca	20	27	0	24	2	0	12	0	7	0	0	0	0	0	0	2	0	11	0	0	0	16
Euchloe belemia	6	14	0	0	0	0	0	13	0	0	24	0	0	0	0	0	4	0	0	18	0	27
Euchloe falloui	12	48	0	8	19	0	11	0	1	4	0	2	0	0	2	0	0	0	0	0	4	2
Freyeria trochylus	32	24	0	0	0	2	0	0	1	0	11	0	0	3	0	0	0	0	0	1	3	53
Gegenes nostrodamus	37	3	0	0	0	0	1	0	0	0	35	0	0	1	1	0	0	0	2	0	1	54
Hypolimnas misippus	10	0	0	1	9	8	0	0	0	0	0	0	0	0	0	0	4	0	1	0	8	68
Iolana alfierii	12	32	4	4	6	0	34	0	0	9	0	8	0	1	0	0	0	0	0	1	0	1

Lampides boeticus	50	11	0	0	1	0	0	0	0	2	12	0	0	0	0	2	0	0	5	0	0	65
Lycaena phlaeas	8	1	0	40	28	0	6	0	2	1	0	8	1	3	0	0	0	0	7	0	0	3
Melitaea deserticola	34	52	0	27	3	1	0	0	1	0	0	2	0	0	4	2	0	0	0	1	2	5
Melitaea trivia	11	42	0	2	23	0	13	0	1	6	0	0	2	0	2	3	0	0	0	0	2	4
Papilio saharae	11	33	0	2	24	0	25	0	2	2	0	3	0	0	0	0	5	0	0	0	0	3
Pelopidas thrax	29	13	0	0	0	0	2	2	0	0	25	0	0	0	0	0	0	0	9	0	0	49
Pieris rapae	43	4	0	0	0	0	3	0	0	0	5	0	0	0	0	1	1	0	1	9	3	73
Plebejus philbyi	14	55	0	4	19	0	13	0	1	2	0	1	0	0	1	0	0	0	0	0	0	4
Pontia daplidice	35	56	0	16	2	0	0	0	4	0	0	0	0	0	0	0	1	2	0	3	0	15
Pontia glauconome	49	39	0	15	2	0	1	5	0	3	8	0	0	2	0	0	0	0	0	10	2	14
Pseudophilotes sinaicus	9	79	1	1	3	0	9	1	0	1	0	4	0	0	0	0	0	0	0	0	0	3
Pseudotergumia pisidice	16	64	4	8	3	0	10	0	0	5	0	0	1	0	0	0	0	0	0	3	0	1
Spialia doris	23	0	0	8	2	3	0	7	4	3	41	0	0	0	0	2	0	0	7	0	4	19
Tarucus rosaceus	37	8	0	0	5	1	4	0	0	0	23	0	0	1	1	2	0	0	6	1	0	48
Vanessa atalanta	17	8	4	0	0	0	1	0	0	0	10	0	0	8	1	0	0	0	0	0	0	67
Vanessa cardui	63	18	0	1	0	0	0	0	0	7	2	0	0	0	0	2	2	0	0	1	3	64
Zizeeria karsandra	41	8	0	3	4	0	5	0	0	0	9	6	0	4	0	0	0	0	2	4	11	42
Mammals:																						
Acinonyx jubatus	35	23	3	0	0	3	7	3	4	0	22	0	1	7	3	0	3	0	0	0	14	7
Acomys cahirinus	106	9	5	1	0	1	3	21	0	0	6	0	2	1	5	1	2	0	2	0	0	42
Acomys dimidiatus	14	1	0	7	60	0	0	0	0	0	0	0	0	11	2	0	0	0	1	1	11	8
Acomys russatus	18	17	0	36	9	0	0	0	0	0	1	0	0	8	0	0	3	1	3	3	10	9
Allactaga tetradactyla	10	3	0	3	2	0	10	0	6	1	0	9	0	35	5	0	0	1	0	0	7	20
Arvicanthis niloticus	47	26	1	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	69
Asellia tridens	42	22	0	0	1	0	1	0	0	0	0	1	0	0	3	0	0	0	0	0	5	65
Canis aureus	17	9	0	0	0	0	3	0	0	0	5	0	0	1	0	0	0	0	0	3	0	77
Canis lupaster	58	30	0	0	0	0	2	0	1	0	9	4	0	0	0	0	0	0	2	0	0	51

Capra nubiana	105	20	0	30	6	0	2	1	4	2	2	4	0	0	1	0	1	0	1	0	11	15
Crocidura olivieri	26	11	0	0	1	1	0	0	1	4	15	0	0	0	5	0	2	0	0	0	3	58
Crocidura religiosa	9	22	0	0	0	0	0	2	0	1	0	0	0	0	3	0	0	0	0	1	0	71
Dipodillus campestris	19	9	0	0	0	0	0	5	0	0	20	0	0	7	23	0	1	4	0	6	0	25
Dipodillus dasyurus	25	26	0	41	8	0	0	1	1	0	6	0	0	2	4	0	0	0	0	0	0	10
Dipodillus simoni	13	5	0	9	2	2	2	1	5	0	0	2	0	0	3	0	0	19	0	0	8	43
Eliomys melanurus	15	30	3	8	19	0	28	0	4	0	0	0	2	0	1	0	0	0	0	0	0	6
Eptesicus bottae	8	0	0	0	0	0	27	0	7	13	0	0	4	10	3	0	0	3	2	6	3	23
Felis chaus	41	19	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	4	0	0	73
Felis margarita	7	0	0	49	0	0	0	0	45	0	0	0	0	0	0	0	0	0	5	0	0	0
Felis silvestris	32	7	0	29	19	0	1	2	0	0	0	0	0	6	0	0	2	0	0	10	3	19
Gazella dorcas	141	14	1	1	1	0	1	4	47	0	1	0	0	4	1	0	1	1	1	2	0	18
Gerbillus amoenus	33	38	0	0	0	1	0	0	1	0	19	0	0	0	0	0	3	0	0	0	0	38
Gerbillus andersoni	57	16	1	6	0	6	2	0	12	1	2	1	0	42	0	0	0	3	0	0	5	3
Gerbillus floweri	18	1	0	11	2	0	0	2	8	6	44	0	0	5	2	0	0	0	1	8	0	9
Gerbillus gerbillus	196	25	2	0	4	1	3	0	3	0	19	0	3	0	2	0	2	2	0	1	2	30
Gerbillus henleyi	44	3	0	7	1	7	0	3	56	2	8	0	0	0	1	0	1	0	0	0	2	9
Gerbillus perpallidus	20	29	0	0	3	1	2	3	0	1	21	0	0	0	1	0	11	16	0	0	2	10
Gerbillus pyramidum	101	40	1	0	4	0	6	4	0	2	3	0	0	4	1	0	0	1	0	0	1	32
Hemiechinus auritus	69	19	0	5	0	5	0	2	9	1	10	0	0	9	2	0	1	1	0	0	2	36
Herpestes ichneumon	29	11	0	0	1	5	0	1	1	3	8	0	1	4	0	0	1	0	0	1	1	63
Ictonyx libyca	22	14	0	1	4	8	0	7	4	0	35	0	0	0	0	0	2	2	1	1	9	12
Jaculus jaculus	124	18	0	1	0	14	3	2	0	0	21	0	3	0	0	0	0	4	1	1	3	26
Jaculus orientalis	25	0	1	6	2	2	3	0	0	1	1	1	0	3	3	0	1	39	1	0	8	28
Lepus capensis	85	14	0	0	1	2	1	2	49	0	2	0	0	1	7	1	5	0	1	2	2	9
Meriones crassus	99	11	1	3	0	0	1	2	29	2	10	0	1	2	5	1	0	1	0	7	9	14
Meriones libycus	25	36	3	3	0	1	2	0	4	0	7	5	0	0	0	0	0	27	0	1	2	9
Meriones shawi	22	11	0	10	5	3	2	0	5	0	0	3	0	0	8	0	0	38	0	0	3	12

Mus musculus	93	23	0	0	4	0	1	1	2	0	7	2	1	0	1	0	0	0	0	0	2	55
Mustela nivalis	21	13	0	0	3	0	0	0	0	0	30	0	0	1	0	0	0	0	0	1	0	52
Nesokia indica	21	27	0	0	0	4	0	0	0	0	12	0	0	0	0	0	3	0	0	1	0	53
Nycteris thebaica	28	4	1	0	0	0	0	0	0	4	2	0	0	0	0	0	0	0	0	0	0	88
Otonycteris hemprichii	16	45	0	0	0	0	0	0	0	0	25	0	0	0	0	0	0	0	0	0	0	30
Pachyuromys duprasi	24	9	0	0	11	8	0	1	1	12	39	0	0	0	0	0	0	0	0	1	1	17
Panthera pardus	22	22	0	27	13	0	2	0	0	1	2	0	0	6	0	0	3	0	1	2	4	17
Paraechinus aethiopicus	33	13	0	6	0	0	0	0	60	0	0	0	0	1	0	2	7	0	2	0	1	8
Pipistrellus kuhlii	30	24	0	0	0	3	0	0	0	0	31	0	0	0	0	0	0	4	0	1	0	36
Plecotus christii	31	42	0	0	6	0	0	0	0	0	1	0	0	0	7	0	0	0	0	3	3	36
Procavia capensis	37	11	0	6	1	0	0	2	23	2	0	0	0	3	0	2	0	0	3	0	6	41
Psammomys obesus	68	7	0	13	3	3	5	0	20	0	0	1	0	9	1	0	2	27	0	0	3	6
Rattus norwegicus	25	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	6	1	5	0	86
Rattus rattus	64	22	0	0	0	0	1	1	0	0	5	0	0	1	2	0	1	0	1	0	0	66
Rhinopoma hardwickii	26	8	0	0	0	2	0	7	0	0	0	1	0	9	0	0	0	0	0	9	10	52
Rhinopoma microphyllum	8	31	0	0	2	0	0	6	0	7	9	0	0	7	6	0	0	2	0	1	6	24
Rousettus aegyptiacus	35	0	0	5	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	91
Sekeetamys calurus	32	9	0	42	5	0	0	0	7	0	0	0	0	0	0	1	2	0	1	0	8	25
Spalax ehrenbergi	19	17	0	6	5	4	0	1	5	0	3	0	0	1	12	0	1	41	0	0	0	4
Taphozous nudiventris	13	41	0	0	0	0	0	2	0	1	9	0	0	0	7	0	0	0	0	0	4	36
Taphozous perforatus	19	1	0	0	0	1	0	2	0	0	1	0	0	6	0	0	0	0	0	12	3	74
Vulpes rueppellii	68	33	0	0	1	19	0	0	0	1	0	1	0	9	0	1	0	0	2	1	13	20
Vulpes vulpes	116	9	0	0	1	5	2	1	1	0	14	0	0	0	3	0	2	0	0	0	1	60
Vulpes zerda	36	48	0	0	0	0	0	2	1	0	12	0	0	10	8	0	1	0	0	3	0	15

Variable key:
1 Altitude
2 Annual mean temperature
3 Mean diurnal temperature range
4 Isothermality
5 Temperature seasonality
6 Maximum temperature of warmest month
7 Minimum temperature of coldest month
8 Annual temperature range
9 Mean temperature of wettest quarter
10 Mean temperature of driest quarter
11 Mean temperature of warmest quarter
12 Mean temperature of coldest quarter
13 Annual precipitation
14 Precipitation of wettest month
15 Precipitation of driest month
16 Precipitation seasonality
17 Precipitation of wettest quarter
18 Precipitation of driest quarter
19 Precipitation of warmest quarter
20 Precipitation of coldest quarter
21 Habitat

10.5 Appendix 7.1

Table 10.5 – A list of the sites visited and their geographical coordinates. Sites where I performed repeat transects (fully-surveyed sites) and sites with incidental records are listed separately.

Site	Longitude	Latitude
Sites with replicate transects:		
Coast near Baltim	31.072	31.599
Farm near Rosetta	30.380	31.459
Farm south of Rosetta	30.453	31.380
Fruit farm	30.432	31.359
Farms near El Zarqa	31.700	31.265
Farms near Lake Manzala	31.800	31.251
Farms near Salamun	31.576	31.122
El Tina	32.290	31.041
Farms west of Ismailia	32.097	30.685
Wadi Bad’	32.252	29.727
Wadi Qena	31.862	29.548
Wadi Abu Fera’	31.726	29.477
Wadi Al Khalal	31.936	29.358
Wadi Abu Remth	31.948	29.211
Wadi Araba	32.075	28.955
Wadi Aldakhal	32.706	28.725
Wadi Abu Had	32.561	28.168
Wadi Abu Sliy	31.075	28.388
Western Desert near Samalut	30.549	28.402
North of Beni Hasan	30.881	27.954
Wadi Kid	34.168	28.351
Sites with incidental records:		
Wadi Natrun (lower)	30.169	30.447
Wadi Natrun (upper)	30.105	30.352
Wadi Shrayg	33.958	28.552
Wadi Arbaein	33.953	28.539
Wadi Itlah	33.933	28.570
Sheikh Mubarak (centre)	31.089	31.591
Landfill site	30.475	31.422
Coastal salt marshes near Baltim	30.376	31.462
Farm in Sheikh Mubarak	31.100	31.587
Near Damietta	31.392	31.428
West of Ismailia	32.096	30.685
Desert between Ain Sukhna and Wadi Qena	32.185	29.642
Matai	30.788	28.417

Table 10.6 – A list of all species sampled during the new survey. More information, including taxonomic authorities, can be found for reptiles and amphibians in Baha El Din (2006), for butterflies in Larsen (1990) and for mammals in Hoath (2003).

Reptiles and amphibians:
Acanthodactylus aegyptius
Acanthodactylus boskianus
Acanthodactylus scutellatus
Cerastes cerastes
Cerastes vipera
Chalcides ocellatus
Chamaeleo africanus
Chamaeleo chamaeleon
Eryx jaculus
Hemidactylus turcicus
Laukadia stellio
Malpolon monspessulanus
Mesalina guttulata
Naja haje
Natrix tessellata
Platyceps florulentus
Psammophis schokari
Psammophis sibilans
Pseudotrapelus sinaitus
Ptychadena mascareniensis
Ptyodactylus guttatus
Ptyodactylus hasselquistii
Ptyodactylus siphonorhina
Rana bedriagae
Scincus scincus
Sphenops sepsoides
Stenodactylus stenodactylus
Tarentola annularis
Trachylepis vittata
Trapelus mutabilis
Varanus griseus
Butterflies:
Colias croceus
Danaus chrysippus
Euchloe aegyptiaca
Lampides boeticus
Leptotes pirithous
Pelopidas thrax
Pieris rapae
Pontia daplidice

Pontia glauconome
Vanessa atalanta
Vanessa cardui
Zizeeria karsandra

Mammals:

Asellia tridens
Capra nubiana
Felis chaus
Gazella dorcas
Gerbillus gerbillus
Hemiechinus auritus
Lepus capensis
Mus musculus
Rattus rattus
Rhinopoma hardwickii

10.6 Appendix 8.1

Table 10.7 – Hoverfly and bird taxa analyzed in Chapter 8. Taxonomies followed those used in Mullarney *et al.* (1999) for birds, and in Stubbs & Falk (2002) for hoverflies.

Birds:
Blackbird (*Turdus merula*)
Blackcap (*Sylvia atricapilla*)
Blue tit (*Cyanistes caeruleus*)
Bullfinch (*Pyrrhula pyrrhula)*
Chaffinch (*Fringilla coelebs*)
Chiffchaff (*Phylloscopus collybita*)
Coal tit (*Periparus ater*)
Dunnock (*Prunella modularis*)
Garden Warbler (*Sylvia borin*)
Goldcrest (*Regulus regulus*)
Great tit (*Parus major*)
Great spotted woodpecker (*Dendrocops major*)
Greenfinch (*Carduelis chloris*)
House sparrow (*Passer domesticus*)
Jay (*Garrulus grandarius*)
Long-tailed tit (*Aegithalos caudatus*)
Marsh tit (*Poecile palustris*)
Nuthatch (*Sitta europaea*)
Redpoll (*Carduelis flammea*)
Reed bunting (*Emberiza schoeniclus*)
Robin (*Erithacus rubecula*)
Song Thrush (*Turdus philomelos*)
Spotted flycatcher (*Muscicapa striata*)
Starling (*Sturnus vulgaris*)
Swallow (*Hirundo rustica*)
Tree sparrow (*Passer montanus*)
Treecreeper (*Certhia familiaris*)
Willow tit (*Poecile montanus*)
Willow warbler (*Phylloscopus trochilus*)
Woodpigeon (*Columba palumbus*)
Wren (*Troglodytes troglodytes*)
Yellowhammer (*Emberiza citrinella*)
Hoverflies:
Anasimyia contracta
Anasimyia interpuncta
Anasimyia lineata
Anasimyia lunulata
Anasimyia transfuga

Arctophila superbiens
Baccha elongata
Blera fallax
Brachyopa bicolor
Brachyopa insensilis
Brachyopa pilosa
Brachyopa scutellaris
Brachypalpoides lentus
Brachypalpus laphriformis
Caliprobola speciosa
Callicera aurata
Callicera rufa
Callicera spinolae
Chalcosyrphus eunotus
Chalcosyrphus nemorum
Chamaesyrphus caledonicus
Chamaesyrphus scaevoides
Cheilosia albipila
Cheilosia albitarsis agg.
Cheilosia antiqua
Cheilosia barbata
Cheilosia bergenstammi
Cheilosia carbonaria
Cheilosia chrysocoma
Cheilosia cynocephala
Cheilosia fraterna
Cheilosia griseiventris
Cheilosia grossa
Cheilosia illustrata
Cheilosia impressa
Cheilosia lasiopa
Cheilosia latifrons
Cheilosia longula
Cheilosia mutabilis
Cheilosia nebulosa
Cheilosia nigripes
Cheilosia pagana
Cheilosia proxima
Cheilosia pubera
Cheilosia sahlbergi
Cheilosia scutellata
Cheilosia semifasciata
Cheilosia soror
Cheilosia urbana
Cheilosia uviformis

Cheilosia variabilis
Cheilosia velutina
Cheilosia vernalis
Cheilosia vicina
Cheilosia vulpina
Chrysogaster cemiteriorum
Chrysogaster solstitialis
Chrysogaster virescens
Chrysotoxum arcuatum
Chrysotoxum bicinctum
Chrysotoxum cautum
Chrysotoxum elegans
Chrysotoxum festivum
Chrysotoxum octomaculatum
Chrysotoxum vernale
Chrysotoxum verralli
Criorhina asilica
Criorhina berberina
Criorhina floccosa
Criorhina ranunculi
Dasysyrphus albostriatus
Dasysyrphus friuliensis
Dasysyrphus hilaris
Dasysyrphus pinastri
Dasysyrphus tricinctus
Dasysyrphus venustus
Didea alneti
Didea fasciata
Didea intermedia
Doros profuges
Epistrophe diaphana
Epistrophe eligans
Epistrophe grossulariae
Epistrophe melanostoma
Epistrophe nitidicollis
Episyrphus balteatus
Eriozona erratica
Eriozona syrphoides
Eristalinus aeneus
Eristalinus sepulchralis
Eristalis abusivus
Eristalis arbustorum
Eristalis cryptarum
Eristalis horticola
Eristalis interruptus

Eristalis intricarius
Eristalis pertinax
Eristalis rupium
Eristalis similis
Eristalis tenax
Eumerus funeralis
Eumerus ornatus
Eumerus sabulonum
Eumerus strigatus
Eupeodes bucculatus agg.
Eupeodes corollae
Eupeodes lapponicus
Eupeodes latifasciatus
Eupeodes lundbecki
Eupeodes luniger agg.
Eupeodes nielseni
Eupeodes nitens
Ferdinandea cuprea
Ferdinandea ruficornis
Hammerschmidtia ferruginea
Helophilus hybridus
Helophilus pendulus
Helophilus trivittatus
Heringia brevidens
Heringia heringi agg.
Heringia latitarsis
Heringia pubescens
Heringia verrucula
Heringia vitripennis
Lejogaster metallina
Lejogaster tarsata
Lejops vittatus
Leucozona glaucia
Leucozona laternaria
Leucozona lucorum
Mallota cimbiciformis
Melangyna arctica
Melangyna barbifrons
Melangyna cincta
Melangyna compositarum/labiatarum
Melangyna ericarum
Melangyna lasiophthalma
Melangyna quadrimaculata
Melangyna umbellatarum
Melanogaster aerosa

Melanogaster hirtella
Melanostoma dubium
Melanostoma mellinum
Melanostoma scalare
Meligramma euchromum
Meligramma guttatum
Meligramma trianguliferum
Meliscaeva auricollis
Meliscaeva cinctella
Merodon equestris
Microdon analis
Microdon devius
Microdon mutabilis agg.
Myathropa florea
Myolepta dubia
Myolepta potens
Neoascia geniculata
Neoascia interrupta
Neoascia meticulosa
Neoascia obliqua
Neoascia podagrica
Neoascia tenur
Orthonevra brevicornis
Orthonevra geniculata
Orthonevra nobilis
Paragus albifrons
Paragus haemorrhous
Paragus tibialis
Parasyrphus annulatus
Parasyrphus lineola
Parasyrphus malinellus
Parasyrphus nigritarsis
Parasyrphus punctulatus
Parasyrphus vittiger
Parhelophilus consimilis
Parhelophilus frutetorum
Parhelophilus versicolor
Pelecocera tricincta
Pipiza austriaca
Pipiza bimaculata
Pipiza fenestrata
Pipiza lugubris
Pipiza luteitarsis
Pipiza noctiluca
Pipizella maculipennis

Pipizella viduata
Pipizella virens
Platycheirus albimanus
Platycheirus ambiguus
Platycheirus angustatus
Platycheirus clypeatus agg.
Platycheirus discimanus
Platycheirus fulviventris
Platycheirus granditarsus
Platycheirus immarginatus
Platycheirus manicatus
Platycheirus melanopsis
Platycheirus peltatus agg.
Platycheirus perpallidus
Platycheirus podagratus
Platycheirus rosarum
Platycheirus scambus
Platycheirus scutatus agg.
Platycheirus sticticus
Platycheirus tarsalis
Pocota personata
Portevinia maculata
Psilota anthracina
Rhingia campestris
Rhingia rostrata
Riponnensia splendens
Scaeva pyrastri
Scaeva selenitica
Sericomyia lappona
Sericomyia silentis
Sphaerophoria bankowskae
Sphaerophoria batava
Sphaerophoria fatarum
Sphaerophoria interrupta
Sphaerophoria loewi
Sphaerophoria philanthus
Sphaerophoria potentillae
Sphaerophoria rueppellii
Sphaerophoria scripta
Sphaerophoria taeniata
Sphaerophoria virgata
Sphegina clunipes
Sphegina elegans
Sphegina sibirica
Sphegina verecunda

Syritta pipiens
Syrphus ribesii
Syrphus torvus
Syrphus vitripennis
Trichopsomyia flavitarsis
Triglyphus primus
Tropidia scita
Volucella bombylans
Volucella inanis
Volucella inflata
Volucella pellucens
Volucella zonaria
Xanthandrus comtus
Xanthogramma citrofasciatum
Xanthogramma pedissequum
Xylota abiens
Xylota florum
Xylota jakutorum
Xylota segnis
Xylota sylvarum
Xylota tarda
Xylota xanthocnema

10.7 Appendix 8.2

10.7.1 Additional results for the study presented in Chapter 8

In addition to models built using only climate variables, presented in the main paper, I also built a set of models for both hoverfly and bird species that included topography, land cover and agriculture variables. Data on land cover in Britain were only available for a single point in time, so changes in land cover could not be incorporated into the models. Only linear terms were fitted in these models because of the large numbers of predictor variables involved and thus the risk of model overfitting. Topography variables (altitude and slope) were calculated based on the Ordnance Survey Digital Elevation Model at 50 m resolution (Ordnance Survey 2009). For land cover we used the Institute of Terrestrial Ecology's (ITE) Land Class Map (Brown *et al.* 2002), which classifies each grid cell into one of 41 land cover classes. We also used the ITE Land Cover Map, which measures the percentage of each 1km grid square covered by each of 10 aggregate land cover types. Additionally, a measure of land class diversity was calculated by drawing a radius of 2 km around each grid square and measuring the diversity of land classes in this radius using a Shannon-Weiner diversity index. We obtained agriculture variables from the Edina agricultural censuses (Anon. 2009b) that recorded total numbers of sheep and cattle and the acreage of cereals grown: censuses were taken in 1976, 1981, 1988, 1994, 1997 and 2004. We used the agriculture census that lay closest to the mid-point of each time period.

Hoverfly models were built using Maxent Version 3.2.9 (Phillips *et al.* 2006). Maxent randomly samples 10,000 grid cells to characterize the background environmental conditions of the study area and does not require absence data (Phillips *et al.* 2006). Models were built using default parameters – a regularization value of 1, a maximum of 500 iterations, a convergence threshold of 0.00001 and a maximum of 10000 random background pseudo-absences (Phillips *et al.* 2006). Bird models were built in R (R Development Core Team 2004), using GLMs with a binomial error distribution and the logit link (McCullagh & Nelder 1989). An automatic backward stepwise selection routine (the 'step' function in R) was used to select simplified models that represented the best trade-off between deviance explained and model complexity, according to Akaike Information Criterion (AIC) values (Akaike 1973; Venables & Ripley 2002).

Initial models predicting contemporary distributions were highly accurate. For hoverflies, average AUC scores were 0.921 ± 0.00462, 0.915 ± 0.00460, 0.896 ± 0.00483, 0.891 ± 0.00520, 0.889 ± 0.00450 and 0.874 ± 0.00582 for each of the six time periods respectively. For birds, average AUC scores were 0.908 ± 0.00968 and 0.875 ± 0.130. Change models, which incorporated changes in the environmental variables to project future and past distributions, were consistently less accurate than control models, which assumed that changes in the environment had no effect on the distributions of species (paired-samples t-tests: in every case $p < 0.05$, and in all but one case $p < 0.001$).

Similarly, contemporary abundances at a single site were predicted well by initial models. Slopes of the relationship between recorded abundance and model predicted probability were all significantly positive. Change models predicted abundance less accurately. 39/43 relationships were positive, of which 27/43 were significantly positive. Control models were more accurate than change models. The relationship between model predicted probability and recorded abundance was always positive, significantly so in 41/43 cases. The AIC for the model of the relationship between abundance and model probability was lower for control models than for change models in 36/43 comparisons.

Although the results were the same as those presented in the main paper, the accuracy of all models – both change and control models, and also models predicting contemporary distributions – was better when land cover, topography and agriculture variables were included in the models. This suggests that these variables have an important influence on the distributions and abundances of species, and accounting for them in attempts to predict the distributions of species in the future must be a priority.

References

Adler P.B., HilleRisLambers J. & Levine J.M. (2007). A niche for neutrality. *Ecology Letters*, 10, 95-104.

Akaike H. (1973). Information theory and an extension of the maximum likelihood. In: *Proceedings of the 2nd International Symposium on Information Theory* (eds. Petrov BN & Cs'aki F) Akademia Kaido, Budapest, pp. 267-281.

Algar A.C., Kerr J.T. & Currie D.J. (2007). A test of Metabolic Theory as the mechanism underlying broad-scale species-richness gradients. *Global Ecology and Biogeography*, 16, 170-178.

Anderson B.J., Arroyo B.E., Collingham Y.C., Etheridge B., Fernandez-De-Simon J., Gillings S., Gregory R.D., Leckie F.M., Sim I.M.W., Thomas C.D., Travis J. & Redpath S.M. (2009). Using distribution models to test alternative hypotheses about a species' environmental limits and recovery prospects. *Biological Conservation*, 142, 488-499.

Anderson R.P., Gómez-Laverde M. & Peterson A.T. (2002a). Geographical distributions of spiny pocket mice in South America: insights from predictive models. *Global Ecology and Biogeography*, 11, 131-141.

Anderson R.P., Peterson A.T. & Gómez-Laverde M. (2002b). Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. *Oikos*, 98, 3-16.

Anderson R.P., Lew D. & Peterson A.T. (2003). Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecological Modelling*, 162, 211-232.

Andrews P. & O'Brien E.M. (2000). Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *Journal of Zoology*, 251, 205-231.

Anon. (2009a). BTO Constant Efforts Sites. URL http://www.bto.org/ringing/ringinfo/ces.

Anon. (2009b). Edina Agricultural Censuses. URL http://edina.ac.uk/agcensus/.

Anon. (2009c). National Biodiversity Gateway. URL http://www.nbn.org.uk/.

Araújo M.B. & Guisan A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, 33, 1677-1688.

Araújo M.B. & Luoto M. (2007). The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, 16, 743-753.

Araújo M.B. & New M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, 22, 42-47.

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

Araújo M.B. & Rahbek C. (2006). How does climate change affect biodiversity? *Science*, 313, 1396-1397.

Araújo M.B. & Williams P.H. (2000). Selecting areas for species persistence using occurrence data. *Biological Conservation*, 96, 331-345.

Araújo M.B., Williams P.H. & Fuller R.J. (2002). Dynamics of extinction and the selection of nature reserves. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 269, 1971-1980.

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

Araújo M.B., Whittaker R.J., Ladle R.J. & Erhard M. (2005b). Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography*, 14, 529-538.

Araújo M.B., Nogués-Bravo D., Diniz-Filho J.A.F., Haywood A.M., Valdes P.J. & Rahbek C. (2008). Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, 31, 8-15.

Araújo M.B., Thuiller W. & Yoccoz N.G. (2009). Reopening the climate envelope reveals macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences of the United States of America*, 106, E45-E46.

Asher J., Warren M., Fox R., Harding P., Jeffcoate G. & Jeffcoate S. (2001). *The Millennium Atlas of Butterflies in Britain and Ireland*. Oxford University Press, Oxford.

Aspinall R.J., Miller J.A. & Franklin J. (2009). Calculations on the back of a climate envelope: Addressing the geography of species distributions. *Proceedings of the National Academy of Sciences of the United States of America*, 106, E44-E44.

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

Austin M. (2007). Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling*, 200, 1-19.

Austin M.P. & Meyers J.A. (1996). Current approaches to modelling the environmental niche of eucalypts: implication for management of forest biodiversity. *Forest Ecology and Management*, 85, 95-106.

Austin M.P., Belbin L., Meyers J.A., Doherty M.D. & Luoto M. (2006). Evaluation of statistical models used for predicting plant species distributions: Role of artificial data and theory. *Ecological Modelling*, 199, 197-216.

Baha El Din S. (2006). *A Guide to the Reptiles and Amphibians of Egypt*. American University in Cairo Press, Cairo.

Bahn V. & McGill B.J. (2007). Can niche-based distribution models outperform spatial interpolation? *Global Ecology and Biogeography*, 16, 733-742.

Bahn V., O'Connor R.J. & Krohn W.B. (2006). Importance of spatial autocorrelation in modeling bird distributions at a continental scale. *Ecography*, 29, 835-844.

Bahn V., Krohn W.B. & O'Connor R.J. (2008). Dispersal leads to spatial autocorrelation in species distributions: A simulation model. *Ecological Modelling*, 213, 285-292.

Bakkenes M., Alkemade J.R.M., Ihle F., Leemans R. & Latour J.B. (2002). Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology*, 8, 390-407.

Ball S. (2009). Hoverfly Recording Scheme. URL http://www.hoverfly.org.uk/.

Bates H.W. (1862). Contributions to an insect fauna of the Amazon valley (Lepidoptera: Heliconidae). *Transactions of the Linnean Society of London*, 23, 495-556.

Beale C.M., Lennon J.J. & Gimona A. (2008). Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 14908-14912.

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.

Beck J. & Kitching I.J. (2007). Correlates of range size and dispersal ability: a comparative analysis of sphingid moths from the Indo-Australian tropics. *Global Ecology and Biogeography*, 16, 341-349.

Beck J., Kitching I.J. & Linsenmair K.E. (2006). Measuring range sizes of South-East Asian hawkmoths (Lepidoptera : Sphingidae): effects of scale, resolution and phylogeny. *Global Ecology and Biogeography*, 15, 339-348.

Bell G. (2001). Neutral macroecology. *Science*, 293, 2413-2418.

Berg Å., Gärdenfors U. & von Proschwitz T. (2004). Logistic regression models for predicting occurrence of terrestrial molluscs in southern Sweden – importance of environmental data quality and model complexity. *Ecography*, 27, 83-93.

Berry P.M., Dawson T.P., Harrison P.A. & Pearson R.G. (2002). Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology and Biogeography*, 11, 453-462.

Best A.S., Johst K., Münkemüller T. & Travis J.M.J. (2007). Which species will successfully track climate change? The influence of intraspecific competition and density dependent dispersal on range shifting dynamics. *Oikos*, 116, 1531-1539.

Beyer H.L. (2004). Hawth's Analysis Tools for ArcGIS. URL http://www.spatialecology.com/htools.

BioMAP (2009). BioMAP Egypt Project. URL http://www.biomapegypt.org/.

Boone R.B. & Krohn W.B. (1999). Modeling the occurrence of bird species: are the errors predictable? *Ecological Applications*, 9, 835-848.

Braby M.F., Vila R. & Pierce N.E. (2006). Molecular phylogeny and systematics of the Pieridae (Lepidoptera : Papilionoidea): higher classification and biogeography. *Zoological Journal of the Linnean Society*, 147, 239-275.

Bro-Jorgensen J. (2007). The intensity of sexual selection predicts weapon size in male bovids. *Evolution*, 61, 1316-1326.

Broennimann O., Treier U.A., Müller-Schärer H., Thuiller W., Peterson A.T. & Guisan A. (2007). Evidence of climatic niche shift during biological invasion. *Ecology Letters*, 10, 701-709.

Brotons L., Thuiller W., Araújo M.B. & Hirzel A.H. (2004). Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography*, 27, 437-448.

Brower A.V.Z. (2000). Phylogenetic relationships among the Nymphalidae (Lepidoptera) inferred from partial sequences of the *wingless* gene. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 267, 1201-1211.

Brown N., Gerard F. & Fuller R. (2002). Mapping of land use classes within the CORINE Land Cover Map of Great Britain. *Cartographic Journal*, 39, 5-14.

Buckley L.B. & Jetz W. (2007). Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 274, 1167-1173.

Burnham K.P. & Anderson D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. 2nd edn. Springer, New York.

Caro T.M. & O'Doherty G. (1999). On the use of surrogate species in conservation biology. *Conservation Biology*, 13, 805-814.

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.

Carrascal L.M., Seoane J., Palomino D., Alonso C.L. & Lobo J.M. (2006). Species-specific features affect the ability of census-derived models to map winter avian distribution. *Ecological Research*, 21, 681-691.

Chape S., Harrison J., Spalding M. & Lysenko I. (2005). Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, 360, 443-455.

Charmantier A., McCleery R.H., Cole L.R., Perrins C., Kruuk L.E.B. & Sheldon B.C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science,* 320, 800-803.

Chase J.M. & Leibold M.A. (2003). *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago.

Chatfield C. (1995). Model uncertainty, data mining and statistical inference. *Journal of the Royal Statistical Society Series A, Statistics in Society*, 158, 419-466.

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.

Chesson P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics,* 31, 343-366.

Connell J.H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, 42, 710-723.

Cottenie K., Michels E., Nuytten N. & de Meester L. (2003). Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. *Ecology*, 84, 991-1000.

Cowley M.J.R., Thomas C.D., Roy D.B., Wilson R.J., León-Cortés J.L., Gutiérrez D., Bulman C.R., Quinn R.M., Moss D. & Gaston K.J. (2001). Density–distribution relationships in British butterflies. I. The effect of mobility and spatial scale. *Journal of Animal Ecology*, 70, 410-425.

Crawley M.J. (2002). *Statistical Computing: An Introduction to Data Analysis Using S-Plus*. John Wiley & Sons, New York.

Currie D.J. (2007). Disentangling the roles of environment and space in ecology. *Journal of Biogeography*, 34, 2009-2011.

Currie D.J., Mittelbach G.G., Cornell H.V., Field R., Guégan J.F., Hawkins B.A., Kaufman D.M., Kerr J.T., Oberdorff T., O'Brien E. & Turner J.R.G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121-1134.

Davis A.J., Jenkinson L.S., Lawton J.H., Shorrocks B. & Wood S. (1998). Making mistakes when predicting shifts in species range in response to global warming. *Nature*, 391, 783-786.

Davis M.B. & Shaw R.G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, 292, 673-679.

Davis M.B., Shaw R.G. & Etterson J.R. (2005). Evolutionary responses to changing climate. *Ecology*, 86, 1704-1714.

den Boer P.J. (1986). The present status of the competitive exclusion principle. *Trends In Ecology & Evolution*, 1, 25-28.

Dennis R.L.H. & Hardy P.B. (1999). Targeting squares far survey: predicting species richness and incidence of species for a butterfly atlas. *Global Ecology and Biogeography*, 8, 443-454.

Dennis R.L.H. & Thomas C.D. (2000). Bias in butterfly distribution maps: the influence of hotspots and recorder's home range. *Journal of Insect Conservation*, 4, 73-77.

Dennis R.L.H., Sparks T.H. & Hardy P.B. (1999). Bias in butterfly distribution maps: the effects of sampling effort. *Journal of Insect Conservation*, 3, 33-42.

Derksen S. & Keselman H.J. (1992). Backward, forward and stepwise automated subset-selection algorithms: frequency of obtaining authentic and noise variables. *British Journal of Mathematical & Statistical Psychology*, 45, 265-282.

Devictor V., Julliard R., Couvet D. & Jiguet F. (2008). Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 275, 2743-2748.

Diniz-Filho J.A.F. & Bini L.M. (2005). Modelling geographical patterns in species richness using eigenvector-based spatial filters. *Global Ecology and Biogeography*, 14, 177-185.

Dormann C.F., McPherson J.M., Araújo M.B., Bivand R., Bolliger J., Carl G., Davies R.G., Hirzel A., Jetz W., Kissling W.D., Kühn I., Ohlemüller R., Peres-Neto P.R., Reineking B., Schröder B., Schurr F.M. & Wilson R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, 30, 609-628.

Dormann C.F., Schweiger O., Arens P., Augenstein I., Aviron S., Bailey D., Baudry J., Billeter R., Bugter R., Bukácek R., Burel F., Cerny M., De Cock R., De Blust G., DeFilippi R., Diekötter T., Dirksen J., Durka W., Edwards P.J., Frenzel M., Hamersky R., Hendrickx F., Herzog F., Klotz S., Koolstra B., Lausch A., Le Coeur D., Liira J., Maelfait J.P., Opdam P., Roubalova M., Schermann-Legionnet A., Schermann N., Schmidt T., Smulders M.J.M., Speelmans M., Simova P., Verboom J., van Wingerden W. & Zobel M. (2008). Prediction uncertainty of environmental change effects on temperate European biodiversity. *Ecology Letters*, 11, 235-244.

Dudík M., Phillips S.J. & Schapire R.E. (2004). Performance guarantees for regularized maximum entropy density estimation. In: *Proceedings of the 17th Annual Conference on Computational Learning Theory* (eds. Shawe-Taylor J & Singer Y). Springer Berlin.

Dullinger S., Dirnböck T. & Grabherr G. (2004). Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. *Journal Of Ecology*, 92, 241-252.

Eaton M.D., Soberón J. & Peterson A.T. (2008). Phylogenetic perspective on ecological niche evolution in American blackbirds (Family Icteridae). *Biological Journal of the Linnean Society*, 94, 869-878.

Egyptian Environmental Affairs Agency (2007). Egyptian Environmental Affairs Agency – Protectorates. URL http://www.eeaa.gov.eg/English/main/protect_desc.asp.

Ehrlich P.R. & Raven P.H. (1964). Butterflies and plants: a study in coevolution. *Evolution*, 18, 586-608.

Elith J. (2002). Quantitative methods for modeling species habitat: comparative performance and an application to Australian plants. In: *Quantitative Methods for Conservation Biology* (ed. Ferson S). Springer-Verlag New York, pp. 39-58.

Elith J., Graham C.H., Anderson R.P., Dudík M., Ferrier S., Guisan A., Hijmans R.J., Huettmann F., Leathwick J.R., Lehmann A., Li J., Lohmann L.G., Loiselle B.A., Manion G., Moritz C., Nakamura M., Nakazawa Y., Overton J.M., Peterson A.T., Phillips S.J., Richardson K., Scachetti-Pereira R., Schapire R.E., Soberón J., Williams S., Wisz M.S. & Zimmermann N.E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129-151.

Elton C.S. (1927). *Animal ecology*. Sidgwick & Jackson, London.

Engler R. & Guisan A. (2009). MIGCLIM: Predicting plant distribution and dispersal in a changing climate. *Diversity and Distributions*, 15, 590-601.

Engler R., Guisan A. & Rechsteiner L. (2004). An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology*, 41, 263-274.

Engler R., Randin C.F., Vittoz P., Czáka T., Beniston M., Zimmermann N.E. & Guisan A. (2009). Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? *Ecography*, 32, 34-45.

Enquist B.J., Sanderson J. & Weiser M.D. (2002). Modeling macroscopic patterns in ecology. *Science*, 295, 1835-1836.

Evans K.L., Rodrigues A.S.L., Chown S.L. & Gaston K.J. (2006). Protected areas and regional avian species richness in South Africa. *Biology Letters*, 2, 184-188.

Evans M.E.K., Smith S.A., Flynn R.S. & Donoghue M.J. (2009). Climate, niche evolution, and diversification of the "bird-cage" evening primroses (*Oenothera*, sections *Anogra* and *Kleinia*). *The American Naturalist*, 173, 225-240.

Feria T.P. & Peterson A.T. (2002). Prediction of bird community composition based on point-occurrence data and inferential algorithms: a valuable tool in biodiversity assessments. *Diversity And Distributions*, 8, 49-56.

Ferrier S. & Watson G. (1997). *An Evaluation of the Effectiveness of Environmental Surrogates and Modeling Techniques in Predicting the Distribution of Biological Diversity*. NSW National Parks And Wildlife Service, Canberra.

Ferrier S., Watson G., Pearce J. & Drielsma M. (2002). Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling. *Biodiversity and Conservation*, 11, 2275-2307.

Ficetola G.F. & Padoa-Schioppa E. (2009). Human activities alter biogeographical patterns of reptiles on Mediterranean islands. *Global Ecology and Biogeography*, 18, 214-222.

Ficetola G.F., Thuiller W. & Miaud C. (2007). Prediction and validation of the potential global distribution of a problematic alien invasive species — the American bullfrog. *Diversity and Distributions*, 13, 476-485.

Ficetola G.F., Thuiller W. & Padoa-Schioppa E. (2009). From introduction to the establishment of alien species: bioclimatic differences between presence and reproduction localities in the slider turtle. *Diversity and Distributions*, 15, 108-116.

Field R., Hawkins B.A., Cornell H.V., Currie D.J., Diniz-Filho J.A.F., Guégan J.F., Kaufman D.M., Kerr J.T., Mittelbach G.G., Oberdorff T., O'Brien E.M. & Turner

J.R.G. (2009). Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, 36, 132-147.

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.

Fielding A.H. & Haworth P.F. (1995). Testing the generality of bird-habitat models. *Conservation Biology*, 9, 1466-1481.

Figueiredo M.S.L. & Grelle C.E.V. (2009). Predicting global abundance of a threatened species from its occurrence: implications for conservation planning. *Diversity and Distributions*, 15, 117-121.

Finch J.M., Samways M.J., Hill T.R., Piper S.E. & Taylor S. (2006). Application of predictive distribution modelling to invertebrates: Odonata in South Africa. *Biodiversity and Conservation*, 15, 4239-4251.

Franco A.M.A., Anderson B.J., Roy D.B., Gillings S., Fox R., Moilanen A. & Thomas C.D. (2009). Surrogacy and persistence in reserve selection: landscape prioritization for multiple taxa in Britain. *Journal of Applied Ecology*, 46, 82-91.

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.

Freitas A.V.L. & Brown K.S. (2004). Phylogeny of the Nymphalidae (Lepidoptera). *Systematic Biology*, 53, 363-383.

García A. (2006). Using ecological niche modelling to identify diversity hotspots for the herpetofauna of Pacific lowlands and adjacent interior valleys of Mexico. *Biological Conservation*, 130, 25-46.

García-Barros E. (2000). Body size, egg size, and their interspecific relationships with ecological and life history traits in butterflies (Lepidoptera : Papilionoidea, Hesperioidea). *Biological Journal of the Linnean Society*, 70, 251-284.

Gaston K.J. & Chown S.L. (2005). Neutrality and the niche. *Functional Ecology*, 19, 1-6.

Gaston K.J., Blackburn T.M., Greenwood J.J.D., Gregory R.D., Quinn R.M. & Lawton J.H. (2000). Abundance–occupancy relationships. *Journal of Applied Ecology*, 37, 39-59.

Gaubert P., Papeş M. & Peterson A.T. (2006). Natural history collections and the conservation of poorly known taxa: Ecological niche modeling in central African rainforest genets (*Genetta* spp.). *Biological Conservation*, 130, 106-117.

Gause G.F. (1934). *The Struggle for Existence*. Williams & Wilkins, Baltimore.

Gavashelishvili A. & Lukarevskiy V. (2008). Modelling the habitat requirements of leopard *Panthera pardus* in west and central Asia. *Journal of Applied Ecology*, 45, 579-588.

Gebremedhin B., Ficetola G.F., Naderi S., Rezaei H.-R., Maudet C., Rioux D., Luikart G., Flagstad Ø., Thuiller W. & Taberlet P. (2009). Combining genetic and ecological data to assess the conservation status of the endangered Ethiopian walia ibex. *Animal Conservation*, 12, 89-100.

Gibbons D.W., Reid J.B. & Chapman R.A. (1993). *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991.* T & A. D. Poyser, London.

Gilbert F. (2007). The evolution of imperfect mimicry. In: *Insect Evolutionary Ecology* (eds. Fellowes M, Holloway G, Rolff J). Wallingford, CABI Publishing.

Gilbert F. & Zalat S. (2007). *The Butterflies of Egypt: Atlas, Red Data Listing and Conservation*. BioMAP, EEAA, Cairo.

Gilbert F., Zalat S. & Bassiouny M. (2008). *The Mammals of Egypt: Atlas, Red Data Listing & Conservation*. BioMAP, EEAA, Cairo.

Ginzburg L.R. & Jensen C.X.J. (2004). Rules of thumb for judging ecological theories. *Trends In Ecology & Evolution*, 19, 121-126.

Gioia P. & Pigott J.P. (2000). Biodiversity assessment: a case study in predicting richness from the potential distributions of plant species in the forests of south-western Australia. *Journal of Biogeography*, 27, 1065-1078.

González-Megías A., Menéndez R., Roy D., Brereton T. & Thomas C.D. (2008). Changes in the composition of British butterfly assemblages over two decades. *Global Change Biology*, 14, 1464-1474.

Graham C.H., Ferrier S., Huettman F., Moritz C. & Peterson A.T. (2004a). New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology & Evolution,* 19, 497-503.

Graham C.H., Ron S.R., Santos J.C., Schneider C.J. & Moritz C. (2004b). Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution*, 58, 1781-1793.

Graham C.H., Elith J., Hijmans R.J., Guisan A., Peterson A.T., Loiselle B.A. & The NCEAS Predicting Species Distributions Working Group (2008). The influence of spatial errors in species occurrence data used in distribution models. *Journal of Applied Ecology*, 45, 239-247.

Green R.E., Collingham Y.C., Willis S.G., Gregory R.D., Smith K.W. & Huntley B. (2008). Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change. *Biology Letters*, 4, 599-602.

Gregory R.D., Willis S.G., Jiguet F., Voříšek P., Klvaňová A., van Strien A., Huntley B., Collingham Y.C., Couvet D. & Green R.E. (2009). An indicator of the impact of climatic change on European bird populations. *PLoS ONE*, 4, e4678.

Grenyer R., Orme C.D.L., Jackson S.F., Thomas G.H., Davies R.G., Davies T.J., Jones K.E., Olson V.A., Ridgely R.S., Rasmussen P.C., Ding T.-S., Bennett P.M., Blackburn T.M., Gaston K.J., Gittleman J.L. & Owens I.P.F. (2006). Global distribution and conservation of rare and threatened vertebrates. *Nature*, 444, 93-96.

Grinnell J. (1917). The niche-relationships of the California Thrasher. *Auk*, 34, 427-433.

Grinnell J. (1924). Geography and evolution. *Ecology*, 5, 225-229.

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

Guisan A. & Thuiller W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8, 993-1009.

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

Guisan A., Edwards T.C. & Hastie T. (2002). Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling*, 157, 89-100.

Guisan A., Broennimann O., Engler R., Vust M., Yoccoz N.G., Lehmann A. & Zimmermann N.E. (2006a). Using niche-based models to improve the sampling of rare species. *Conservation Biology*, 20, 501-511.

Guisan A., Lehmann A., Ferrier S., Austin M., Overton J.M.C., Aspinall R. & Hastie T. (2006b). Making better biogeographical predictions of species' distributions. *Journal of Applied Ecology*, 43, 386-392.

Gulve P.S. (1994). Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. *Ecology*, 75, 1357-1367.

Gutiérrez D., Fernández P., Seymour A.S. & Jordano D. (2005). Habitat distribution models: are mutualist distributions good predictors of their associates? *Ecological Applications*, 15, 3-18.

Hampe A. (2004). Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography*, 13, 469-471.

Hansen M.C., Defries R.S., Townshend J.R.G. & Sohlberg R. (2000). Global land cover classification at 1 km spatial resolution using a classification tree approach. *International Journal of Remote Sensing*, 21, 1331-1364.

Hanski I. (1991). Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society*, 42, 17-38.

Hanski I., Pakkala T., Kuussaari M. & Lei G.C. (1995). Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos*, 72, 21-28.

Harmon J.P., Moran N.A. & Ives A.R. (2009). Species response to environmental change: impacts of food web interactions and evolution. *Science*, 323, 1347-1350.

Harvey P.H. & Pagel M.D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.

Hawkes L.A., Broderick A.C., Coyne M.S., Godfrey M.H. & Godley B.J. (2007). Only some like it hot — quantifying the environmental niche of the loggerhead sea turtle. *Diversity and Distributions*, 13, 447-457.

Hawkins B.A. & Porter E.E. (2003). Does herbivore diversity depend on plant diversity? The case of California butterflies. *The American Naturalist*, 161, 40-49.

Hawkins B.A., Field R., Cornell H.V., Currie D.J., Guégan J.F., Kaufman D.M., Kerr J.T., Mittelbach G.G., Oberdorff T., O'Brien E.M., Porter E.E. & Turner J.R.G. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105-3117.

Hawkins B.A., Diniz-Filho J.A.F., Bini L.M., De Marco P. & Blackburn T.M. (2007). Red herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology. *Ecography*, 30, 375-384.

He F. & Gaston K.J. (2007). Estimating abundance from occurrence: An underdetermined problem. *The American Naturalist*, 170, 655-659.

Heikkinen R.K., Luoto M., Virkkala R., Pearson R.G. & Körber J.H. (2007). Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecology and Biogeography*, 16, 754-763.

Helmus M.R., Savage K., Diebel M.W., Maxted J.T. & Ives A.R. (2007). Separating the determinants of phylogenetic community structure. *Ecology Letters*, 10, 917-925.

Hepinstall J.A., Krohn W.B. & Sader S.A. (2002). Effects of niche width on the performance and agreement of avian habitat models. In: *Predicting Species Occurrences: Issues of Accuracy and Scale* (eds. Scott JM, Heglund PJ, Morrison ML, Haufler JB, Raphael MG, Wall WA & Samson FB). Island Press Washington, pp. 593-606.

Herborg L.M., Rudnick D.A., Siliang Y., Lodge D.M. & MacIsaac H.J. (2007). Predicting the range of Chinese mitten crabs in Europe. *Conservation Biology*, 21, 1316-1323.

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.

Hernandez P.A., Franke I., Herzog S.K., Pacheco V., Paniagua L., Quintana H.L., Soto A., Swenson J.J., Tovar C., Valqui T.H., Vargas J. & Young B.E. (2008). Predicting species distributions in poorly-studied landscapes. *Biodiversity and Conservation*, 17, 1353-1366.

Hijmans R.J. (2009). Diva GIS. URL http://www.diva-gis.org/.

Hijmans R.J. & Graham C.H. (2006). The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, 12, 2272-2281.

Hijmans R.J., Garrett K.A., Huamán Z., Zhang D.P., Schreuder M. & Bonierbale M. (2000). Assessing the geographic representativeness of genebank collections: the case of Bolivian wild potatoes. *Conservation Biology*, 14, 1755-1765.

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, 1965-1978.

Hijmans R.J., Cameron S.E. & Parra J.L. (2009). Worldclim - global climate data. URL http://www.worldclim.org/.

Hirzel A. & Guisan A. (2002). Which is the optimal sampling strategy for habitat suitability modelling. *Ecological Modelling*, 157, 331-341.

Hirzel A.H. & Le Lay G. (2008). Habitat suitability modelling and niche theory. *Journal of Applied Ecology*, 45, 1372-1381.

Hirzel A.H., Helfer V. & Metral F. (2001). Assessing habitat-suitability models with a virtual species. *Ecological Modelling*, 145, 111-121.

Hoath R. (2003). *A Field Guide to the Mammals of Egypt*. American University in Cairo Press, Cairo.

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.

Holmes R.T., Marra P.P. & Sherry T.W. (1996). Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. *Journal of Animal Ecology*, 65, 183-195.

Hortal J., Jiménez-Valverde A., Gómez J.F., Lobo J.M. & Baselga A. (2008). Historical bias in biodiversity inventories affects the observed environmental niche of the species. *Oikos*, 117, 847-858.

Hubbell S.P. (1997). A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs*, 16, S9-S21.

Hubbell S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.

Hubbell S.P. (2005). Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology*, 19, 166-172.

Hunt G., Roy K. & Jablonski D. (2005). Species-level heritability reaffirmed: a comment on "On the heritability of geographic range sizes". *The American Naturalist*, 166, 129-135.

Huntley B. (1995). Plant species' response to climate change: implications for the conservation of European birds. *Ibis*, 137, S127-S138.

Huntley B., Green R.E., Collingham Y.C., Hill J.K., Willis S.G., Bartlein P.J., Cramer W., Hagemeijer W.J.M. & Thomas C.J. (2004). The performance of models relating species geographical distributions to climate is independent of trophic level. *Ecology Letters*, 7, 417-426.

Huntley B., Green R.E., Collingham Y.C. & Willis S.G. (2007). *A Climatic Atlas of European Breeding Birds*. Durham University, the RSPB and Lynx Edicions, Barcelona.

Hurlbert A.H. & White E.P. (2007). Ecological correlates of geographical range occupancy in North American birds. *Global Ecology and Biogeography*, 16, 764-773.

Hutchinson G.E. (1957). Concluding Remarks. *Cold Spring Harbor Symposium On Quantitative Biology*, 22, 415-427.

IPCC (2007). *Intergovernmental Panel on Climate Change 4th Assessment Report*.

Iverson L.R., Prasad A. & Schwartz M.W. (1999). Modeling potential future individual tree-species distributions in the eastern United States under a climate change scenario: a case study with *Pinus virginiana*. *Ecological Modelling*, 115, 77-93.

Jablonski D. (1987). Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. *Science*, 238, 360-363.

James M., Gilbert F. & Zalat S. (2003). Thyme and isolation for the Sinai baton blue butterfly (*Pseudophilotes sinaicus*). *Oecologia*, 134, 445-453.

Jenkins D.G., Brescacin C.R., Duxbury C.V., Elliott J.A., Evans J.A., Grablow K.R., Hillegass M., LyonO B.N., Metzger G.A., Olandese M.L., Pepe D., Silvers G.A., Suresch H.N., Thompson T.N., Trexler C.M., Williams G.E., Williams N.C. &

Williams S.E. (2007). Does size matter for dispersal distance? *Global Ecology and Biogeography*, 16, 415-425.

Jenks G.F. (1967). Visualizing statistical distributions and generalizing process. *Annals of the Association of American Geographers*, 57, 179-179.

Jetz W. & Rahbek C. (2002). Geographic range size and determinants of avian species richness. *Science*, 297, 1548-1551.

Jetz W., Kreft H., Ceballos G. & Mutke J. (2009). Global associations between terrestrial producer and vertebrate consumer diversity. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 276, 269-278.

Johnson C.N., Vernes K. & Payne A. (2005). Demography in relation to population density in two herbivorous marsupials: testing for source–sink dynamics versus independent regulation of population size. *Oecologia*, 143, 70-76.

Joseph L. & Stockwell D. (2002). Climatic modelling of the distribution of some *Pyrrhura* parakeets of northwestern South America with notes on their systematics and special reference to *Pyrrhura caeruleiceps* Todd, 1947. *Ornitologia Neotropical*, 13, 1-8.

Kadmon R., Farber O. & Danin A. (2003). A systematic analysis of factors affecting the performance of climatic envelope models. *Ecological Applications*, 13, 853-867.

Kadmon R., Farber O. & Danin A. (2004). Effect of roadside bias on the accuracy of predictive maps produced by bioclimatic models. *Ecological Applications*, 14, 401-413.

Karl J.W., Svancara L.K., Heglund P.J., Wright N.M. & Scott J.M. (2002). Species commonness and the accuracy of habitat-relationship models. In: *Predicting Species Occurrences: Issues of Accuracy and Scale* (eds. Scott JM, Heglund PJ, Morrison ML, Haufler JB, Raphael MG, Wall WA & Samson FB). Island Press Washington, pp. 573-580.

Keil P., Dziock F. & Storch D. (2008). Geographical patterns of hoverfly (Diptera, Syrphidae) functional groups in Europe: inconsistency in environmental correlates and latitudinal trends. *Ecological Entomology*, 33, 748-757.

Keith D.A., Akçakaya H.R., Thuiller W., Midgley G.F., Pearson R.G., Phillips S.J., Regan H.M., Araújo M.B. & Rebelo T.G. (2008). Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*, 4, 560-563.

Keitt T.H., Bjørnstad O.N., Dixon P.M. & Citron-Pousty S. (2002). Accounting for spatial pattern when modeling organism-environment interactions. *Ecography*, 25, 616-625.

Kelly C.K., Bowler M.G., Pybus O. & Harvey P.H. (2008). Phylogeny, niches, and relative abundance in natural communities. *Ecology*, 89, 962-970.

Kershaw M., Mace G.M. & Williams P.H. (1995). Threatened status, rarity and diversity as alternative selection measures for protected areas: a test using Afrotropical antelopes. *Conservation Biology*, 9, 324-334.

Kéry M. (2002). Inferring the absence of a species—a case study of snakes. *Journal Of Wildlife Management*, 66, 330-338.

Kissling W.D., Field R. & Böhning-Gaese K. (2008). Spatial patterns of woody plant and bird diversity: functional relationships or environmental effects? *Global Ecology and Biogeography*, 17, 327-339.

Kivinen S., Luoto M., Kuussaari M. & Helenius J. (2006). Multi-species richness of boreal agricultural landscapes: effects of climate, biotope, soil and geographical location. *Journal of Biogeography*, 33, 862-875.

Kivinen S., Luoto M., Kuussaari M. & Saarinen K.M. (2007). Effects of land cover and climate on species richness of butterflies in boreal agricultural landscapes. *Agriculture Ecosystems & Environment*, 122, 453-460.

Klar N., Fernández N., Kramer-Schadt S., Herrmann M., Trinzen M., Büttner I. & Niemitz C. (2008). Habitat selection models for European wildcat conservation. *Biological Conservation*, 141, 308-319.

Knouft J.H., Losos J.B., Glor R.E. & Kolbe J.J. (2006). Phylogenetic analysis of the evolution of the niche in lizards of the *Anolis sagrei* group. *Ecology*, 87, S29-S38.

Körner C. (2007). The use of 'altitude' in ecological research. *Trends In Ecology & Evolution*, 22, 569-574.

Kozak K.H., Graham C.H. & Wiens J.J. (2008). Integrating GIS-based environmental data into evolutionary biology. *Trends In Ecology & Evolution*, 23, 141-148.

Kraft N.J.B., Cornwell W.K., Webb C.O. & Ackerly D.D. (2007). Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *The American Naturalist*, 170, 271-283.

Kreuzer M.P. & Huntly N.J. (2003). Habitat-specific demography: evidence for source-sink population structure in a mammal, the pika. *Oecologia*, 134, 343-349.

Kupfer J.A. & Farris C.A. (2007). Incorporating spatial non-stationarity of regression coefficients into predictive vegetation models. *Landscape Ecology*, 22, 837-852.

Kuussaari M., Heliölä J., Luoto M. & Pöyry J. (2007). Determinants of local species richness of diurnal Lepidoptera in boreal agricultural landscapes. *Agriculture Ecosystems & Environment*, 122, 366-376.

La Sorte F.A., Lee T.M., Wilman H. & Jetz W. (2009). Disparities between observed and predicted impacts of climate change on winter bird assemblages. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 276, 3167-3174.

Larsen T.B. (1990). *The Butterflies of Egypt*. The American University Press, Cairo.

Leathwick J.R. & Austin M.P. (2001). Competitive interactions between tree species in New Zealand's old-growth indigenous forests. *Ecology*, 82, 2560-2573.

Lee T.M., Sodhi N.S. & Prawiradilaga D.M. (2007). The importance of protected areas for the forest and endemic avifauna of Sulawesi (Indonesia). *Ecological Applications*, 17, 1727-1741.

Legendre P. (1993). Spatial autocorrelation: trouble or new paradigm? *Ecology*, 74, 1659-1673.

Leibold M.A. (1995). The niche concept revisited: mechanistic models and community context. *Ecology*, 76, 1371-1382.

Leibold M.A. (2008). Return of the niche. *Nature*, 454, 39-41.

Leibold M.A. & McPeek M.A. (2006). Coexistence of the niche and neutral perspectives in community ecology. *Ecology*, 87, 1399-1410.

Lennon J.J. (2000). Red-shifts and red herrings in geographical ecology. *Ecography*, 23, 101-113.

Lester S.E., Ruttenberg B.I., Gaines S.D. & Kinlan B.P. (2007). The relationship between dispersal ability and geographic range size. *Ecology Letters*, 10, 745-758.

Levinsky I., Skov F., Svenning J.C. & Rahbek C. (2007). Potential impacts of climate change on the distributions and diversity patterns of European mammals. *Biodiversity and Conservation*, 16, 3803-3816.

Lichstein J.W., Simons T.R., Shriner S.A. & Franzreb K.E. (2002). Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs*, 72, 445-463.

Linares-Palomino R. & Kessler M. (2009). The role of dispersal ability, climate and spatial separation in shaping biogeographical patterns of phylogenetically distant plant groups in seasonally dry Andean forests of Bolivia. *Journal of Biogeography*, 36, 280-290.

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

Lobo J.M., Lumaret J.-P. & Jay-Robert P. (2002). Modelling the species richness distribution of French dung beetles (Coleoptera, Scarabaeidae) and delimiting the predictive capacity of different groups of explanatory variables. *Global Ecology and Biogeography*, 11, 265-277.

Lobo J.M., Jiménez-Valverde A. & Real R. (2008). AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 17, 145-151.

Loiselle B.A., Howell C.A., Graham C.H., Goerck J.M., Brooks T., Smith K.G. & Williams P.H. (2003). Avoiding pitfalls of using species distribution models in conservation planning. *Conservation Biology*, 17, 1591-1600.

Losos J.B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, 11, 995-1003.

Losos J.B., Leal M., Glor R.E., de Queiroz K., Hertz P.E., Schettino L.R., Lara A.C., Jackman T.R. & Larson A. (2003). Niche lability in the evolution of a Caribbean lizard community. *Nature*, 424, 542-545.

Loyn R.H., McNabb E.G., Volodina L. & Willig R. (2001). Modelling landscape distributions of large forest owls as applied to managing forests in north-east Victoria, Australia. *Biological Conservation*, 97, 361-376.

Loyola R.D., Kubota U. & Lewinsohn T.M. (2007). Endemic vertebrates are the most effective surrogates for identifying conservation priorities among Brazilian ecoregions. *Diversity and Distributions*, 13, 389-396.

Luoto M., Pöyry J., Heikkinen R.K. & Saarinen K. (2005). Uncertainty of bioclimate envelope models based on the geographical distribution of species. *Global Ecology and Biogeography*, 14, 575-584.

Lütolf M., Kienast F. & Guisan A. (2006). The ghost of past species occurrence: improving species distribution models for presence-only data. *Journal of Applied Ecology*, 43, 802-815.

MacArthur R.H. (1972). *Geographical Ecology*. Harper & Row, New York.

MacKenzie D.I., Nichols J.D., Lachman G.B., Droege S., Royle J.A. & Langtimm C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83, 2248-2255.

Mackey B.G. & Lindenmayer D.B. (2001). Towards a hierarchical framework for modelling the spatial distribution of animals. *Journal of Biogeography*, 28, 1147-1166.

Maddison W.P. & Maddison D.R. (2007). Mesquite: a modular system for evolutionary analysis. Version 2.01. URL http://mesquiteproject.org.

Manel S., Dias J.M., Buckton S.T. & Ormerod S.J. (1999a). Alternative methods for predicting species distribution: an illustration with Himalayan river birds. *Journal of Applied Ecology,* 36, 734-747.

Manel S., Dias J.M. & Ormerod S.J. (1999b). Comparing discriminant analysis, neural networks and logistic regression for predicting species distributions: a case study with a Himalayan river bird. *Ecological Modelling*, 120, 337-347.

Manel S., Williams H.C. & Ormerod S.J. (2001). Evaluating presence–absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology*, 38, 921-931.

Margules C.R. & Pressey R.L. (2000). Systematic conservation planning. *Nature*, 405, 243-253.

Marshall A.J. (2009). Are montane forests demographic sinks for Bornean white-bearded gibbons *Hylobates albibarbis*? *Biotropica*, 41, 257-267.

Martin T.G., Wintle B.A., Rhodes J.R., Kuhnert P.M., Field S.A., Low-Choy S.J., Tyre A.J. & Possingham H.P. (2005). Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecology Letters*, 8, 1235-1246.

Martínez-Meyer E. & Peterson A.T. (2006). Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition. *Journal of Biogeography*, 33, 1779-1789.

Martínez-Meyer E., Peterson A.T. & Hargrove W.W. (2004a). Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecology And Biogeography*, 13, 305-314.

Martínez-Meyer E., Townsend Peterson A. & Hargrove W.W. (2004b). Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecology and Biogeography*, 13, 305-314.

Martins E.P. (2004). COMPARE, version 4.6b. Computer programs for the statistical analysis of comparative data. URL http://compare.bio.indiana.edu/.

May R.M. (1997). The dimensions of life on earth. In: *Nature and Human Society* (ed. Raven PH). National Academy Press Washington D.C., pp. 30-45.

McCauley S.J. (2006). The effects of dispersal and recruitment limitation on community structure of odonates in artificial ponds. *Ecography*, 29, 585-595.

McCullagh P. & Nelder J.A. (1989). *Generalized Linear Models*. Chapman & Hall, London.

McGill B.J. (2003). A test of the unified neutral theory of biodiversity. *Nature*, 422, 881-885.

McPherson J.M. & Jetz W. (2007). Effects of species' ecology on the accuracy of distribution models. *Ecography*, 30, 135-151.

McPherson J.M., Jetz W. & Rogers D.J. (2004). The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? *Journal of Applied Ecology*, 41, 811-823.

Menéndez R., González-Megías A., Collingham Y., Fox R., Roy D.B., Ohlemüller R. & Thomas C.D. (2007). Direct and indirect effects of climate and habitat factors on butterfly diversity. *Ecology*, 88, 605-611.

Meynard C.N. & Quinn J.F. (2007). Predicting species distributions: a critical comparison of the most common statistical models using artificial species. *Journal of Biogeography*, 34, 1455-1469.

Miles L., Grainger A. & Phillips O. (2004). The impact of global climate change on tropical forest biodiversity in Amazonia. *Global Ecology and Biogeography*, 13, 553-565.

Mitchell M.S., Lancia R.A. & Gerwin J.A. (2001). Using landscape-level data to predict the distribution of birds on a managed forest: effects of scale. *Ecological Applications*, 11, 1692-1708.

Mitikka V., Heikkinen R.K., Luoto M., Araújo M.B., Saarinen K., Pöyry J. & Fronzek S. (2008). Predicting range expansion of the map butterfly in Northern Europe using bioclimatic models. *Biodiversity and Conservation*, 17, 623-641.

Moisen G.G. & Frescino T.S. (2002). Comparing five modelling techniques for predicting forest characteristics. *Ecological Modelling*, 157, 209-225.

Moore K.A. (2009). Fluctuating patch boundaries in a native annual forb: the roles of niche and dispersal limitation. *Ecology*, 90, 378-387.

Moore R.P., Robinson W.D., Lovette I.J. & Robinson T.R. (2008). Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecology Letters*, 11, 960-968.

Mullarney K., Svensson L., Zetterström D. & Grant P.J. (1999). *Bird Guide*. HarperCollins, London.

Munguía M., Peterson A.T. & Sánchez-Cordero V. (2008). Dispersal limitation and geographical distributions of mammal species. *Journal of Biogeography*, 35, 1879-1887.

Murphy H.T. & Lovett-Doust J. (2007). Accounting for regional niche variation in habitat suitability models. *Oikos,* 116, 99-110.

Mustin K., Benton T.G., Dytham C. & Travis J.M.J. (2009). The dynamics of climate-induced range shifting; perspectives from simulation modelling. *Oikos*, 118, 131-137.

Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. & Kent J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858.

Nix H. (1986). A biogeographic analysis of Australian elapid snakes. In: *Atlas of Elapid Snakes of Australia* (ed. Longmore R). Australian Government Publishing Service Canberra, pp. 4-15.

Nogués-Bravo D. & Araújo M.B. (2006). Species richness, area and climate correlates. *Global Ecology and Biogeography*, 15, 452-460.

Nogués-Bravo D., Araújo M.B., Romdal T. & Rahbek C. (2008a). Scale effects and human impact on the elevational species richness gradients. *Nature*, 453, 216-219.

Nogués-Bravo D., Rodríguez J., Hortal J., Batra P. & Araújo M.B. (2008b). Climate change, humans, and the extinction of the woolly mammoth. *PLoS Biology*, 6, 685-692.

Nyári A., Ryall C. & Peterson A.T. (2006). Global invasive potential of the house crow *Corvus splendens* based on ecological niche modelling. *Journal of Avian Biology*, 37, 306-311.

Ordnance Survey (2009). Ordnance survey digital terrain model. URL http://www.ordnancesurvey.co.uk/oswebsite/products/landformprofile/.

Orme C.D.L., Davies R.G., Burgess M., Eigenbrod F., Pickup N., Olson V.A., Webster A.J., Ding T.-S., Rasmussen P.C., Ridgely R.S., Stattersfield A.J., Bennett P.M., Blackburn T.M., Gaston K.J. & Owens I.P.F. (2005). Global hotspots of species richness are not congruent with endemism or threat. *Nature*, 436, 1016-1019.

Osborn D.J. & Helmy I. (1980). The contemporary land mammals of Egypt (including Sinai). *Fieldiana Zoology*, 5, 1-579.

Osborne P.E., Alonso J.C. & Bryant R.G. (2001). Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. *Journal of Applied Ecology*, 38, 458-471.

Osborne P.E., Foody G.M. & Suárez-Seoane S. (2007). Non-stationarity and local approaches to modelling the distributions of wildlife. *Diversity and Distributions*, 13, 313-323.

Owen J. (1991). *Ecology of a Garden*. Cambridge University Press, Cambridge.

Özesmi U. & Mitsch W.J. (1997). A spatial habitat model for the marsh-breeding red-winged blackbird (*Agelaius phoeniceus* L.) in coastal Lake Erie wetlands. *Ecological Modelling*, 101, 139-152.

Page R.D.M. (1996). TreeView: an application to display phylogenetic trees on personal computers. *Computer Applications in the Biosciences*, 12, 357-358.

Papeş M. & Gaubert P. (2007). Modelling ecological niches from low numbers of occurrences: assessment of the conservation status of poorly known viverrids (Mammalia, Carnivora) across two continents. *Diversity and Distributions*, 13, 890-902.

Park T. (1948). Experimental studies of interspecies competition. 1. Competition between populations of the flour beetles, *Tribolium confusum* Duval and *Tribolium castaneum* Herbst. *Ecological Monographs*, 18, 265-307.

Parmesan C. & Yohe G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37-42.

Parolo G., Rossi G. & Ferrarini A. (2008). Toward improved species niche modelling: *Arnica montana* in the Alps as a case study. *Journal of Applied Ecology*, 45, 1410-1418.

Pawar S., Koo M.S., Kelley C., Ahmed M.F., Chaudhuri S. & Sarkay S. (2007). Conservation assessment and prioritization of areas in Northeast India: Priorities for amphibians and reptiles. *Biological Conservation*, 136, 346-361.

Peach W., du Feu C. & McMeeking J. (1995). Site tenacity and survival rates of Wrens *Troglodytes troglodytes* and Treecreepers *Certhia familiaris* in a Nottinghamshire wood. *Ibis*, 137, 497-507.

Pearce J. & Ferrier S. (2000a). Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling,* 133, 225-245.

Pearce J. & Ferrier S. (2000b). An evaluation of alternative algorithms for fitting species distribution models using logistic regression. *Ecological Modelling*, 128, 127-147.

Pearce J., Ferrier S. & Scotts D. (2001). An evaluation of the predictive performance of distributional models for flora and fauna in north-east New South Wales. *Journal of Environmental Management*, 62, 171-184.

Pearman P.B., Guisan A., Broennimann O. & Randin C.F. (2008a). Niche dynamics in space and time. *Trends In Ecology & Evolution*, 23, 149-158.

Pearman P.B., Randin C.F., Broennimann O., Vittoz P., van der Knaap W.O., Engler R., Le Lay G., Zimmermann N.E. & Guisan A. (2008b). Prediction of plant species distributions across six millennia. *Ecology Letters*, 11, 357-369.

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

Pearson R.G. & Dawson T.P. (2004). Bioclimate envelope models: what they detect and what they hide - response to Hampe (2004). *Global Ecology and Biogeography*, 13, 471-473.

Pearson R.G., Dawson T.P. & Liu C. (2004). Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography*, 27, 285-298.

Pearson R.G., Thuiller W., Araújo M.B., Martínez-Meyer E., Brotons L., McClean C., Miles L., Segurado P., Dawson T.P. & Lees D.C. (2006). Model-based uncertainty in species range prediction. *Journal Of Biogeography*, 33, 1704-1711.

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

Pech P., Fric Z., Konvička M. & Zrzavý J. (2004). Phylogeny of *Maculinea* blues (Lepidoptera : Lycaenidae) based on morphological and ecological characters: evolution of parasitic myrmecophily. *Cladistics*, 20, 362-375.

Peery M.Z., Beissinger S.R., House R.F., Bérubé M., Hall L.A., Sellas A. & Palsbøll P.J. (2008). Characterizing source-sink dynamics with genetic parentage assignments. *Ecology*, 89, 2746-2759.

Penman T.D., Mahony M.J., Towerton A.L. & Lemckert F.L. (2005). Bioclimatic analysis of disjunct populations of the giant burrowing frog, *Heleioporus australiacus*. *Journal of Biogeography*, 32, 397-405.

Perry M. & Hollis D. (2006). The generation of monthly gridded datasets for a range of climatic variables over the United Kingdom. URL http://www.metoffice.gov.uk/climatechange/science/downloads/Monthly_gridded_datasets_UK.pdf.

Petersen I., Masters Z., Hildrew A.G. & Ormerod S.J. (2004). Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Applied Ecology*, 41, 934-950.

Peterson A.T. (2003). Projected climate change effects on Rocky Mountain and Great Plains birds: generalities of biodiversity consequences. *Global Change Biology*, 9, 647-655.

Peterson A.T. (2006). Uses and requirements of ecological niche models and related distributional models. *Biodiversity Informatics*, 3, 59-72.

Peterson A.T. & Cohoon K.P. (1999). Sensitivity of distributional prediction algorithms to geographic data completeness. *Ecological Modelling*, 117, 159-164.

Peterson A.T. & Holt R.D. (2003). Niche differentiation in Mexican birds: using point occurrences to detect ecological innovation. *Ecology Letters*, 6, 774-782.

Peterson A.T. & Kluza D.A. (2003). New distributional modelling approaches for gap analysis. *Animal Conservation*, 6, 47-54.

Peterson A.T. & Nakazawa Y. (2008). Environmental data sets matter in ecological niche modelling: an example with *Solenopsis invicta* and *Solenopsis richteri*. *Global Ecology and Biogeography*, 17, 135-144.

Peterson A.T. & Robins C.R. (2003). Using ecological-niche modeling to predict barred owl invasions with implications for spotted owl conservation. *Conservation Biology*, 17, 1161-1165.

Peterson A.T. & Shaw J. (2003). *Lutzomyia* vectors for cutaneous leishmaniasis in Southern Brazil: ecological niche models, predicted geographic distributions, and climate change effects. *International Journal for Parasitology*, 33, 919-931.

Peterson A.T. & Vieglais D.A. (2001). Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *Bioscience*, 51, 363-371.

Peterson A.T., Navarro-Sigüenza A.G. & Benítez-Díaz H. (1998). The need for continued scientific collecting; a geographic analysis of Mexican bird specimens. *Ibis*, 140, 288-294.

Peterson A.T., Soberón J. & Sánchez-Cordero V. (1999). Conservatism of ecological niches in evolutionary time. *Science*, 285, 1265-1267.

Peterson A.T., Sánchez-Cordero V., Soberón J., Bartley J., Buddemeier R.W. & Navarro-Sigüenza A.G. (2001). Effects of global climate change on geographic distributions of Mexican Cracidae. *Ecological Modelling*, 144, 21-30.

Peterson A.T., Ball L.G. & Cohoon K.P. (2002a). Predicting distributions of Mexican birds using ecological niche modelling methods. *Ibis*, 144, E27-E32.

Peterson A.T., Ortega-Huerta M.A., Bartley J., Sánchez-Cordero V., Soberón J., Buddemeier R.H. & Stockwell D.R.B. (2002b). Future projections for Mexican faunas under global climate change scenarios. *Nature*, 416, 626-629.

Peterson A.T., Sánchez-Cordero V., Ben Beard C. & Ramsey J.M. (2002c). Ecologic niche modeling and potential reservoirs for Chagas disease, Mexico. *Emerging Infectious Diseases*, 8, 662-667.

Peterson A.T., Sánchez-Cordero V., Martínez-Meyer E. & Navarro-Sigüenza A.G. (2006). Tracking population extirpations via melding ecological niche modeling with land-cover information. *Ecological Modelling*, 195, 229-236.

Peterson A.T., Papeş M. & Eaton M. (2007). Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography*, 30, 550-560.

Peterson A.T., Barve N., Bini L.M., Diniz-Filho J.A.F., Jiménez-Valverde A., Lira-Noriega A., Lobo J., Maher S., de Marco P., Martínez-Meyer E., Nakazawa Y. & Soberón J. (2009). The climate envelope may not be empty. *Proceedings of the National Academy of Sciences of the United States of America*, 106, E47-E47.

Pfennig D.W., Harcombe W.R. & Pfennig K.S. (2001). Frequency-dependent Batesian mimicry. *Nature*, 410, 323-323.

Pfennig D.W., Harper G.R., Brumo A.F., Harcombe W.R. & Pfennig K.S. (2007). Population differences in predation on Batesian mimics in allopatry with their model: selection against mimics is strongest when they are common. *Behavioral Ecology and Sociobiology*, 61, 505-511.

Phillips S.J., Dudík M. & Schapire R.E. (2004). A maximum entropy approach to species distribution modelling. In: *Proceedings of the 21st International Conference on Machine Learning*. ACM Press New York, pp. 655-662.

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

Pierce N.E., Braby M.F., Heath A., Lohman D.J., Mathew J., Rand D.B. & Travassos M.A. (2002). The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). *Annual Review of Entomology*, 47, 733-771.

Pineda E. & Lobo J.M. (2009). Assessing the accuracy of species distribution models to predict amphibian species richness patterns. *Journal of Animal Ecology*, 78, 182-190.

Pinto M.P., Diniz-Filho J.A.F., Bini L.M., Blamires D. & Rangel T.F.L.V.B. (2008). Biodiversity surrogate groups and conservation priority areas: birds of the Brazilian Cerrado. *Diversity and Distributions*, 14, 78-86.

Pollock D.D., Watt W.B., Rashbrook V.K. & Iyengar E.V. (1998). Molecular phylogeny for *Colias* butterflies and their relatives (Lepidoptera: Pieridae). *Annals of the Entomological Society of America*, 91, 524-531.

Post E. & Pedersen C. (2008). Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 12353-12358.

Pöyry J., Luoto M., Heikkinen R.K. & Saarinen K. (2008). Species traits are associated with the quality of bioclimatic models. *Global Ecology and Biogeography*, 17, 403-414.

Pressey R.L., Humphries C.J., Margules C.R., Vanewright R.I. & Williams P.H. (1993). Beyond opportunism: Key principles for systematic reserve selection. *Trends In Ecology & Evolution*, 8, 124-128.

Prinzing A., Durka W., Klotz S. & Brandl R. (2001). The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 268, 2383-2389.

Prudic K.L. & Oliver J.C. (2008). Once a Batesian mimic, not always a Batesian mimic: mimic reverts back to ancestral phenotype when the model is absent. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 275, 1125-1132.

Prys-Jones, O.E. & Corbet S.A. (1991). *Naturalists' Handbooks 6: Bumblebees*. Richmond Publishing, Oxford.

Pulliam H.R. (1988). Sources, sinks, and population regulation. *The American Naturalist*, 132, 652-661.

Pulliam H.R. (2000). On the relationship between niche and distribution. *Ecology Letters*, 3, 349-361.

Qian H. (2007). Relationships between plant and animal species richness at a regional scale in China. *Conservation Biology*, 21, 937-944.

Qian H. & Ricklefs R.E. (2000). Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature*, 407, 180-182.

Qian H. & Ricklefs R.E. (2007). A latitudinal gradient in large-scale beta diversity for vascular plants in North America. *Ecology Letters*, 10, 737-744.

Qian H., Wang X., Wang S. & Li Y. (2007). Environmental determinants of amphibian and reptile species richness in China. *Ecography*, 30, 471-482.

Quinn R.M., Gaston K.J. & Roy D.B. (1998). Coincidence in the distributions of butterflies and their foodplants. *Ecography*, 21, 279-288.

R Development Core Team (2004). R: A language and environment for statistical computing. URL http://www.r-project.org/.

Raes N. & ter Steege H. (2007). A null-model for significance testing of presence-only species distribution models. *Ecography*, 30, 727-736.

Raes N., Roos M.C., Ferry Slik J.W., van Loon E.E. & ter Steege H. (2009). Botanical richness and endemicity patterns of Borneo derived from species distribution models. *Ecography*, 32, 180-192.

Rahbek C., Gotelli N.J., Colwell R.K., Entsminger G.L., Rangel T.F.L.V.B. & Graves G.R. (2007). Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 274, 165-174.

Randin C.F., Dirnböck T., Dullinger S., Zimmermann N.E., Zappa M. & Guisan A. (2006). Are niche-based species distribution models transferable in space? *Journal of Biogeography*, 33, 1689-1703.

Randin C.F., Engler R., Normand S., Zappa M., Zimmermann N.E., Pearman P.B., Vittoz P., Thuiller W. & Guisan A. (2009). Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology*, 15, 1557-1569.

Raxworthy C.J., Martínez-Meyer E., Horning N., Nussbaum R.A., Schneider G.E., Ortega-Huerta M.A. & Peterson A.T. (2003). Predicting distributions of known and unknown reptile species in Madagascar. *Nature*, 426, 837-841.

Raxworthy C.J., Pearson R.G., Rabibisoa N., Rakotondrazafy A.M., Ramanamanjato J.-B., Raselimanana A.P., Wu S., Nussbaum R.A. & Stone D.A. (2008a). Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. *Global Change Biology*, 14, 1703-1720.

Raxworthy C.J., Pearson R.G., Zimkus B.M., Reddy S., Deo A.J., Nussbaum R.A. & Ingram C.M. (2008b). Continental speciation in the tropics: contrasting biogeographic patterns of divergence in the *Uroplatus* leaf-tailed gecko radiation of Madagascar. *Journal of Zoology*, 275, 423-440.

Reddy S. & Dávalos L.M. (2003). Geographical sampling bias and its implications for conservation priorities in Africa. *Journal Of Biogeography*, 30, 1719-1727.

Reilly J., Stone P.H., Forest C.E., Webster M.D., Jacoby H.D. & Prinn R.G. (2001). Uncertainty and climate change assessments. *Science*, 293, 430-433.

Rice N.H., Martínez-Meyer E. & Peterson A.T. (2003). Ecological niche differentiation in the *Aphelocoma* jays: a phylogenetic perspective. *Biological Journal of the Linnean Society*, 80, 369-383.

Richards C.L., Carstens B.C. & Knowles L.L. (2007). Distribution modelling and statistical phylogeography: an integrative framework for generating and testing alternative biogeographical hypotheses. *Journal of Biogeography*, 34, 1833-1845.

Richardson B.J., Zabka M., Gray M.R. & Milledge G. (2006). Distributional patterns of jumping spiders (Araneae: Salticidae) in Australia. *Journal of Biogeography*, 33, 707-719.

Ritchie E.G., Martin J.K., Johnson C.N. & Fox B.J. (2009). Separating the influences of environment and species interactions on patterns of distribution and abundance: competition between large herbivores. *Journal of Animal Ecology*, 78, 724-731.

Rodríguez J.P., Brotons L., Bustamante J. & Seoane J. (2007). The application of predictive modelling of species distribution to biodiversity conservation. *Diversity and Distributions*, 13, 243-251.

Ruggiero A. & Hawkins B.A. (2008). Why do mountains support so many species of birds? *Ecography*, 31, 306-315.

Ruxton G.D., Sherratt T.N. & Speed M.P. (2004). *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals & Mimicry*. Oxford University Press, Oxford.

Ryti R.T. (1992). Effect of the focal taxon on the selection of nature reserves. *Ecological Applications*, 2, 404-410.

Saetersdal M., Birks H.J.B. & Peglar S.M. (1998). Predicting changes in Fennoscandian vascular-plant species richness as a result of future climatic change. *Journal of Biogeography*, 25, 111-122.

Sánchez-Fernández D., Lobo J.M., Abellán P., Ribera I. & Millán A. (2008). Bias in freshwater biodiversity sampling: the case of Iberian water beetles. *Diversity and Distributions*, 14, 754-762.

Sánchez-Flores E. (2007). GARP modeling of natural and human factors affecting the potential distribution of the invasives *Schismus arabicus* and *Brassica tournefortii* in 'El Pinacate y Gran Desierto de Altar' Biosphere Reserve. *Ecological Modelling*, 204, 457-474.

Sanderson E.W., Jaiteh M., Levy M.A., Redford K.H., Wannebo A.V. & Woolmer G. (2002). The human footprint and the last of the wild. *BioScience*, 52, 891-904.

Sastre P. & Lobo J.M. (2009). Taxonomist survey biases and the unveiling of biodiversity patterns. *Biological Conservation*, 142, 462-467.

Schmidt M., König K. & Müller J.V. (2008). Modelling species richness and life form composition in Sahelian Burkina Faso with remote sensing data. *Journal of Arid Environments*, 72, 1506-1517.

Schouten M.A., Verweij P.A., Barendregt A., Kleukers R., Kalkman V.J. & de Ruiter P.C. (2009). Determinants of species richness patterns in the Netherlands across multiple taxonomic groups. *Biodiversity and Conservation*, 18, 203-217.

Schwartz M.W., Iverson L.R., Prasad A.M., Matthews S.N. & O'Connor R.J. (2006). Predicting extinctions as a result of climate change. *Ecology*, 87, 1611-1615.

Schweiger O., Settele J., Kudrna O., Klotz S. & Kühn I. (2008). Climate change can cause spatial mismatch of trophically interacting species. *Ecology*, 89, 3472-3479.

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

Segurado P., Araújo M.B. & Kunin W.E. (2006). Consequences of spatial autocorrelation for niche-based models. *Journal of Applied Ecology*, 43, 433-444.

Seo C., Thorne J.H., Hannah L. & Thuiller W. (2009). Scale effects in species distribution models: implications for conservation planning under climate change. *Biology Letters*, 5, 39-43.

Seoane J., Carrascal L.M., Alonso C.L. & Palomino D. (2005). Species-specific traits associated to prediction errors in bird habitat suitability modelling. *Ecological Modelling*, 185, 299-308.

Sharrock J.T.R. (1976). *The Atlas of Breeding Birds in Britain and Ireland.* T. & A. D. Poyser, Berkhamsted.

Skelly D.K., Joseph L.N., Possingham H.P., Freidenburg L.K., Farrugia T.J., Kinnison M.T. & Hendry A.P. (2007). Evolutionary responses to climate change. *Conservation Biology*, 21, 1353-1355.

Snyder R.E. & Chesson P. (2003). Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. *Ecology Letters*, 6, 301-309.

Soberón J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, 10, 1115-1123.

Soberón J. & Peterson A.T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, 2, 1-10.

Soberón J.M., Llorente J.B. & Oñate L. (2000). The use of specimen-label databases for conservation purposes: an example using Mexican Papilionid and Pierid butterflies. *Biodiversity and Conservation*, 9, 1441-1466.

Solano E. & Feria T.P. (2007). Ecological niche modeling and geographic distribution of the genus *Polianthes* L. (Agavaceae) in Mexico: using niche modeling to improve assessments of risk status. *Biodiversity and Conservation*, 16, 1885-1900.

Soria-Auza R.W. & Kessler M. (2008). The influence of sampling intensity on the perception of the spatial distribution of tropical diversity and endemism: a case study of ferns from Bolivia. *Diversity and Distributions*, 14, 123-130.

Southgate R., Paltridge R., Masters P. & Carthew S. (2007). Bilby distribution and fire: a test of alternative models of habitat suitability in the Tanami Desert, Australia. *Ecography*, 30, 759-776.

Steiner F.M., Schlick-Steiner B.C., VanDerWal J., Reuther K.D., Christian E., Stauffer C., Suarez A.V., Williams S.E. & Crozier R.H. (2008). Combined modelling of distribution and niche in invasion biology: a case study of two invasive *Tetramorium* ant species. *Diversity and Distributions,* 14, 538-545.

Stockwell D.R.B. & Noble I.R. (1992). Induction of sets of rules from animal distribution data: a robust and informative method of data analysis. *Mathematics and Computers in Simulation,* 33, 385-390.

Stockwell D. & Peters D. (1999). The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographical Information Science*, 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.

Stubbs A. & Falk S. (2002). *British Hoverflies: An Illustrated Identification Guide*. British Entomological and Natural History Society, Reading.

Svenning J.-C. & Skov F. (2004). Limited filling of the potential range in European tree species. *Ecology Letters*, 7, 565-573.

Svenning J.-C., Normand S. & Skov F. (2008). Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. *Ecography*, 31, 316-326.

Syartinilia & Tsuyuki S. (2008). GIS-based modeling of Javan Hawk-Eagle distribution using logistic and autologistic regression models. *Biological Conservation,* 141, 756-769.

Terribile L.C., Diniz-Filho J.A.F., Rodríguez M.Á. & Rangel T.F.L.V.B. (2009). Richness patterns, species distributions and the principle of extreme deconstruction. *Global Ecology and Biogeography*, 18, 123-136.

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

Thomson J.R., Fleishman E., Mac Nally R. & Dobkin D.S. (2007). Comparison of predictor sets for species richness and the number of rare species of butterflies and birds. *Journal of Biogeography*, 34, 90-101.

Thorn J.S., Nijman V., Smith D. & Nekaris K.A.I. (2009). Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: *Nycticebus*). *Diversity and Distributions*, 15, 289-298.

Thuiller W. (2003). BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, 9, 1353-1362.

Thuiller W. (2007). Biodiversity: Climate change and the ecologist. *Nature*, 448, 550-552.

Thuiller W., Araújo M.B., Pearson R.G., Whittaker R.J., Brotons L. & Lavorel S. (2004a). Uncertainty in predictions of extinction risk. *Nature*, 430.

Thuiller W., Brotons L., Araújo M.B. & Lavorel S. (2004b). Effects of restricting environmental range of data to project current and future species distributions. *Ecography*, 27, 165-172.

Thuiller W., Lavorel S., Araújo M.B., Sykes M.T. & Prentice I.C. (2005a). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 8245-8250.

Thuiller W., Richardson D.M., Pyšek P., Midgley G.F., Hughes G.O. & Rouget M. (2005b). Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology*, 11, 2234-2250.

Thuiller W., Richardson D.M., Rouget M., Procheş Ş. & Wilson J.R.U. (2006). Interactions between environment, species traits, and human uses describe patterns of plant invasions. *Ecology*, 87, 1755-1769.

Tilman D. (1976). Ecological competition between algae: experimental confirmation of resource-based competition theory. *Science*, 192, 463-465.

Tilman D. (2004). Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 10854-10861.

Titeux N., Dufrene M., Radoux J., Hirzel A.H. & Defourny P. (2007). Fitness-related parameters improve presence-only distribution modelling for conservation practice: The case of the red-backed shrike. *Biological Conservation*, 138, 207-223.

Tognelli M.F. & Kelt D.A. (2004). Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. *Ecography*, 27, 427-436.

Traba J., de la Morena E.L.G., Morales M.B. & Suárez F. (2007). Determining high value areas for steppe birds in Spain: hot spots, complementarity and the efficiency of protected areas. *Biodiversity and Conservation*, 16, 3255-3275.

Tsoar A., Allouche O., Steinitz O., Rotem D. & Kadmon R. (2007). A comparative evaluation of presence-only methods for modelling species distribution. *Diversity and Distributions*, 13, 397-405.

Turner J.R.G., Gatehouse C.M. & Corey C.A. (1987). Does solar energy control organic diversity? Butterflies, moths and the British climate. *Oikos*, 48, 195-205.

Uehara-Prado M., Brown K.S. & Freitas A.V.L. (2007). Species richness, composition and abundance of fruit-feeding butterflies in the Brazilian Atlantic Forest: comparison between a fragmented and a continuous landscape. *Global Ecology and Biogeography*, 16, 43-54.

van Jaarsveld A.S., Freitag S., Chown S.L., Muller C., Koch S., Hull H., Bellamy C., Krüger M., Endrödy-Younga S., Mansell M.W. & Scholtz C.H. (1998). Biodiversity assessment and conservation strategies. *Science*, 279, 2106-2108.

van Rensburg B.J., Chown S.L. & Gaston K.J. (2002). Species richness, environmental correlates, and spatial scale: a test using South African birds. *The American Naturalist*, 159, 566-577.

Vandermeer J.H. (1972). Niche theory. *Annual Review of Ecology and Systematics*, 3, 107-132.

VanDerWal J., Shoo L.P., Graham C. & William S.E. (2009a). Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? *Ecological Modelling*, 220, 589-594.

VanDerWal J., Shoo L.P., Johnson C.N. & Williams S.E. (2009b). Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. *The American Naturalist*, 174, 282-291.

Vanreusel W., Maes D. & Van Dyck H. (2007). Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. *Conservation Biology*, 21, 201-212.

Venables W.N. & Ripley B.D. (2002). *Modern Applied Statistics with S*. Springer, Berlin.

Visscher D.R. (2006). GPS measurement error and resource selection functions in a fragmented landscape. *Ecography*, 29, 458-464.

Visser M.E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 275, 649-659.

Wahlberg N., Weingartner E. & Nylin S. (2003). Towards a better understanding of the higher systematics of Nymphalidae (Lepidoptera: Papilionoidea). *Molecular Phylogenetics and Evolution*, 28, 473-484.

Wahlberg N., Braby M.F., Brower A.V.Z., de Jong R., Lee M.-M., Nylin S., Pierce N.E., Sperling F.A.H., Vila R., Warren A.D. & Zakharov E. (2005). Synergistic effects of combining morphological and molecular data in resolving the phylogeny of butterflies and skippers. *Proceedings of the Royal Society of London Series B, Biological Sciences,* 272, 1577-1586.

Walther B.A., Schäffer N., van Niekerk A., Thuiller W., Rahbek C. & Chown S.L. (2007a). Modelling the winter distribution of a rare and endangered migrant, the Aquatic Warbler *Acrocephalus paludicola*. *Ibis*, 149, 701-714.

Walther G.-R., Gritti E.S., Berger S., Hickler T., Tang Z.Y. & Sykes M.T. (2007b). Palms tracking climate change. *Global Ecology and Biogeography*, 16, 801-809.

Watkinson A.R., Lonsdale W.M. & Andrew M.H. (1989). Modelling the population dynamics of an annual plant *Sorghum intrans* in the wet-dry tropics. *Journal Of Ecology*, 77, 162-181.

Watkinson A.R. & Sutherland W.J. (1995). Sources, sinks and pseudo-sinks. *Journal of Animal Ecology,* 64, 126-130.

Webb C.O. (2000). Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *The American Naturalist,* 156, 145-155.

Webb T.J. & Gaston K.J. (2003). On the heritability of geographic range sizes. *The American Naturalist,* 161, 553-566.

Whittaker R.J., Willis K.G. & Field R. (2001). Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, 28, 453-470.

Wieczorek J., Guo Q.G. & Hijmans R.J. (2004). The point-radius method for georeferencing locality descriptions and calculating associated uncertainty. *International Journal of Geographical Information Science,* 18, 745-767.

Wiens J.J. (2008). Commentary on Losos (2008): niche conservatism déjà vu. *Ecology Letters*, 11, 1004-1005.

Wiley E.O., McNyset K.M., Peterson A.T., Robins C.R. & Stewart A.M. (2003). Niche modelling and geographic range predictions in the marine environment using a machine-learning algorithm. *Oceanography*, 16, 120-127.

Williams P.H., Margules C.R. & Hilbert D.W. (2002). Data requirements and data sources for biodiversity priority area selection. *Journal Of Biosciences*, 27, 327-338.

Willis C.G., Ruhfel B., Primack R.B., Miller-Rushing A.J. & Davis C.C. (2008). Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 17029-17033.

Willis S.G., Thomas C.D., Hill J.K., Collingham Y.C., Telfer M.G., Fox R. & Huntley B. (2009). Dynamic distribution modelling: predicting the present from the past. *Ecography*, 32, 5-12.

Wilson D.E. & Reeder D.M. (2005a). Mammal Species of the World. A Taxonomic and Geographic Reference. URL http://www.bucknell.edu/msw3/.

Wilson D.E. & Reeder D.M. (2005b). *Mammal Species of the World: A Taxonomic and Geographic Reference*. 3rd edn. Johns Hopkins University Press, Baltimore.

Wilson K.A., Underwood E.C., Morrison S.A., Klausmeyer K.R., Murdoch W.W., Reyers B., Wardell-Johnson G., Marquet P.A., Rundel P.W., McBride M.F., Pressey R.L., Bode M., Hoekstra J.M., Andelman S., Looker M., Rondinini C., Kareiva P., Shaw M.R. & Possingham H.P. (2007). Conserving biodiversity efficiently: what to do, where, and when. *PLoS Biology*, 5, 1850-1861.

Wintle B.A. & Bardos D.C. (2006). Modeling species–habitat relationships with spatially autocorrelated observation data. *Ecological Applications*, 16, 1945-1958.

Wintle B.A., McCarthy M.A., Parris K.M. & Burgman M.A. (2004). Precision and bias of methods for estimating point survey detection probabilities. *Ecological Applications*, 14, 703-712.

Wintle B.A., Elith J. & Potts J.M. (2005). Fauna habitat modelling and mapping: A review and case study in the Lower Hunter Central Coast region of NSW. *Austral Ecology*, 30, 719-738.

Wisz M.S., Hijmans R.J., Li J., Peterson A.T., Graham C.H. & Guisan A. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, 14, 763-773.

Wootton J.T. (2005). Field parameterization and experimental test of the neutral theory of biodiversity. *Nature*, 433, 309-312.

Zaniewski A.E., Lehmann A. & Overton J.M. (2002). Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecological Modelling*, 157, 261-280.