BIOGEOGRAPHY OF BENT-WING BAT COMPLEX (MINIOPTERUS SCHREIBERSII) (CHIROPTERA: VESPERTILIONIDAE) IN ASIA MINOR AS INFERRED FROM ECOLOGICAL NICHE MODELLING PREDICTIONS

by
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ABSTRACT

In this thesis, ecological niche modelling is used to analyze factors, which affect the current distributions of two morphologically similar, but genetically distinct species; *Miniopterus schreibersii schreibersii* and *M. s. pallidus* in Asia Minor and Thrace. In addition, projections are done for the past and future climatic conditions. The current predictions intend to help to determine variables responsible for the allopatry of *M. s. schreibersii* and *M. s. pallidus*, the projections to the past (the Last Glacial Maximum) aim to provide hints regarding phylogeography of these taxa, and projections to the future intend to assess their vulnerability under the global climate change conditions. The results suggest that *M. s. pallidus*, in comparison to *M. s. schreibersii,* is capable of utilizing a much wider range of climatic conditions. The past projections support earlier suggestions that these species survived the Last Glacial Maximum in the distinct glacial refugia; *M. s. schreibersii* in Thrace and southern Anatolia, and *M. s. pallidus* on the southern coast of the Caspian Sea. Under the climate warming scenarios, distribution of *M. s. schreibersii* is rapidly shrinking, while distribution of *M. s. pallidus* is expanding, replacing the former. As it is not possible to evaluate models' discrimination capacity for other than current conditions, species-specific properties and models' transferability are assessed by projections to already known distributions. *Miniopterus s. schreibersii* distribution is compared with known distributions in Europe. *Miniopterus s. pallidus* distribution in the Last Glacial Maximum is compared with literature. Typically, candidate models, which are used in the projections to future climatic conditions, are selected according to their high AUC values. Projections for *M. s. schreibersii*, however, imply that higher AUC values may not always be a correct indicator for successful projections. Therefore, the future (and the past) projections outcomes should always be treated with extreme caution.

ÖZET

Bu tezde ekolojik niş modellemesi kullanılarak morfolojik olarak benzer ama genetik olarak farklı olan *Miniopterus schreibersii schreibersii* ve *M. s. pallidus* türlerinin, Anadolu'daki ve Trakya'daki dağılımlarını etkileyen faktörler saptanmıştır. Ek olarak, geçmiş ve gelecek iklim koşullarına projeksiyonlar yapılmıştır. Simdiki zaman tahminleri *M. s. schreibersii* ve *M. s. pallidus*’un allopatrik yalıtımından sorumlu değişkenlerin belirlenmesi amacıyla, geçmiş zaman tahminleri (Son Buzul Maksimum) bu taksonların filocoğrafyasına ilişkin ipuçları sağlamak amacıyla, gelecek zaman tahminleri küresel ısınmaya karşı türlerin hassasiyetini belirlemek amacıyla yapılmıştır. Sonuçlar *M. s. pallidus*’un *M. s. schreibersii*’ye kıyasla çok daha geniş iklim koşullarından faydalanabildiğini önermektedir. Geçmiş zaman projeksiyonları, bu iki türün Son Buzul Maksimum dönemini, *M. s. schreibersii*’nin Trakya’da ve güney Anadolu’da, *M. s. pallidus*’un Hazar Denizi’nin güney kıyılarında olmak üzere farklı barınaklarda geçirdiklerini savunan önceki önermeleri desteklemektedir. Küresel ısınma senaryolarında, *M. s. schreibersii*’nin dağılımı hızla daralırken, *M. s. pallidus*’un dağılımı öncekinin yerini alarak genişlemektedir. Şimdiki zaman projeksiyonlarının dışındaki projeksiyonlarda modellerin ayırtedebilme kapasitesini ölçmek mümkün olmadığından, türe özgü nitelikler ve modelin aktarılabilirliği, dağılımı bilinen yerlere projeksiyonlar yapılarak değerlendirilmiştir. *Miniopterus s. schreibersii* dağılımı Avrupa’daki bilinen dağılımla kıyaslanmıştır. *Miniopterus s. pallidus* dağılımı, literatürdeki Son Buzul Maksimum dönemi dağılımı ile kıyaslanmıştır. Tipik olarak, gelecek zaman projeksiyonları için aday olan modeler, yüksek AUC değerlerine sahip olmalarına göre seçilirler, fakat *M. s. schreibersii* ile yapılan projeksiyonlar, yüksek AUC değerlerinin her zaman başarılı projeksiyonlar için doğru gösterge olamadığını göstermiştir. Bu yüzden, gelecek ve geçmiş zaman projeksiyonlarının sonuçları her zaman çok dikkat ederek yorumlanmalıdır.

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ABBREVIATIONS

Abbreviation	**Explanation**
AUC	Area Under Curve
CART	Classification and Regression Tree
CEM	Climate Envelope Model
ENM	Ecological Niche Model
GAM	Generalized Additive Model
GARP	Genetic Algorithm for Rule-set Prediction
GBIF	Global Biodiversity Information Facility
GIS	Geographic Information System
GLM	Generalized Linear Model
IPCC	Intergovernmental Panel on Climate Change
ISCGM	International Steering Committee for Global Mapping
KC	Kulczynski's coefficient
LGM	Last Glacial Maximum
MARS	Multivariate Adaptive Regression Spline
ROC	Receiver Operating Characteristics
SDM	Species Distribution Model

1. INTRODUCTION

Understanding patterns of species distribution and predicting them is a fundamental element of the ecological research and a starting point for taking the correct management decisions in conservation efforts. Knowing species habitat requirements, finding priority areas for protection, and predicting changes of species ranges under various climatic conditions become more important as the speed of species extinction seems to be steadily increasing. Assessing the vulnerability of species or the importance of ecosystems is a complex process, which, among others, includes ecological modelling, a method for examining patterns and distributions of species. Although ecological modelling cannot answer many questions posed by the ecological research and conservation, it can still provide some insights regarding species' habitats, history, vulnerability, and responses to possible climatic changes.

1.1. Niches and spatial distribution of species

Environmental conditions and species physiology determine ecological niches, which in turn determine species distribution. The term 'niche' was coined by Joseph Grinnell in 1917 (Grinnell, 1917) to define all suitable habitats in which species occur (Pulliam, 2000). Hutchinson (1957), however, suggested that a niche defines the range of a species tolerance, which 'could be modeled as an imaginary space with many dimensions, in which each dimension or axis represents the range of some environmental condition or resource that is required by the species' (in Thuiller et al., 2004). Within the species niche, its growth rate can vary from none to maximum, but outside the niche, it is always negative (Hirzel and Le Lay, 2008).

The concept of a species niche is frequently considered in two categories: a realized and a fundamental niche. The fundamental niche is defined as 'the response of all physiological processes of a species to the synergistic effects of environmental factors' (Helaouet and Beaugrand, 2009). The fundamental niche concept does not consider interactions among species, whereas the realized niche concept does. Accordingly, the latter takes into account interspecific competition, predation, diseases, and parasites.

Because a species distribution is affected by other species, the realized and fundamental niches are generally very different (Pulliam, 2000). The realized niche is smaller than fundamental niche, if:

- there is a factor, affected by environmental conditions, which directly or indirectly increases mortality or decreases reproduction (Helaouet and Beaugrand, 2009);
- the species is dispersal limited;
- there are limited resources (e.g. food);
- there is competitive exclusion between neighboring species.

When species dispersal is high, however, the realized niche can be bigger than the fundamental niche (Pulliam, 2000), governed by the source-sink dynamics when species migrate from suitable to unsuitable habitats (Fig. 1.1).

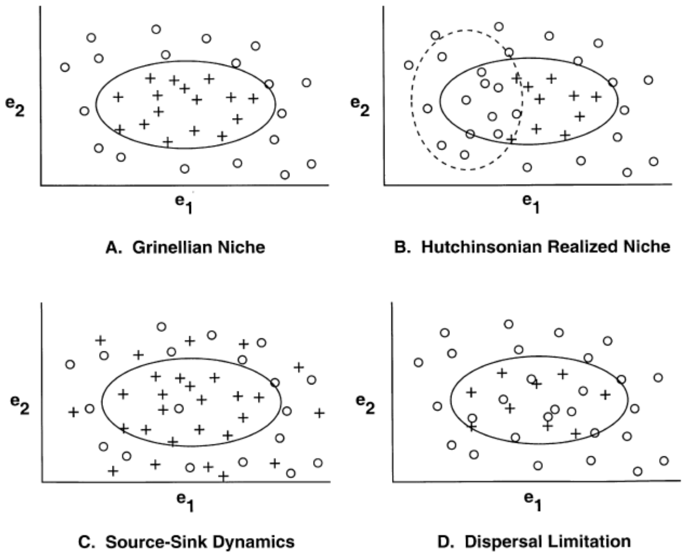


Figure 1.1. The relationship between a species niche and its distribution (Pulliam, 2000); plus signs indicate presence and zeroes indicate absence of species, 'e_1' and 'e_2' are independent environmental variables measured along rectangular coordinates.

Fundamental niches of species tend to evolve slowly under circumscribed conditions and they can stay conserved over long timescales (Holt and Gaines, 1992; Wiens and Graham, 2005), which is known as niche conservatism (Losos *et al.*, 2003; Bohning-Gaese *et al.*, 2003; Graham *et al.*, 2004). Peterson *et al.* (1999) combined museum locality data of 21 pairs of birds sister taxa, 11 mammals taxa, and five butterflies taxa from southern Mexico, with climatic data, and used the niche modelling to test the degree to which ecological characteristics of one taxon were able to predict the geographic distribution of its sister taxon. The results suggested that niches evolve at, or around, the time of speciation events, and that sister taxa were successful in approximating each other's distribution. Because outside of the fundamental niche, the rate of extinction generally exceeds the rate of adaptation, migration and extinction, rather than evolution, were the main responses to Quaternary climate changes (Svenning *et al.*, 2008).

When projections are applied to other time spans and geographical areas to predict distribution of alien species, refugia and climate change effects, it is implicitly assumed that niches of species are conserved.

1.2. Ecological modelling for predicting distribution and patterns

The species-environment relationship can be quantified in species distribution models (SDMs), which predict not only distributions of species across landscapes, but also population sizes and potential impact of habitat changes (Guisan and Thuiller, 2005). Because only a few species have been studied in detail in terms of biological responses to environmental change, and because of intrinsic variations in species responses to changing environmental factors, ecological modelling is the best approach to explore the effects of environmental change on species (in Guisan and Zimmermann, 2000).

Indeed, ecological modelling can be seen as 'operational applications of the ecological niche' (Hirzel and Le Lay, 2008). In an ecological niche, environmental variables are related to the fitness of species; in ecological models, environmental variables are related to probability of their occurrence. Accordingly, the realized niche of species can be calculated from environmental variables known from the location of species, and then it can be used in ecological modelling to produce suitability maps. The strength of the distribution-niche link depends on the ecology of species, local constraints, and historical events (Hirzel and Le Lay, 2008).

1.3. How does it work?

To find a potential niche of a particular species, the presence/absence data are compared with data cells, which represent an environmental map. To produce the probabilistic distribution map, the results are projected to secondary environmental maps. There are three main components of SDMs: environmental data, species occurrence data, and statistical models. Selection of these components affects modelling output.

1.3.1. Environmental data

Environmental data summarizes habitat properties, such as temperature, vegetation, precipitation, topography, etc. These are called independent variables, predictors, or covariates. In Climate Envelope Models (CEMs) only climatic variables are used as model predictors, whereas in Ecological Niche Models (ENMs) a wider range of variables, including vegetation and topographical layers, are used. The variables are generally in the form of Geographic Information System (GIS) layers. Every GIS layer represents a habitat condition, and every pixel in a layer has a specific value describing each condition. Accordingly, GIS layers are two dimensional maps that define values of a specific environmental condition for a particular geographic area.

Whereas environmental climatic data can be obtained from WorldClim website (http://www.worldclim.org/), vegetation, land cover, and land use data can be found in the site of the International Steering Committee for Global Mapping (ISCGM, www.iscgm.org/). Environmental layers can be prepared using a number of dedicated GIS tools.

1.3.2. Species data

Species data required for a model construction depend on the approach taken in building a particular distribution model. The models can be either mechanistic or correlative (Fig. 1.2). In mechanistic modelling, fitness values for different physical parameters are found. Species-related data are physiological or behavioral parameters, derived from laboratory experiments by relating responses of individuals to different tested variables, such as temperature, humidity, and so on. Because fundamental niche is a function of species physiological performance, mechanistic modelling projects fundamental niche (Guisan and Zimmermann, 2000). In correlative modelling, species-related data are derived from actually known, however incomplete, locations of species (absence/presence data for latitude/longitude pairs). Because the occurrences are field observations, biotic interactions are implicitly involved, and correlative modelling projects the realized niche of species (Guisan and Zimmermann, 2000). This approach is advantageous, because detailed knowledge of species physiology is not needed.

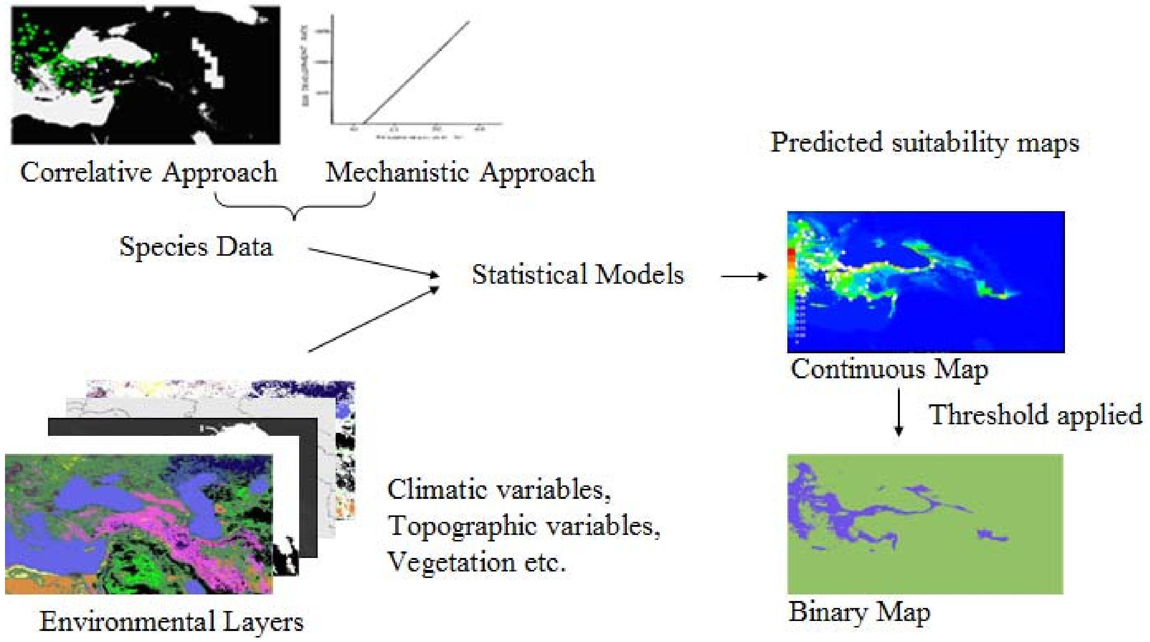


Figure 1.2. Correlative and mechanistic approaches to species distribution modelling.

Various species data can be obtained from Global Biodiversity Information Facility (GBIF, www.gbif.org), HerpNet databases (www.herpnet.org), and SpeciesLink (http://splink.cria.org.br/).

1.3.3. Statistical models

Statistical models are the most important part of a model construction, as they establish functional relationships between species-related data and environmental data. These functional relations are the mathematical representation of a species' potential niche that can be projected to geographic space and time in order to obtain the distribution of suitable conditions for species.

The presence/absence data in the correlative approach or fitness values in mechanistic approach are statistically compared to data from the environmental map cells to find a potential niche of the species. The result is projected to locations where the species occurrence is not known and consequently becomes a probabilistic niche map with continuous values or binary values, if the threshold value is applied.

1.4. Climate change

1.4.1. Reasons for climate change

The Earth's climate is a dynamic system that changes continuously due to variations in its radiation balance. Changes in the radiation balance arise from the three main factors: solar radiation received by the Earth, fraction of solar radiation that is reflected by the Earth, and change in long wave radiation from Earth back towards space. Any changes in these factors, along with the redistribution of heat in ocean circulation, and heat transport, can trigger abrupt changes in the Earth climate (Intergovernmental Panel on Climate - Climate Change 2007 [IPCC]).

The variations in the Sun or in the Earth's orbit affect the solar radiation received by the Earth. For example, the global cooling and warming cycles during the Quaternary, known as Milankovitch oscillations, were caused by the precession, obliquity, and eccentricity of the Earth's orbit. The effect of the orbital variations was further amplified by the atmospheric carbon dioxide concentration, global ice volume, and surface albedo. Furthermore, plate tectonics of oceanic and atmospheric flows determined the mean climate over these oscillations. The Milankovitch oscillations peak every 10 to 100 thousand years and stable conditions last for only a few thousand (Jansson *et al*., 2002). The most recent peak, the Last Glacial Maximum (LGM), reached its maximum ca. 18.000-21.000 years ago. Then, the climate was drier, colder, the sea levels were lower, and continents in the northern hemisphere were mostly covered with ice sheets.

Variations in cloud cover, atmospheric particles, vegetation, continental drift, and volcanic eruptions can cause change in solar radiation reflected by earth by affecting surface albedo. Albedo is the ratio of reflected solar radiation from the Earth's surface. For example, the albedo of a forested land is lower than of an open land; the greater leaf area and multiple reflections in a forested land result in more absorption of shortwave radiation (IPCC, 2007a).

Some gases absorb long wave radiation that is emitted from the surface then emit that radiation back to Earth, making the planet more hospitable. These gases are called greenhouse gases. Changes in greenhouse gas concentrations can cause changes in a long wave radiation reflected from the Earth to space. Primary greenhouse gases are water vapor, carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), and ozone (O_3). The concentration of greenhouse gases can be affected by the movement of continents and volcanic eruptions.

Greenhouse gases concentration decreased at the beginning of the ice ages (ca. 190 ppm [IPCC, 2007a]), and rose when the ice sheets retreated (ca. 280 ppm [IPCC, 2007a]), thus contributing to the glacial-interglacial cycles by amplifying the initial effect of orbital forcing. The available evidence implies a close correlation between Antarctic temperature and atmospheric concentrations of CO_2 and CH_4 (Petit *et al.*, 1999).

While there are many natural causes of the climate changes, the human activities have also their own impact on them. After the industrial revolution, greenhouse gas levels began to increase steadily. Atmospheric concentration of CO_2 increased from pre-industrial value of ca. 280 ppm to ca. 380 ppm in 2005. The current CO_2 concentration is higher than in the last 650,000 years. Methane concentration, stable at 700 ppb for the last 1,000 years, steadily increased to 1,745 ppb in 1998 (IPCC, 2001) and to 1,774 ppb in 2005; it is now higher than in the last half-million years of glacial-interglacial cycles. Global atmospheric concentration of N_2O increased from the pre-industrial value of ca. 270 ppb to ca. 320 ppb in 2005. More than 30% of all N_2O emissions are anthropogenic and are primarily due to agriculture (IPCC, 2007a).

In fact, at any time during the last half-million years, levels of all greenhouse gases were lower than those in the 1990s (Petit *et al.*, 1999). Indeed, some greenhouse gases, such as synthetic halocarbons, did not even exist in the past. In addition, for the last 50 years the linear warming trend accelerates and is faster than in the last 100 years; the average temperature raised by about 0.76 °C between the years 1850-1899 and 2001-2005. Still, a more dramatic effect of a global climate change is observed in the recent years. Since 1850, the warmest 11 years were recorded between 1995 and 2006 (IPCC, 2007b). It is predicted that the temperature will increase further by 1.4 to 5.8 ^{o}C between 1990 and 2100. Because of the complexity in forecasting climate, Intergovernmental Panel on Climate Change (IPCC) developed 40 scenarios considering different storylines of demographic, societal, economic and technical-change growth, categorized under four scenario families (A1, A2, B1 and B2). These scenarios are projected through year 1990 to 2100 (Nakicenovic *et al.*, 2000).

1.4.2. Impact of climate change on species

Climatic factors, as well as physical factors, affect species' distribution and their population structure. The effects of global warming, combined with human impacts (land development, over-exploitation, species translocations, and pollution) are expected to be the main reason for species extinctions in the 21st century (IUCN, http://iucn.org/). The current species extinction rate is about 1,000-10,000 times higher than the natural one (IUCN, http://iucn.org/). In consequence, 20 to 30% of plant and animal species are likely to be at high risk of extinction if the mean global temperatures exceed pre-industrial levels by 2-3 ^{o}C (IPCC, 2007b).

The current distribution of species and their population structure are typically determined by the past events and species responses to those events. Understanding species responses to the past climatic changes are also crucial for predicting their responses to future climatic changes. The way organisms respond to global climate change can be somehow predicted by referring to the species' responses to the past climate changes (Waltari *et al.*, 2007). Clades migrate, merge, become extinct, or split due to rapid climate change. Organisms that are more likely to go extinct are those moving slowly, encountering a geographical barrier, or depending on specific, restricted, and rare habitats

(Jansson and Dynesius, 2002). For instance, during the LGM, many species went extinct because of reduction and fragmentation of their habitats caused by a drier and colder climate, which exceeded their physiological tolerance (Waltari *et al.*, 2007).

The magnitude of climatic changes that a region is exposed to determines the types of species that inhabit it, species richness, and the endemism. In highly variable areas, only generalist species are successful. On the other hand, specialist species are favored in climatically stable places, such as the tropics. Furthermore, the number of endemic species increases with decreasing amplitude of climate oscillations (Jansson and Dynesius, 2002). Therefore, the areas that were exposed to relatively small climatic changes during the glacial and interglacial periods served as the species shelters. Medail and Diadema (2009) found significant association between phylogeographically defined refugia/shelters and regional hotspots of biodiversity. Consequently, the conservation of refugial areas is very important for long term persistence of species and their genetic diversity. Major shelters in the colder and drier climate of the ice ages were mountainous areas, which provided suitable conditions with altitudinal shifts; and deep gorges and closed valleys, which provided continuous moisture availability (Jansson and Dynesius, 2002; Medail and Diadema, 2009). Of the 52 refugia identified by Medail and Diadema, 33 were situated in the Mediterranean submontane and mountain margins. Similarly, the mountainous Iberian and Italian peninsulas, the Balkans (including Thrace and north-western Anatolia), and the lowlands of western Georgia were the most important refugia for the ancestors of extant European populations.

1.5. Challenges and limitations of SDMs

1.5.1. Biotic Interactions

Both, the mechanistic and correlative approaches to species distribution modelling ignore the importance of biotic interactions (Jeschke and Strayer, 2008). In the mechanistic approach, physiological tolerances are measured in the laboratory and so, they do not incorporate biotic interactions. In the correlative approach, biotic interactions are implicitly included in the realized niche calculation and they are assumed to stay constant over space and time.

1.5.2. Change in genetic and phenotypic composition of species

Both the mechanistic and correlative approaches assume that genetic and phenotypic composition of species stay constant (Jeschke and Strayer, 2008). When a species' potential niche is produced from its distribution, it incorporates the species adaptations only for a particular time span, place, or environmental conditions, and does not take into consideration any possible changes to these settings.

1.5.3. No dispersal limitation

Both the mechanistic and correlative approaches assume that a species can exist in all suitable locations without taking its dispersal capacity into account. Yet, many species are unable to reach some of the putatively suitable, but spatially distant locations (Jeschke and Strayer, 2008). For example, in Europe, only the range of widespread northern tree species is in equilibrium with the climate (Svenning *et al.*, 2008).

1.6. Thesis Objectives

Here, using the ecological niche modelling, I intend to find which of the environmental variables are the most important in explaining the occurrence of two bat subspecies: *Miniopterus schreibersii schreibersii* (type locality: Kolumbacs cave, Romania; Kuhl, 1817) and *M. s. pallidus* (type locality: South coast of Caspian Sea, Iran; Thomas, 1907). I also aim to project my findings to the past and to the future climatic conditions. Using the past climatic data (from the period of the LGM) might help to find locations of the putative glacial refugia of these taxa. Using the future climatic conditions might help to predict the possible changes in their distributional ranges in response to the forecasted change of climate.

2. LITERATURE REVIEW

Relating species distribution to environmental factors has been used to explain distributional patterns of various plant and animal species (Salisbury, 1926; Guisan and Zimmermann, 2000). Statistically quantifying this relationship and projecting it on a map is the main idea of ecological modelling.

A few decades ago, development of powerful and easily accessible processors initiated computer-based ecological modelling. The main types of computer-based applications included bio-geo-chemical and static/dynamic population models (Jorgensen, 2008). From that point on, the number of species distribution models increased in parallel to developments in computer technology and statistical sciences (Guisan and Thuiller, 2005) and to availability of species data, environmental data, and online databases. Indeed, whereas 40 years ago, *Ecological Modelling* journal was publishing *ca*. 300 pages *per* year of papers related to modelling, nowadays it is publishing *ca*. 4000 pages *per* year (Fig. 2.1) (after Jorgensen, 2008).

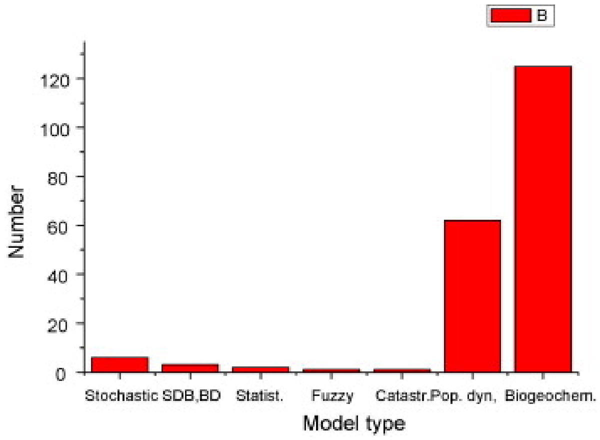


Figure 2.1. The number of papers related modelling published in the period 1975–1982. The statistical approaches used in those papers covered stochastic models, spatial distribution models and structurally dynamic models (SDBBD), models based on the use of statistics, fuzzy models, models using catastrophe theory, population dynamic models and bio-geo-chemical models (after Jorgensen, 2008).

Over the years, the ecological modelling has been successfully applied to predict species occurrence for current, past, and future scenarios, to find possible dispersal of invasive species (Peterson and Vieglais, 2001), to understand the effect of landscape features to distribution (Jaberg and Guisan, 2001, Kanuch *et al.*, 2008), to assess changes in biodiversity (Guisan and Zimmermann, 2000; Pineda and Lobo, 2009), to identify potential migration pathways (Krebs *et al.*, 2004; Peterson *et al.*, 2004; Waltari *et al.*, 2007), to explore hybridization (Swenson, 2006; Richards *et al.*, 2007), to investigate speciation (Graham *et al.*, 2004; Richards *et al.*, 2007), to analyze diversity gradients (Weins *et al.*, 2006; Richards *et al.*, 2007), to predict extinction (Bond *et al.*, 2006; Richards *et al.*, 2007), to estimate the effects of climate change on species (Walther *et al.*, 2002), and to gather data for conservation purposes (Greaves *et al.*, 2006; Chefaoui *et al.*, 2005). When combined with coalescent simulations to analyze genetic data, the ecological modelling can be used to generate and test alternative phylogeographic hypotheses (Richards *et al.*, 2007; Flanders *et al.*, 2010).

Ecological models can be categorized in many ways. One of the possibilities is to divide them according to the type of data used for species occurrence. Models can also be categorized by discrimination and profile techniques they utilize (using presence-absence or presence-only occurrence data). Some examples of discrimination techniques include models based on a discriminant functions analysis, Generalized Linear Models (GLMs), Generalized Additive Models (GAMs), Multivariate Adaptive Regression Spline (MARS), and decision-tree based methods (Navarro-Cerrillo *et al.*, 2010). Examples of profile techniques are climate envelope models. Many datasets have only presence data, such as studies consisting of poorly sampled regions, rare species, and undetectable species. When absence data is not reliable, using the profile technique is advantageous (Jeschke and Strayer, 2008; Farber and Kadmon, 2003). But when abundant and reliable absence data is available, using discrimination techniques is better (Jeschke and Strayer, 2008).

Another way of categorizing models is to divide them according to dynamic or static change in time parameter. Dynamic models based on a non-equilibrium concept, and in which time parameter is explicitly involved, simulate dispersal, competition, and movement of species. As a result, they can predict the species response to a stochastically and dynamically changing environment. On the other hand, in static models, the equilibrium state is assumed, time parameter is not involved, and after a long constant input, the system reaches a steady state. Species that react slowly to environmental changes are less restricted by this assumption (Guisan and Zimmermann, 2000).

Models can also be grouped into empirical, mechanistic, and analytical models according to their intrinsic properties, such as generality, reality, and precision (Levins, 1966). Of these three properties, only two can be improved simultaneously (Fig. 2.2). Models focusing on reality and precision are called empirical models; their formulation does not aim to describe cause and effect between parameters and response, but rather to condense empirical facts. Models focusing on reality and generality are called mechanistic models; their predictions are based on real cause-effect relationships, which are judged on the theoretical correctness of the predicted response. Models focusing on generality and precision are called analytical models; these models predict accurate responses. The Lotka-Volterra equations are an example of the last type of models (Guisan and Zimmermann, 2000). The correlative modelling approach can be categorized as empirical.

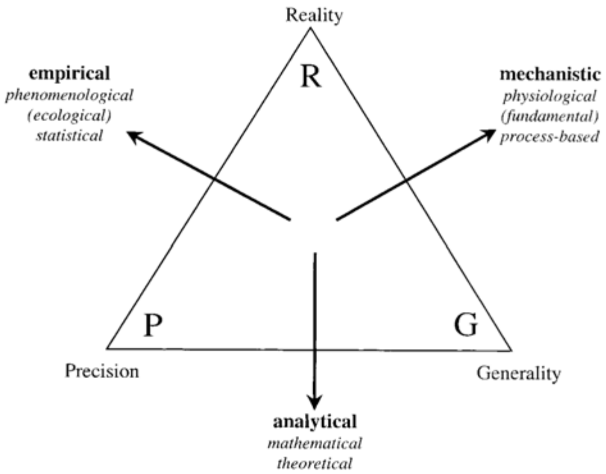


Figure 2.2. Models classification based on their intrinsic properties (Guisan and Zimmermann, 2000).

On the other hand, Loehle (1983) categorized models as calculating tools and theoretical models. Calculating tools are synonymous with empirical models, while theoretical models are an equivalent of mechanistic models from Levins' categorization (Guisan and Zimmermann, 2000). These classifications can be useful in determining the context of modelling. According to the intended response and goal of modelling, an adequate model type and desired ecological gradients can be selected.

Ecological gradients can refer to a resource, direct or indirect species' needs. Resource gradients depend on matter and energy that are consumed, such as nutrients or water. Direct gradients depend on factors, such as climate, temperature or pH, which have a physiological importance for species. Climatic factors are particularly important, especially for plants, as they influence the physiology of organisms to a great degree, (Hirzel and Le Lay, 2008). A particular ecological gradient can have a varied influence on different species. For example, gradients derived from digital elevation models (e.g. slope, aspect, convexity, elevation or topography) are crucial for plants as they affect light, wetness, soil, or stability. Their effect on animals can be direct, by affecting locomotion, or indirect, by affecting vegetation (Hirzel and Le Lay, 2008). Similarly, land cover data can also diversely influence ecological niches. It can represent food, shelter, breeding sites, disturbance, locomotion, etc. (Hirzel and Le Lay, 2008). Organisms compensate for climatic differences by changing their locations in indirect gradients. Hence, the use of resource and direct gradients makes the model more mechanistic, general, and applicable over larger areas (Guisan and Zimmermann, 2000; Phillips *et al.*, 2006).

2.1. Statistical Models

A statistical approach used to construct a particular model depends on the available species data and the aim of the study. Guisan and Zimmermann (2000) categorized models into generalized regressions, classification techniques, environmental envelopes, ordination techniques, bayesian approaches, neural networks, and mixed approaches.

In generalized regressions, the classical least square regression approach is used when the response variable is normally distributed and the variance does not change as a function of the mean (Guisan and Zimmermann, 2000). In GLMs, a binary response variable is a linear function of the independent variables. Here, in addition to normal distribution, the response variable can have Gaussian, binomial, gamma and Poisson distributions. In GAMs, a response variable is the additive combination of the functions of independent variables. GAMs allow non-parametric fitting. This method offers less transparency and interpretability, but greater modelling flexibility (Guisan and Zimmermann, 2000). GLMs and GAMs are commonly used with presence-absence datasets. They are also used with 'background pixels', or 'pseudo absences', which are randomly selected pixels from the background (Phillips *et al.*, 2006)

Classification techniques include classification and regression tree (CART), rule based classification, and maximum likelihood classification (Guisan and Zimmermann, 2000). In CART analysis, data are split into homogenous subsets and subsequently a binary decision tree is generated.

Ordinary techniques are predominantly based on canonical correspondence analysis and are appropriate for datasets with many absences. Distribution of species is assumed to be Gaussian (Guisan and Zimmermann, 2000).

Bayesian models use prior probabilities to find the occurrence probability of species related to each environmental predictor. Prior probabilities can be found in literature or by reference to previous researches (Guisan and Zimmermann, 2000).

Neural networks and genetic algorithms are powerful approaches, but their predictions are difficult to interpret (Jeschke and Strayer, 2008). According to Lek *et al.* (1996) neural network models are more successful than multiple regression models when modelling non-linear relationships (Guisan and Zimmermann, 2000). One of the most frequently used modelling algorithms is Genetic Algorithm for Rule-set Prediction (GARP). GARP is a machine learning method that uses genetic algorithms to select rules that optimally predict species distribution (Stockwell and Peters, 1999; Elith *et al.*, 2006). Presence-only data are used with randomly sampled pseudo-absence data. Sets of rules are developed with randomly selected training and testing subsets through an iterative process of evaluations. The chosen method (logistic regression, range rules, etc.) is first applied to training data for rule development. Predictive accuracy is evaluated based on 1250 points resampled from test data and 1250 pseudo-absence points. Change in predictive accuracy is used to decide whether to incorporate the selected rule in the model. Iteration continues until convergence, or for a fixed number of iterations (Peterson *et al.*, 2007).

Environmental/climatic conditions at locations where species are present are interpolated to environmental/climatic envelopes (niches). ANUCLIM, BIOCLIM, DOMAIN, FEM, HABITAT, and Mahalanobis Distance are examples of environmental envelope techniques.

BIOCLIM model is a climate envelope model developed initially to model distribution of plant species in Australia (Guisan and Zimmermann, 2000). It can be used to describe the climatic conditions in which species exist and to predict their potential distributions (Fig. 2.3). BIOCLIM is a range-based model and describes the envelope as a rectilinear volume (Beaumont *et al.,* 2005). It can produce up to 35 climatic parameters derived from maximum temperature, minimum temperature, rainfall, solar radiation, and pan evaporation. However, using all 35 variables can result in the over-fitting of the model (ANU, http://fennerschool.anu.edu.au/publications/software/anuclim/doc/bioclim.html). Beaumont *et al.* (2005) modeled the distribution of 25 Australian butterfly species with different numbers of climatic variables (the full set of 35 climatic variables, customized selection of most relevant variables, and a subset of eight parameters) and included random selection to explore the effect of over-fitting. They found that the size of distribution was negatively correlated with the number of parameters added to the model. Accordingly, when measuring the actual distribution of a species the number of parameters is critical, but when averaged over multiple species, the number of parameters has little effect on the distributions. The problem with BIOCLIM is that the bioclimatic envelope can incorrectly include or exclude some points (Walker and Cocks, 1991), as it assumes that the suitability of all combinations within the rectilinear envelope is equal (Farber and Kadmon, 2003). For example, point A can be excluded from a core climate whereas point B, which is dissimilar to other presence locations, can be included (Carpenter *et al.*, 1993) (Fig. 2.3). BIOCLIM can interpret cool-wet and hot-dry environments as suitable for organisms that exist in hot-wet and cool-dry environments. Climate envelope models are not able to cope with correlations and interactions of variables. Rectilinear envelopes can lead to overestimated distributions of species when variables are correlated (Farber and Kadmon, 2003).

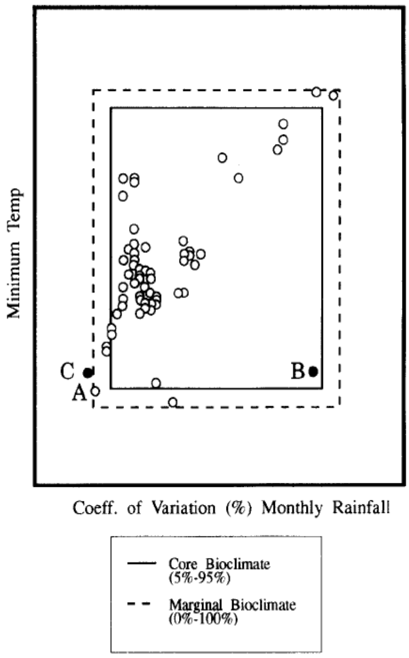


Figure 2.3. A representation of a hypothetical two dimensional bioclimatic envelope of BIOCLIM. Dots represent the temperature-rainfall pairs where species presence is recorded (Carpenter *et al.*, 1993).

As an alternative to BIOCLIM, the HABITAT environmental technique can be used. HABITAT uses non-climatic attributes as well as soil, vegetation, land use, etc. It uses 'convex hull of record sites' to fit the bioclimate envelope to the presence records better than BIOCLIM (Carpenter *et al.*, 1993) (Fig. 2.4). Here, point A is included and point B is excluded from 'convex hull of record sites'. HABITAT uses CART to eliminate parameters that are not successful in determining species absence and presence.

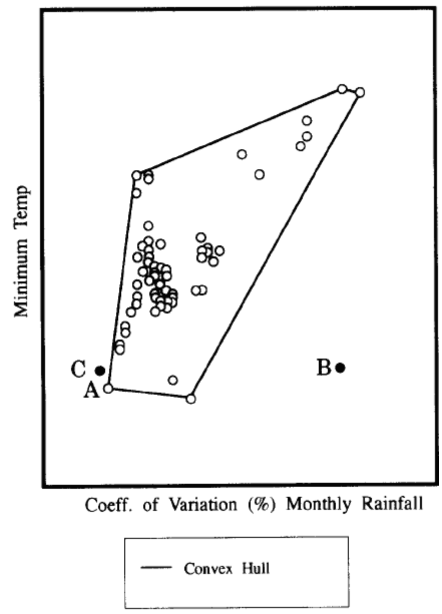


Figure 2.4. A representation of a hypothetical two dimensional convex hull bioclimatic envelope of HABITAT. Dots represent the temperature-rainfall pairs where species presence is recorded (Carpenter *et al.*, 1993).

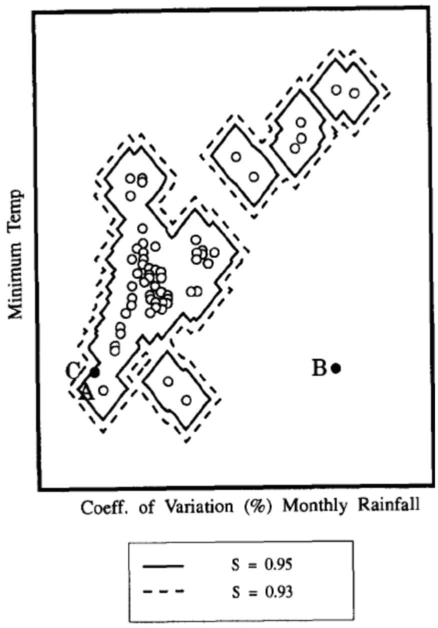


Figure 2.5. A representation of a hypothetical two dimensional bioclimatic envelope of DOMAIN. Dots represent the temperature – rainfall pairs where species presence is recorded (Carpenter *et al.*, 1993).

When the availability of records is limited, DOMAIN model developed by Carpenter *et al.* (1993), is more suitable (Fig. 2.5). Instead of CART, it uses multivariate distance measures known as ‘point-to-point similarity metric’ (Guisan and Zimmermann, 2000).

Farber and Kadmon (2003) used Mahalanobis Distance to model distributions of 192 species of woody plants in Israel. Mahalanobis Distance uses an oblique ellipse envelope for defining species distribution and can cope with interactions and correlations between variables. It relies on multivariate mean and covariance matrix rather than the boundaries of distribution. It fits well with the ecological theory because the ‘principle of continuity’ is assumed which asserts that species are distributed optimally along niche axes, optimal conditions are around mean, and deviation from mean are categorized as having lower suitability.

Finally, Maxent is one of the most accurate general-purpose methods which works well with small sample sizes, using the presence-only data. With the use of a conditional model, it can also be applied to presence-absence data. It makes inferences from incomplete information aiming to find the probability distribution of maximum entropy that is most spread out, or closest to uniform. Maxent applies the second law of thermodynamics by adapting it to ecological processes. Constraints in the model are features (functions of environmental layers) having the same mean under probability distribution as observed empirically. As empirical feature means are approximations to true means, Maxent can be prone to over-fitting. To prevent over-fitting, constraints can be relaxed by a constant regularization parameter. This regularization parameter is determined by the sum of weights of features. Hence, models that have fewer parameters are less likely to be over fit. One of the advantages of Maxent is allowing users to change the regularization parameter (Phillips *et al.*, 2006). Another advantage is that it can utilize both continuous and categorical data. The outputs of Maxent are continuous. Setting a specific threshold value can produce binary predictions (Phillips *et al.*, 2006).

In Maxent, goodness of fit is measured by the gain, which is closely related to deviance. Maxent starts with a uniform distribution of the presence probability values and improves the model fit iteratively. The uniform distribution constant is subtracted from the average log probability of the presence samples to calculate gain. The average likelihood of the presence samples is exp (gain) times higher than that of a random background pixel (Phillips, http://www.cs.princeton.edu/~schapire/maxent/).

2.2. Evaluating the model

Model utility depends on evaluation of model’s performance. Selections of environmental variables are also determined by evaluation measurements, such as comparing how much variance is explained by each variable. Initially, a model is run with training data set and then its performance is evaluated with testing data set. Training and testing data sets are generated by partitioning methods (randomization, re-substitution, bootstrapping, and k-fold partitioning). There is, however, a tradeoff between training and testing datasets. Large training sets increase model accuracy and give better results, but large test sets also ‘reduce the variance of the error estimates’. For testing data, it is the best to use an independent dataset, not used in fitting the model. Furthermore, partitioning training data decreases modelling performance (Fielding and Bell, 1997). Also unbiased data should be used in order to prevent errors. Biases like distribution of samples and accessibility to reach them can affect model output.

Model’s performance determines range of areas over which a model can be used. For conservation studies of endangered species, false negative errors (omission errors and under-predictions) are more important than false positive errors (commission errors and over-predictions). Thus a model that has a high rate of false negative errors is not preferred for locating endangered species. Performance is determined by model’s discrimination capacity and reliability. Discrimination capacity is model’s ability to discriminate presences from absences. Accuracy measures are calculated from correctly and falsely predicted cases. Reliability is ‘capability of the predicted probabilities to reflect the observed proportion of sites occupied by the subject species’ (Liu *et al.*, 2009). Both discrimination capacity and reliability can be assessed with continuous outputs, whereas only discrimination capacity can be assessed with binary outputs (Liu *et al.*, 2009). Continuous prediction values vary from 0 to 1, and they can be dichotomized by applying a threshold value. Change in threshold value results in a change in a confusion matrix (Table 2.1). This threshold value can be changed according to the aim of the study. For example, when dealing with endangered species, a threshold value can be changed in such a way as to decrease false negative errors at the expanse of increase in false positive errors (Fielding and Bell, 1997). Some of approaches used in selection of a threshold value are: fixed threshold approach (0.5), kappa maximization approach, overall prediction success approach, prevalence approach, average probability approach, mid-point probability approach, sensitivity-specificity sum maximization approach, sensitivity-specificity equality approach, ROC plot-based approach, precision-recall break-even point approach, P-R plot-based approach, and F maximization approach (Liu *et al.*, 2005).

Table 2.1. An example of a confusion matrix

	Actual		
Predicted		Presence	Absence
	Presence	a	b
	Absence	c	d

Accuracy measures can be divided into threshold-dependent and threshold-independent indices. In threshold-dependent indices, a specific threshold value is applied, whereas threshold-independent indices are directly applied to continuous situations (Liu *et al.*, 2009).

Overall accuracy, sensitivity, specificity, false positive rate, false negative rate, odds ratio, positive predictive power, negative predictive power, Kappa, and F measure are examples of the threshold-dependent measures (Table 2.2). Prevalence (ratio of presence data to all data) also effects these accuracy measurements.

Maximum overall accuracy, Gini index, Point biserial correlation coefficient are examples of threshold-independent measures (Liu *et al.*, 2009). One of the most frequently used threshold-independent tests to evaluate discrimination ability is based on the Receiver Operating Characteristic curve (ROC) and on values of the area under ROC function (AUC). Sensitivity values (measured as a fraction of true positives) and specificity values (measured as a fraction of false positives) are plotted for all relevant thresholds. The minimum value of AUC, 0.5, indicates that the prediction is not better than random guessing. The maximum value of 1 gives a perfect prediction (Fielding *et al.*, 1997). In general, higher values of AUC indicate better discrimination of suitable versus unsuitable areas (Phillips *et al.*, 2006).

Table 2.2. Measures of classification accuracy

Measure	Calculation	Reference
Prevalence	(a+c)/N	Fielding and Bell (1997)
Overall accuracy	(a+d)/N	Liu *et al.* (2009)
Sensitivity	a/(a+c)	Fielding and Bell (1997)
Specificity	d/(b+d)	Fielding and Bell (1997)
False positive rate	b/(b+d)	Fielding and Bell (1997)
False negative rate	c/(a+c)	Fielding and Bell (1997)
Positive predictive power	a/(a+b)	Fielding and Bell (1997)
Negative predictive power	d/(c+d)	Fielding and Bell (1997)
Odds ratio	(ad)/(cb)	Fielding and Bell (1997)

2.3. Geographical Area of the study

The geographic area selected for this thesis corresponds to the distribution of two bat species, *M. s. schreibersii* and *M. s. pallidus*. The models focus on Turkey (Asia Minor and Thrace) and Iran, and extend to Europe.

2.3.1. Turkey

Surrounded by seas from three sides, lying at the junction of three continents, having Euro-Siberian, Mediterranean, and Irano-Turanian bio-geographical zones (MED-O-MED, http://medomed.org/), and having mountainous topography with several microclimates, Turkey is a very rich country in terms of biological diversity. In the glacial-interglacial periods, the region was a contact zone for isolated populations from the glacial refugia located in Thrace, Transcaucasia, and probably in Southern Anatolia. There are about 11,000 plant species (4,000 endemic) in Turkey, whereas in whole Europe there are about 12,500 of them (Uzun and Bayır, 2009). Most of the endemic species are found in the Mediterranean and the Irano-Turanian biogeographical regions (CBD, www.cbd.gov.tr/thematic/documents/FOREST_MOUNTAIN.doc).

In reference to geographical and climatic properties, Turkey is divided into seven regions: the Aegean, the Black Sea, Central Anatolia, Eastern Anatolia, Marmara, Mediterranean, and Southeastern Anatolia. The factors affecting Turkish climate are: west to east oriented high mountains along the northern and southern coasts of Asia Minor, the Black Sea and Mediterranean basins, and the Anatolian plateau with a mean elevation of 1130 m (Türkeş, 1996).

The central and eastern parts of Asia Minor have a continental climate with long and cold winters (Sensoy *et al.* 2008). The Central Anatolia region is a semi-arid region (Türkeş, 1996). The Central, Eastern and Southeastern Anatolia regions are within the boundries of Irano-Turanian biogeographical zone (Uzun and Bayır, 2009). Irano-Turanian biogeographical zone extends from Central Anatolia to Mongolia and steppe plants are dominant in this region. The Black Sea region is in the Euro-Siberian biogeographical zone and has the highest amount of annual rainfall in Turkey. The region is covered largely by forests (Sensoy *et al.* 2008). In Thrace and the Western Black Sea regions, longoz mixed forest ecosystems are found (CBD, www.cbd.gov.tr/thematic/documents/FOREST_MOUNTAIN.doc). The Aegean and Mediterranean regions have cool, rainy winters, and hot, moderately dry summers (Avcı, 2005). The Southern part of Thrace, including the Gallipoli peninsula and the western and southern part of Anatolia remain in the Mediterranean biogeographical zone (Avcı, 2005). Humid, semi-humid coniferous forests, dry forests (oak, black and red pine), and shrubby areas are found there (CBD, www.cbd.gov.tr/thematic/documents/FOREST_MOUNTAIN.doc).

2.3.2. Iran

Iran has a complex topography accompanied by various climatic regimes. Iran’s landscape is dominated by mountain ranges. The Elburz Mountains lay in the northwest-northeast direction along the northern border of Iran, and the Zagros Mountains lay in the northwest-southeast direction along the western border of Iran. These two mountain ranges block moist air entering into the high Iranian plateau and are responsible for non-uniform distribution of precipitation. The plateau slopes down gradually and becomes a desert.

Inland areas have a continental climate with hot and dry summers and very cold winters. Except for the coastal areas and western Iran, the climate is arid or semi-arid. Iran can be divided into four biogeographical zones: Hyrcanian, Khalij-o-Omani, Zagross, and Irano-Turanian. The Hyrcanian zone constitutes of the Alborz Range forest steppe, the Caspian Hyrcanian mixed forest, and the Caspian lowland desert. The Zagros zone has a semi-arid climate and temperate winter. Kurdo-Zagrosian steppe-forests are mainly composed of dense deciduous, broad-leaved trees or shrubs. The Khalij-o-Omani zone is dominated by sub-equatorial climate (Heshmati, 2007). The Irano-Turanian zone has a dry climate with cold winters.

2.4. Bats as a target species

Bats are important to every ecosystem they inhabit, they pollinate flowers, disperse seeds over long distances and many of them are considered to be ‘keystone species’ (Bat Conservation International, http://www.batcon.org/index.php/media-and-info/bats-archives.html?task=viewArticle&magArticleID=203).). They are also the main consumers of night-flying insects in temperate and tropical ecosystems. Cave dwelling bats are very important for cave ecology.

Bats constitute ca. 20% of all classified mammals and more than 1,100 bat species exist worldwide (Bat Conservation Trust, http://www.bats.org.uk/pages/bats_of_the_world.html). Although they are small, they are long-lived. They are also characterized by low fecundity and high survivorship (Findley, 1993). Identifying distribution of bats is a challenging process as they are nocturnal, small-bodied and fast moving mammals (Hill *et al.*, 2005). Bats live in stable and predictable habitats, so that they maintain steady populations close to the carrying capacity of their environment (Findley, 1993). Because monitoring of bats is difficult, species-habitat relationships can be used to model and predict their distributions, using a set of selected habitat descriptors (Guisan and Zimmermann, 2000). The typical prediction models applied for bats include climatic conditions, elevation, and woodland cover (Jaberg and Guisan, 2001; Greaves *et al.*, 2006; Kanuch *et al.*, 2008).

Bent-wing bats (*Miniopterus schreibersii)* form a species complex, which has been reputed to range from Europe to Australia. However, the recent molecular studies proved that its distribution is limited to Europe, northern Africa, and Asia Minor (Furman *et al.*, 2010a). *Miniopterus schreibersii* in Asia Minor consists of two morphologically similar but genetically diverged lineages: *M. s. schreibersii* and *M. s. pallidus*. The lineages are allopatric and meet along a contact zone passing through Central Anatolia. The separation of the lineages does not follow any obvious geographical barriers. Molecular data shows that the lineages split ca. 2.0 to 0.5 Myr BP, 'implying separation in disjunct Pleistocene glacial refugia' (Furman *et al.*, 2010a; Furman *et al.*, 2009).

Most of known *M. s. schreibersii* colonies are found in coastal low altitude locations with wet Mediterranean and Black Sea climate supporting shrub-land vegetation (Furman *et al.*, 2010b) and *M. s. pallidus* are found semiarid regions of higher altitude (Furman *et al.*, 2010a).

3. MATERIALS AND METHODS

Using ecological modelling, this study aims to find and analyze distributions of *M. s. schreibersii* and *M. s. pallidus* under the current, past (the LGM), and future climatic conditions. Predicting the current distribution and analyzing the variables, which are the most important in these predictions, can give us an insight into the ecology of the modeled species. Predicting the past distributions gives us hints about the natural history of the modeled species and their responses to different climatic conditions; it can also point out to the reservoirs of the species genetic diversity. Finally, predicting the future distributions can warn us about the putative effects of the global climate change on the modeled species and offer guidance for the conservation efforts. Still, all predictions are to be taken cautiously, as correlative modelling can be very challenging when species-specific, geography-specific, and time-specific conditions are not incorporated into the models.

3.1. Modelling

Ecological niche was modeled with the maximum entropy software, Maxent v. 3.3.3 (http://www.cs.princeton.edu/~schapire/maxent). This program was selected because of its discrimination capacity success for presence-only data and for small sample sets. Maxent uses threshold-dependent ‘omission and predicted area curve,’ and threshold-independent ‘ROC curve’ for the model evaluation. In this thesis, AUC values were interpreted as: excellent if AUC > 0.90, good if 0.80 < AUC < 0.90, fair if 0.70 < AUC < 0.80, poor if 0.60 < AUC < 0.70, and fail if AUC < 0.60 (Randin *et al.* 2006). For selection of the most effective variables, I used jackknife plots (for training, testing data and AUC analysis) and response curves. Jackknife tests produce bar chart graphs that show gain with, and without, a particular variable. Variables that are contributing similarly in training and testing jackknife analyses are more transferable in space and time. These variables are more suitable when projections are made to other time spans or different geographical area. Response curves give a graph of predicted probabilities of suitable conditions against the corresponding variable, when the other variables are set to their average values (Phillips, http://www.cs.princeton.edu/~schapire/maxent/).

Four group of models were run. The first group consisted of current time span models, which were used to select the most important variables determining distributions of *M. s. schreibersii* and *M. s. pallidus*. Models were run in Asia Minor and Thrace with all bioclimatic variables, elevation, land use, land cover and vegetation data. For evaluation, a 10% test data set was randomly selected from the training data. The setting of a random seed option ensured that a different testing set was used in each run. Variable contribution analysis, jackknife plots for gains, and response curves were used to select the variables. The accuracy of the models was accessed by ROC plots. Models were run with ten replicates with cross validation to check the transferability of the selected variables. Data were split into 'folds' and then models were created leaving out each fold in turn (Phillips, http://www.cs.princeton.edu/~schapire/maxent/).

The second group of models was used to assess modelling transferability. With six variables selected, the models, which were run in Asia Minor and Thrace, were projected to Europe (and vice versa) to test transferability in space. Predicted distributions were compared with projected distributions in order to check their full transferability. The criteria used to assess full transferability were: (1) internal evaluations of models for similarity, (2) models' internal evaluations for comparability with external evaluations, (3) and internal and external predictions within each region for matching (Randin *et al.*, 2006). Randin's (2006) transferability index was used to check first and second criteria of full transferability (Eq. 3.1).

$$\mathrm{T1} = \frac{\frac{1}{2}\left(\left(1-\frac{\left|\mathrm{AUC}_{\mathrm{regA}\to\mathrm{regA}}-\mathrm{AUC}_{\mathrm{regA}\to\mathrm{regB}}\right|}{0.5}\right)+\left(1-\frac{\left|\mathrm{AUC}_{\mathrm{regB}\to\mathrm{regB}}-\mathrm{AUC}_{\mathrm{regB}\to\mathrm{regA}}\right|}{0.5}\right)\right)}{1+\left\|\frac{\mathrm{AUC}_{\mathrm{regA}\to\mathrm{regA}}-\mathrm{AUC}_{\mathrm{regA}\to\mathrm{regB}}}{0.5}\right|-\left|\frac{\mathrm{AUC}_{\mathrm{regB}\to\mathrm{regB}}-\mathrm{AUC}_{\mathrm{regB}\to\mathrm{regA}}}{0.5}\right\|} \tag{3.1}$$

$\mathrm{AUC}_{\mathrm{regA}\to\mathrm{regA}}$ ($\mathrm{AUC}_{\text{AsiaMinor and Thrace} \to \text{AsiaMinor and Thrace}}$) and $\mathrm{AUC}_{\mathrm{regB}\to\mathrm{regB}}$ ($\mathrm{AUC}_{\text{Europe} \to \text{Europe}}$) are internal evaluations, when the model is fitted and evaluated in the same region. $\mathrm{AUC}_{\mathrm{regA}\to\mathrm{regB}}$ ($\mathrm{AUC}_{\text{Asia Minor and Thrace} \to \text{Europe}}$) and $\mathrm{AUC}_{\mathrm{regB}\to\mathrm{regA}}$ ($\mathrm{AUC}_{\text{Europe} \to \text{Asia Minor and Thrace}}$) are external evaluations, when the model is fitted in one region and evaluated in another region. The T1 index values vary between 0 and 1; 1 indicating that a difference between internal and external evaluation is null.

Kulczynski's coefficient (KC) was used to check the third criteria of full transferability (Eq. 3.2). Two KC values were produced. One for predicted and projected probability distribution for Asia Minor and Thrace, the other for predicted and projected probability distribution for Europe.

$$KC_{jk} = \frac{\sum_{i=1}^{n} X_{ij} - \sum_{i=1}^{n} \min(X_{ij}, X_{ik})}{\sum_{i=1}^{n} X_{ij}} \tag{3.2}$$

J and k are predicted and projected map distributions (comparison of internal and external predictions). Xij and Xjk are the habitat suitability for cell i for maps j and k of total number of n cells.

The third group of models included projections to the LGM under CCSM and MIROC climate models. The models were run with six selected variables and intended to locate putative glacial refugia of *M. s. schreibersii* and *M. s. pallidus*. The average of the projection maps was calculated to obtain the consensus distribution model.

Finally, the fourth group of models included future projections for the years 2020, 2050, and 2080. The projections were done under HADCM3, CCCMA, and CSIRO climate models, with addition of a2a and b2a scenarios. Percentage areas covered by different probability (threshold) values (≥ 0.3, ≥ 0.4, ≥ 0.5, ≥ 0.6, ≥ 0.7, and ≥ 0.8) were analyzed in order to determine the effect of global climate change on populations' expansions and contractions. Here, a consensus map was also calculated.

3.2. Input Data

3.2.1. Environmental Layers

Models were developed using climatic, land cover, elevation, land use, and vegetation data (Table 3.1, Table 3.2, Table 3.3, and Table 3.4). Current climatic variables, past climatic data (for the LGM period under CCSM and MIROC climate models), and future climatic conditions (for the years 2020, 2050, and 2080 under HADCM3, CCCMA, CSIRO climate models, and A2A and B2A scenarios) were obtained from WorldClim.

Other variables were obtained from International Steering Committee for Global Mapping (ISCGM, Global Map V.0 data). In all the models, bioclimatic variables were used as climate layers. Bioclimatic variables are derived from monthly temperature and rainfall values and represent annual trends, seasonality, and extreme or limiting environmental factors (Table 3.1) (Worldclim, http://www.worldclim.org/bioclim). Some of the models were run with bioclimatic variables already prepared by Worldclim (Table 3.5). Other models used bioclimatic variables derived from climate data with DIVA-GIS software using methodology described in Ramirez and Bueno (2009).

Bioclimate, land cover, land use, and vegetation are variables, which directly affect the availability of the fundamental primary resources (such as heat, water, and nutrients) and their impact can be generalized. Conversely, elevation is an indirect variable, which is not suitable for generalizations since organisms can compensate for climatic differences by changing their locations in indirect gradients (Guisan and Zimmermann, 2000; Phillips *et al.*, 2006). The validity of projections, which use the elevation variable, depends on geographic extent and preservation of collinearity between the direct-resource variables and elevation. In different geographical regions and under varying environmental conditions, the same altitudinal position can reveal the different combinations of direct-resource gradients (the law of relative site constancy; Walter and Walter [1953], Guisan and Zimmermann [2000]). Elevation is also a topographic variable that is more likely to affect species distributions at meso- and topo- scales (Phillips *et al.*, 2006). Hence, the elevation layer is not suitable for projections.

Predictors used for modelling had a resolution of 2.5 arc-minutes (arc min) and 30 arc-seconds (arc sec). The selection of predictors' resolution was based on the mobility of species and the availability of species occurrence data as suggested by Santana *et al.* (2008). Bats are highly mobile organisms; therefore they are associated with relatively large areas (Findley, 1993). Whenever available, 2.5 arc min grids (an equivalent to 21 km^2 at the equator) were selected.

Table 3.1. Bioclimatic variables (www.worldclim.org)

Bioclimatic Variables
(1) annual mean temperature
(2) mean diurnal range
(3) isothermality
(4) temperature seasonality
(5) maximum temperature of the warmest month
(6) minimum temperature of the coldest month
(7) temperature annual range
(8) mean temperature of the wettest quarter
(9) mean temperature of the driest quarter
(10) mean temperature of the warmest quarter
(11) mean temperature of the coldest quarter
(12) annual precipitation
(13) precipitation of the wettest month
(14) precipitation of the driest month
(15) precipitation seasonality
(16) precipitation of the wettest quarter
(17) precipitation of the driest quarter
(18) precipitation of the warmest quarter
(19) precipitation of the coldest quarter

Table 3.2. Definition of land use variable (http://www.iscgm.org/)

Value	Definition
Forest	Area dominated by trees higher than shrubs with a canopy cover greater than or equal to 10%.
Mixture	Area where more than two classes are mixed including Non-vegetated area, Agricultural area, Grassland/Shrub and Wetland. This class is not applied where one class dominates.
Grassland/shrub	Area covered by trees with canopy cover less than l0%.
Agricultural area	Area where agricultural activities are implemented constantly.
Wetland	Area where underground water level is near the ground surface, or area with humid soil.
Barren area	Non-vegetated area where no artificial structures exist.
Built-up area	Area where artificial structures occupy significant surfaces.
Drainage/water	Area inside coastline forming water surface.
Ocean	Area outside coastline forming water surface.

Table 3.3. Definition of vegetation variable (http://www.iscgm.org/)

Value	Definition
Tropical rainforest	Evergreen forest which has high rainfall and high humidity throughout the year. This class has an upper canopy formed by trees from 30 to 40m tall and may have occasional emerging trees taller than the upper canopy.
Hydrotropic forest	Deciduous broad-leaved trees which are defoliated in dry season and foliate in rainy season.
Grassland in tropical or sub-tropical zone	Grassland which has a long dry season and is heavily dried. Trees are only sparsely distributed. Plant density depends on dryness.
Semi desert in tropical or sub-tropical zone	Plants are sparsely distributed in the area which has a little rainfall and is heavily dried.
Desert in tropical or sub-tropical zone	Plants are very sparsely distributed in the area which has a little rainfall and is extremely dried.
Evergreen thick-leaved forest	Forest which has high rainfall in the rainy season and is relatively dried in summer. Trees which have evergreen thick and hard leaves dominate this forest.
Evergreen broad-leaved forest	Forest in the warm temperate zone which has high rainfall in summer, or is humid throughout the year. Broad-leaved trees which have a little larger leaves than evergreen thick-leaved trees are the main component of this forest.
Deciduous broad-leaved forest	Forest which mainly consists of trees defoliated in winter. This forest appears in the area which has sufficient rainfall in cool temperate zone.
Grassland in temperate zone	Grassland in drier climates in temperate zone. No trees grow.
Semi-desert in temperate zone	Heavily dried area in the temperate zone. Grasses, such as mugwort and pigweed cover this area.
Desert in temperate zone	Extremely dried area in temperate zone. Grasses, such as mugwort and pigweed cover this area.
Northern coniferous forest	Coniferous trees in semi-frigid zone which has very cold and long winter. Trees in this forest are usually evergreen.
Tundra	Plant colony consists of shrub, grass with broad leaves, moss and lichen. Trees cannot become tall due to severe cold.
Water body	Water surfaces, such as rivers and lakes.
Ice and snow	Area which is covered with snow and ice throughout the year.
Wetland	Vegetated area with waterlogged soils or surface water for significant periods of the year.
Mixed forest	Forest containing a mixture of types. Usually deciduous and coniferous.
Mixed land	Area containing a mosaic of other types.
Non natural	Cultivated, urban or otherwise modified vegetation.
Unclassified	Areas not included in other classifications. For example, baren land.

Table 3.4. Definition of land cover variable (http://www.iscgm.org/)

Value	Definition
Evergreen Needleleaf Forest	Lands dominated by trees with a percent canopy cover > 60% and height exceeding 2 meters. Almost all trees remain green all year. Canopy is never without green foliage.
Evergreen Broadleaf Forest	Lands dominated by trees with a percent canopy cover > 60% and height exceeding 2 meters. Almost all trees remain green all year. Canopy is never without green foliage.
Deciduous Needleleaf Forest	Lands dominated by trees with a percent canopy cover > 60% and height exceeding 2 meters. Consists of seasonal needleleaf tree communities with an annual cycle of leaf-on and leaf-off periods.
Deciduous Broadleaf Forest	Lands dominated by trees with a percent canopy cover > 60% and height exceeding 2 meters. Consists of seasonal broadleaf tree communities with an annual cycle of leaf-on and leaf-off periods.
Mixed Forest	Lands dominated by trees with a percent canopy cover > 60% and height exceeding 2 meters. Consists of tree communities with interspersed mixtures or mosaics of the other four forest cover types. None of the forest types exceeds 60% of the landscape.
Closed Shrublands	Lands with woody vegetation less than 2 meters tall and with shrub canopy cover > 60%. The shrub foliage can be either evergreen or deciduous.
Open Shrublands	Lands with woody vegetation less than 2 meters tall and with shrub canopy cover between 10-60%. The shrub foliage can be either evergreen or deciduous.
Woody Savannas	Lands with herbaceous and other understory systems and with forest canopy cover between 3-60%. The forest cover height exceeds 2 meters.
Savannas	Lands with herbaceous and other understory systems, and with forest canopy cover between 10-30%. The forest cover height exceeds 2 meters.
Grasslands	Lands with herbaceous types of cover. Tree and shrub cover is less than 10%.
Permanent Wetlands	Lands with a permanent mixture of water and herbaceous or woody vegetation that cover extensive areas. The vegetation can be present in either salt, brackish, or fresh water.
Croplands	Lands covered with temporary crops followed by harvest and a bare soil period (e.g., single and multiple cropping systems). Note that perennial woody crops will be classified as the appropriate forest or shrub land cover type.
Urban and Built-Up	Land covered by buildings and other man-made structures.
Cropland/Natural Vegetation Mosaic	Lands with a mosaic of croplands, forests, shrub lands, and grasslands in which no one component comprises more than 60% of the landscape.
Snow and Ice	Lands under snow and/or ice cover throughout the year.
Barren or Sparsely Vegetated	Lands with exposed soil, sand, rocks, or snow and never has more than 10% vegetated cover during any time of the year.
Water Bodies	Oceans, seas, lakes, reservoirs, and rivers. Can be either fresh or salt water bodies.

Table 3.5. The list of environmental variables used in modelling (Only resolution 2.5 arc min and 30 arc sec were considered. Available data are marked with 'x'. Pink colored layers were used to determine the most important variables to explain the distribution of *M. s. schreibersii* and *M. s. pallidus*. Blue colored layers were used for past projection and green colored layers were used for future projections).

	Past(LGM-CCSM,MIROC)		**Current**		**Future (HADCM3, CCCMA, CSIRO)**	
	2.5 arc min	**30 arc sec**	**2.5 arc min**	**30 arc sec**	**2.5 arc min**	**30 arc sec**
Worldclim						
Tmin	-	-	x	x	x	x
Tmax	-	-	x	x	x	x
Prec	-	-	x	x	x	x
Bioclim(Ready to use from WorldClim)	x	-	x	x	-	-
Bioclim(Derived from Tmin, Tmax, Prec)	-	-	x	x	x	x
ISCGM						
Vegetation	-	-	-	x	-	-
Land Cover	-	-	-	x	-	-
Land Use	-	-	-	x	-	-
Elevation	-	-	-	x	-	-

For the current distribution projections, variables with 30 arc sec resolutions were used. After selecting the most important variables for determining species' distribution, 2.5 arc min resolution layers were used to test transferability of *M. s. schreibersii* between Europe and Asia Minor and Thrace. For the past climatic projections, variables had a resolution of 2.5 arc min. For the future projections, precipitation, minimum temperature and maximum temperature data were available in a resolution of 2.5 arc min, while other variables were derived from them. The variables used in various projections are listed in Table 3.5.

3.2.2. Species Data

All species occurrence data used to construct models and check their transferability were derived from 198 recorded locations of *M. s. schreibersii* and 45 recorded locations of *M. s. pallidus* (Fig. 3.1B). Predictions for Asia Minor and Thrace were based on 83 locations of *M. s. schreibersii* and 45 locations of *M. s. pallidus*. Only the presence data were used to run the models. The presence data were obtained from the GBIF database (www.gbif.org), and literature reviews (Albayrak and Coskun, 2000; Benda *et al.*, 2006; Benda and Horacek, 1998; Bilgin *et al.*, 2008; DeBlase, 1980; Furman et al., 2009; Karatas and Sözen, 2004).

Out of 3,777 *M. schrebersii* records obtained from GBIF database and 259 records from the literature review, only 198 records were selected to ensure homogenous distribution of locations density (equal sampling per unit size) and to minimize spatial autocorrelation (Fig. 3.1). Spatial autocorrelation arises when ‘probability of occurrence in one unit is not independent of the probability of occurrence in neighboring unit’ (Fielding and Bell, 1997). Violation of spatial autocorrelation is a leading source of problems in test statistics (Fielding and Bell, 1997). Hence, the area of the study was divided into five by five degree areas and records were randomly selected for each area.

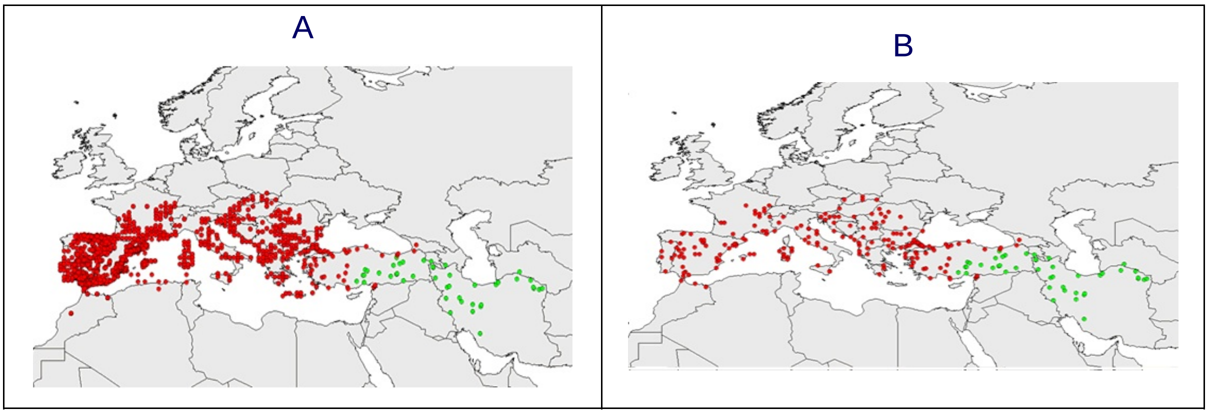


Figure 3.1. A) Available location data of *M. s. schreibersii* (red points) and *M. s. pallidus* (green points). B) The locations of *M. s. schreibersii* used for modelling, after removal of some sites from the data set. These data consist of all occurrence points that were used for model construction and checking transferability.

4. RESULTS

4.1. Selecting the Variables

To determine the most important predictors affecting distribution of bats, variables were eliminated one by one, each time a model was run. With six variables were left, elimination of one more variable resulted in considerable decrease in gain and in AUC values compared to previous eliminations.

The most important variables for explaining the current distribution of both, *M. s. schreibersii* and *M. s. pallidus* were annual temperature range, mean temperature of wettest quarter, mean temperature of driest quarter, and annual precipitation. Variables specific to each lineage were isothermality and precipitation of driest quarter for *M. s. schreibersii*, and elevation and precipitation seasonality for *M. s. pallidus*. The AUC values for the models based on these six variables were high for both lineages, indicating excellent discrimination capacity of suitable versus unsuitable habitats. For *M. s. schreibersii* the regularized training gain was 1.873 and the training AUC was 0.950. For *M. s. pallidus* the regularized training gain was 1.625, and the training AUC was 0.946.

Replications with cross validation analyses for *M. s. pallidus* revealed that elevation contributed the least to the test gain in jackknife analysis, although this variable contributed the most to the model (32.1%) (Fig. 4.1). The elevation, however, is an indirect variable and not too suitable for generalizations. Therefore, using elevation in projections to other geographical spaces or time zones could produce misleading results. Thus, for projections, only climate variables were used and the elevation variable was removed from the list. For *M. s. schreibersii,* the test jackknife results were parallel to the training jackknife results (Fig. 4.2). A new model for *M. s. pallidus* (without the elevation layer) included isothermality, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, annual precipitation, and precipitation of the warmest quarter. The model had the regularized training gain of 1.531 and the training AUC of 0.943. The threshold values, 0.3 for *M. s. schreibersii and* 0.4 for *M. s. pallidus* was selected because these values maximized the agreement between observed and predicted distributions in Asia Minor and Thrace trained models (Fig. 4.3).

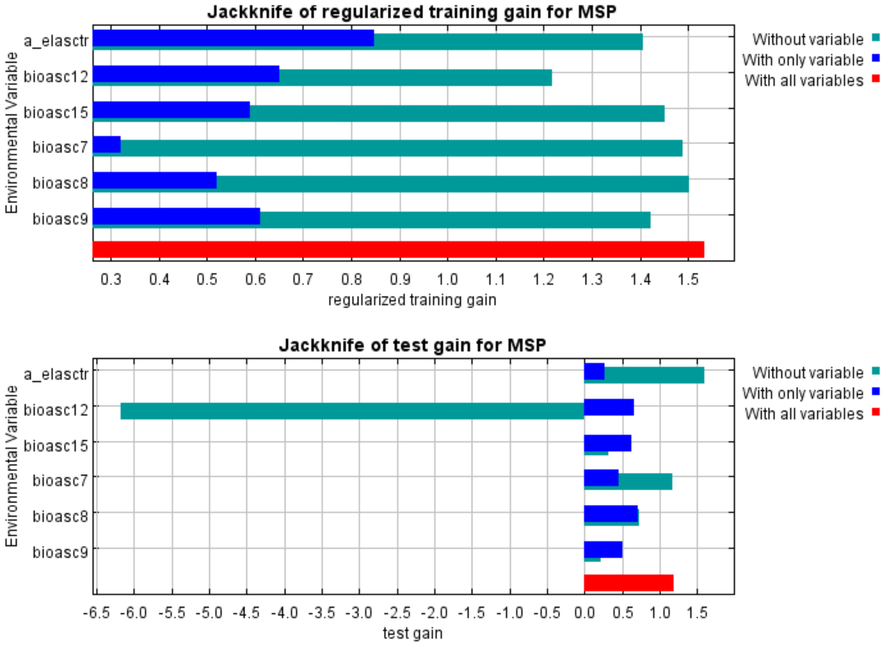


Figure 4.1. Jackknife analysis of the training and test gain for *M. s. pallidus*. Replication with cross-validation. Elevation is coded as ‘a_elasctr.’

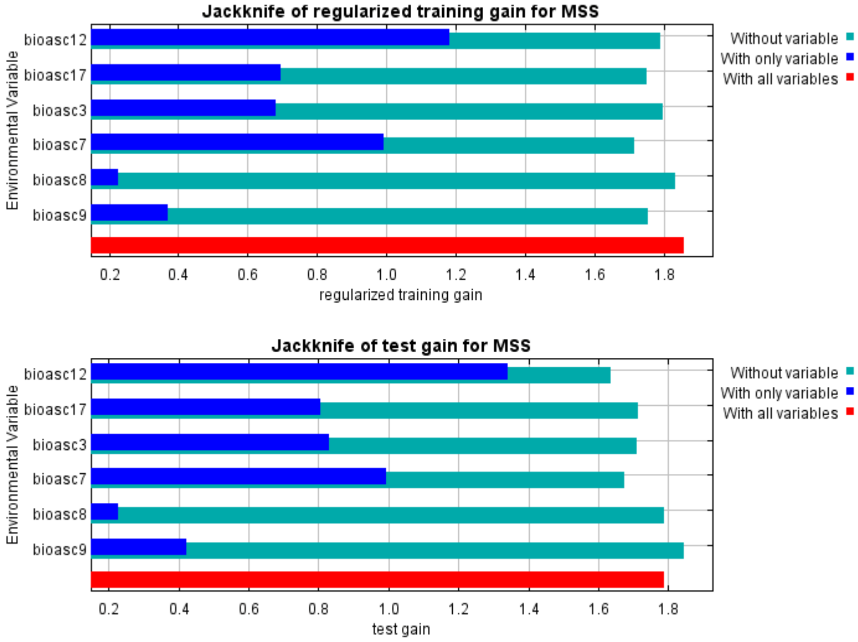


Figure 4.2. Jackknife analysis of training and test gain for *M. s. schreibersii*. Replication with cross-validation.

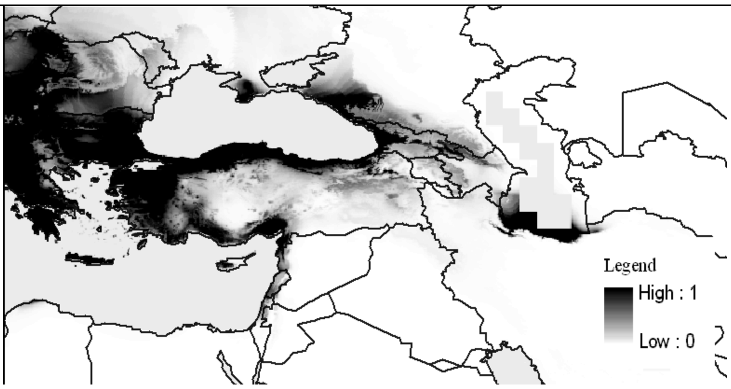
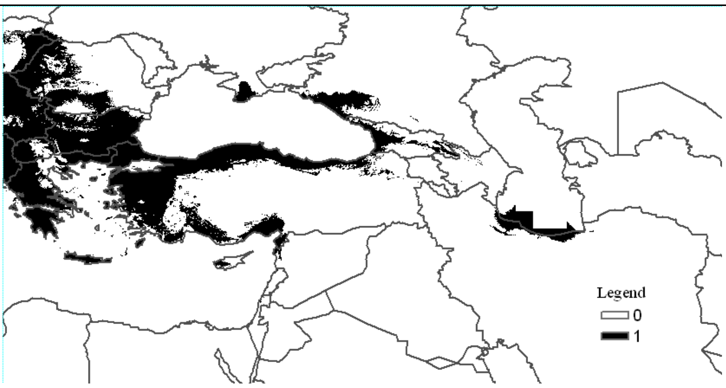
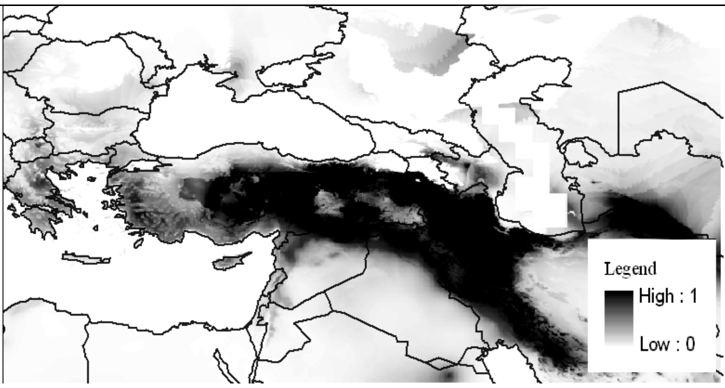
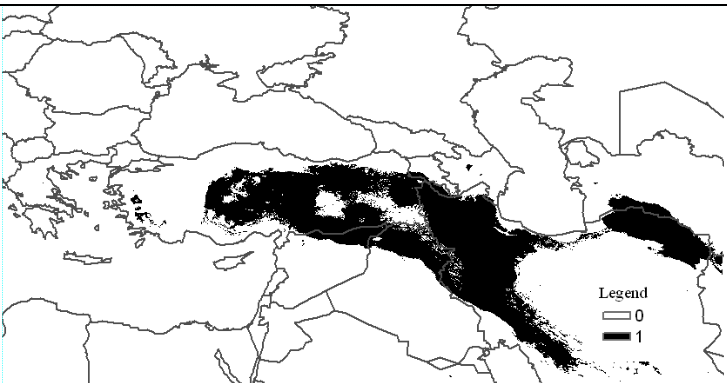
M. s. schreibersii	
M. s. schreibersii Threshold applied (0.3)	
M. s. pallidus	
M. s. pallidus Threshold applied (0.4)	

Figure 4.3. The predicted current distributions of *M. s. schreibersii* and *M. s. pallidus* in Asia Minor and Thrace.

4.2. Testing transferability

When predicting distribution by projection it was assumed that the niche of a species was conserved. Furman *et al.* (2010b) analyzed 547 sequences from the eastern (Thrace, the Black Sea, Central Anatolia and Mediterranean) and western (Iberian Peninsula) colonies of *M. s. schreibersii*. They found shallow genetic differentiation (< 1%) between eastern and western colonies, indicating that the *M. s. schreibersii* only recently colonized Europe. Niches evolve over long periods of time with exposure to adaptation and genetic variation. Very recent colonization therefore indicates niche conservatism, which ensures more accurate projections.

To check for full transferability, two models were run with the six most important variables; the first model constructed from Asia Minor and Thrace data was projected to Europe and the second model was constructed from European data and projected to Asia Minor and Thrace. The predicted outputs of both models were then compared (Fig. 4.4).

The difference between predicted and projected maps was not caused by the difference in success of internal evaluation of models in these regions (Fig. 4.5). The similarity of internal evaluations of models was checked with the transferability index (Eq. 4.1). The result was better than average, indicating the similarity of internal evaluations and comparability of internal and external evaluations.

$$\mathrm{T} = \frac{\frac{1}{2}\left(\left(1-\frac{|0.952-0.770|}{0.5}\right)+\left(1-\frac{|0.823-0.918|}{0.5}\right)\right)}{1+\left\|\frac{0.952-0.770}{0.5}\right|-\left|\frac{0.823-0.918}{0.5}\right\|} \tag{4.1}$$

$$\mathrm{T} = \frac{0.723}{1.174} = 0.616$$

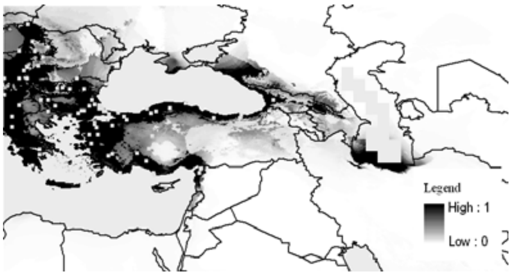
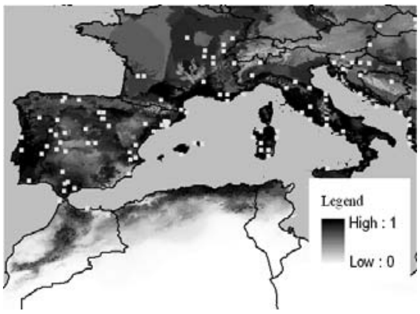
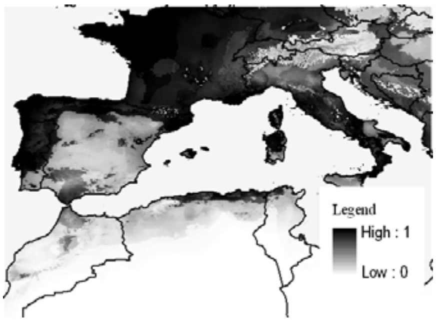
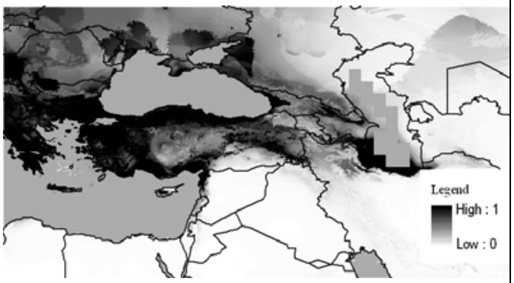
	Model fitted to Asia Minor and Thrace and then projected to Europe	Model fitted to Europe and then projected to Asia Minor and Thrace
Internal AUC	A Regularized training gain = 1.867, $\text{AUC}_{\text{Asia Minor and Thrace} \rightarrow \text{Asia Minor and Thrace}}$ = 0.952-excellent  	B Regularized training gain = 0.603, $\text{AUC}_{\text{Europe} \rightarrow \text{Europe}}$ = 0.823-good 
External AUC	C $\text{AUC}_{\text{Asia Minor and Thrace} \rightarrow \text{Europe}}$ = 0.770-fair  	D $\text{AUC}_{\text{Europe} \rightarrow \text{Asia Minor and Thrace}}$ = 0.918-excellent 
Kulczynski	Europe – Europe → Asia Minor and Thrace - Europe 0.34	Asia Minor and Thrace – Asia Minor and Thrace → Europe – Asia Minor and Thrace 0.08

Figure 4.4. Maps of models that were run to check full transferability (The model constructed from Asia Minor and Thrace data (A) was projected to Europe (C). The model constructed from European data (B) was projected to Asia Minor and Thrace (D). C-B and A-D were compared).

Although the model predicting distribution of *M. s. schreibersii* in Asia Minor and Thrace had an excellent discrimination capacity (the regularized training gain was 1.867 and the $\text{AUC}_{\text{Asia Minor and Thrace} \rightarrow \text{Asia Minor and Thrace}}$ was 0.952), its projection had only a fair discrimination capacity ($\text{AUC}_{\text{Asia Minor and Thrace} \rightarrow \text{Europe}} = 0.770$). The model for predicting European distribution had good discrimination capacity (the regularized training gain was 0.603 and the $\text{AUC}_{\text{Europe} \rightarrow \text{Europe}}$ was 0.823) and its projection had excellent discrimination capacity (AUC $_{\text{Europe} \rightarrow \text{Asia Minor and Thrace}}$ = 0.918). The KC value for Asia Minor and Thrace was 0.08 and the KC value for Europe was 0.34. These KC values satisfied asymmetrical transferability, which means that transferability was good from one region to another but not vice versa. The difference in predictions was perhaps caused by the geographical dissimilarity of these two regions. For example, the Mediterranean Basin is heterogeneous in terms of climate and geography, which poses challenges for prediction modelling. A similar problem can arise when making projections for different geographical areas. Maxent uses exponential modelling and can give very large predicted values for conditions that are outside the typical ranges. Accordingly, projections should be 'clamped' and set at the upper or lower bound of the training range (Phillips *et al.* 2006).

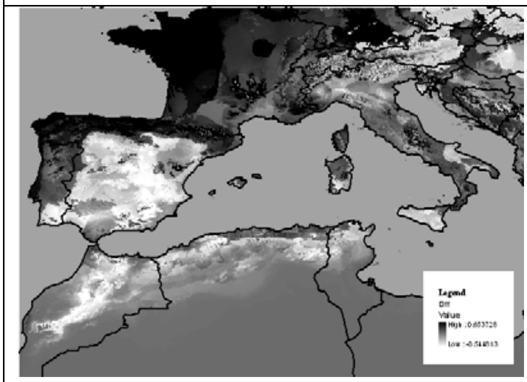
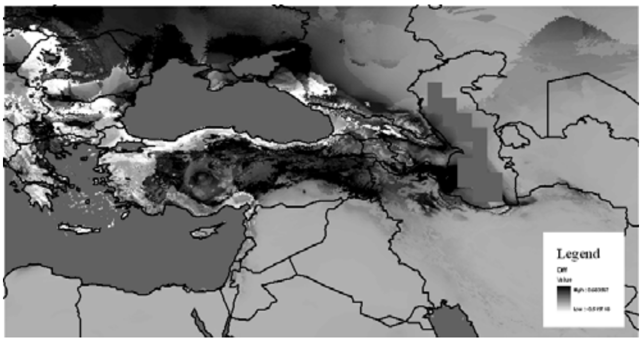
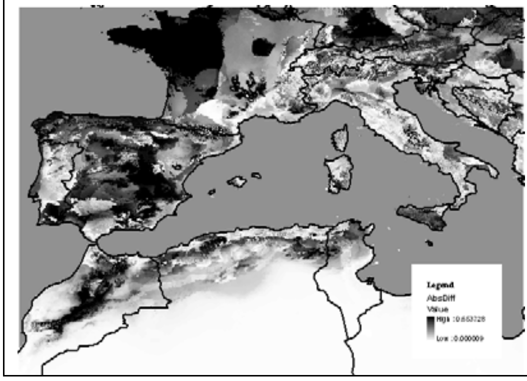
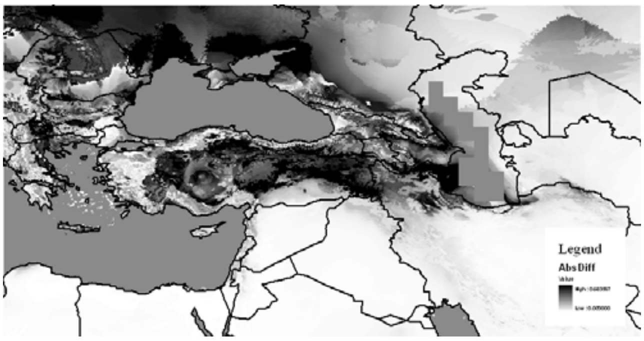
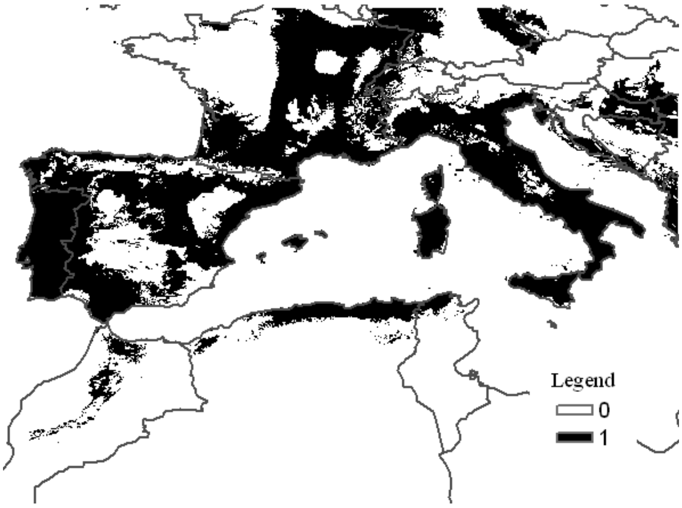
Difference of B-C	Difference of A-D
	
Absolute value 	Absolute value 

Figure 4.5. Maps showing the difference of predicted and projected distributions.

With the threshold set to 0.5, which maximized the agreement between observed and predicted distributions for the model trained in Europe, that projection was successful in predicting the distribution of *M. s. schreibersii* in Asia Minor and Thrace (Fig. 4.6). The AUC $_{\text{Europe} \rightarrow \text{Asia Minor and Thrace}}$ value was 0.918 and could be categorized as having excellent discrimination capacity. Projection to Europe with the Asia Minor and Thrace trained model had the $\text{AUC}_{\text{Asia Minor and Thrace} \rightarrow \text{Europe}}$ of 0.770 (fair) and was not as successful in predicting distribution in Europe as when the threshold value of 0.3 was applied (Fig. 4.7). The threshold value of 0.3 maximized the agreement between observed and predicted distributions of *M. s. schreibersii* in Asia Minor and Thrace trained model. These results were consistent with KC values of 0.08 (Asia Minor and Thrace) and 0.34 (Europe), satisfying asymmetrical transferability.

Model trained in Europe, Threshold = 0.5

$\text{AUC}_{\text{Europe} \rightarrow \text{Europe}}$ = 0.823-good



$\text{AUC}_{\text{Europe} \rightarrow \text{Asia Minor and Thrace}}$ = 0.918-excellent

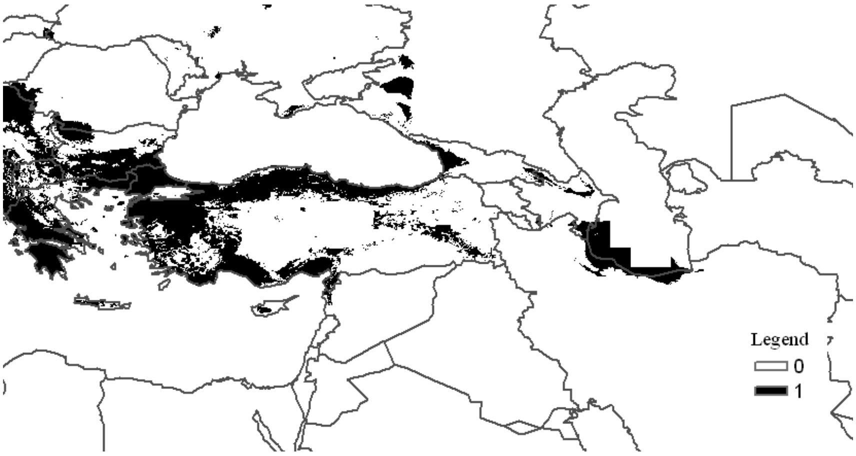
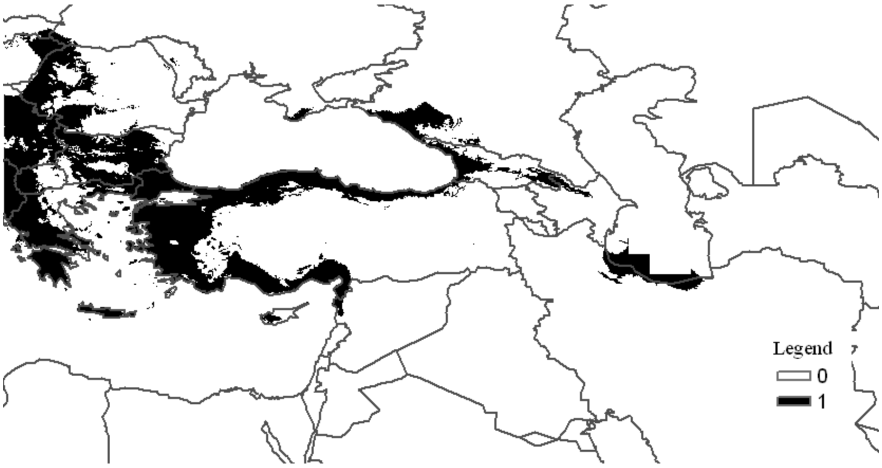


Figure 4.6. Prediction maps of the model trained in Europe and projected to Asia Minor and Thrace with the threshold value of 0.5.

Model trained in Asia Minor and Thrace, Threshold = 0.3

$\text{AUC}_{\text{Asia Minor and Thrace} \rightarrow \text{Asia Minor and Thrace}}$ = 0.952-excellent



$\text{AUC}_{\text{Asia Minor and Thrace} \rightarrow \text{Europe}}$ = 0.770-fair

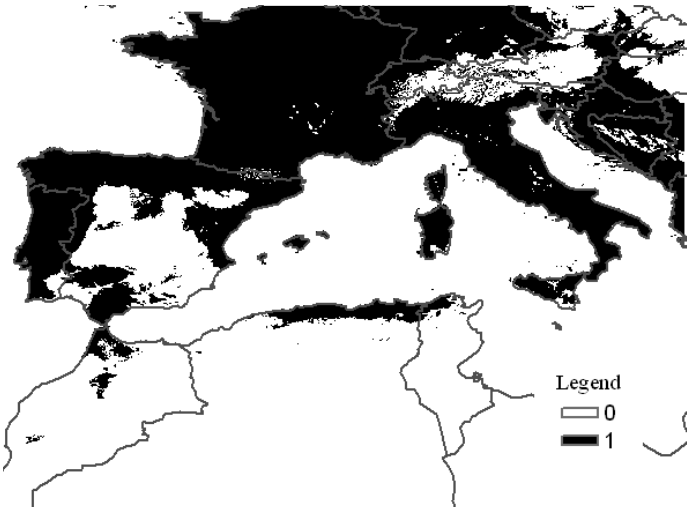
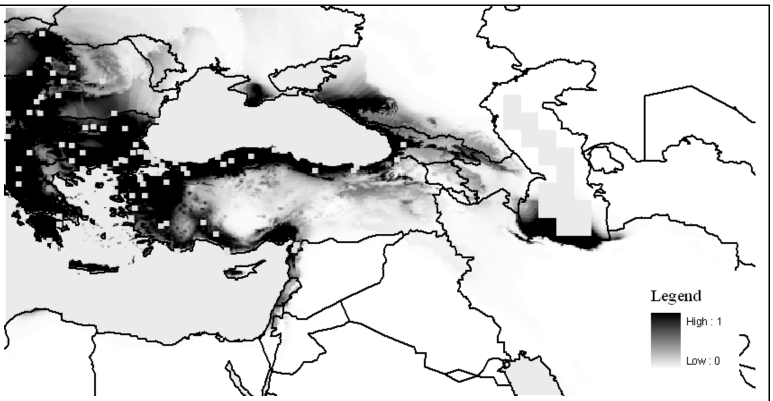


Figure 4.7. Prediction maps of the model trained in Asia Minor and Thrace and projected to Europe with the threshold value of 0.3.

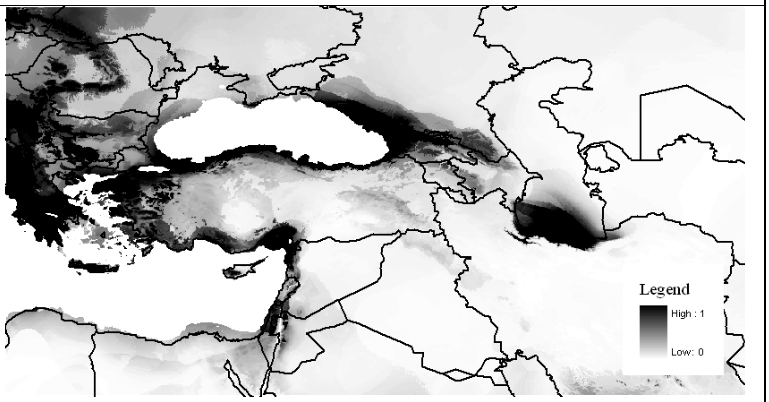
4.3. Predicting the LGM distributions

To identify locations of the putative refugia of *M. s. schreibersii* and *M. s. pallidus* during the LGM, projections were made with CCSM and MIROC models and the outcomes were averaged. For *M. s. schreibersii*, the regularized training gain was 1.867, and the training AUC was 0.952. For *M. s. pallidus*, the regularized training gain was 1.433 and the training AUC was 0.933. The projections are presented on Fig. 4.8 and Fig. 4.9.

Current



LGM



LGM

Threshold applied (0.3)

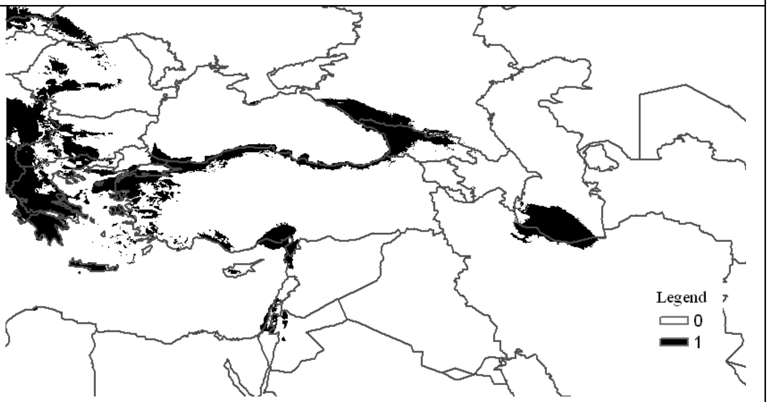


Figure 4.8. The projected distribution of *M. s. schreibersii* during the LGM. The projections were done with six bioclimatic variables.

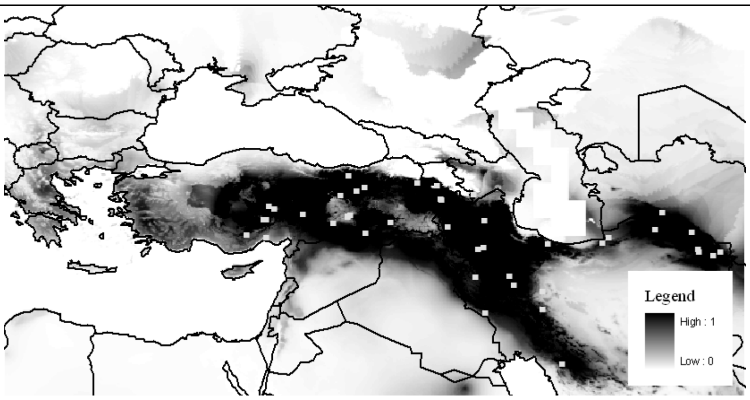
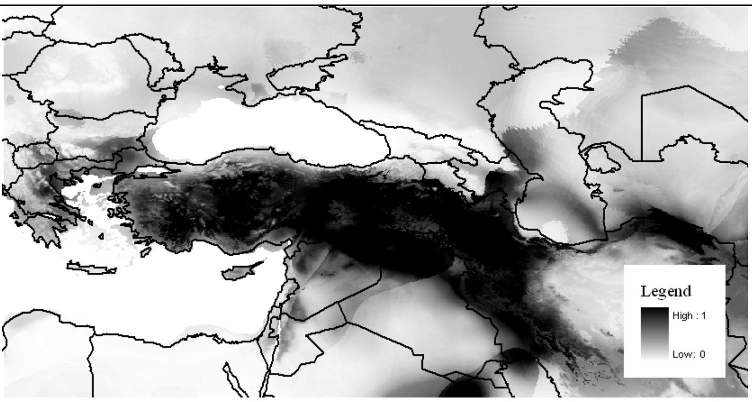
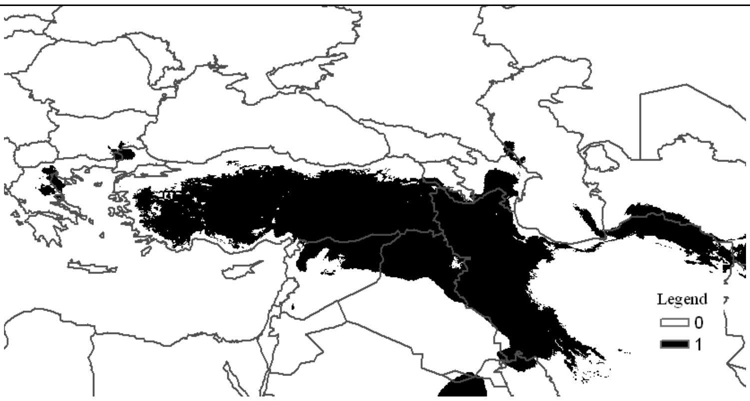
Current	
LGM	
LGM Threshold applied (0.4)	

Figure 4.9. The projected distribution of *M. s. pallidus* during the LGM. The projections were done with six bioclimatic variables.

The predicted distribution of *M. s. schreibersii* during the LGM corresponded to the putative location of the glacial refugia from literature review. The predicted distribution of *M. s. pallidus*, however, was clearly over-predicted (the high commission error). The overestimation was probably caused by species-specific requirements that were not incorporated into the correlative modelling approach. To cover a wider range of parameters, new models were run with all bioclimatic variables. The new projections indicated that the distribution of *M. s. pallidus* distribution was determined by wider range of climatic variables than the distribution of *M. s. schreibersii*. Apparently, whereas there was no noticeable difference in the distribution of *M. s. schreibersii* projected from the six and from all bioclimatic variables; there was a considerable difference in the distribution of *M. s. pallidus*. The regularized training gain was 1.912 and the training AUC was 0.959 for *M. s. schreibersii*. For *M. s. pallidus*, the regularized training gain was 1.575 and the training AUC was 0.947. The results are presented on Fig. 4.10 and Fig. 4.11.

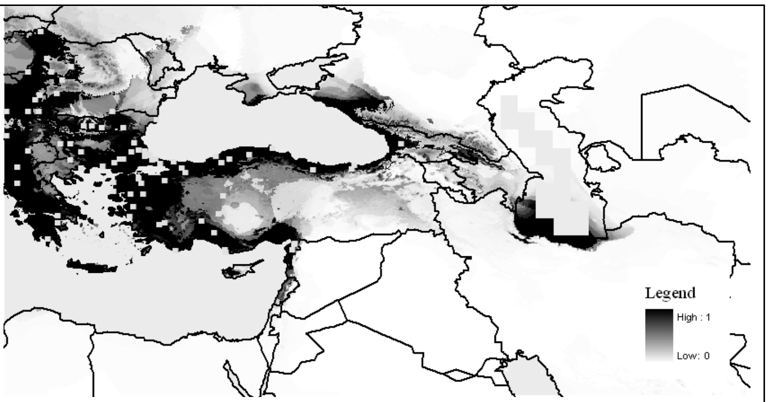
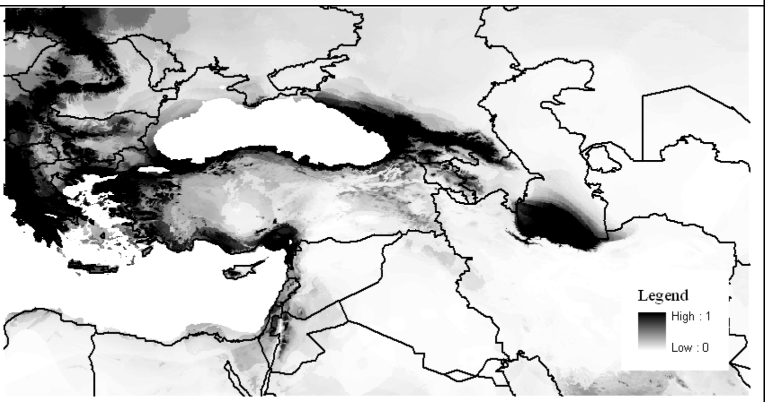
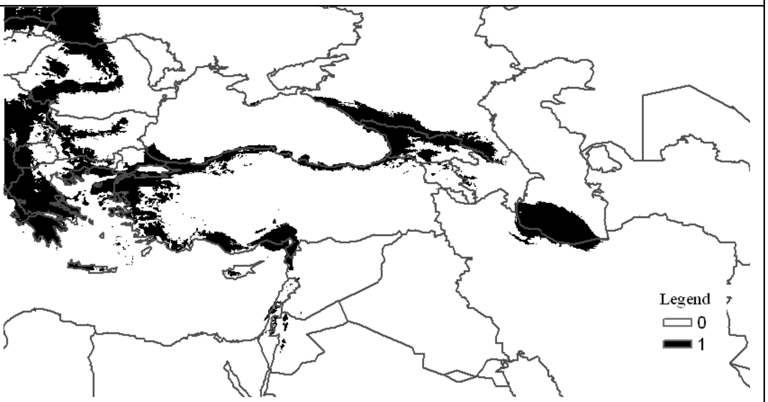
Current	
LGM	
LGM Threshold applied (0.3)	

Figure 4.10. The projected distribution of *M. s. schreibersii* during the LGM. The projections were done with all bioclimatic variables.

The predicted distribution of *M. s. schreibersii* was in agreement with the genetic study of Furman *et al.* (2010b). Accordingly, it is possible that *M. s. schreibersii* survived the LGM not only in Thrace, but also in Transcaucasia and Southern Anatolia. The Thracian refugium was probably located in the Bosphorus and Dardanelles Strait and the Trans-Caucasian refugium somewhere in the Colchis region of today's eastern Georgia (Krebs *et al.*, 2004). The Southern Anatolian refugium or refugia was/were located along the Mediterranean coasts of Turkey, Syria and Lebanon (Krebs *et al.*, 2004; Medail and Diadema, 2009; Tzedakis, 2009).

The locations with the highest *presence* probability within the distribution of *M. s. pallidus*, during the LGM, pointed out to the southern part of the Caspian Sea and to the region along the Turkish-Syrian border. The former location is a part of the Trans-Caucasian refugium and overlaps with the type locality of *M. s. pallidus*, the latter location does not correspond to any know glacial shelters. This result was only in partial agreement with genetic study of Furman *et al.* (2010a), which excluded the presence of *M. s. pallidus* in the south of Turkey before, or during the LGM, and estimated the approximate time of occurrence of *M. s. pallidus* in Southern Anatolia to about 13,000 years BP. It was suggested that the late arrival of *M. s. pallidus* to Anatolia was caused by the high altitude of the region or scarcity of suitable underground habitats (Furman *et al.*, 2010a). Accordingly, the disagreement between the model projection and genetic data might result from inability of the static models to incorporate dispersal limiting factors into the classifier. The disagreement might also arise from the specificity of the projected region; the Mediterranean Basin, Anatolia, the western Irano-Turanian region, and the Zagros region are very heterogeneous in terms of climate and geography, which poses a considerable challenge for the refugia modelling (Medail and Diadema, 2009). The areas of the putative glacial refugia in the Mediterranean Basin have a numerous range of microhabitats with varied topography (Tzedakis, 2009; Medail and Diadema, 2009), and the areas in Anatolia and Iran are mountainous and have continental climate, where favorable microclimate niches may have existed in marginal positions (Krebs *et al.*, 2004).

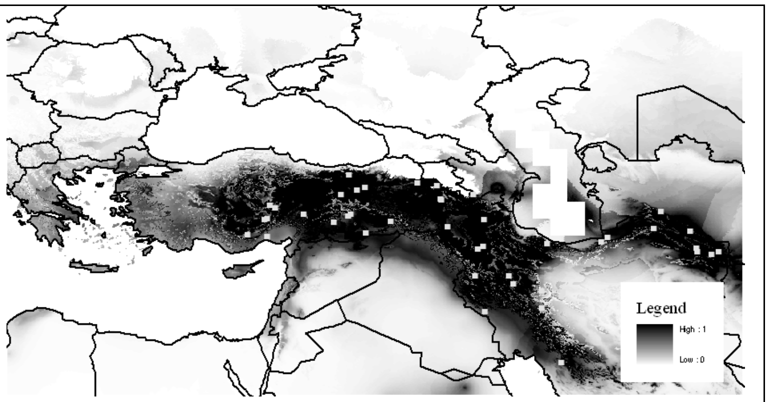
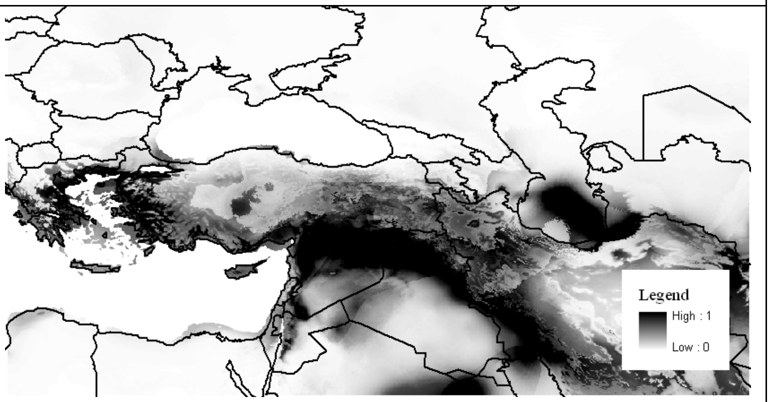
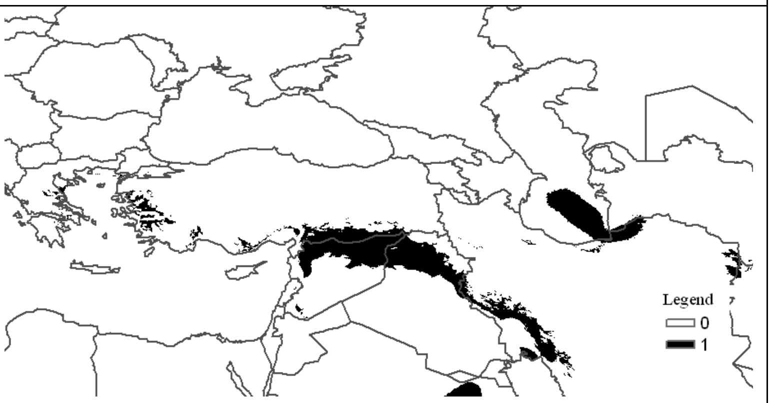
Current	
LGM	
LGM Threshold applied (0.4)	

Figure 4.11. The projected distribution of *M. s. pallidus* during the LGM. The projections were done with all bioclimatic variables.

4.4. Predicting distribution under global climate change scenarios

The models for predicting distributions of *M. s. schreibersii* and *M. s. pallidus* under the global climate change scenarios were run with all bioclimatic variables. The regularized training gain was 1.802 and the training AUC was 0.949 for *M. s. schreibersii*. For *M. s. pallidus*, the regularized training gain was 1.383 and the training AUC was 0.927. The predictions were derived from three climate models (HADCM3, CCCMA, and

CSIRO) run under the A2A and B2A scenarios; the outputs from each climate models were averaged (Fig. 4.12, Fig. 4.13, Fig. 4.14, and Fig. 4.15).

For both the A2A and B2A scenarios, distribution of *M. s. schreibersii* was shrinking dramatically with only a small proportion of its population remaining in the coastal area of western Asia Minor (Fig. 4.12, Fig. 4.13, Fig. 4.14, Fig. 4.15, Fig. 4.16, and Table 4.1). The scenario A2A was more pessimistic than the scenario B2A. By the year 2080, the predicted presence values (higher than 0.3) decreased by 76% in the A2A scenario and by 57% in the B2A scenario (Table 4.1). The value of 0.3 was selected as a model threshold, because it maximized the current observed and predicted distributions. *Miniopterus s. schreibersii* distribution was shrinking with nearly a constant rate under the A2A scenario, and with a decreasing rate under the B2A scenario (for A2A, current to 2020: -2.5%, 2020 to 2050: -3.0%, 2050 to 2080: -2.5%; for B2A, current to 2020: -4.7 %, 2020 to 2050: -1.0 %, 2050 to 2080: -0.3%).

Unlike in the predictions for *M. s. schreibersii*, distribution of *M. s. pallidus* was expanding under both scenarios (Fig. 4.12, Fig. 4.13, Fig. 4.14, Fig. 4.15, Fig. 4.16, and Table 4.1). By the year 2080, for the predicted presence probability values higher than 0.4, *M. s. pallidus* distribution was expanding by 13% under the A2A scenario and by 9% under the B2A scenario (derived from Table 4.1). The value of 0.4 maximized agreement between the currently observed and predicted distributions for *M. s. pallidus*. Distribution of *M. s. pallidus* was expanding in all periods, except for years 2050 to 2080 under the B2A scenario (for A2A, current to 2020: 0.7%, 2020 to 2050: 0.6%, 2050 to 2080: 0.4%; for B2A, current to 2020: 0.8%, 2020 to 2050: 0.7%, 2050 to 2080: -0.5%). Apparently, *M. s. pallidus* was expanding and shifting its distributional range towards northwestern Turkey, where currently *M. s. schreibersii* is present (Fig. 4.12, Fig. 4.13, Fig. 4.14, and Fig. 4.15).

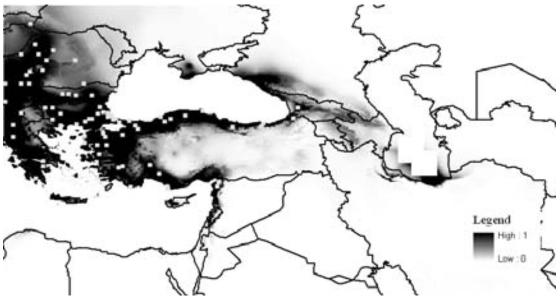
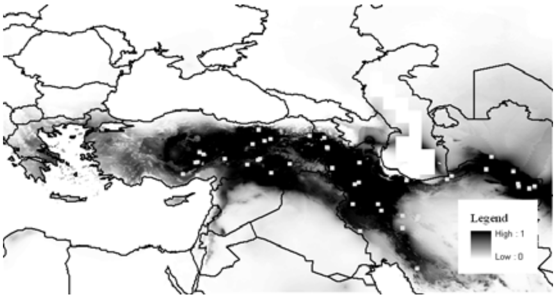
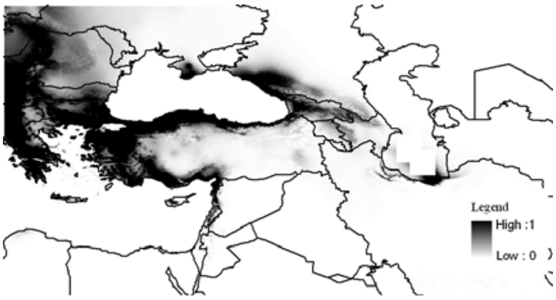
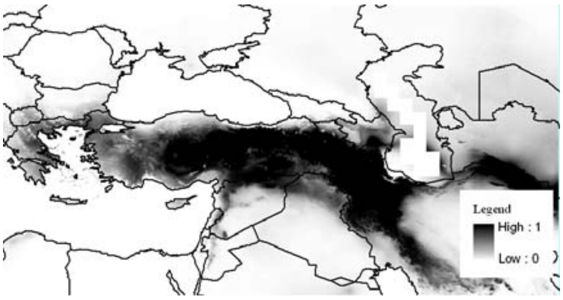
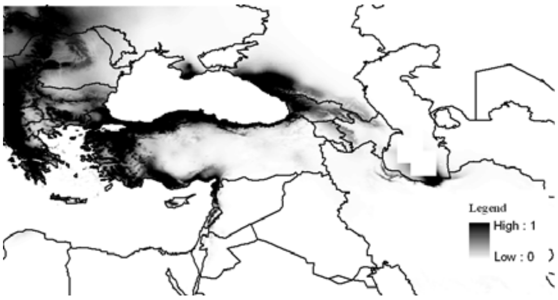
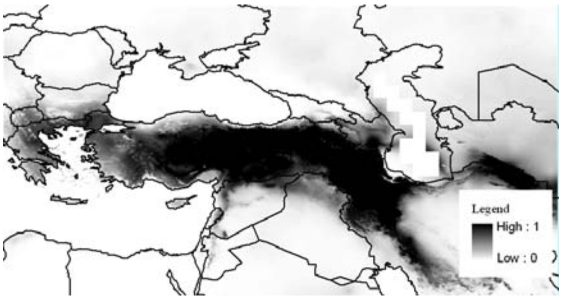
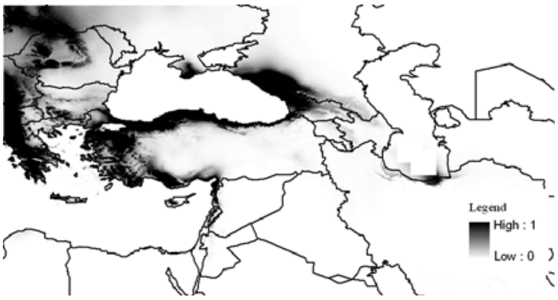
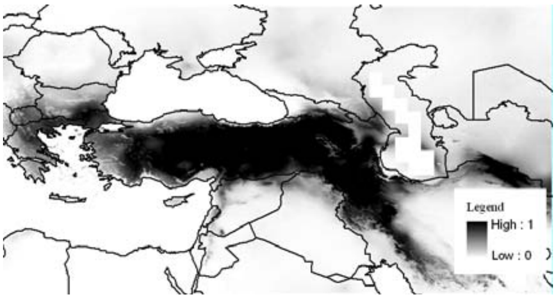
AVERAGE – A2A scenario	
M. s. schreibersii	***M. s. pallidus***
Current 	**Current** 
2020 	**2020** 
2050 	**2050** 
2080 	**2080** 

Figure 4.12. Distribution of *M. s. schreibersii* and *M. s. pallidus* under A2A scenario.

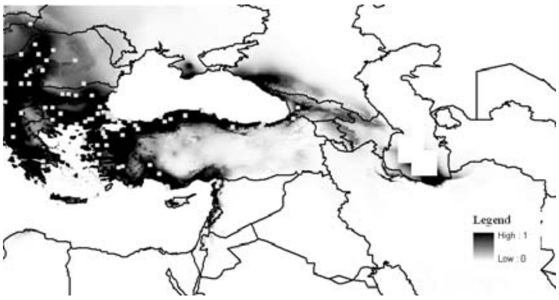
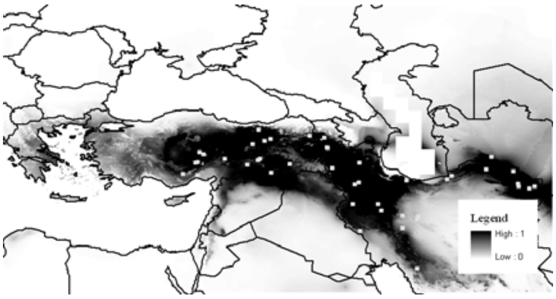
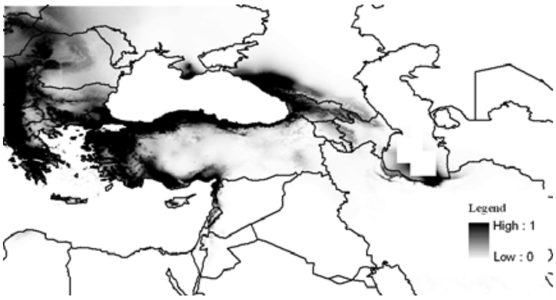
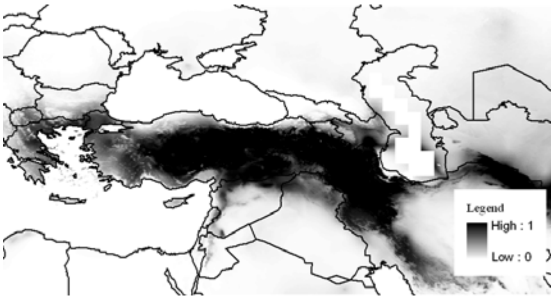
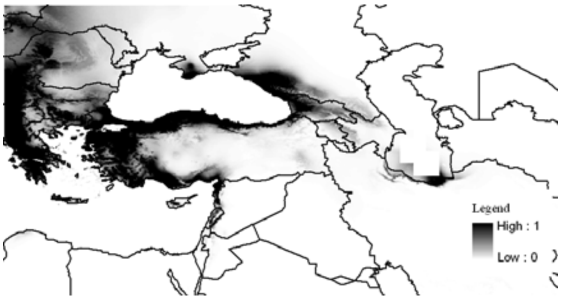
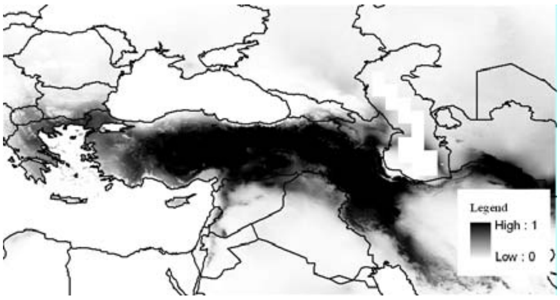
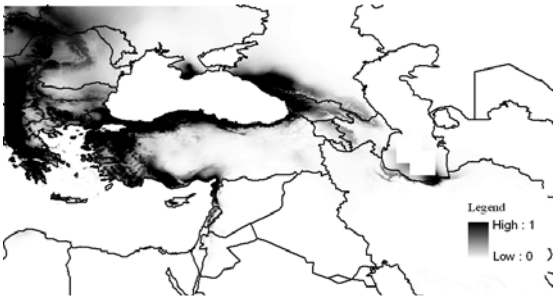
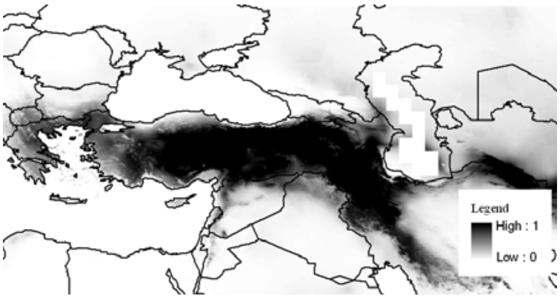
AVERAGE – B2A scenario	
M. s. schreibersii	***M. s. pallidus***
Current  	**Current** 
2020  	**2020** 
2050  	**2050** 
2080  	**2080** 

Figure 4.13. Distribution of *M. s. schreibersii* and *M. s. pallidus* under B2A scenario.

AVERAGE – A2A scenario	
M. s. schreibersii	***M. s. pallidus***
Current 	**Current** 
2020 	**2020** 
2050 	**2050** 
2080 	**2080** 

Figure 4.14. Binary maps with thresholds values, 0.3 for *M. s. schreibersii* and 0.4 for *M. s. pallidus* under A2A scenario.

<table>
<tr><th colspan="2">AVERAGE – B2A scenario</th></tr>
<tr><th>M. s. schreibersii</th><th>M. s. pallidus</th></tr>
<tr><td>Current
 </td><td>Current
 </td></tr>
<tr><td>2020
 </td><td>2020
 </td></tr>
<tr><td>2050
 </td><td>2050
 </td></tr>
<tr><td>2080
 </td><td>2080
 </td></tr>
</table>

Figure 4.15. Binary maps with thresholds values, 0.3 for *M. s. schreibersii* and 0.4 for *M. s. pallidus* under B2A scenario.

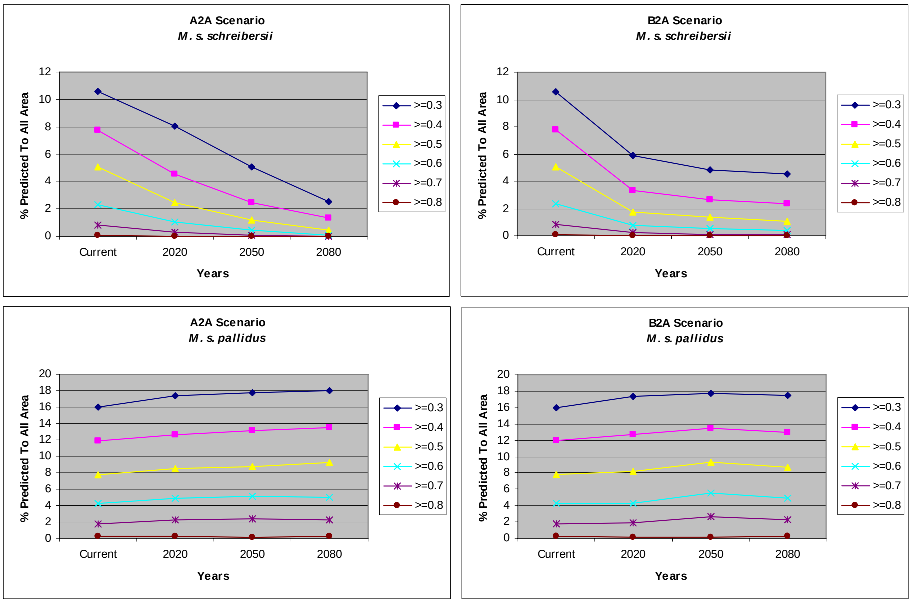


Figure 4.16. Summary of distribution maps of *M. s. schreibersii* and *M. s. pallidus* for future scenarios. A percent of the total are occupied by each species was calculated for the different occurrence probability values (i.e. $p \geq 0.3, \geq 0.4, \geq 0.5, \geq 0.6, \geq 0.7$, and ≥ 0.8).

Table 4.1. A percent of the total are occupied by *M. s. schreibersii* and *M. s. pallidus* for the different occurrence probability values (i.e. $p \geq 0.3, \geq 0.4, \geq 0.5, \geq 0.6, \geq 0.7$, and ≥ 0.8)

A2A *M. s. schreibersii*						
	$p \geq 0.3$	$p \geq 0.4$	$p \geq 0.5$	$p \geq 0.6$	$p \geq 0.7$	$p \geq 0.8$
Current	10.6	7.8	5.1	2.3	0.8	0.1
2020	8.1	4.6	2.5	1.0	0.3	0
2050	5.1	2.5	1.2	0.5	0.1	0
2080	2.5	1.3	0.5	0.1	0	0
B2A *M. s. schreibersii*						
	$p \geq 0.3$	$p \geq 0.4$	$p \geq 0.5$	$p \geq 0.6$	$p \geq 0.7$	$p \geq 0.8$
Current	10.6	7.8	5.1	2.3	0.8	0.1
2020	5.9	3.3	1.8	0.7	0.2	0
2050	4.9	2.7	1.4	0.5	0.1	0
2080	4.6	2.3	1.1	0.4	0.1	0
A2A *M. s. pallidus*						
	$p \geq 0.3$	$p \geq 0.4$	$p \geq 0.5$	$p \geq 0.6$	$p \geq 0.7$	$p \geq 0.8$
Current	15.9	11.9	7.8	4.3	1.8	0.2
2020	17.4	12.6	8.5	4.9	2.2	0.2
2050	17.7	13.2	8.8	5.1	2.4	0.1
2080	17.9	13.6	9.2	5.0	2.3	0.3
B2A *M. s. pallidus*						
	$p \geq 0.3$	$p \geq 0.4$	$p \geq 0.5$	$p \geq 0.6$	$p \geq 0.7$	$p \geq 0.8$
Current	15.9	11.9	7.8	4.3	1.8	0.2
2020	17.3	12.7	8.2	4.3	1.9	0.1
2050	17.8	13.4	9.4	5.5	2.6	0.2
2080	17.5	12.9	8.6	4.9	2.2	0.2

5. DISCUSSION AND CONCLUSION

Ecological modelling is a robust approach, which can generate, suggest, and test alternative biogeographical hypotheses. Here, ecological modelling is used to investigate climatic variables responsible for the current distributions of *M. s. schreibersii* and *M. s. pallidus*, to project their distributions during the LGM, and to predict their distributions in future, under the global climate change scenarios. When modelling, a special care is taken to consider species-specific and variable-specific features in the ecological context in order to minimize the weaknesses and shortcomings of the chosen modelling approach.

This study found that the most important factors determining distributions of both, *M. s. schreibersii* and *M. s. pallidus* are temperature annual range, the mean temperature of the wettest and driest quarters, and annual precipitation. The factors specific for each species are isothermality and precipitation of the driest quarter for *M. s. schreibersii,* and elevation and precipitation seasonality for *M. s. pallidus*. Although the elevation variable is a very important variable in predicting distribution of *M. s. pallidus*, it is also the least transferable. Accordingly, projections using the elevation variable can be only applied within a limited geographic area and/or only under the current climatic conditions. Even though the current distribution of *M. s. pallidus* overlaps well with altitude (above 1,100 m), using altitude for larger areas or other time periods can be misleading since the preservation of collinearity between this and other direct variables cannot be verified. For example, during the LGM, the mean temperature in Anatolia was about 4 to 5^{o}C lower, and the regions above 2,200 m were covered with ice sheets. Even the regions located above 1,500 m had harsh climate, which was not suitable for bats. Thus, in my projections, the elevation is not among the used variables.

Without the elevation variable, the most important factors affecting distributions of *M. s. schreibersii* and *M. s. pallidus* are isothermality, temperature annual range, the mean temperature of wettest and driest quarters, and annual precipitation. The variables specific for each species are precipitation of the warmest quarter (*M. s. pallidus*) and precipitation of driest quarter (*M. s. schreibersii*). These factors have both, direct and indirect effect on the distribution of bats. As bats hibernate, winter temperature does not have a direct affect on bats. Temperature, however, determines distribution of vegetation. Precipitation can affect bats indirectly by influencing the vegetation growth, and directly by affecting their foraging activity. The isothermality and temperature annual range variables represent yearly and monthly variability of temperature; the arid regions with continental climate have higher variability of temperature, while the temperate wet regions have lower variability. The results suggesting the importance of the factors related to temperature and its variability on the distribution of the modeled bats seem to be meaningful, as *M. s. schreibersii* is typically found in the wet coastal areas and *M. s. pallidus* is mainly found in the arid-semiarid inlands.

It is not possible to evaluate a model's performance for future projection. However, projections made to already known distributions can give an idea of its transferability. In this thesis, geographical transferability is tested by evaluating predictions within and between two geographical regions. Accordingly, *M. s. schreibersii* distribution in Asia Minor and Thrace is projected to Europe and vice versa. Although discrimination capacity of the model trained in Asia Minor and Thrace is excellent (AUC = 0.952), its projection to Europe is only fair in predicting the current distribution (AUC = 0.770). When the model fitted in Europe is projected to Asia Minor and Thrace, its discrimination capacity increases from good to excellent (from AUC = 0.823 to AUC = 0.918), showing asymmetrical transferability. This result shows that higher internal AUC value (discrimination capacity between *presences* and *absences*) may not always be a right indicator of successful projections. Yet, the determination capacity becomes crucial in the interpretations of future projections. Accordingly, as it is not possible to evaluate projections models, which are selected according to their high discrimination capacity in most of the studies, outcomes should always be treated with extreme caution. A success or failure of projection depends on the regional specificities, the range of environmental predictors, the existence of ecotypes, the dependence on biotic interactions, the species-specific reasons, and impact of land use history (Randin *et al.*, 2006), which most of the time cannot be included in the models.

The predicted distribution of *M. s. schreibersii*, during the LGM, hints to the presence of glacial refugia in Thrace, Transcaucasia (Colchis region), and Southern Anatolia. This outcome is in good agreement with the molecular data of *M. s. schreibersii*

(Furman *et al.* (2010b). The predicted distribution of *M. s. pallidus*, during the LGM, points out to the southern part of the Caspian Sea and Mesopotamia. Because *M. s. pallidus* probably only recently colonized Anatolia, as indicated by molecular studies (Furman *et al.*, 2010a), the location of the latter refugium is rather unrealistic. Although, in principle, *M. s. pallidus* might have been present in Mesopotamia during the LGM, in reality there is no evidence, which could support it. Static models are not able to incorporate historical processes or dispersal limitations into the classifier. Another possible location of the glacial refugium for *M. s. pallidus* (on the southern cost of the present Caspian Sea) is in good agreement with the molecular data (Furman *et al.*, 2010a). During the LGM, the change in evaporation, precipitation, and runoff of rivers reduced the area of the Caspian Sea by about 50% (Kislov and Toropov, 2007). As during that time the climate was more arid and the Caspian Sea smaller, *M. s. pallidus* probably adapted to more arid conditions than *M. s. schreibersii* which stayed in the wetter coastal areas. The current allopatric distributions of *M. s. schreibersii* and *M. s. pallidus* might be partly a consequence of different climatic preferences these species acquired during the LGM. Apparently, *M. s. pallidus* is capable to utilize a variety of climatic conditions, ranging from the coastal wet areas to the arid or semiarid highlands.

The affect of global climate change on *M. s. schreibersii* and *M. s. pallidus* is determined with all bioclimatic variables under two different climate change scenarios, and projected for the years 2020, 2050 and 2080. Under both scenarios the range of *M. s. schreibersii* is drastically reduced. In the year 2080, *M. s. schreibersii* is present only in the coastal regions of the Mediterranean and the Black Sea. In contrary, under both scenarios the range of *M. s. pallidus* increases. In the year 2080, *M. s. pallidus* is present in all Anatolia, Thrace, and the Balkans, replacing *M. s. schreibersii*. Thus, *M. s. schreibersii* will not be only affected by the global warming, but will also have to compete with *M. s. pallidus*. *Miniopterus s. schreibersii* is already declining in most of the European countries and it is listed as near-threatened in the IUCN Red List. It is estimated that the population decline rate of *M. s. schreibersii* approaches 30% (in Furman *et al.*, 2010a). As the estimation also includes Anatolian populations, the predicted range contraction of *M. s. schreibersii* in Turkey might have an extremely damaging effect on entire species. Furthermore, Turkish colonies of *M. s. schreibersii* have much higher genetic diversity than European colonies. Accordingly, if the projections for the future of *M. s. schreibersii* (under the global climate change scenarios) prove to be true, most of its genetic polymorphism will be lost. Apparently, *M. s. schreibersii* has survived the previous glacial in interglacial periods in Thrace, the Balkans, and in the coastal areas of Southern Anatolia. Thus, to ensure the existence of *M. s. schreibersii*, special conservation efforts should be directed towards the conservation of populations in these regions.

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APPENDIX: MAPS

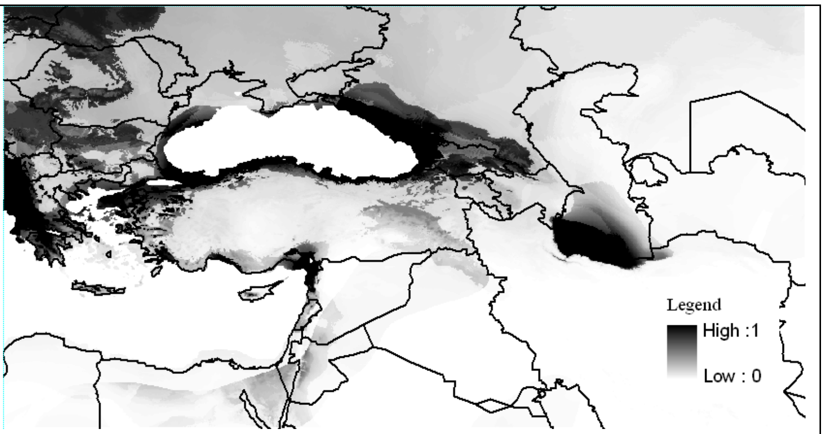
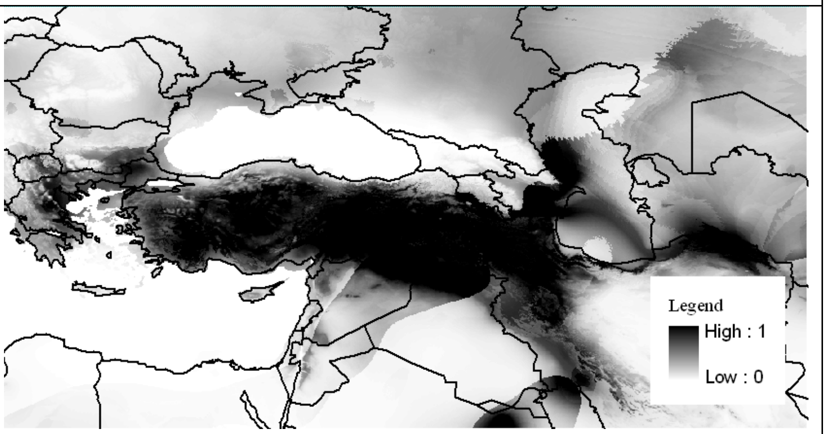
M. s. schreibersii	
M. s. pallidus	

Figure 1A. CCSM with six variables.

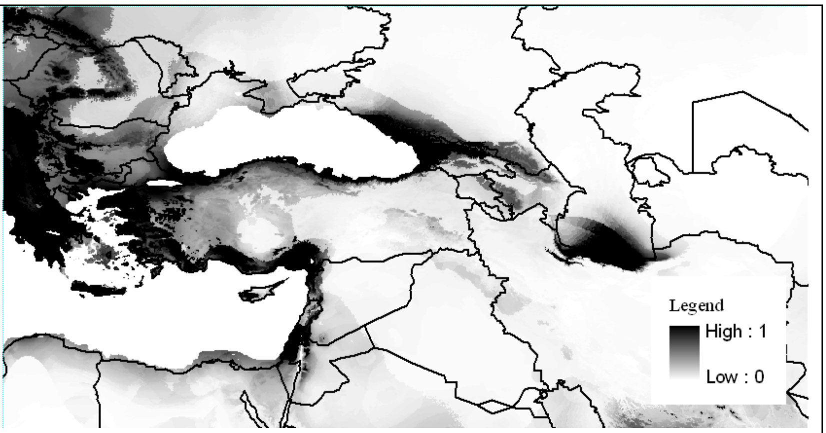
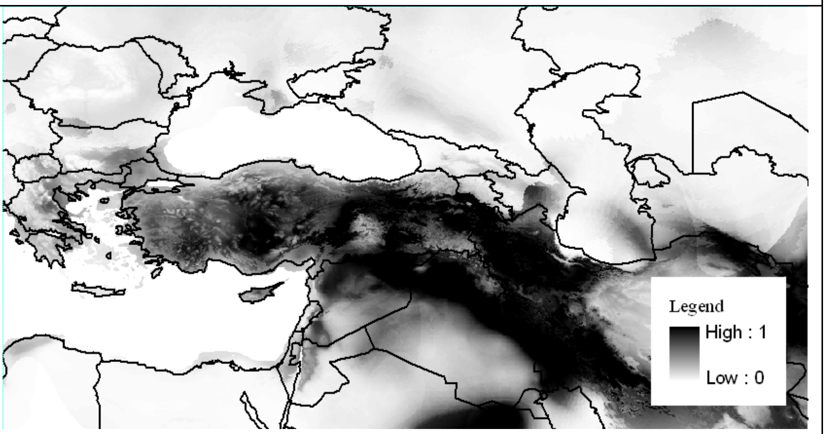
M. s. schreibersii	
M. s. pallidus	

Figure 1B. MIROC with six variables.

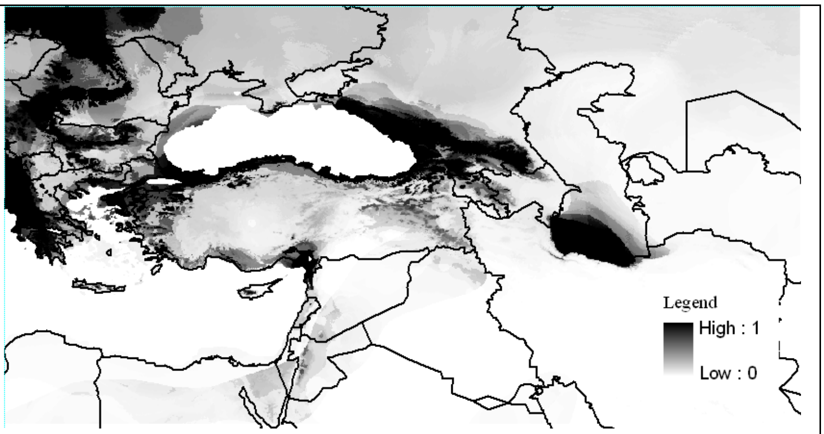
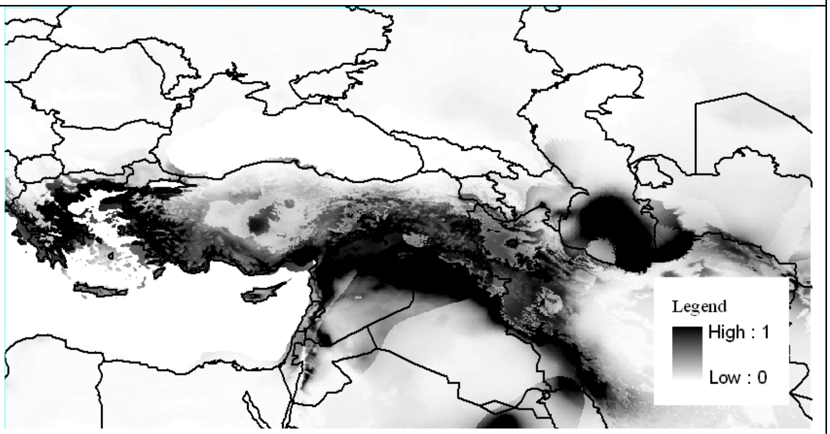
M. s. schreibersii	
M. s. pallidus	

Figure 1C. CCSM with all variables.

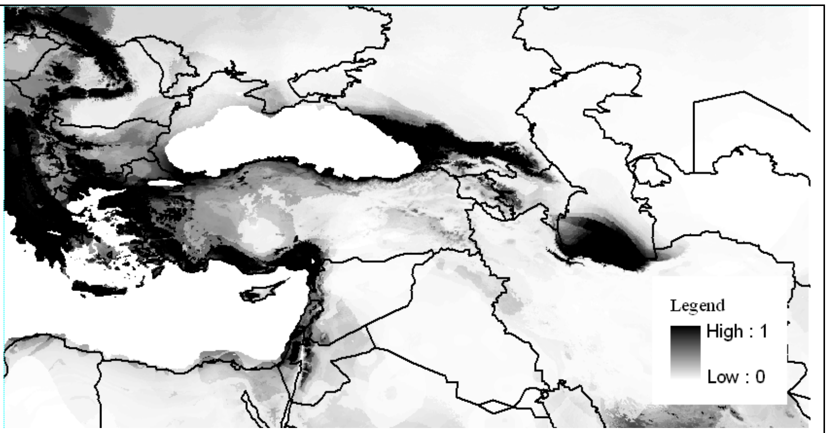
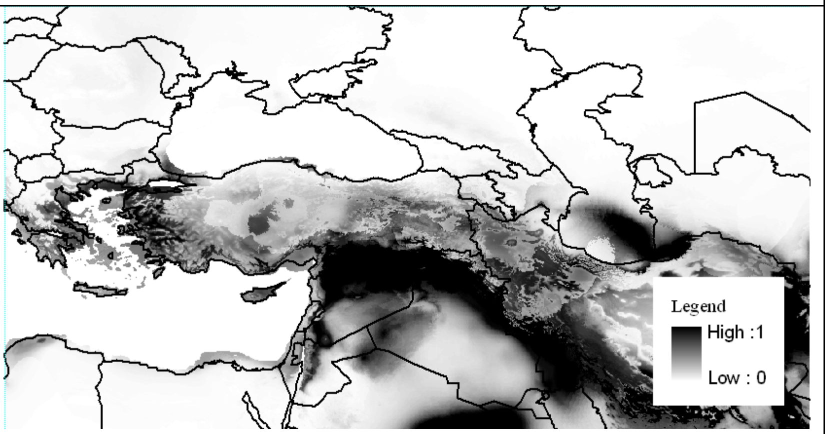
M. s. schreibersii	
M. s. pallidus	

Figure 1D. MIROC with all variables.

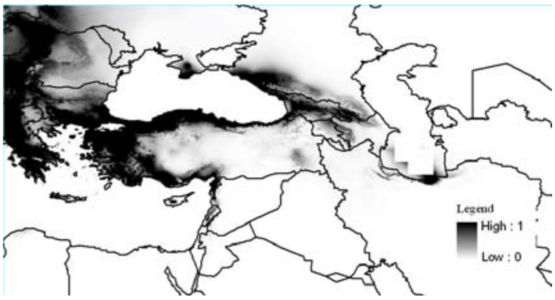
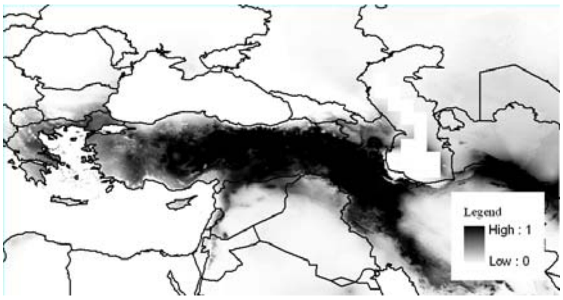
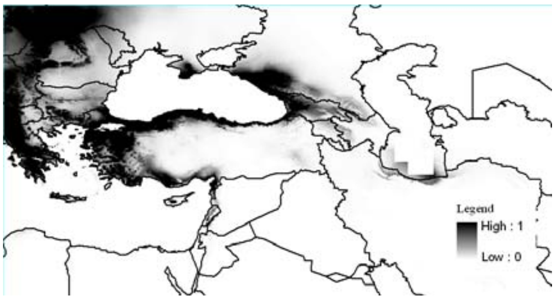
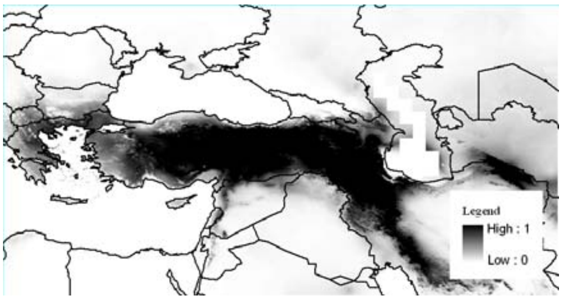
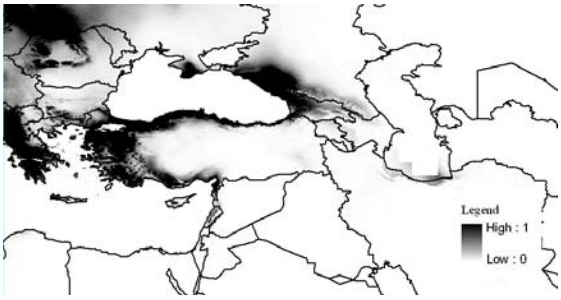
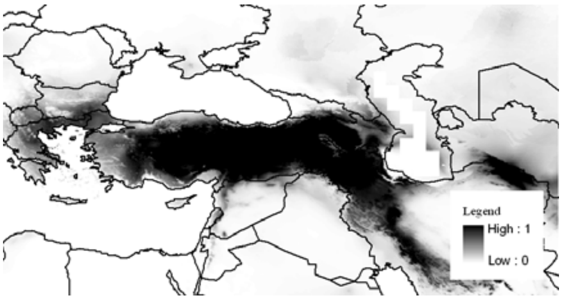
M. s. schreibersii	***M. s. pallidus***
2020  	**2020** 
2050  	**2050** 
2080  	**2080** 

Figure 2A. CCCMA – A2A scenario.

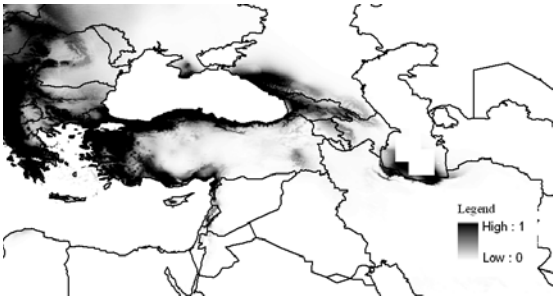
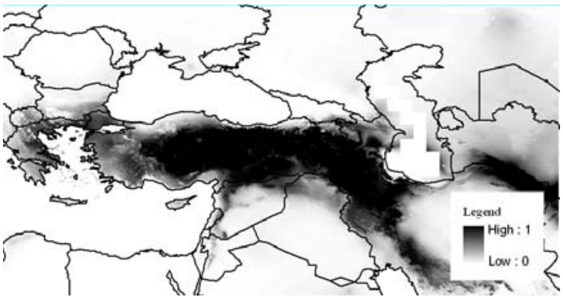
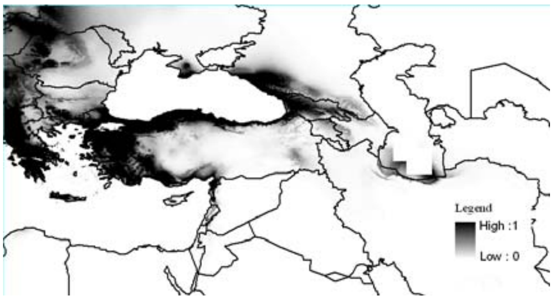
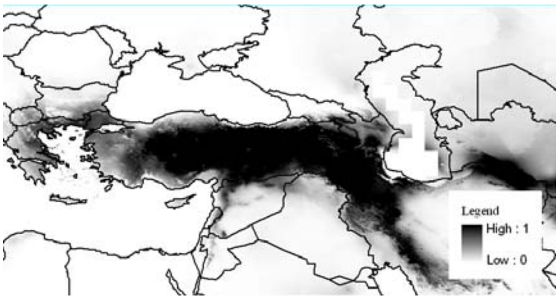
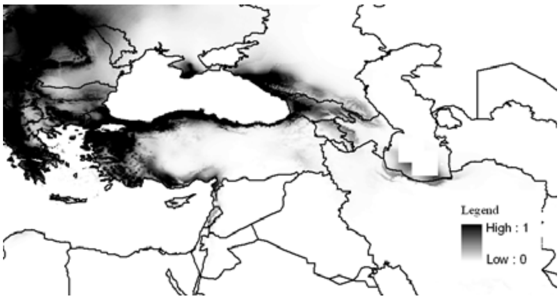
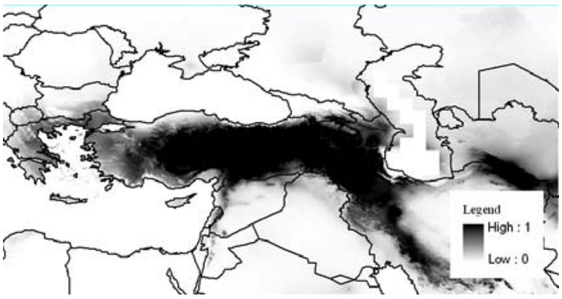
M. s. schreibersii	***M. s. pallidus***
2020  	**2020** 
2050  	**2050** 
2080  	**2080** 

Figure 2B. CCCMA – B2A scenario.

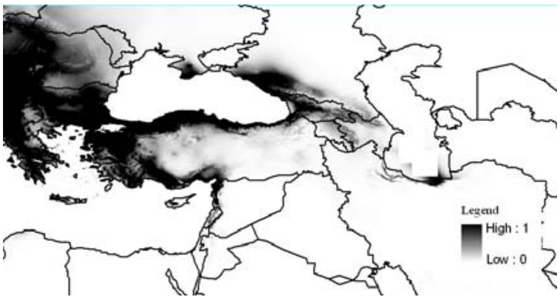
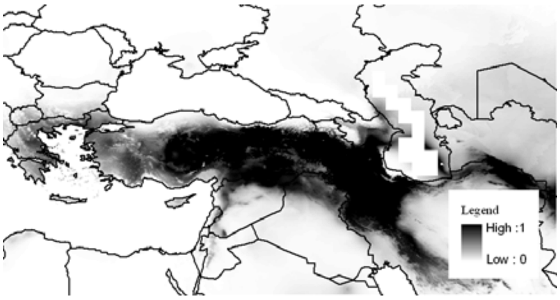
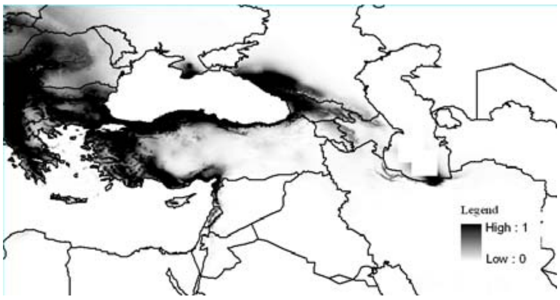
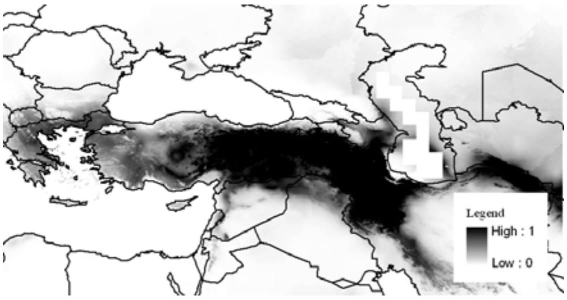
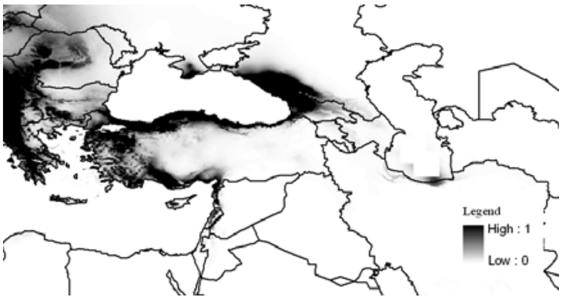
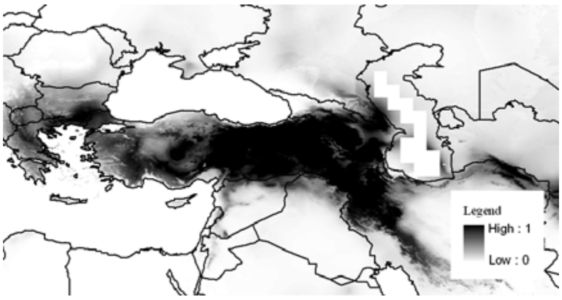
M. s. schreibersii	***M. s. pallidus***
2020  	**2020** 
2050  	**2050** 
2080  	**2080** 

Figure 2C. CSIRO – A2A scenario.

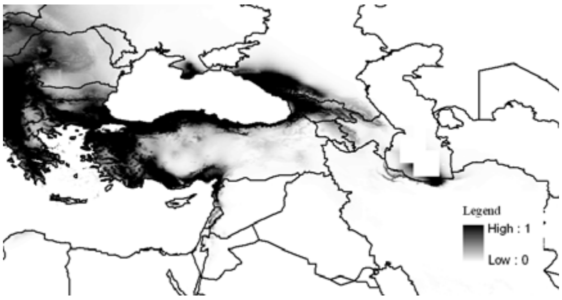
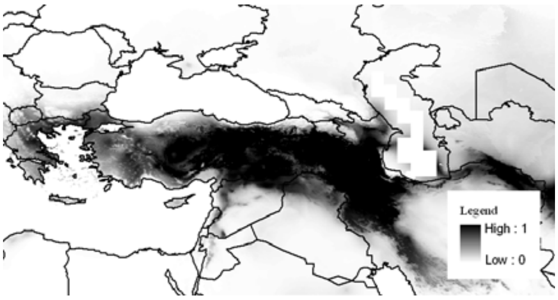
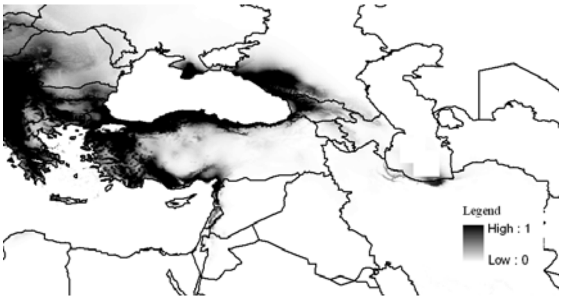
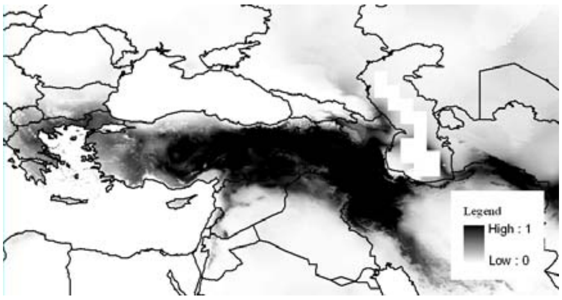
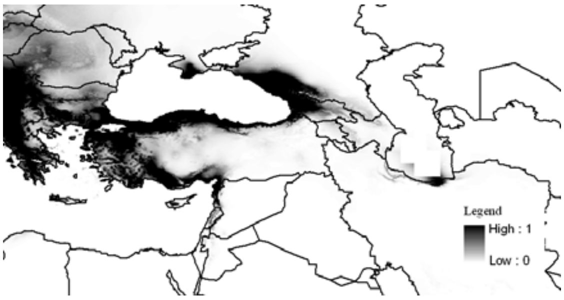
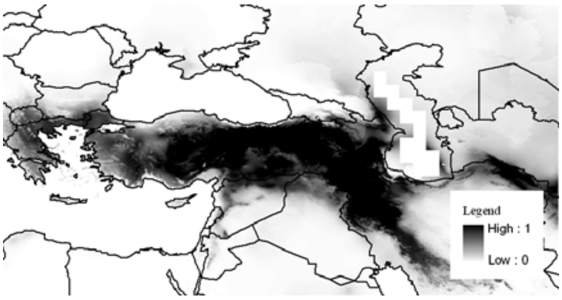
M. s. schreibersii	*M. s. pallidus*
2020  	**2020** 
2050  	**2050** 
2080  	**2080** 

Figure 2D. CSIRO – B2A scenario.

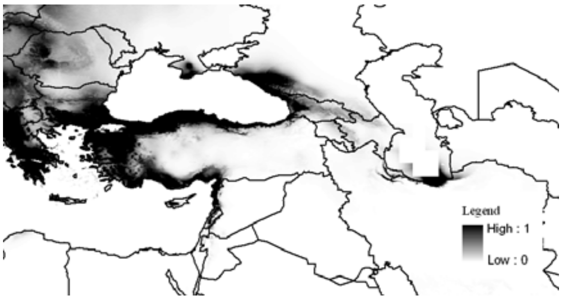
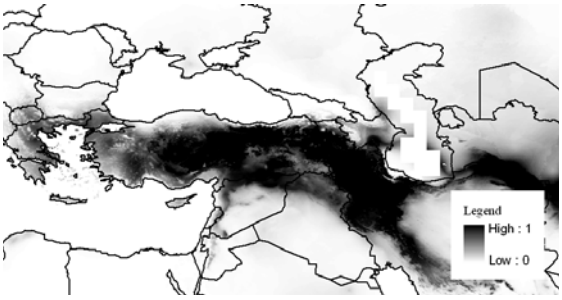
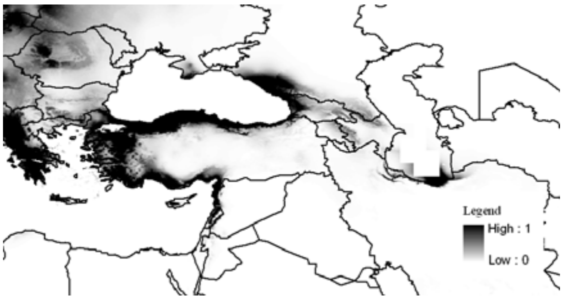
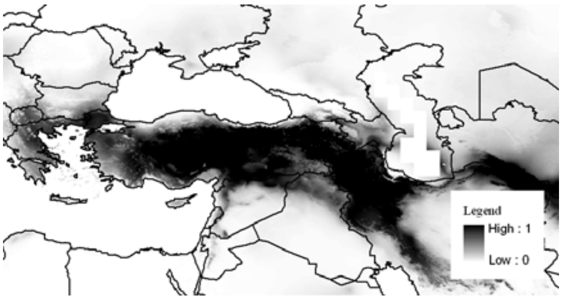
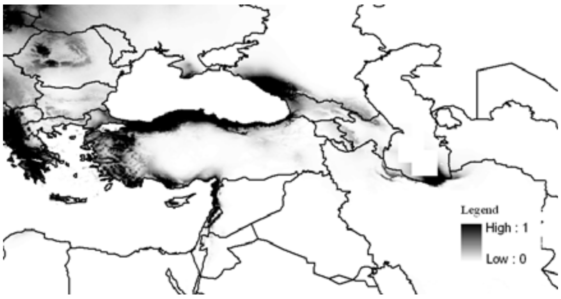
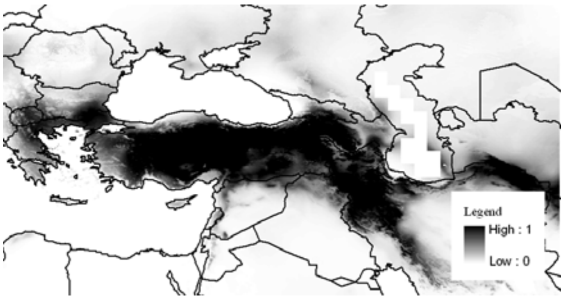
M. s. schreibersii	***M. s. pallidus***
2020  	**2020** 
2050  	**2050** 
2080  	**2080** 

Figure 2E. HADCM3 – A2A scenario.

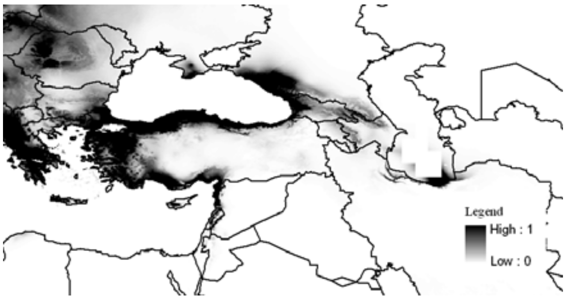
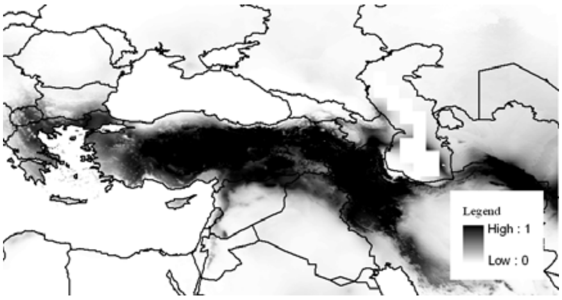
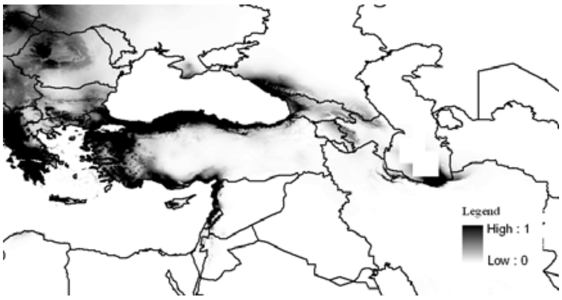
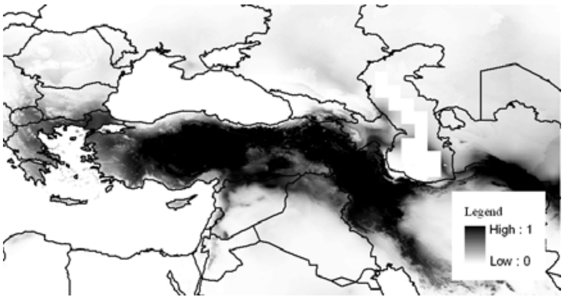
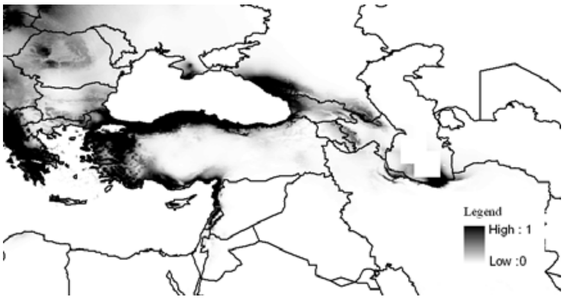
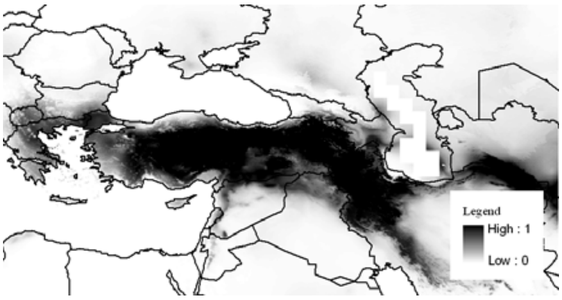
M. s. schreibersii	*M. s. pallidus*
2020  	**2020** 
2050  	**2050** 
2080  	**2080** 

Figure 2F. HADCM3 – B2A scenario.