PHYLOGEOGRAPHY OF ROCK NUTHATCHES: AN INTEGRATED APPROACH

KAYA SIVACI KUŞLARININ FİLOCOĞRAFYASI: BÜTÜNLEYİCİ BİR YAKLAŞIM

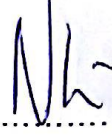## CAN ELVERİCİ

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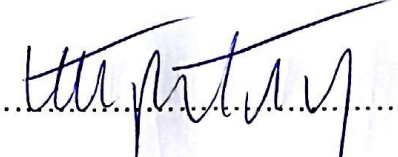for the Award of the Degree of Master of Sciences
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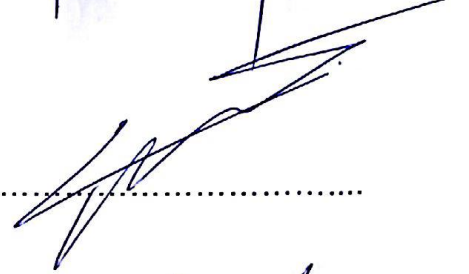
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ABSTRACT

PHYLOGEOGRAPHY OF ROCK NUTHATCHES: AN INTEGRATED APPROACH

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In this study, morphological and genetic variations of Eastern Rock Nuthatch (*Sitta tephronota* Sharpe, 1872) and Western Rock Nuthatch (*Sitta neumayer* Michahelles, 1830) were evaluated. To this end, historical biogeography of the species has been discussed using phylogeography and ecological niche modeling.

Climatic fluctuations in the Quaternary have caused many species to shift their ranges across Palearctic ecosystem. In the Last Glacial Maximum some species have expanded their distribution areas. A large part of the species, on the other hand, had to narrow their distribution areas. The impact of the Last Integlacial period is rarely studied in this respect. Moreover, how bird species distributed across southern latitudes known as refugial areas have historically changed their distributional areas have not been a popular subject. It is possible to test these changes in the distribution areas of species with ecological niche models and phylogenetic analyzes. In this thesis, morphological

variation, genetic diversity and distributional patterns of these two bird species have been examined in detail.

The genetic diversity patterns of the species and therefore phylogenetic inferences about species were done by using ND2 and ND3 regions of the mitochondrial DNA (mtDNA). As a result of the phylogenetic evaluation of the genetic diversity patterns revealed by these two gene regions, cryptic genetic diversity patterns were found for both species. Accordingly, Balkan, Anatolian and Zagros (Iran) population of *S. neumayer* formed a monophyletic group. The same pattern was also found for *S. tephronota* as Zagros and eastern population of the species formed a monophyletic group. Phylogenetic results were highly consistent with morphological results.

With the use of species specific occurrence data and the maximum entrophy machine learning algorithm (MAXENT),an ecological niche model is developed to predict the geographic distribution of these nuthatch species under reconstructed past (the Last Interglacial, ~ 130000 to 116000 years ago and the Last Glacial Maximum, 22000 years ago) and present (1960 to 1990) bioclimatic conditions. Co-evaluation of the results of the ecological niche model and phylogeography reveals reliable conclusions about the evolutionary history of species. Ecological niche model results for both species showed that they had narrower distributions in the Last Interglacial Period when compared to the Present and the Last Glacial Maximum distributions.

When the results obtained are evaluated altogether and combined with previous taxonomic studies; *Sitta n. tschitscherini*, which has been previously proposed in the Zagros region for *Sitta neumayer,* and *Sitta t. dresseri* which has been proposed for *Sitta tephronota* in the same region, should be examined as species rather than subspecies.

Keywords: mitochondrial DNA, ecological niche modeling, climate change, Last Glacial Maximum, Last Interglacial Period, Middle Eastern biogeography, *Sitta neumayer*, *Sitta tephronota*

ÖZET

KAYA SIVACI KUŞLARININ FİLOCOĞRAFYASI: BÜTÜNLEYİCİ BİR YAKLAŞIM

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Yüksek Lisans, Biyoloji Bölümü

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Haziran 2018, 69 sayfa

Bu çalışmada, Büyük Kaya Sıvacısı'nın (*Sitta tephronota* Sharpe, 1872) ve Kaya Sıvacısı'nın (*Sitta neumayer* Michahelles, 1830) morfolojik ve genetik varyasyonu değerlendirilmiştir. Bu amaç doğrultusunda, filocoğrafya ve ekolojik niş modellemesinden yararlanılarak, türlerin tarihsel biyocoğrafyası tartışılmıştır.

Kuvaterner'deki iklimsel dalgalanmalar, birçok türün Palearktik ekosistemi boyunca dağılım alanlarını değiştirmesine neden olmuştur. Son Buzul Maksimumu'nda bazı türler dağılım alanlarını genişletmiştir. Öte yandan türlerin büyük bir kısmı dağılım alanlarını daraltmak zorunda kalmıştır. Son Buzullar Arası dönemin bu açıdan etkileri ise literatürde nadiren çalışılmıştır. Ayrıca, sadece sığınak olarak tanımlanan güney enlemlerde dağılan kuş türlerinin dağılım alanlarını tarihsel olarak nasıl değiştirdikleri de çok fazla çalışmaya konu olmamıştır. Türlerin dağılım alanlarındaki bu değişimleri ekolojik niş modellemesi ve filogenetik analizlerle test etmek mümkündür. Bu tez çalışmasıyla, bu iki kuş türünün morfolojik varyasyon, genetik çeşitlilik ve dağılım örüntüleri detaylı bir biçimde incelenmiştir.

Türlerin genetik çeşitlilik örüntüleri ve dolayısıyla tür hakkındaki filocoğrafi çıkarımlar mitokondriyel DNA'nın (mtDNA) ND2 ve ND3 bölgeleri dikkate alınarak gerçekleştirilmiştir. İki gen bölgesinin ortaya koyduğu genetik çeşitlilik örüntüsünün filogenetik değerlendirilmesi sonucunda iki tür içinde kriptik genetik çeşitlilik örüntüsü ortaya çıkmıştır. Buna göre, *S. neumayer* için Balkanlar ile Anadolu'nun tamamı ve İran'ın Zagros popülasyonu monofiletik bir grup oluşturmuştur. Benzer durum *S. tephronota* için de geçerli olmuş, bu türün dağılım alanının doğusundaki popülasyonlar ile Zagros popülasyonları monofiletik bir grup oluşturmuştur. Filogenetik sonuçlar morfolojik sonuçlarla büyük ölçüde örtüşmüştür.

Türlere özgü dağılım verileri ve maksimum entropi makine öğrenme algoritması (MAXENT) kullanılarak, bu sıvacı kuşu türlerinin yeniden yapılandırılmış geçmiş biyoiklimsel koşullarındaki (~130000-116000 yıl önce Son Buzullar Arası dönemde ve ~22000 yıl önce Son Buzul Maksimumu sırasında) ve günümüzdeki (1960-1990 arası) coğrafi dağılımlarını test etmek için ekolojik niş modeli yaklaşımı benimsenmiştir. Ekolojik niş modeli ve filocoğrafya sonuçlarının beraber değerlendirilmesi, türlerin evrimsel tarihi hakkında güvenilir sonuçlar ortaya koymaktadır. Her iki türün ekolojik niş modeli sonuçları, türlerin Son Buzullar Arası dönemde günümüz ve Son Buzul Maksimumu'ndan daha dar bir dağılıma sahip olduklarını göstermiştir.

Elde edilen sonuçlar bir bütün olarak değerlendirildiğinde ve daha önceki taksonomik çalışmalarla birleştirildiğinde, *Sitta neumayer* için Zagros bölgesinde alttür olarak önerilmiş olan *Sitta n. tschitscherini*'nin ve aynı bölgede *Sitta tephronota*'nın alttürü olarak önerilmiş olan *Sitta t. dresseri*'nin alttürden ziyade tür olarak dikkate alınması gerektiği sonucuna varılmıştır.

Anahtar Kelimeler: mitokondriyel DNA, ekolojik niş modeli, iklim değişimi, Son Buzul Maksimumu, Son Buzullarası Dönem, Orta Doğu biyocoğrafyası, *Sitta neumayer*, *Sitta tephronota*

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SYMBOLS AND ABBREVIATIONS

ENM	Ecological Niche Modeling
LGM	Last Glacial Maximum
AMNH	American Museum of Natural History
ZFMK	Zoological Research Museum Alexander Koenig
MNB	Museum für Naturkunde, Berlin
MNHAT	British Museum of Natural History at Tring
NR	Naturhistoriska Riksmuseet, Sweden
BL	Beak Length
NL	Nostril Length
WL	Wing Length
TL	Tail Length
TRS	Tarsus Length
PCA	Principle Component Analysis
PC1	Principle Component 1
PCR	Polymerase Chain Reaction
ND2	NADH dehydrogenase subunit 2
ND3	NADH dehydrogenase subunit 3
GBIF	Global Biodiversity Information Facility
LIG	Last Interglacial
GCM	Global Climate Model
CCSM4	Community Climate System Model version 4
MIROC-ESM	An Earth System Model
MPI-ESM-P	Max Planck Institute Earth System Model
L	Linear
Q	Quadratic

P	Product
H	Hinge
AIC	Akaike Information Criterion
AUC	Area Under Curve

1. INTRODUCTION

1.1 Studies of the Biological Diversity

Biogeography studies the geographical patterns of the biological diversity. In other words, biogeography studies the distributions of organisms both in the past and the present. The study of the past distributions of organisms can be classified as historical biogeography and the present distributions can be classified as ecological biogeography [1, 2]. Practically, ecological biogeography asks the question "Why is the organism living in the area where it lives today?"; historical biogeography asks "How did it get there?" [3].

After the overseas explorations began in the European history, naturalists began to collect and categorise organisms. As they interpreted the geographical and distributinal patterns of organisms, they produced new theories about the history of life on Earth. As an example Carl Linnaeus believed that all life must be coming from a mountain located in tropics because environmental conditions change more rapidly in mountain slopes than flat surfaces [1, 4]. Second example is the opposing idea which was suggested by Comte de Buffon. He observed that there were some species that are adapted to specific habitats, such as mesic montane forests, and some areas, for example deserts, can restrict those species to colonize northern deciduous and coniferous forests. Thereby, he proposed that life should be originated and expanded from the North in a time when continents were connected. Later, he speculated that when climates cooled, species colonized sourhern areas [1]. Also as there were a diversity of different animals in ecologically similar areas, he proposed the first principle of biogeography which states that environmentally similar but unconnected regions have different mammals and birds [1, 5]. Many studies continued to increase the diversity of biological patterns in the 18th century. However, many questions which were asking the reasons behind the biological patterns had insufficient answers. After the 19th century better conjectures on the age of the Earth and new insigths about the movements and the nature of the

continents were found. These prepared the rise of the evolutionary theory. Today, many tools for understanding biological diversity are ready for the use of the biologist. Also specimens from a wide range of geographies can be reached fairly easily from natural history museums or private collections.

1.2 Climatic Changes and Responses of Organisms

Climate is a dynamicaly changing phenomenon which is affected by many factors, including carbondioxide concentrations [6], diverging geometric variation of the Earth's orbit [7], changing number of sunspots of the Sun [8], difference in concentrations of some athmospheric chemicals, formation of highlands as a result of plate tectonics. Generally, two of these parameters are very important; formation of highlands and variation of insolation (incoming solar radiation). Evidences of climate change can ve found via the glaciers, fluctuations in the sea level, sediment cores obtained from sea-floor, results of statigraphy, distributions of living organisms and modelling the past streams, winds and soils.

Distributions of living organisms are dependent on climatic factors. The Earth is currently occupied by about 8.7 million species [9] and every species have their own ecological niche. Niche is basicaly defined as the role of a species in its environment and this term was first used by Roswell [10]. Later the term was developed by many researchers and three concepts emerged; The Grinnellian Niche [11], The Eltonian Niche [12] and The Hutchinsonian Niche [13].

The ecological niche is defined as a n-dimensional hypervolume formed by biotic and abiotic factors that maintains a population to persist in its habitat according to Hutchinson[14]. These abiotic factors can be moisture, soil type, wind velocity and temperature. Climatic models are mostly used for modeling the climatic niche of a species [15]. As climate is a dynamicaly changing phenomenon, species have to adapt to these changes and/or disperse to new suitable areas. Otherwise, extinction is a crystal-clear fact.

The ecological niche modeling (ENM) predicts the distribution of species by using statistical algorithms such as regression based models or machine learning techniques. Simply, it uses the current distribution of species and relates it with environmental variables. Hypotheticaly, BAM diagrams are appropriate to explain the ecological niche (See Figure 1). In the niche space there is an area where species can be able to survive and that area is defined by the intersection of biotic, abiotic and movement factors [16]. In ENM approaches, mostly climatic models are used to define the suitable areas for the species. This demolishes the effects of biotic interactions but they still give crucial information. Also it is very important to use the dispersal (M-area) of the species and this can be implemented to an ENM [17].
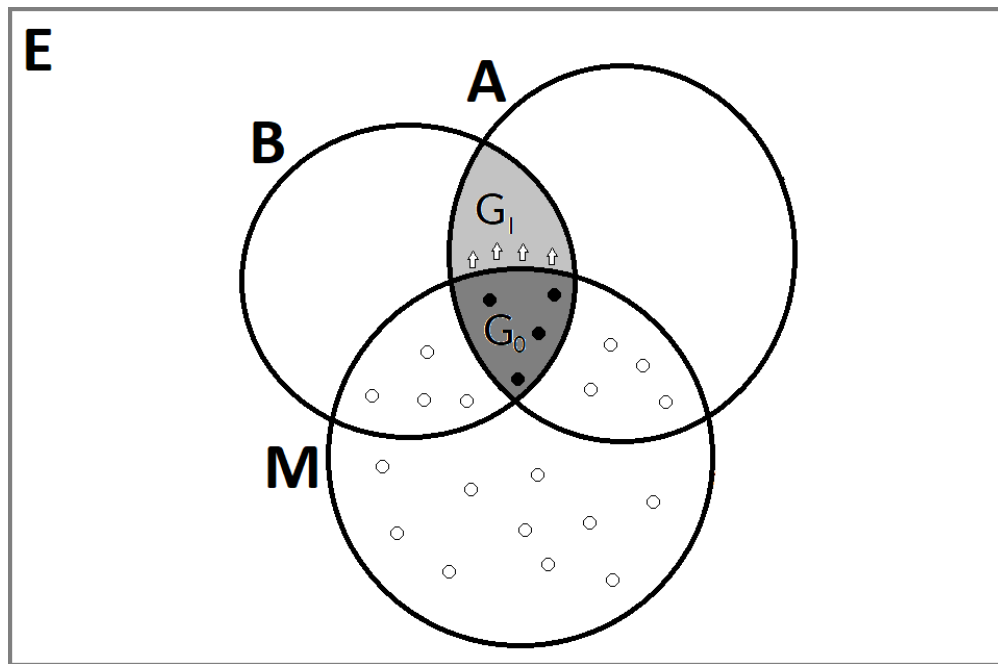
Figure 1 A hypothetical BAM diagram depicting biotically suitable areas (B), abiotically suitable areas (A) and movement areas of the species (M) in a Venn diagram. G0 is the occupied area, GI is the invadable area for the species. Solid circles are showing presences and open circles are showing absences of the species. This diagram was modified from Peterson et. al. [16]

Quaternary climatic oscillations also known as Late-Cenozoic glacial cycles includes major climatic variations. These oscillations caused differences in ice volumes, air temperatures, sea levels and so on. Collected data on these

differences show some correlation and these can be seen on Figure 2. In the glacial ages glaciers formed in the poles, especially in the Northern Hemisphere, and moved to Southern temperate regions. This had a huge effect on many organisms [18]. Many became extinct and many had to move down to suitable environments to survive. Extinctions can be detected by paleontological studies. Additionaly, major dispersal patterns of many animals and plants can be tracked via phylogeographical studies [19].
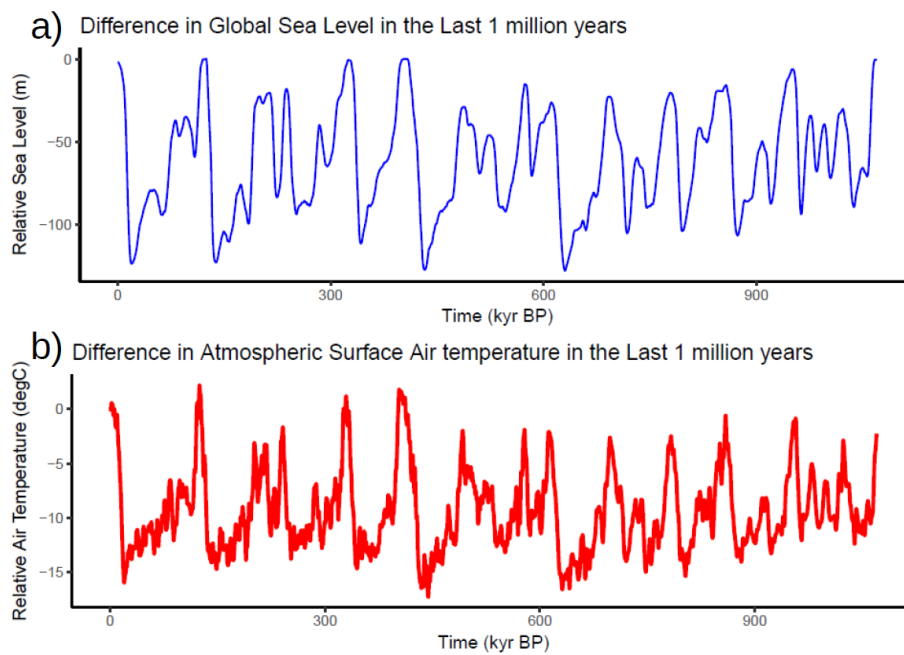
Figure 2 Difference in global sea level in the last 1 million years can be seen in a. Difference in athmospheric surface air temperature in the last 1 million years can be seen in b. Data was taken from Bintanja et al [20]. Graphs were created by using ggplot2 package in R [21, 22].

Phylogeography is a scientific field which analyzes at a high spatial scale. It examines the geographical distributions of lineages between populations of the same species or closely related species and helps to make biogeographic inferences on behalf of the studied group [23] and it is affected by many factors which are classified as abiotic and biotic factors according to Kumar&Kumar [24] (See Figure 3). However, phylogeography can not do the temporal analysis with a high precision. At this juncture, ENMs help to identify temporal patterns [25]. Using phylogeography together with ENM provide important results for understanding the evolutionary history of

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species [26]. Additionaly, these tools have the potential to reveal how climate change will affect the distributions of species in the future. When the results obtained from both phylogeography and ENMs are combined, results may not only reveal the distributions of the species, they may give insights about how the genetic diversity will be effected in the future.

It is known that there are significant changes in the distributions of species in the last glacial period just before the Pleisocene-Holocene transition [27]. These changes in the distributions of species, during the Last Glacial Maximum (LGM), led to distributional contractions and the loss of genetic diversity for many populations. Some geographies were climatically suitable for some populations and acted as refugia [28] and led to increased genetic diversity patterns. Phylogeographical studies by using neutral markers (independent of natural selection) can give important results for distinct populations.

PHYLOGEOGRAPHIC
FACTORS

ABIOTIC

Topographic variations
Phylogeographic breaks
Latitudinal gradient
Glacial refuge
Geographic position of striats
Climatic oscillations

BIOTIC

Population expansion
Population contraction
Gene movements
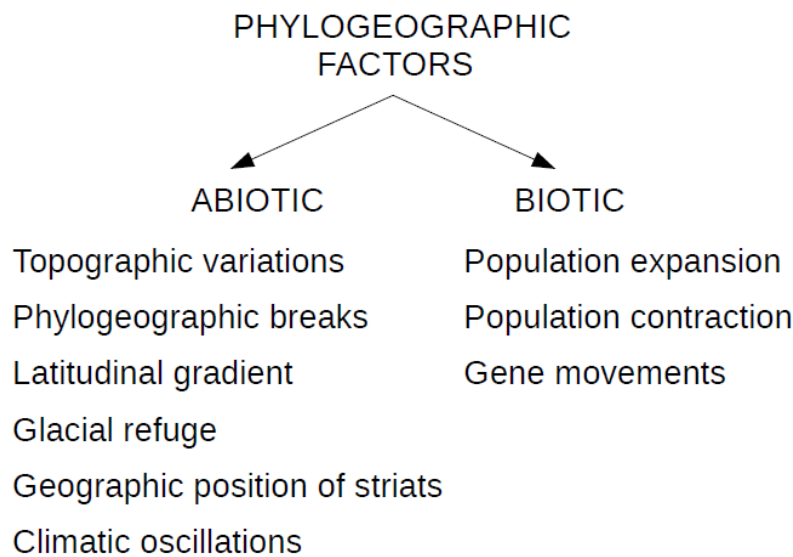
Figure 3 Phylogeographic factors which affect the distribution of organisms. See Kumar&Kumar for further details[24].

The role of LGM in the diversification of species is still being discussed [29]. For this reason geographical identification of refugial areas where populations reached their highest genetic diversities in the LGM, is very important for questions of evolutionary biology and conservation biology. The glacial refugia hypothesis [27] (see Brito [19]) suggests that temperate species which are widespread in Western Europe had to survive in the

southern regions like Southern Iberia, Italy, Balkans, Caucasus and Anatolia [30-33]. This hypothesis has been tested for many different organisms and supporting results were published which were confirming the roles of refugia from Iberian Peninsula to the Caucasus [19, 34-37].

The role of Anatolia, which is thought to have served as an important refugium for many groups in the LGM (~22,000 years before present), has been studied in terms of many living groups including plants, birds and mammals [3, 35, 36, 38-40]. It is argued that Anatolia has a forest- and steppe-dominated vegetation during the LGM and thus it is an important refugium which is protecting the diversity of life at the time [3, 35, 38]. For this reason Anatolia has an important position to test mechanisms of species formation and the hypothesis about its habitat diversity and climatic structure in the glacial periods. There some studies about testing the glacial refugia hypothesis in vertebrates of Anatolia but there are many vertebrates to be studied. As Anatolia is rich in animal species and is also a geographical region that contains many endemic species [3]. Anatolia is in an extraordinary position in terms of biodiversity when compared to other temperate zones [41] because it is in the intersection point of different continents and phytogeographic regions. The presence of Anatolian Diagonal, the topography and the microclimatic diversity in specific areas are the most widely used arguments for explaining Anatolia's biological diversity.

1.3 Study Species

Remnants of the Therapoda, flying dinosaurs of the latest 165-150 million years which are birds [42] have 10978 species in the wild [43]. Class of birds, *Aves,* is commonly divided into 36 orders. These orders host 241 families and more than half of it, 137 families, belong to Passeriformes making this group the richest (6662 of 10978 species in 30 July 2017) in the class.

In this study 2 species of Nuthatches (*Sittidae),* which belong to Passeriformes, were examined. There are 32 species that are classified into 3 genera; *Salpornis* which has 2 species, *Tichodroma* has only 1 species and

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the rest of the species in the family are classified in the *Sitta* [2]. Members of the *Sittidae* family are found on Palearctic, Oriental and Nearctic zoogeographic regions [44, 45].

Most members of the *Sittidae* are persisting their lives on forest habitats. However there are some exceptions which are species belonging to *Salpornis* and *Tichodroma* genera and two species of *Sitta* genus. Subjects of this thesis *Sitta neumayer* and *Sitta tephronota* prefer habitats mostly composed of rocky and mountainous areas [44]. On the one hand most of the species in *Sitta* generally forage in trees, on the other hand *S. neumayer* and *S. tephronota* forage on the ground, trying to find seeds, arachnids, snails (Gastropoda) and insects [46, 47].

Sitta neumayer is found on the west when compared to its sister species as the English name Western Rock Nuthatch suggests. Being a resident species, *S.neumayer* is found across Croatia, Montenegro, Albania, Greece, Turkey, Syria, Northern Iraq, Lebanon, Northern Israel and Iran. Six well known geographical forms or variants are defined according to their morphological differences; *S. n. neumayer, S. n. zarudnyi, S. n. syriaca, S. n. rupicola, S. n. tschitscherini* and *S. n. plumbea.* See Figure 4 to view their distributions.
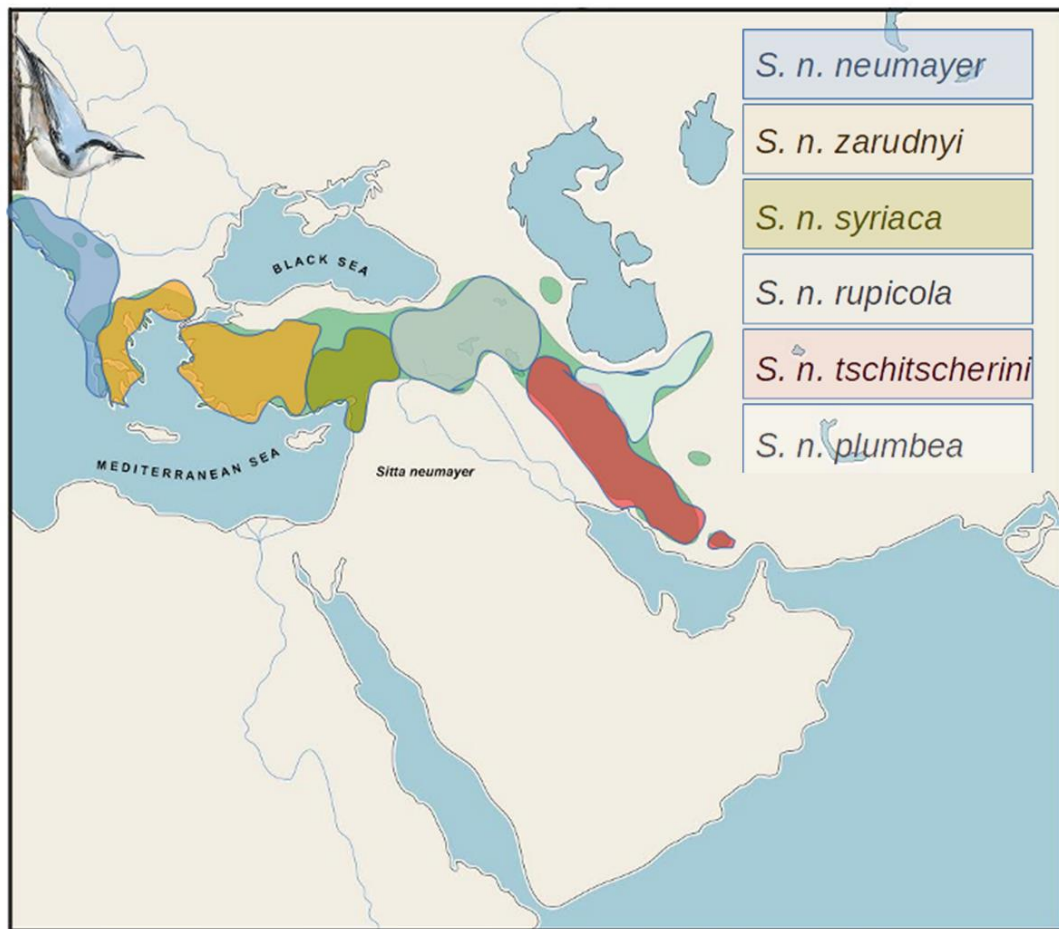
Figure 4 Distributions of the variants of *S. neumayer.*

S. n. neumayer, the nominate form, shows the known characteristics of the species. It has grey upperpart, black eyestripe, creamy-whitish breast and rufous cinnamon thigh. It is the biggest when compared to other forms. Individuals of this form is found on the European part of the species distributional range. *S. n. zarudnyi*, is found on Eastern Greece to Western Turkey. It has a little bit smaller body size and its colors are generally paler than the nominate form. *S. n. syriaca,* is found on South Eastern part of Turkey, Syria to Northern Israel. It has quite similar body size to the nominate form but has smaller bill size. Also it has slightly paler upper and underparts than western forms. *S. n. rupicola,* is found on North-North East Turkey to Northern Iraq covering Armenia, Azerbaijan and North Iran. Its colors are paler than the nominate but darker than *S. n. syriaca* and *S. n. zarudnyi. S.*

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n. tschitscherini is in found on West – Central to South Iran, constituting the population found on the Zagros mountains. It has paler colors, smaller body size and very reduced eyestripe; may be absent in some specimens. *S. n. plumbea* is found on Central and Southern mountains of Iran. It has darker upperparts and greyish (rather than white) belly, smaller body size than the western forms and shows very reduced eyestripe like *S. n. tschitscherini* [47].

Sitta tephronota, the Eastern Rock Nuthatch, is mostly found across Afghanistan, Turkmenistan, Iran, Azerbaijan, Northern Iraq and Turkey. There are four well known geographical forms; *S. t. dresseri, S. t. obscura, S. t. iranica* and *S. t. tephronota.* See Figure 5 to view the distributions of these forms.
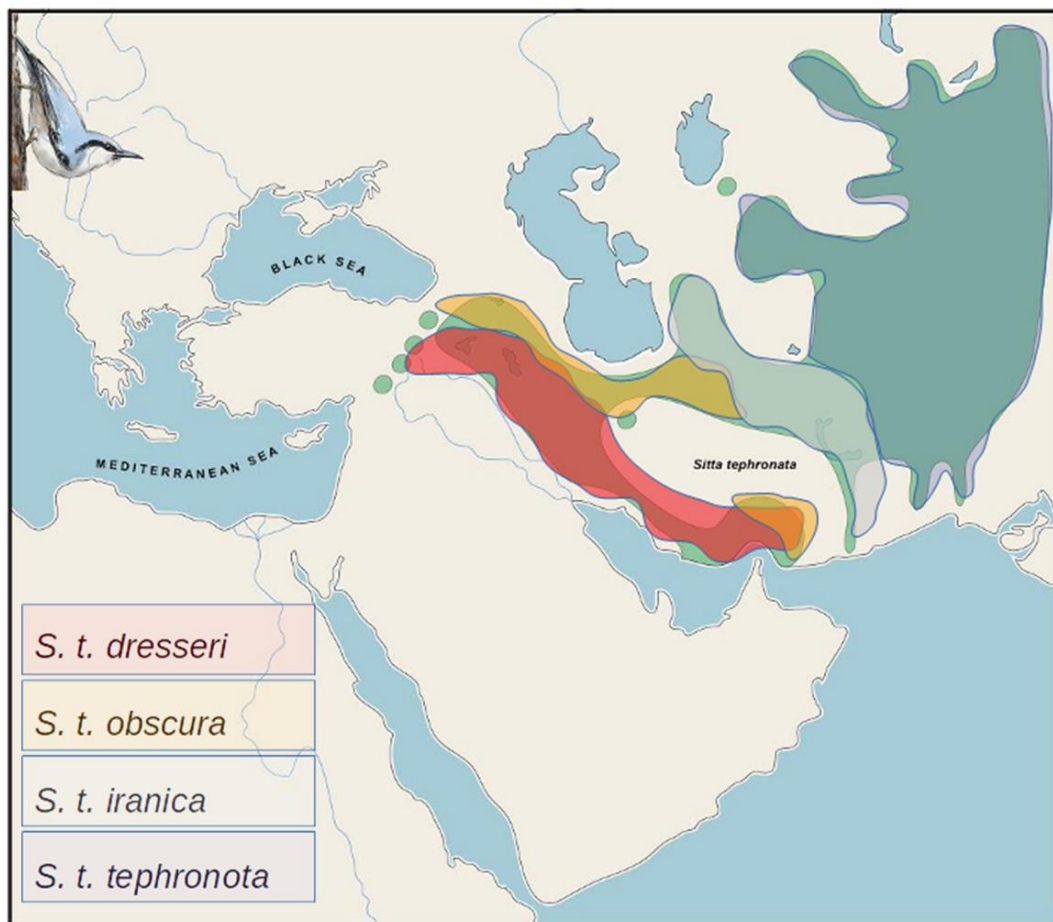
Figure 5 Distributions of the variants of *S. tephronota.*

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When compared to *S. neumayer,* this species have slight differences in their body and bill sizes, vocalisations, size prominance of their eyestripes and colourisations. The nominate form, *Sitta t. tephronota* lives in the easternmost part of the distribution (Afghanistan, Turkmenistan, West Pakistan, Kazakhstan and North Eastern extreme of Iran) and is very similar to *S. neumayer.* Specimens found from east to the west are *S. t. iranica*, *S. t. obscura* and S*. t. dresseri,* respectively. In these forms *S. t. iranica* is the smallest, has less prominent eyestripe than western forms. *S. t. obscura* is found on Southern and Central Iran, North Eastern Turkey and South Azerbaijan and Armenia. Its morphology is intermediate of western and eastern form. *S. t. dresseri* is found on South Eastern Turkey, Southern and Northern Iraq, and Western Iran; especially lives in Zagros mountains. It is the biggest form, having largest bill and most prominent and biggest eye stripe when compared to eastern forms [46, 48].

When both of these two species are compared, it can be seen that there is a contrast between sympatry and morphological characters. In coexistance *Sitta neumayer* becomes smaller, has smaller, less prominent eyestripe and beak, conversely *Sitta tephronota* becomes larger, has bigger, more prominent eyestripe and has bigger beak. This difference was a challenge for early explorers but Sarudny and Härms untangled it [49]. Although there was different taxonomical status for these two species at the time, Sarudny and Härms stated in 1923 that it is easy to separate sympatric populations [49]. Later, Vaurie inspected museum collections and linked this contrast in characters to ecology, especially validated David Lack's observation on Darwin's finches, which stated that two closely related species should have different characteristics to survive in coexistance, by examining *Sitta neumayer* and *Sitta tephronota* [50, 51]. Also several other researchers has seen this pattern but did not name the consept until Brown and Wilson, 1956. They called this pattern "character displacement" and reviewed many examples of it [52]. They described the term as "*Character displacement is the situation in which, when two species of animals overlap geographically, the differences between them are accentuated in the zone of sympatry and weakened or lost entirely in the parts of their ranges outside this zone.*" [52].

Main examples which were given in the study included two monophyletic groups: *Sitta neumayer* - *Sitta tephronota* and *Lasius nearcticus – Lasius flavus.* After this study, some other researchers regarded the case of *Sitta neumayer* and *Sitta tephronota* as the classical case of character displacement, but some found this classical case had insuffcent support and suggested that character difference to be related more to clinal variation[53-56]. Also the term character displacement has not also been agreed upon because Darwin has also noted a similar pattern in his work and called the term as the "divergence of character"[57] and this excited attention of Mayr and he termed it as "character divergence"[58]*.* Independently from these arguments, *S. neumayer* and *S. tephronota* clearly shows niche partitioning as their diets are significantly different [55]. Later, Yousefi et al. (in 2017) pointed out that in addition to this trophic niche partitioning, there is spatial niche partitioning between these two species because they prefer different microhabitats [56].

2. MATERIALS AND METHODS

2.1.1 Morphological Characters

This study was done by measuring rock nuthatch samples which were obtained from American Museum of Natural History (AMNH), Zoological Research Museum Alexander Koenig (ZFMK), Museum für Naturkunde Berlin (MNB), British Museum of Natural History at Tring (MNHAT) and Naturhistoriska riksmuseet Sweden (NR).

Five characters of *S. neumayer* and *S. tephronota* were measured which were beak (BL), nostril (NL), wing (WL), tail (TL) and tarsus (TRS) lengths by using electronic caliper, steel ruler and center screw compass according to Lars Svensson [59]. The total number of samples were 132 for *S. neumayer,* 22 of them were *S. n. tschitscherini*, and 171 for *S. tephronota*, 42 of them were *S. t. dresseri* (See Table 1 for male and female numbers. Also descriptives and histograms of the data can be seen in Supplementary tables 1-4). Many geographic ranges were tried to be covered and sample localities were georeferenced if the exact collection localities were found. To detect collection localities in the map Vertnet Search Portal (AMNH Bird Collection) and published materials were used which state expedition localities of collectors were used [48, 50, 60, 61]. Google Earth Pro version 7.3.1.4507 was used to georeference them. See Figure 6 for sampling locations and Figure 7 for measured morphological characters.

Table 1 Sample numbers according to their sexes.

		Sex	
		Male	Female
		Number	Number
Species	S. neumayer	67	43
	S. n. tschitscherini	19	3
	S. tephronota	73	56
	S. t. dresseri	24	18
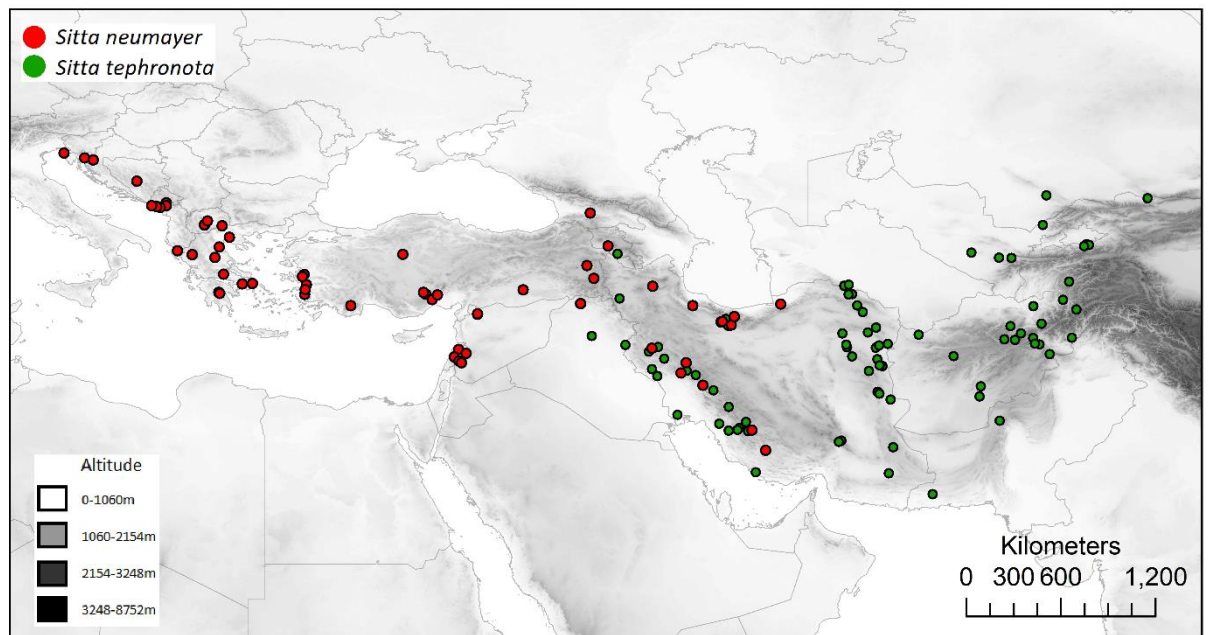
Figure 6 Sampling locations of *S. neumayer* and *S. tephronota* for morphological study which consists of beak, nostril, wing, tail and tarsus lenghts. [62, 63]
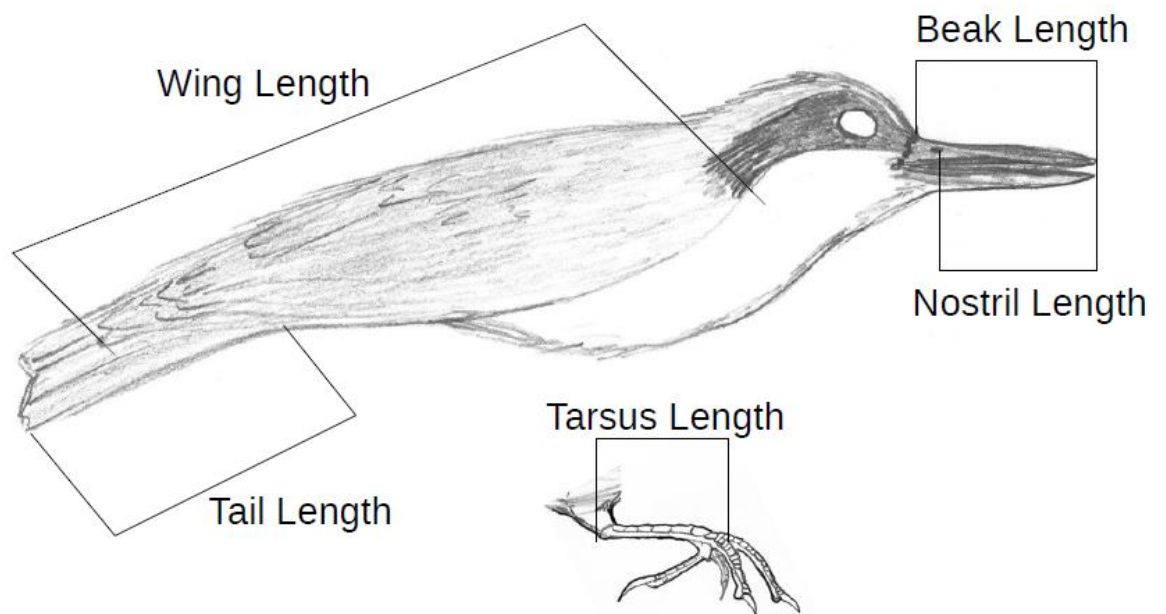
Figure 7 Morphological characters used in this thesis. See Svensson [59] for details.

2.1.2 Statistical Analyses

Statistical analyses were performed by using SPSS software version 23. The variables were investigated by using visual (histograms, probability plots) and analytical (Lilliefors Kolmogorov-Smirnov test, Shapiro-Wilk test) methods for determining if variables were showing normal distributions or not.

In the first test, I wanted to find out whether males and females were different by means of five morphological characters. For *S. neumayer* males were not showing normal distribution for NL and females were not showing normal distribution for BL. Thereby, non-parametric Kruskal-Wallis Test was used for these two variables. The others were normally distributed so Independent-Samples T Test was used for them. The same methodology was used for *S. tephronota*.

Freeman and Jackson have pointed out that univariate measurements are not adequate for measuring avian body size [64]. Therefore, individual measurements were not used to deduce divergence of studied species and a new allometric size variable was produced by Principle Component Analysis (PCA) to reduce dimensionality and complexity of the data and to compare Zagros populations and the rest for both of the species [65].

BL and NL are very closely related data and males had shown deviation from normal distribution in NL. Therefore, non-parametric Spearman test was used. Correlation between them may causes multicollinearity during PCA.

2.2 Phylogeography

Key areas for study species were selected covering 30 geographical areas and museums provided those samples for our studies. (See Figure 8 (Samples were obtained from Natural History Museum Wien, Zoological Research Museum Alexander Koenig and American Museum of Natural History)). By using QIAGEN DNeasy Extraction Kit, total genomic DNA was isolated from 60 samples which were toe pads and some of them were skin

samples. In this step, standard protocol set by the manufacturer (QIAGEN) was followed. 306 bp portion of the ND2 region from 45 samples and 313 bp portion of the ND3 region from 33 samples were amplified by polymerase chain reaction (PCR) with the primers L-5215 and H-5578 for ND2 [66]; ND3-10755-L and ND3-11151-H for ND3 [67]. As the samples were old, the annealing temperature of primers showed some variation. PCR amplifications were performed under following ingredients: 9.1µL PCR grade water, 4.8µL 5x Promega GreenTaq reaction buffer, 2µL 20 uM MgCl, 2µL 10 mM dNTP, 1µL per primer, 0.12µL hotstartTaq and 5µL DNA isolate(Promega).Then, all PCR reactions were performed in a SimpliAmp Thermal Cycler (Applied Biosystems) with the following conditions: denaturation at 95°C for 3 minutes; 8 cycles at 95°C for 15 seconds, 58°C for 20 seconds, 72°C for 20 seconds; 8 cycles at 95°C for 15 seconds, 56°C for 20 seconds, 72°C for 20 seconds; 38 cycles at 95°C for 15 seconds, 54°C for 20 seconds, 72°C for 20 seconds; and a final 72°C for 2 minutes. The results were checked by 1% agarose gel electrophoresis. If they contained the portions we targeted, they were sent for Sanger Sequencing to the companies (Medsantek and BM Labosis).
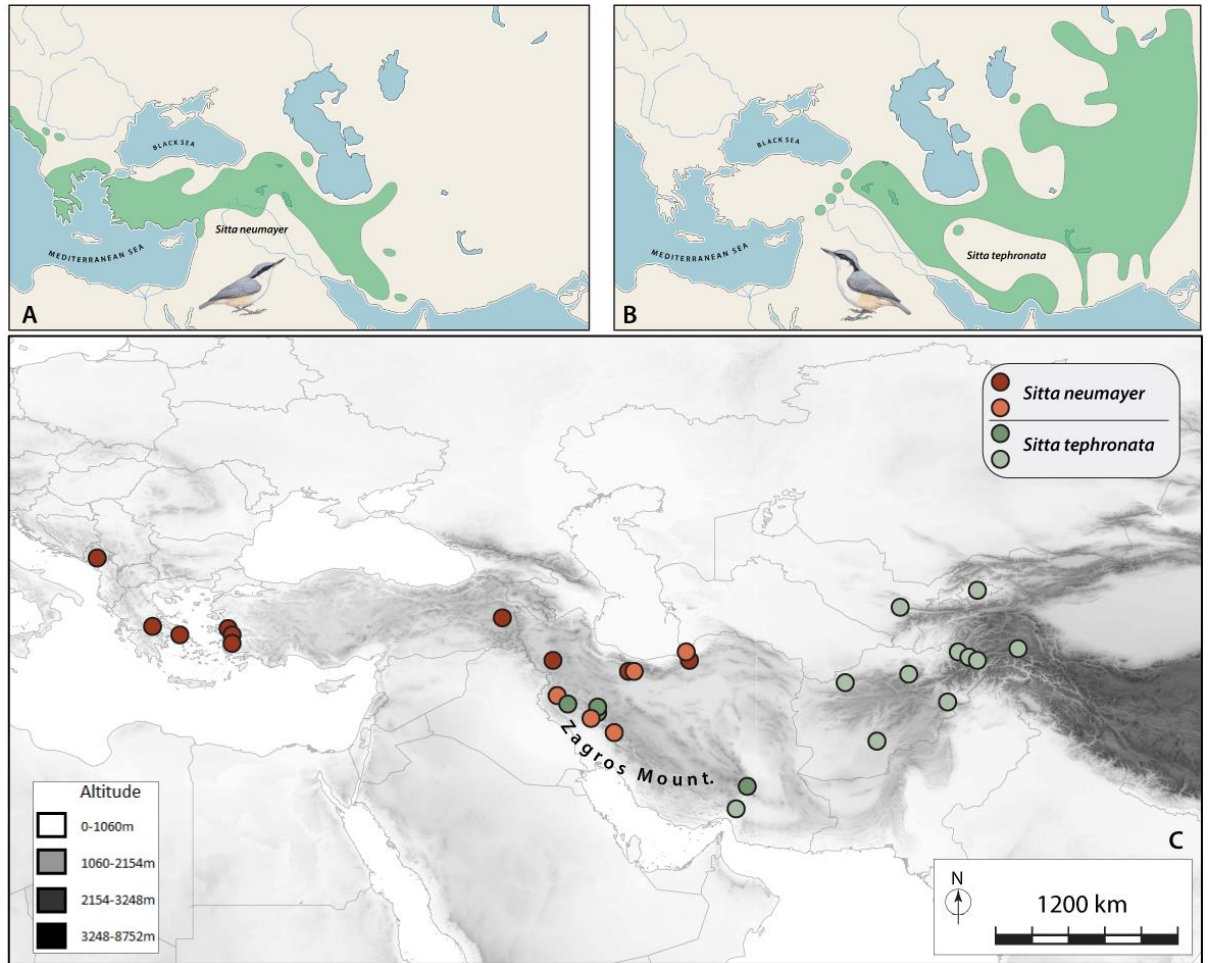
Figure 8 Distributions of *S. neumayer* and *S. tephronota* are shown in A and B, respectively [46, 47]. Locations of sample collection areas are shown in C. Colors of points indicate lineages (See 3.2).

2.2.1 Analysis

Raw sequences were edited by using Sequencher v.5.2 [68] and Unipro UGENE v.1.28.0 [69]. Then they were checked by eye. Contig was extracted as a fasta file and converted to different file formats (i.e. NEXUS) for further analysis.

Numbers of haplotypes were calculated using FaBOX 1.41 (www.birc.au.dk/software/fabox) [70] (See Table 4). For populations with sample sizes 3 and above, DNA polymorphism measures were calculated by using DNAsp version 5 [71]. These included values of nucleotide diversity, haplotype diversity, Tajima's D and Fu's Fs.

After determining the number of haplotypes for each species, the relationship between the haplotypes was determined by maximum parsimony method and for both mtDNA genes. For this, PAUP [72] was used to infer minimum length trees for both genes. *Sitta carolinensis* (GenBank accession number NC_024870) [73] was used as an outgroup. Trees were found using a heuristic search procedure in which simple sequence addition in a stepwise procedure, followed by tree bisection-reconnection (TBR). The stability of phylogenetic structure was tested by bootstrap procedure (100 replicates).

2.3 Ecological Niche Modeling

2.3.1 Input Data

The occurrence data of studied species were downloaded from Global Biodiversity Information Facility's online database (GBIF). Observation records which were entered before 1950 were removed. Duplicates in the sample were removed. By checking with eye, clustering of records were eliminated and records which were staying outside the bioclimatic data were removed. An outline of this procedure is given below:

1- Download georeferenced species occurrence data from www.gbif.org.
2- Remove every point locality which were collected before 1950 (1950-2017 data were used.)
3- Remove point localities which were collected from the same location by using SDMtoolbox [74] in ArcGIS version 10.2.2 [62].
4- Inspect clustering of point localities and delete ones which form clusters by using random numbers approach.
5- Remove points on the sea because they stand outside the climatic variables which will be used in ENM.

This procedure was followed for both *S. neumayer* and *S. tephronota.* As an example you can inspect the input and output point locations in Figure 9. There were 4019 records for *S. neumayer* and 659 records for *S. tephronota.*

After using the procedure above these numbers fell down to 458 and 109, respectively.
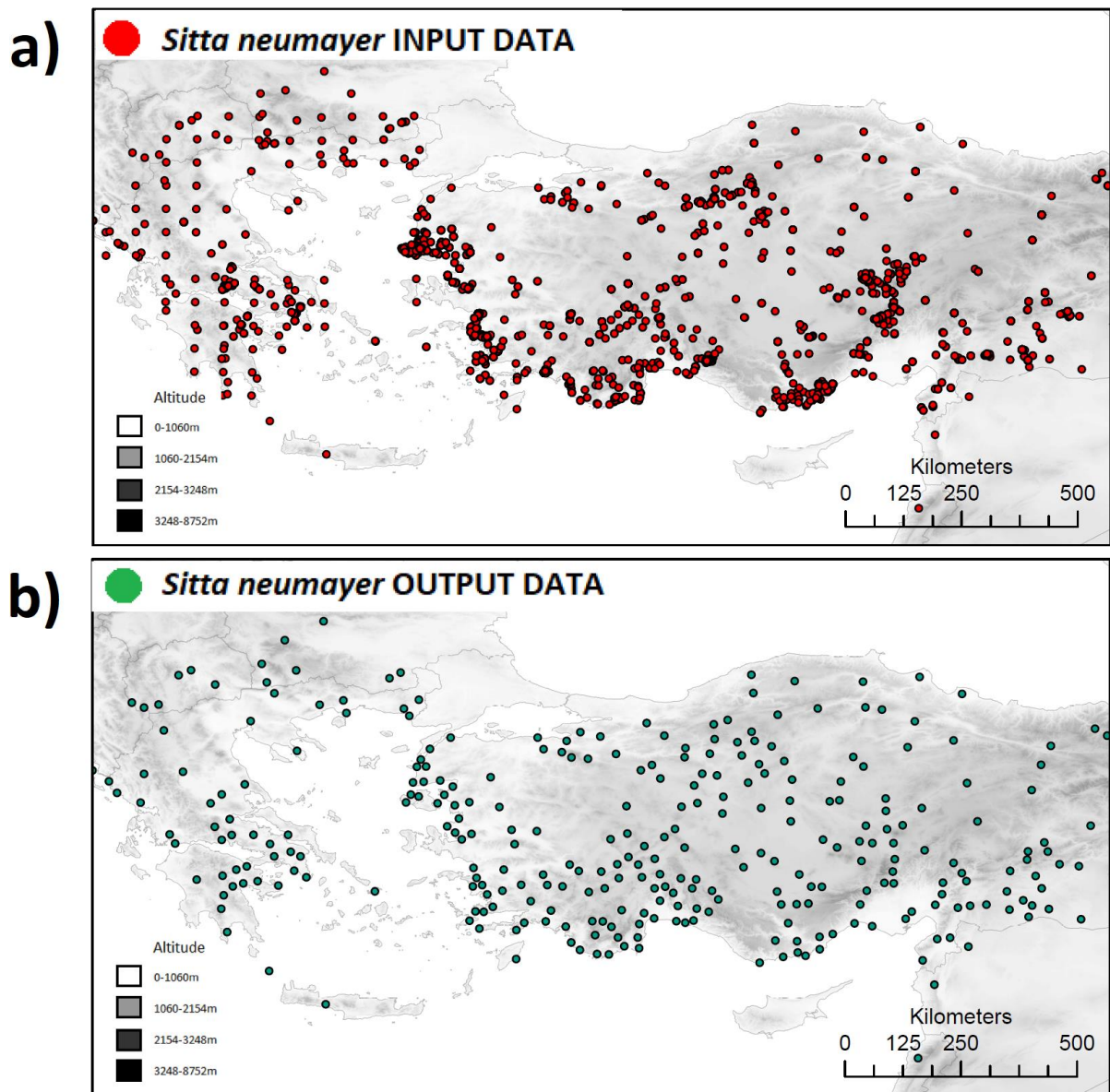
Figure 9 Raw point locations (n=4019) for *S. neumayer* can be seen in a. Output point locations(n=463) of *S. neumayer* can be seen in b.

Both Zagros populations of S. neumayer and S. tephronota has shown unique characteristics compared to the rest of their populations. Hence, Zagros populations of both species were treated as different groups in the ENM. S. neumayer was divided into Zagros population and the rest. The former had 436 records and the latter had 22 records. By using the same approach on S. tephronota, 90 records were used for the eastern population

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and 19 records were used for the Zagros population. To summarise, 6 different populations were classified as:

- *S. neumayer*
- *S. neumayer* without Zagros population
- *S. neumayer's* Zagros population (*S. n. tscihtscherini*)
- *S. tephronota*
- *S. tephronota* without Zagros population
- *S. tephronota's* Zagros Population (*S. t. dresseri*)

Bioclimatic variables at a spatial resolution of 2.5 arc minutes were downloaded from WorldClim database version 1.4 [75] for current (~1960-1990), Last Glacial Maximum (~22000 years before present, LGM). Also Last Interglacial (LIG) data was downloaded in 30 arc second spatial resolution. This was later downscaled to 2.5 arc minutes by using SDMtoolbox [74] in ArcGIS version 10.2.2 [62]. For LGM three Global Climate Models (GCMs) were used; Community Climate System Model version 4 (CCSM4) [76], an Earth System Model (MIROC-ESM) [77] and a Max Planck Institute Earth System Model (MPI-ESM-P) [78]. Previous studies has indicated that a CCSM model was used in the construction of the LIG model [79]. Later, bioclimatic data were masked in the extent of 55° to 15° North and 7° to 90° East.

2.3.2 Modeling the Past and the Present Distributions

M-area (See Figure 1),which specifies the accessible area for the species, was created by following Barve et. al [17]. It was generated by using "Sample by buffered MCP (Minimum Convex Polygon)" function in SDMtoolbox [74]. Buffer distance was assumed to be 200 km when the species needs and potential bird dispersal range are considered [43, 80, 81]. By using "Remove Highly Correlated Variables" function in SDMtoolbox, correlated bioclimatic variables were removed based on 0.85 correlation coefficient. Model test and calibration was done by using MaxEnt version 3.3.3k [82] and ENMTools version 1.4.4 [83]. In this step, algorithm parameters were calibrated.

Different feature types (Linear (L), quadratic (Q), product (P) and hinge (H) features) with regularization multipliers (0.5, 1, 2, 5 and 10) were tested. Models with the lowest Akaike Information Criterion (AIC) scores were preferred.

ENM was operated by running MaxEnt in SDMtoolbox. Non correlated bioclimatic variables were used. CCSM4, MIROC-ESM and MPI-ESM-P scenarios of the LGM and CCSM scenario of the LIG was used for projecting the past climates. Spatial Jackknifing, clamping and extrapolation were switched off. Replicate numbers were increased to 10 and "crossvalidate" was used as the replicate type.

3. RESULTS

3.1 Morphological Characters

In the first test, the difference between the characters of males and females was investigated. Males characters of *S. neumayer* except NL and female characters of it except BL were not normally distributed. TRS for males and TRS and WL for females were non-normally distributed in *S. tephronota* and others were normal. Normally distributed were tested with Independent Samples t-test and non-normally distributed ones were tested with Kruskal-Wallis test.

In the data of *S. neumayer,* the equality of variances was tested by Levene's Test and variances were assumed to be homogenious ($p>0.05$). Independent Samples t-test gave difference only in terms of WL with a p-value of 0.049 (t = 1.985, df = 130) . There was no difference between males and females in terms of TL (t = -0.062, df = 129, p = 0.951) and TRS (t = -0.720, df = 120, p = 0.473) (See Supplementary Table 5). No difference in terms of BL (p = 0.603) and NL (p = 0.804) was found as a result of Kruskal-Wallis Test (See Supplementary Table 6). Boxplots of these characters were shown in figures 10-14.
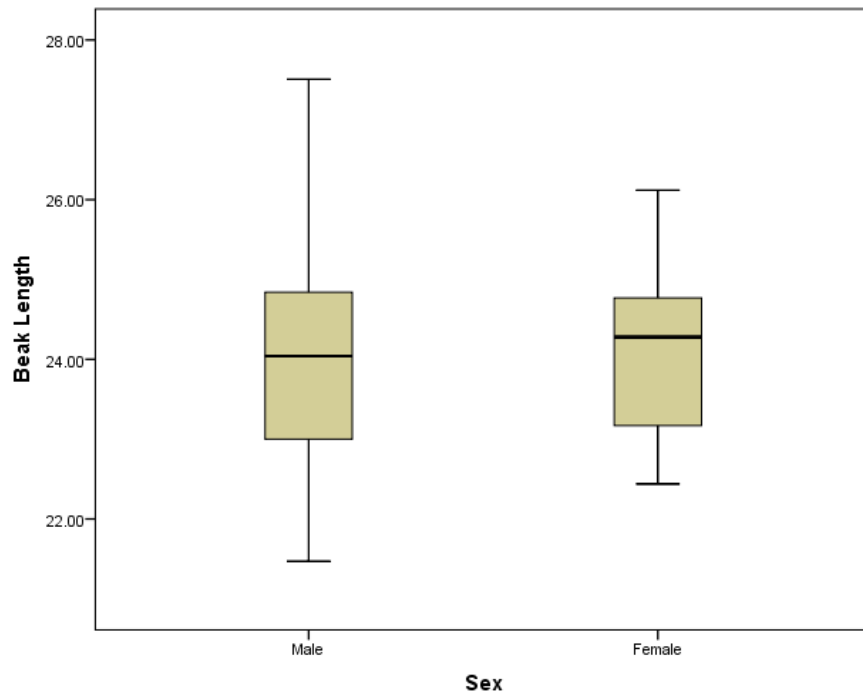
Figure 10 Differences between the sexes in *S. neumayer* in terms of BL.
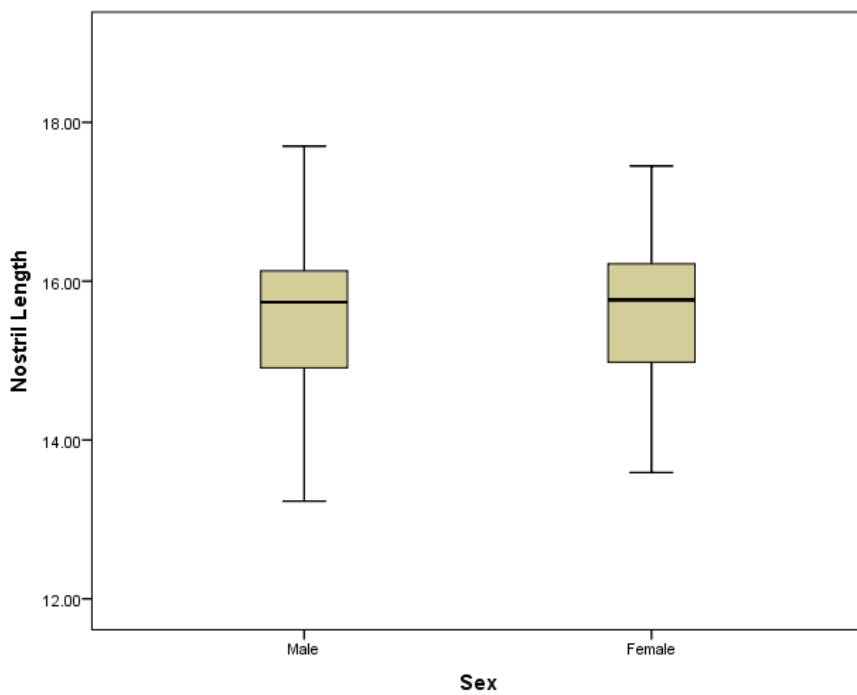
Figure 11 Differences between the sexes in *S. neumayer* in terms of NL.
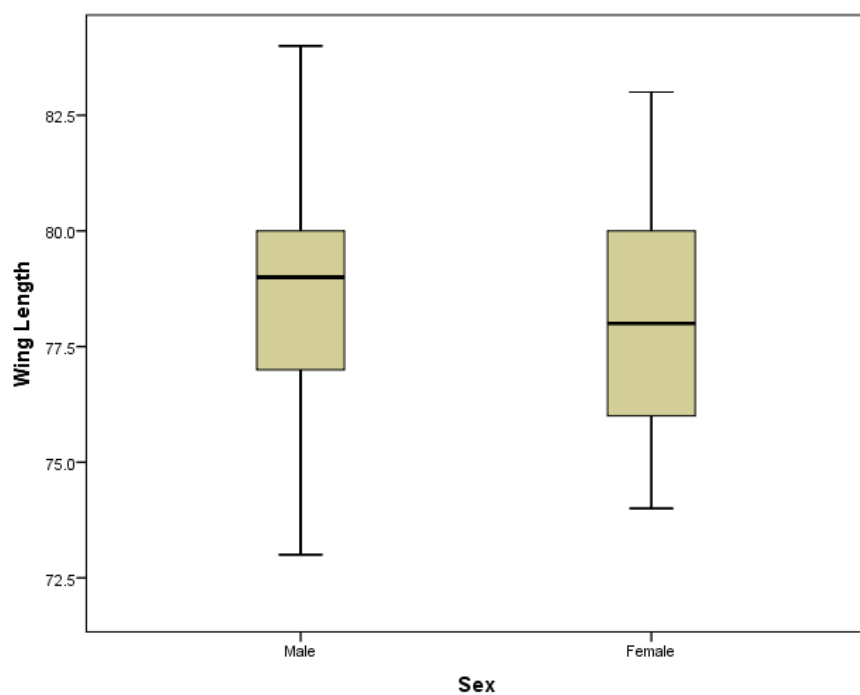
Figure 12 Differences between the sexes in *S. neumayer* in terms of WL.
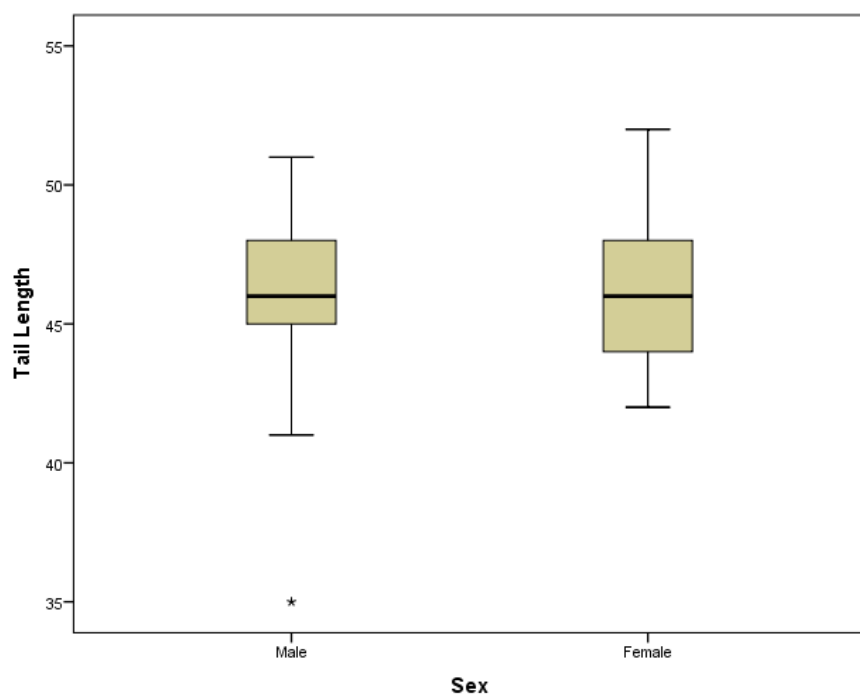
Figure 13 Differences between the sexes in *S. neumayer* in terms of TL.
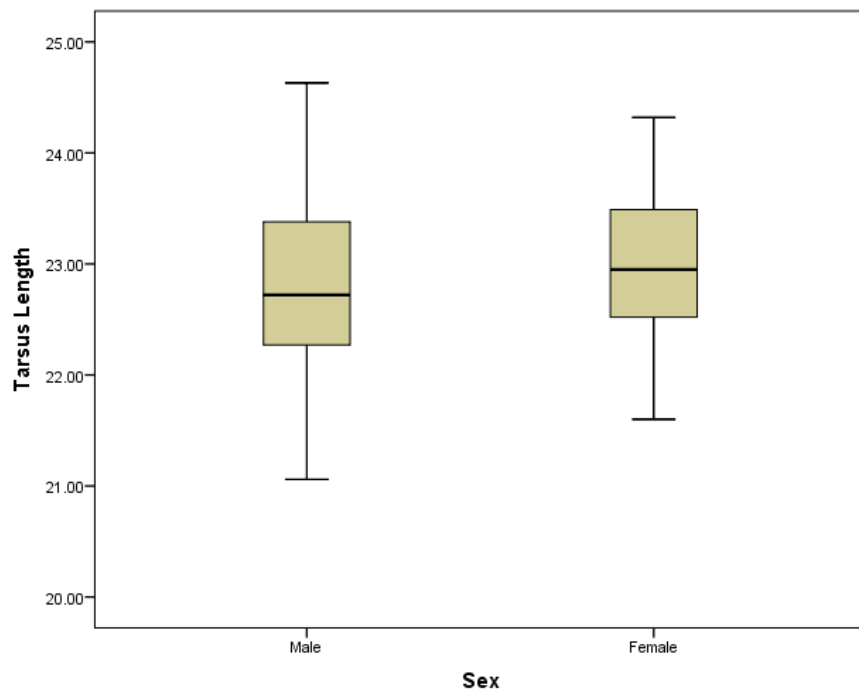
Figure 14 Differences between the sexes in *S. neumayer* in terms of TRS.

In the data of *S. tephronota*, the equality of variances was tested by Levene's Test and variances were assumed to be homogenious (p>0.05) in Independent Samples t-test. As a result BL (t = 2.017, df = 169, p = 0.045), TL (t = 2.727, df = 168, p = 0.007) and WL (p = 0.011) had difference. NL (t = 1.158, df = 169, p = 0.249) and TRS (p=0.078) has not shown any difference. See Supplementary Tables 7 and 8.). Boxplots of these characters were shown in figures 15-19.
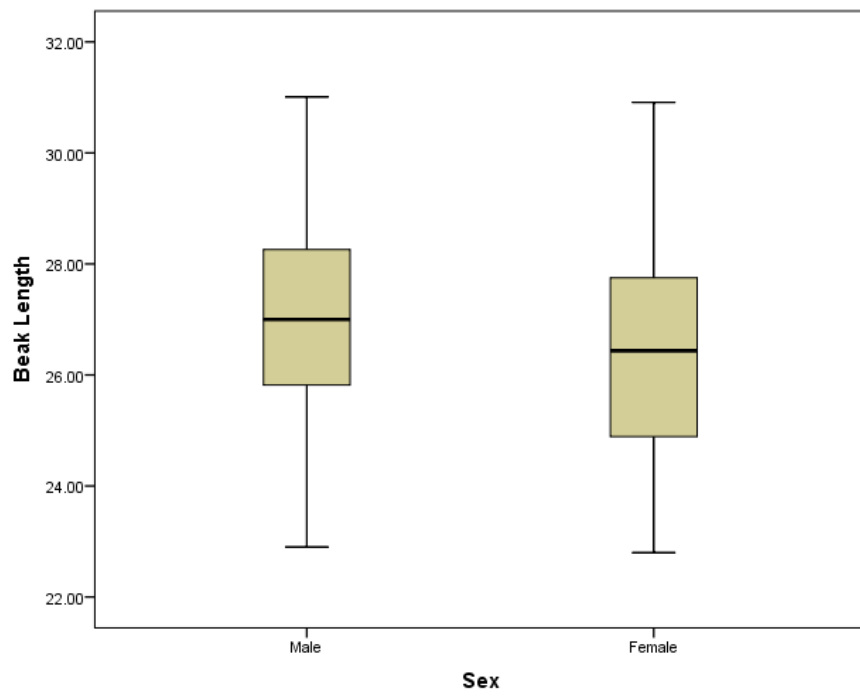
Figure 15 Differences between the sexes in *S. tephronota* in terms of BL.
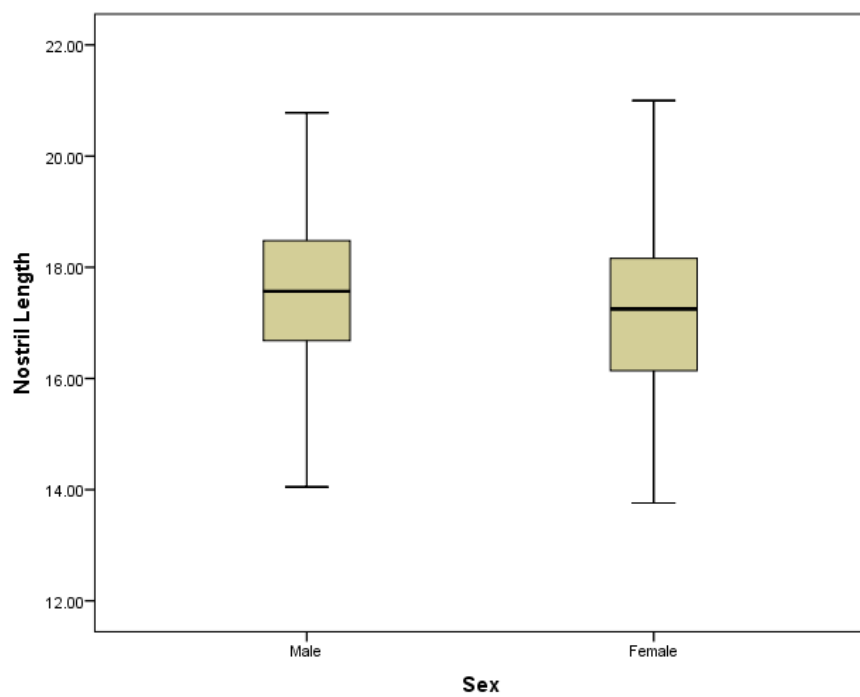
Figure 16 Differences between the sexes in *S. tephronota* in terms of NL.
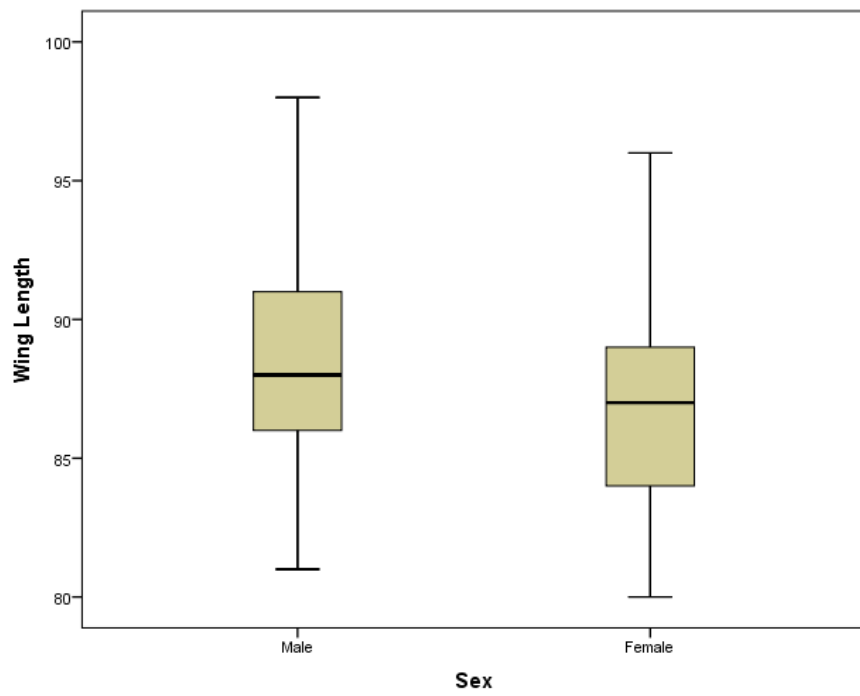
Figure 17 Differences between the sexes in *S. tephronota* in terms of WL.
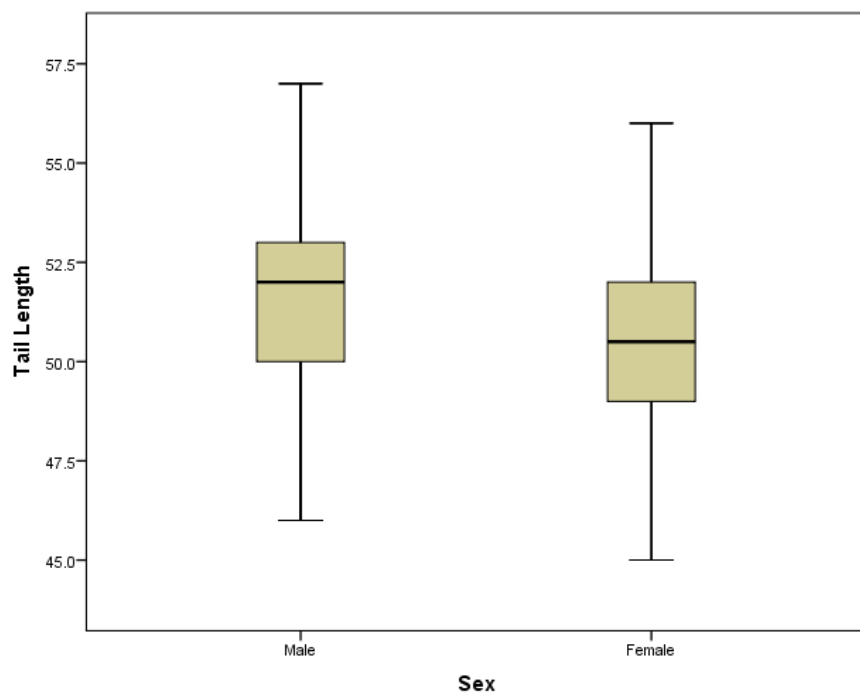
Figure 18 Differences between the sexes in *S. tephronota* in terms of TL.
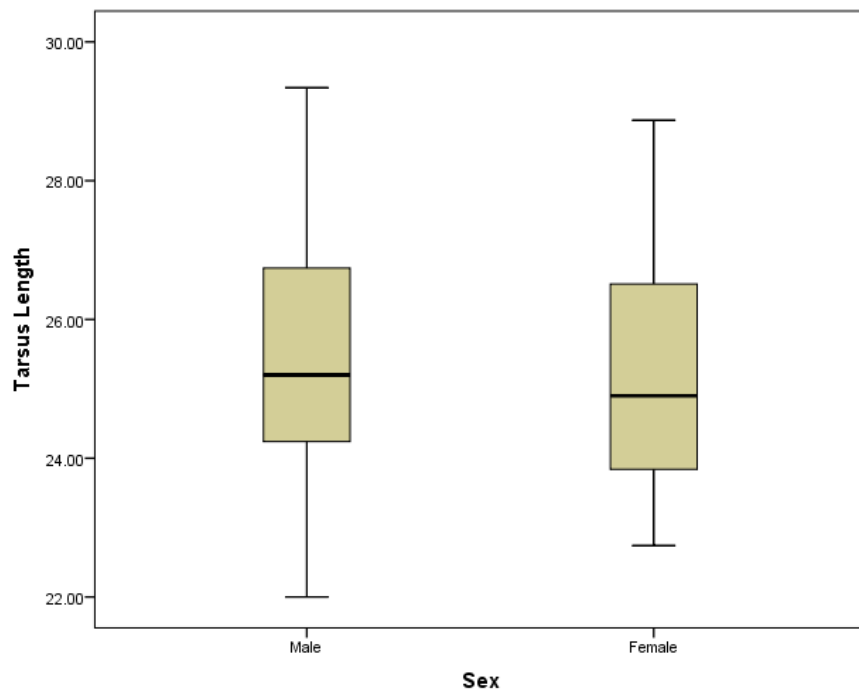
Figure 19 Differences between the sexes in *S. tephronota* in terms of TRS.

Since there was difference between sexes for WL in *S. neumayer,* only male data was used. The associations between BL and NL was investigated with Spearman Test for the males of *S. neumayer* since those variables are very related to each other. Spearman test showed a significant correlation between these two variables with a correlation coefficient of 0.865. The same method was used for other variables and correlations can be seen on Figure 20 (for details see Supplementary Table 9.).
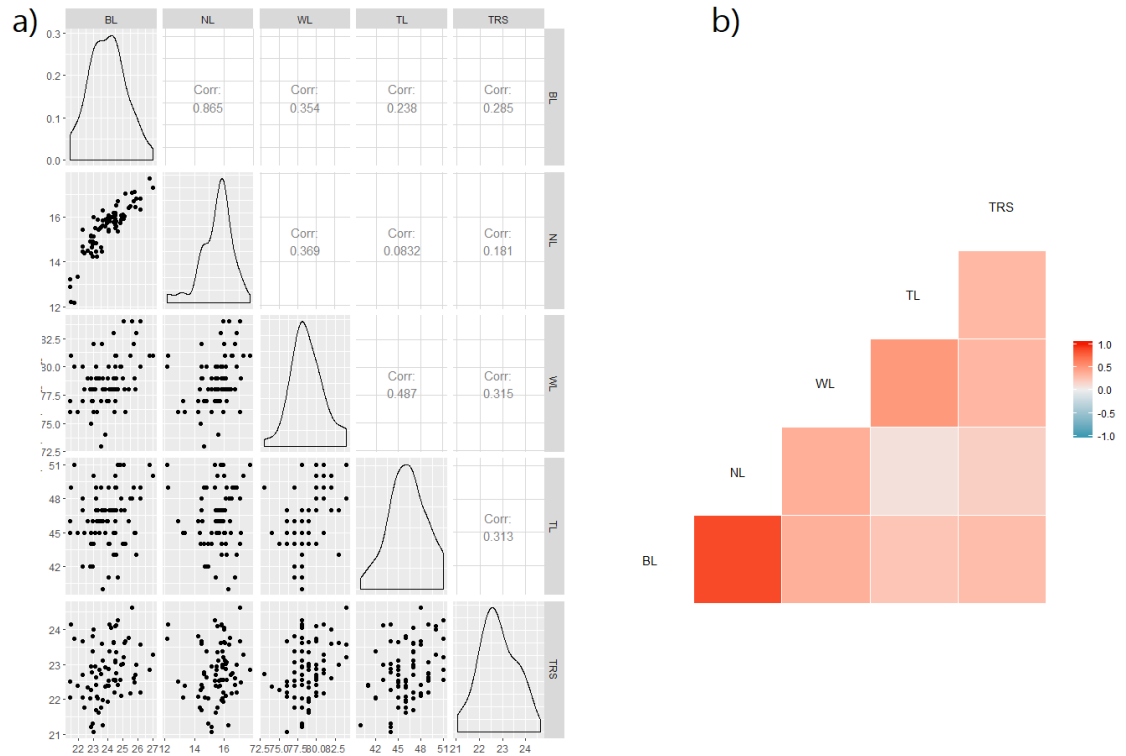
Figure 20 Relationship between BL, NL, WL, TL and TRS for the males of *S. neumayer.* a) Scatterplots and correlation coefficients are shown. b) Visualization of correealations. Figures were created by using Ggally package extension of ggplot2 in R [22, 84].

Because of the high correlation between BL and NL; NL was removed to discard overemphasis and multicollinearity. BL, WL, TL and TRS was used to create a new allometric size variable using PCA. As a difference between sexes have been found in *S. tephronota* for BL, TL and WL; both of the species were treated as dimorphic and females were removed from the data. Also there was not enough females for comparing Zagros with the rest. There were several outliers in the data so they were removed to reduce their influence on PCA (1 sample from *S. neumayer,* 3 samples from *S. tephronota)*. Since no transformations were done for any of the variables, the correlation matrix was used [65]. The PCA produced a new allometric size and shape variables. Component matrix of each variable on these new variables can be seen in Table 2 and 3. First principle component (PC1) was used as allometric size variable for each species and second principle component was used as the shape variable. On the one hand, the first component explains 53.1% of the total variance for *S.neumayer.* On the other hand, the first principle component of *S. tephronota* explains 57.1% of the total variance.

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Table 2 Principal component loadings (PC1) from a PCA of 4 external morphological measurements of 76 *S. neumayer* and 78 *S. tephronota* males.

Characters	PC1	
	S. neumayer	*S.tephronota*
BL	0.677	0.843
WL	0.799	0.878
TL	0.740	0.086
TRS	0.692	0.892
Eigenvalue	2.125	2.285
% of variance	53.117	57.122

Table 3 Principle component loadings (PC2) from a PCA of 4 external morphological measurements of 76 *S. neumayer* and 78 *S. tephronota* males.

Characters	PC2	
	S. neumayer	*S.tephronota*
BL	0.652	-0.201
WL	0.136	0.185
TL	-0.317	0.983
TRS	-0.456	-0.087
Eigenvalue	0.752	1.049
% of variance	18.800	26.231

In phylogeography analysis, 2 different lineages for both species (Zagros and the rest) have been found and because of this I investigated whether there were any differences between those lineages in terms of morphological features (PC1). Normalities of these newly created allometric size variables (PC1) were checked and no deviations from normality were found for both of the species Lilliefors Kolmogorov-Smirnov and Shapiro-Wilk results were used in testing normality. (See Supplementary Tables 10 and 11). For testing differences between Zagros populations and the rest, Independent Samples t-test was used. Males of *S. n. tschitscherini* (t = 2.651, df = 74, p=0.01) and

S. t. dresseri (t = -9.921, df = 86, p<0.001) has shown difference from their main populations. Both of the variances were assumed to be equal according to the Levene's Test of equality of variances (See Supplementary Tables 12-13).

PC2 represents the shape variable and to visualise the difference between populations new graphs were created by using allometric size and shape variables. (See Figures 21 and 22.)
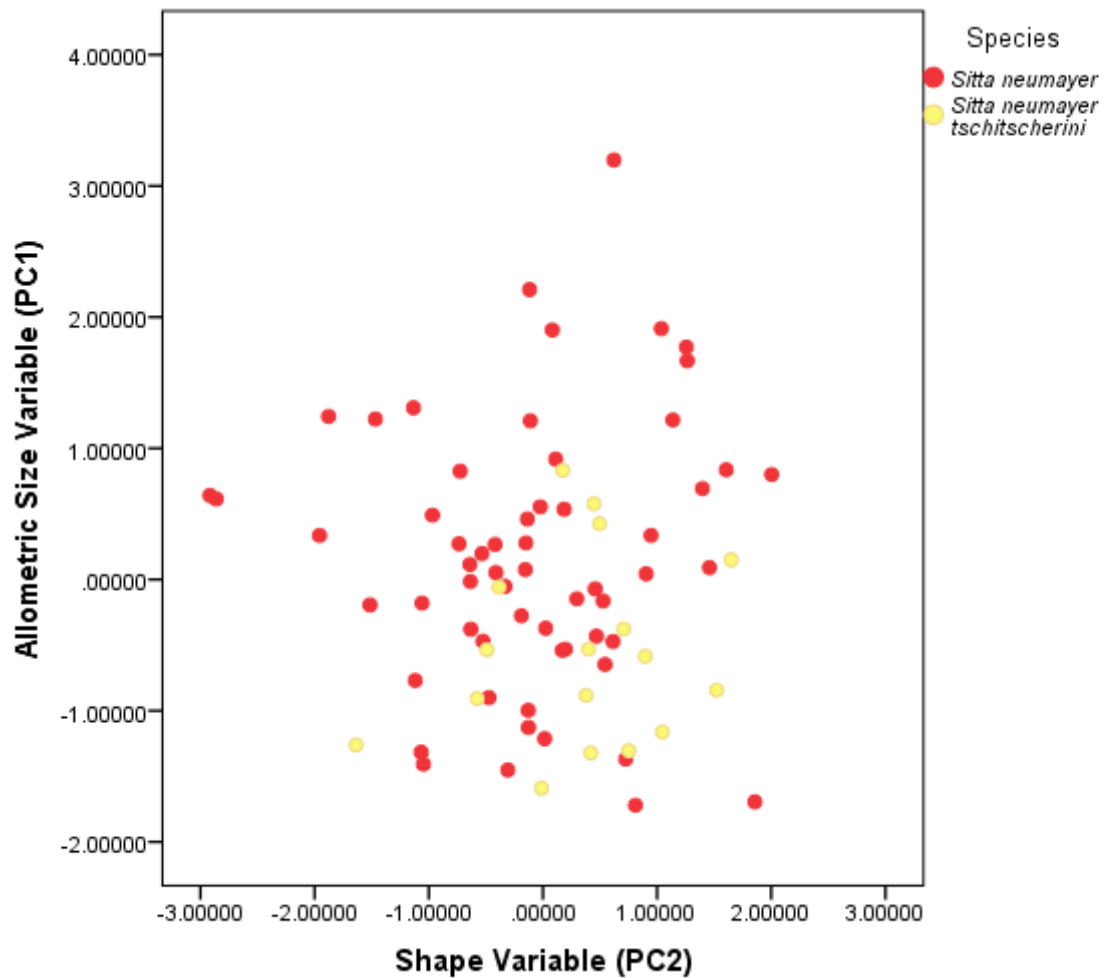
Figure 21 Comparison of *S. neumayer* and *S. n. tschitscherini* by using allometric size and shape variables.
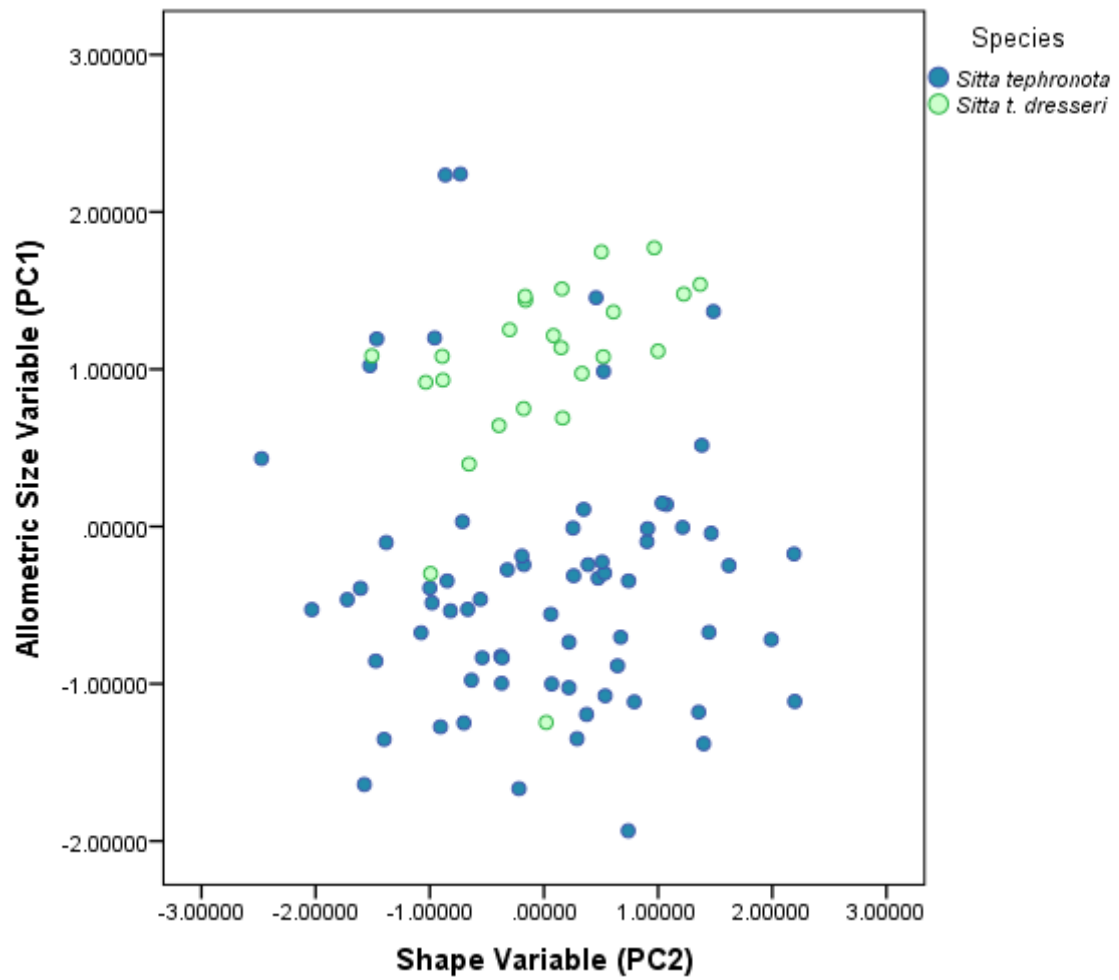
Figure 22 Comparison of *S. tephronota* and *S. t. dresseri* by using allometric size and shape variables.

3.2 Phylogeography

32 samples of *S. neumayer* and 28 samples of *S. tephronota* was studied which were covering most of the range of both species. Populations for both species were divided as Zagros and non-Zagros populations. Non-Zagros samples of *S. neumayer* included samples from Montenegro, Greece, Western and Eastern Anatolia and Zagros samples, which were consistent with the distribution of *S. n. tschitscherini* were collected from Zagros mountains, Tehran and Gorgan. *S. t. dresseri* included samples from South Iran and Zagros mountains. The non-Zagros category of *S. tephronota* included 6 populations including samples from Uzbekistan, Western, Eastern, Southern, Northern and Northeastern Afghanistan. Populations were divided as *S. neumayer – S. n. tschitscherini* and *S. tephronota – S. t. dresseri* by considering species distributions and a preliminary tree created with PAUP [72], as there were not enough samples from some locations to do phylogeographical analysis. All DNA polymorphism measures with sample sizes and population informations can be seen in Table 4.

S. neumayer had 6 different ND2 and 8 different ND3 haplotypes for *S. n. tschitscherini* and western population. As a result the similar pattern of haplotype diversities for both populations were detected. However, haplotype diversity of the western population was bigger than the eastern population (see Table 4).

S. tephronota had 10 different ND2 and 17 different ND3 haplotypes for eastern and Zagros populations and values for haplotype diversities has shown a similar pattern as *S. neumayer*. Haplotype diversity of the western population was higher than the eastern population (see Table 4).

A parsimony analysis of 14 haplotypes of *S. neumayer* and 27 haplotypes of *S. tephronata*, plus an outgroup sequence, produced a set of 5 trees for ND2 (of 306 total charactes: 26 variable characters were parsimony informative), and a set of 8 trees for ND3 (of 313 total charactes: 32 variable characters were parsimony informative). In all trees, Zagros sequences separated from

others with good bootstrap support for both species (Figure 23 and 24). However, Mazandaran region had haplotypes from eastern and western lineages for *S. neumayer*.

Table 4 DNA polymorphism measures and results of neutrality tests for *S. neumayer* (S.n.) and *S. tephronota* (S.t). n is the number of samples, hn is the haplotype number, h is the haplotype divesity, µ is the nucleotide diversity, D is Tajima's D and Fs is Fu's. (* means significant. t. is *S. n. tschitscherini* and d. is *S. t. dresseri*.)

	ND2 (306 bases)						ND3 (313 bases)					
S. n.	n	hn	H	Pi	D	Fs	N	Hn	H	Pi	D	Fs
t.	8	2	0.250	0.00085	-1.05482	-0.182	7	3	0.286	0.00092	-1.00623	-0.095
W.	18	4	0.608	0.00237	-0.46640	-0.841	6	5	0.867	0.00715	0.97428	-0.439
Total	26	6	0.751	0.00519	-0.08695	-0.611	13	8	0.782	0.01349	1.35453	0.596
S. t.	n	hn	H	Pi	D	Fs	N	Hn	h	Pi	D	Fs
d.	9	5	0.722	0.00436	-1.7278*	-1.784	6	4	0.600	0.00226	-1.13197	-0.858
E.	10	5	0.356	0.00157	0.01499	0.417	14	13	0.769	0.00872	0.12331	0.397
Total	19	10	0.743	0.03102	1.39885	4.029	20	17	0.879	0.03883	1.46507	2.441

When differences of ND2 gene regions' haplotypes between *S. neumayer – S. n. tschitscherini* are inspected according to their codon numbers, there has been 3 mutations between them and all of them were in the third base of their codons. There were 12 mutations betweeen *S. tephronota – S. t. dresseri* and 9 of them were in the third base of the codon and 3 of them were in the first base of the codon.

ND3 gene had 7 mutations between *S. neumayer – S. n. tschitscherini.* 6 of them were in the third base of their codons and only one was in the first base of its codon. There were 11 mutations between *S. tephronota – S. t. dresseri* and all of them were in the third base of their codons.
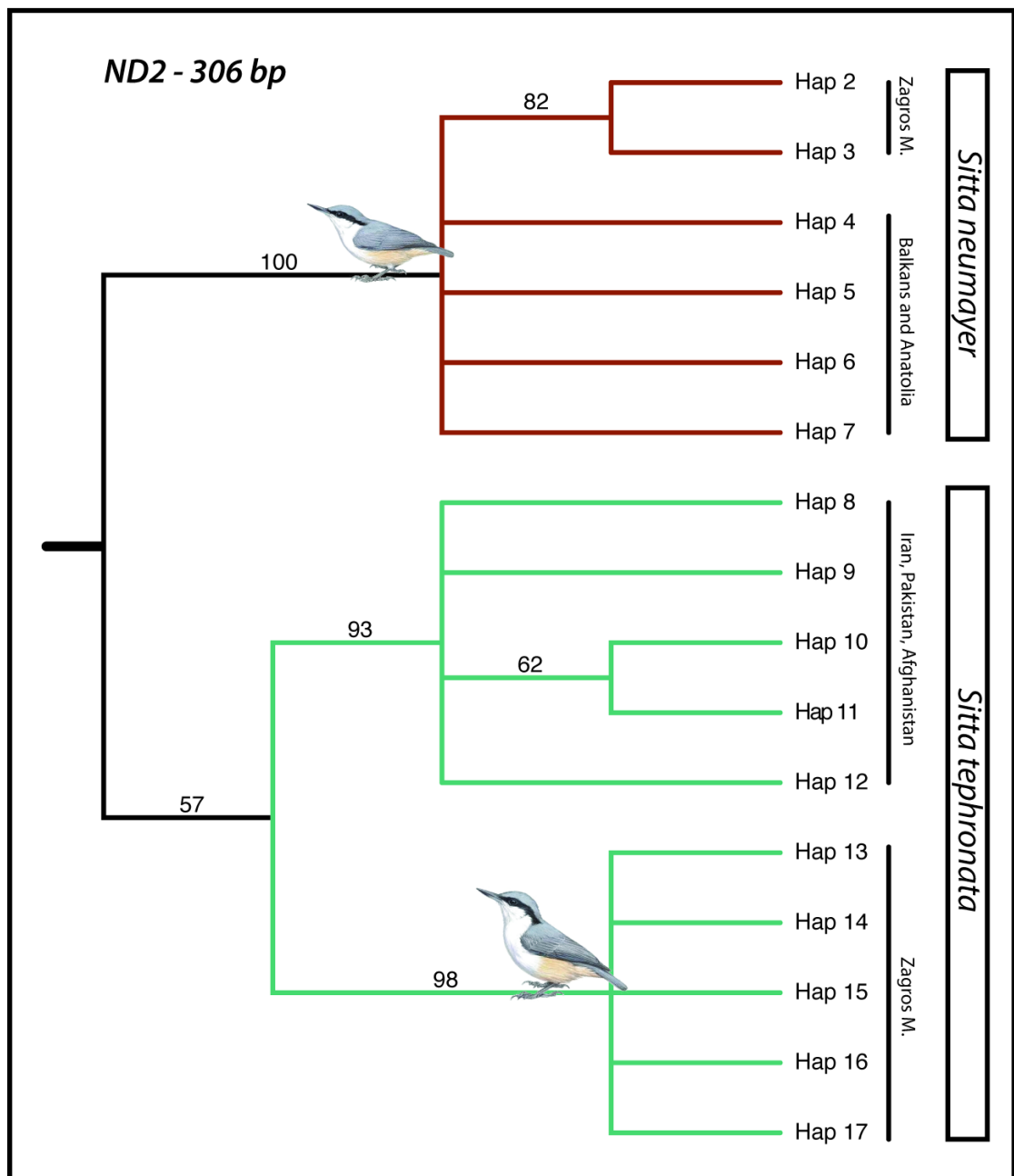
Figure 23 Parsimony bootstrap proportions for the two major clades are shown below the branches within *S. neumayer* and *S. tephronota* for ND2. Major haplotype groupings are indicated by different colours.
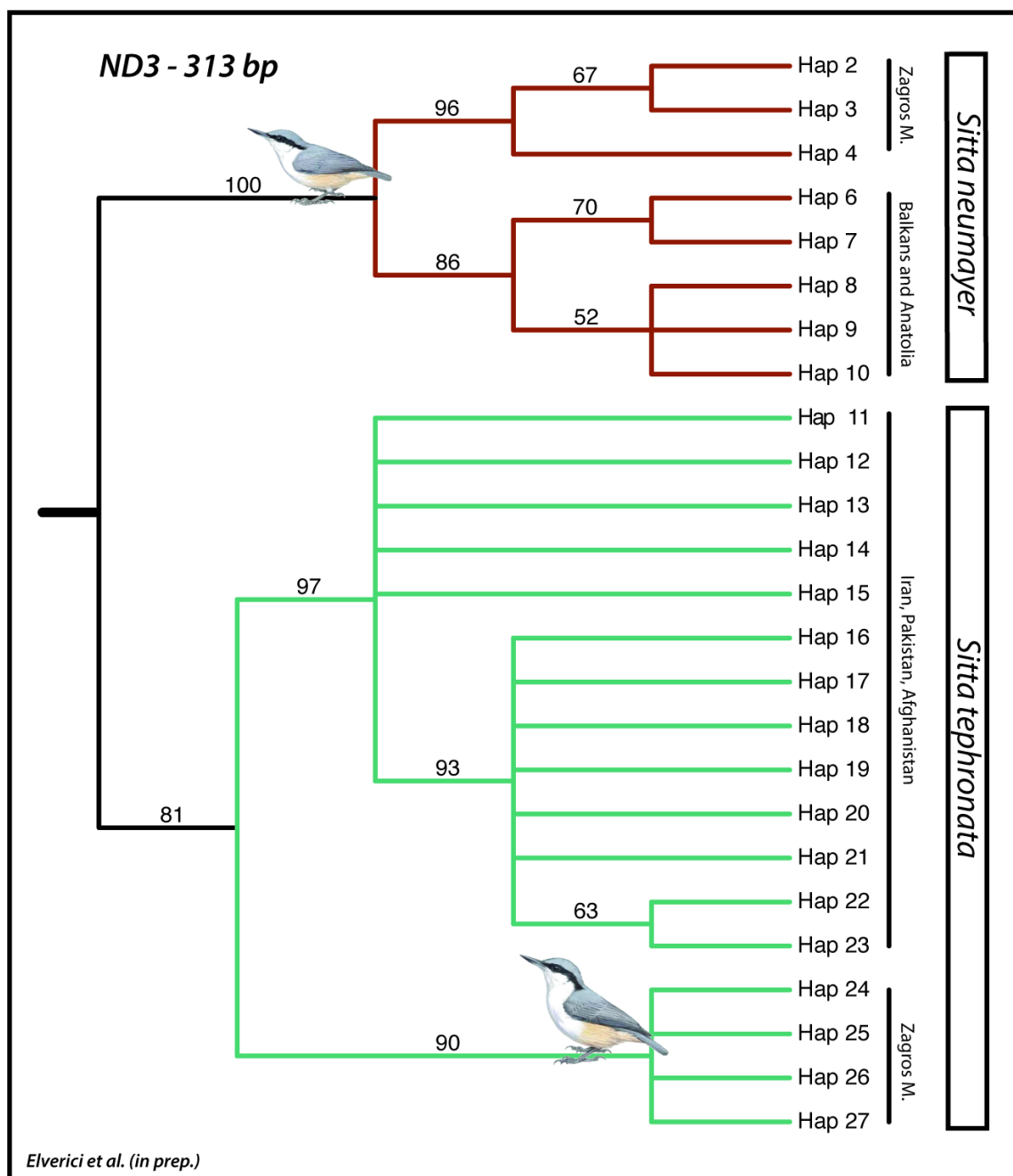
Figure 24 Parsimony bootstrap proportions for the two major clades are shown below the branches within *S. neumayer* and *S. tephronota* for ND3. Major haplotype groupings are indicated by different colours.

3.3 Ecological Niche Modeling

Models with the lowest AICc scores were shown in Supplementary Tables 14-19 for both species and Zagros populations. The ENM estimated better than the random predictions with Area Under Curve (AUC) values ranging from 0.785 to 0.9. Individual AUC results can be seen in Table 5. According to Swets, AUC values are classified as excellent for values over 0.9, good for values between 0.8-0.9, fair for values between 0.7-0.8, poor for values between 0.6-0.7 and failed for values under 0.6 [85, 86]. The response curves showed that BIO19 (precipitation of the coldest quarter) contributed most to *S. tephronota* (all occurrences), its Zagros population and *S. neumayer* without Zagros population. Also BIO18 (precipitation of the warmest quarter) contributed most to the *S. neumayer* (all occurrences) and *S. tephronota* without Zagros population. *S. neumayer'*s Zagros population was affected mostly by BIO8 (mean temperature of the wettest quarter).

Table 5 AUC values for 6 different models.

Models	AUC
S. neumayer (All occurrences*)*	0.872
S. neumayer without Zagros population	0.785
S. neumayer 's Zagros population	0.821
S. tephronota (All occurrences*)*	0.844
S. tephronota without Zagros population	0.861
S. tephronota 's Zagros population	0.900

Under present bioclimatic conditions the model prediction was almost concordant with species' known distributions (Figures 25-30). Under past climatic conditions, the model prediction showed that there was no difference between the present and the LGM for both species and Zagros populations. However, the LIG prediction showed a distributional contraction pattern for both species. Additionaly, the LIG prediction for Zagros populations of both species showed no evidence of suitable conditions. The LGM scenarios of Figures 25-30 were created by combining CCSM4, MIROC-ESM and MPI-ESM-P GCMs. Individual results for these GCMs can be seen in Figures 31-36.
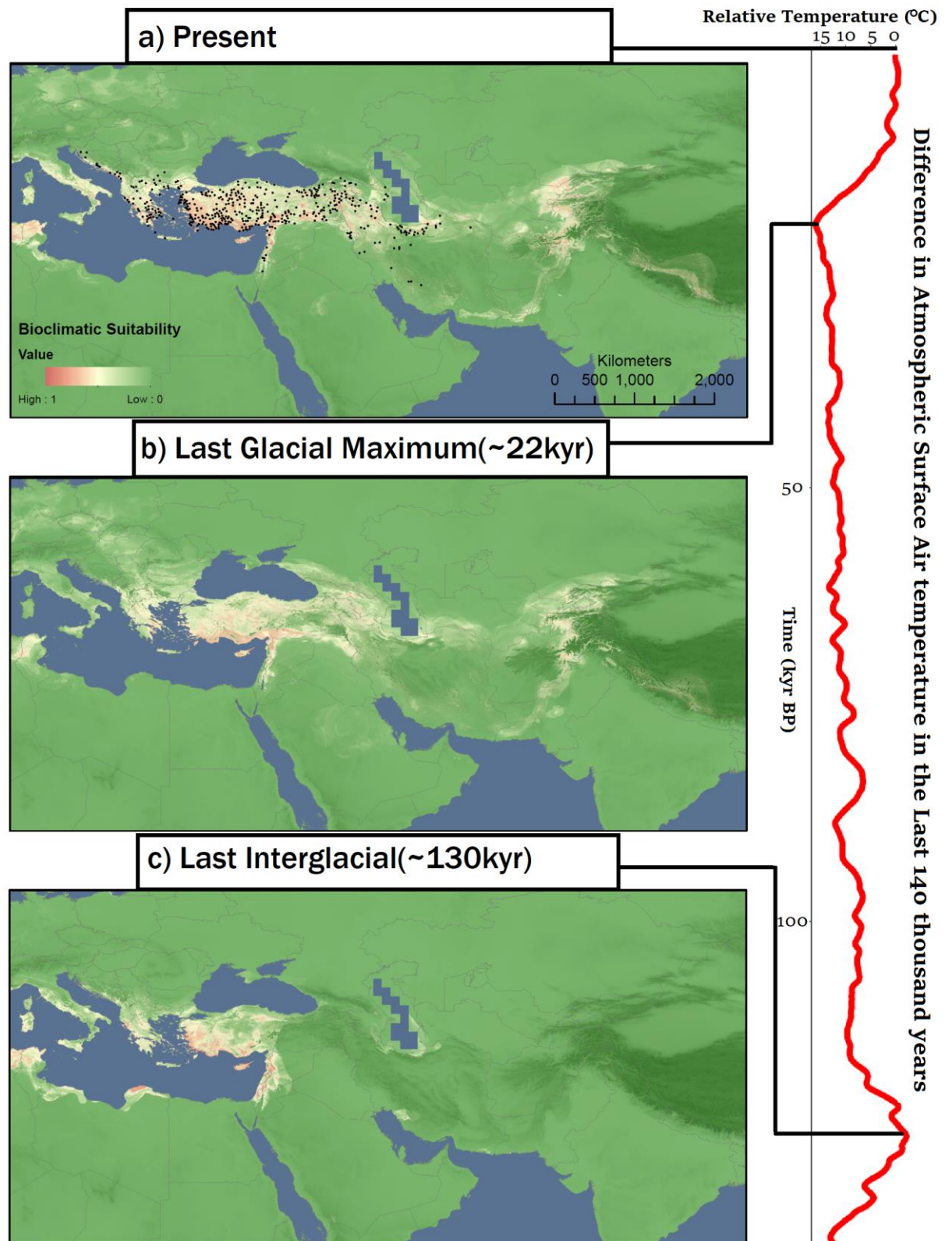
Figure 25 ENM showing the suitable conditions for *S. neumayer* for present(~1960-1990) and the reconstructed past bioclimatic conditions. Here LGM is obtained by combining CCSM4, MIROC-ESM and MPI-ESM-P GCMs.
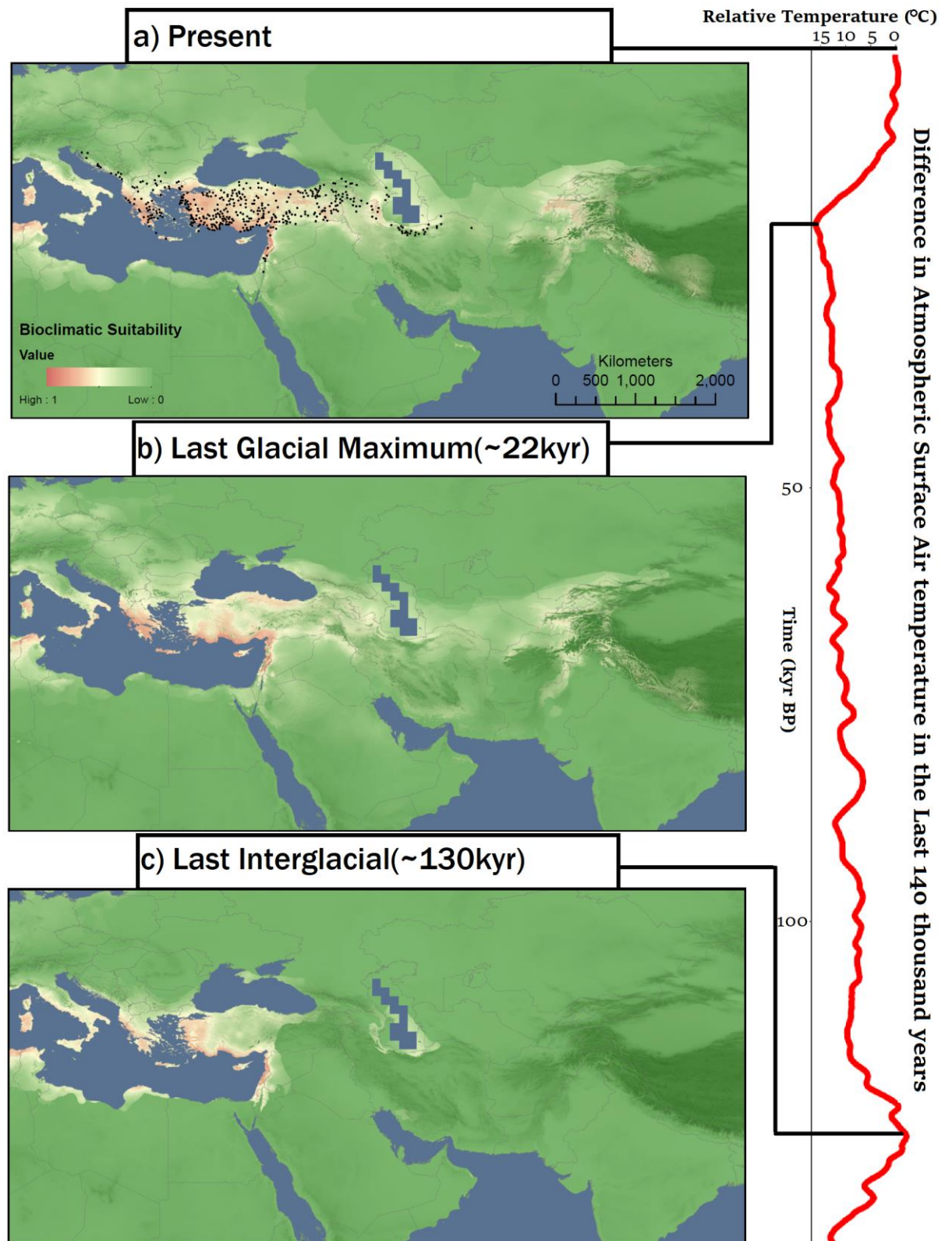
Figure 26 ENM showing the suitable conditions for *S. neumayer* without Zagros population for present(~1960-1990) and the reconstructed past bioclimatic conditions. Here LGM is obtained by combining CCSM4, MIROC-ESM and MPI-ESM-P GCMs.
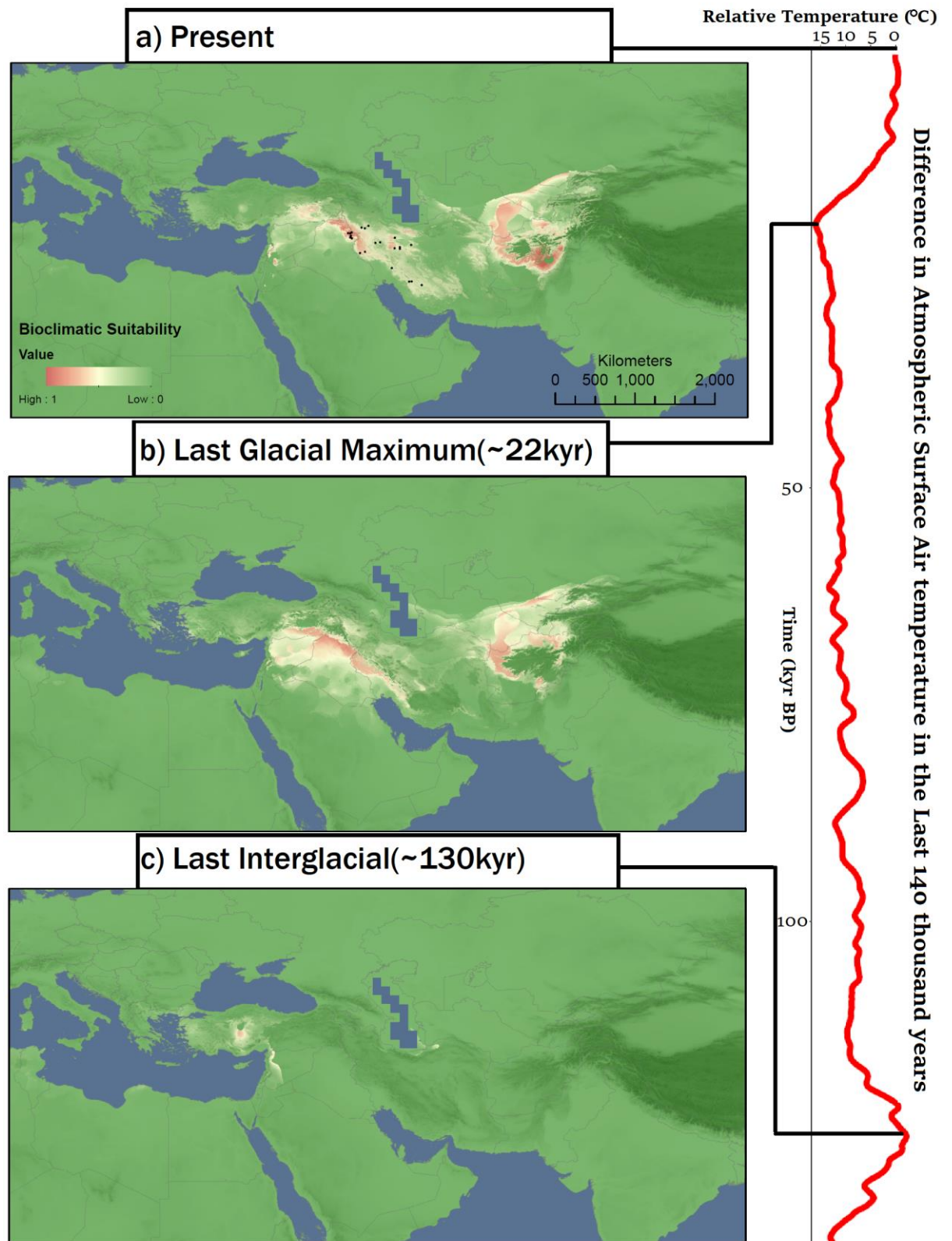
Figure 27 ENM showing the suitable conditions for *S. neumayer*'s Zagros population for present(~1960-1990) and the reconstructed past bioclimatic conditions. Here LGM is obtained by combining CCSM4, MIROC-ESM and MPI-ESM-P GCMs.
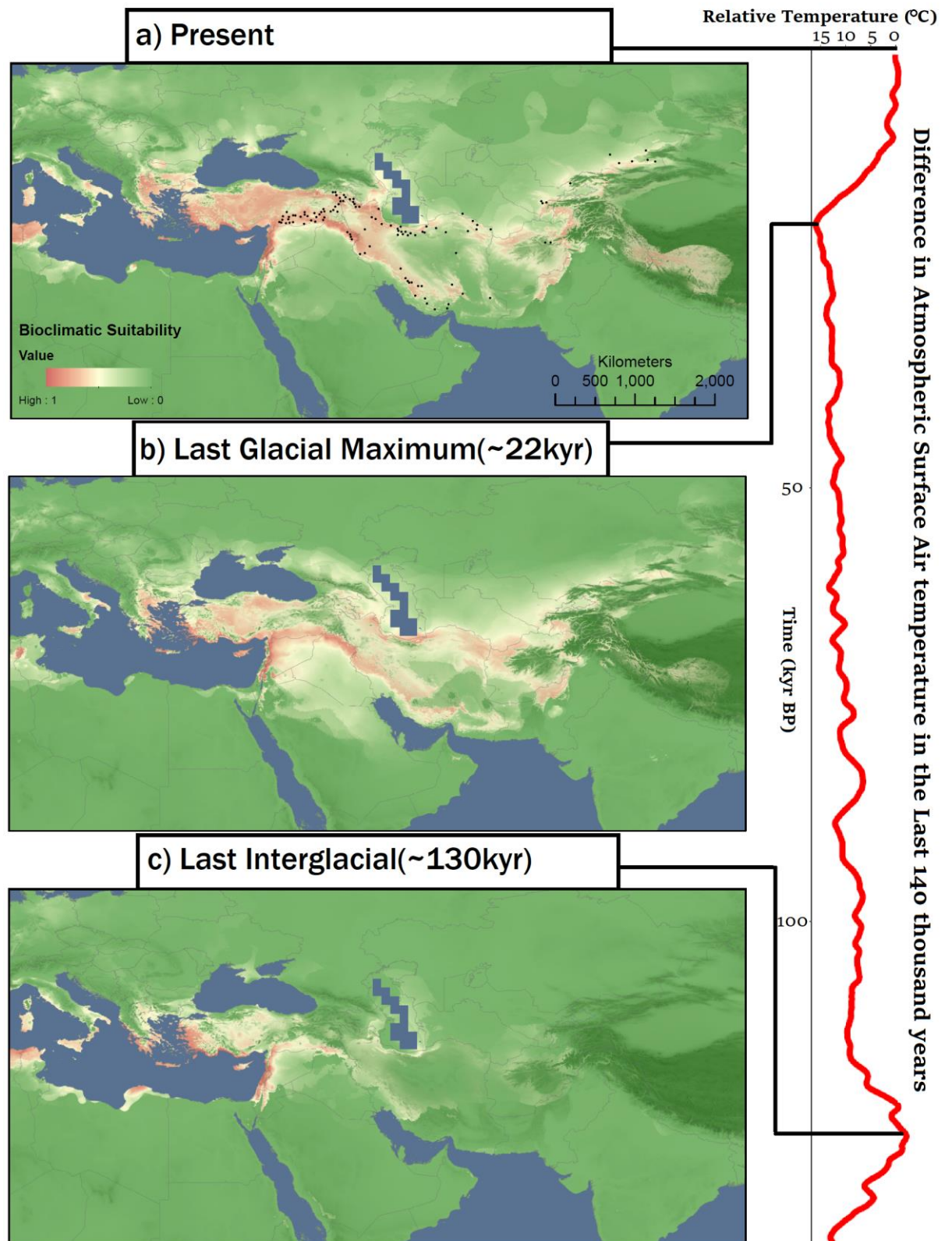
Figure 28 ENM showing the suitable conditions for *S. tephronota* for present(~1960-1990) and the reconstructed past bioclimatic conditions. Here LGM is obtained by combining CCSM4, MIROC-ESM and MPI-ESM-P GCMs.
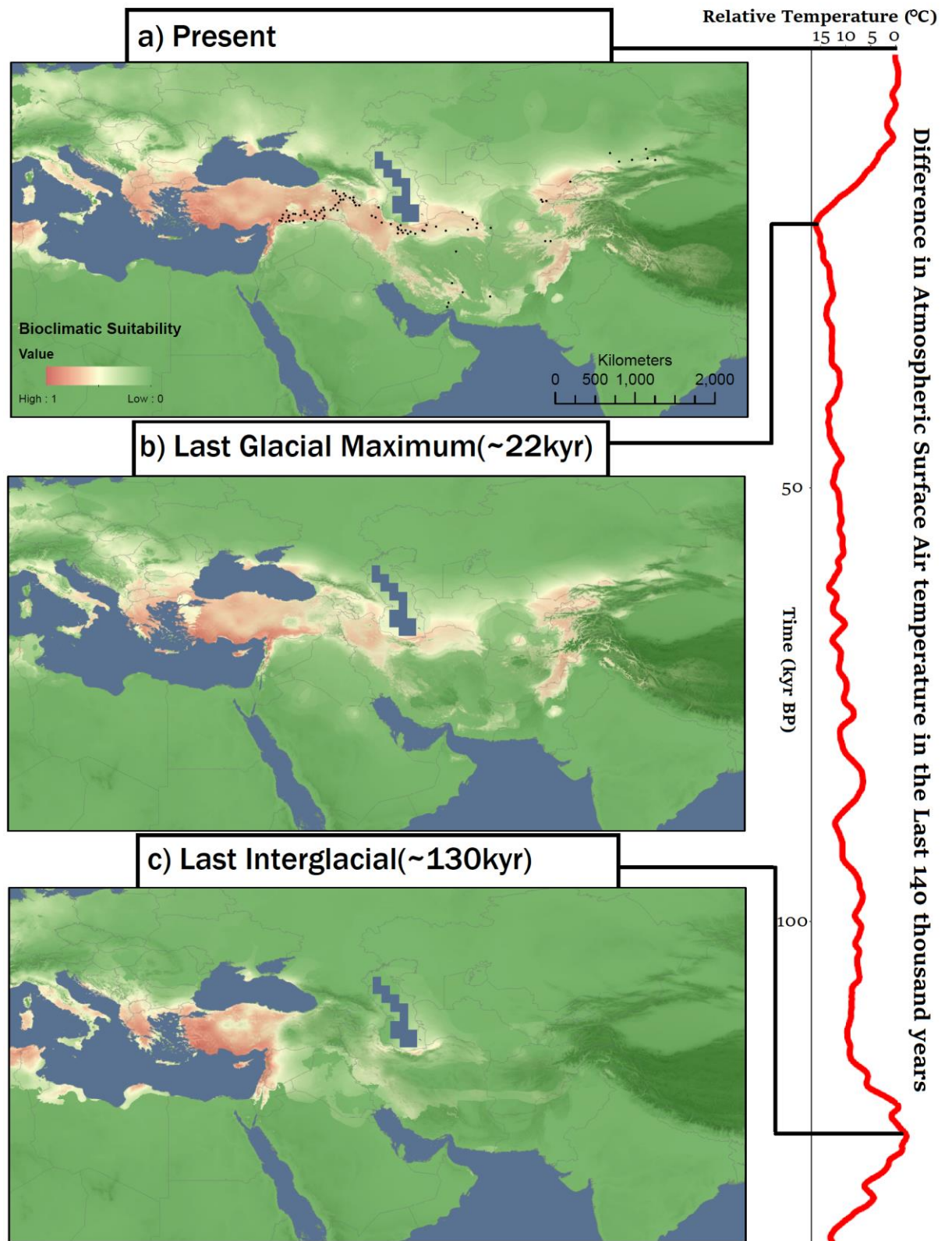
Figure 29 ENM showing the suitable conditions for *S. tephronota* without Zagros population for present(~1960-1990) and the reconstructed past bioclimatic conditions. Here LGM is obtained by combining CCSM4, MIROC-ESM and MPI-ESM-P GCMs.
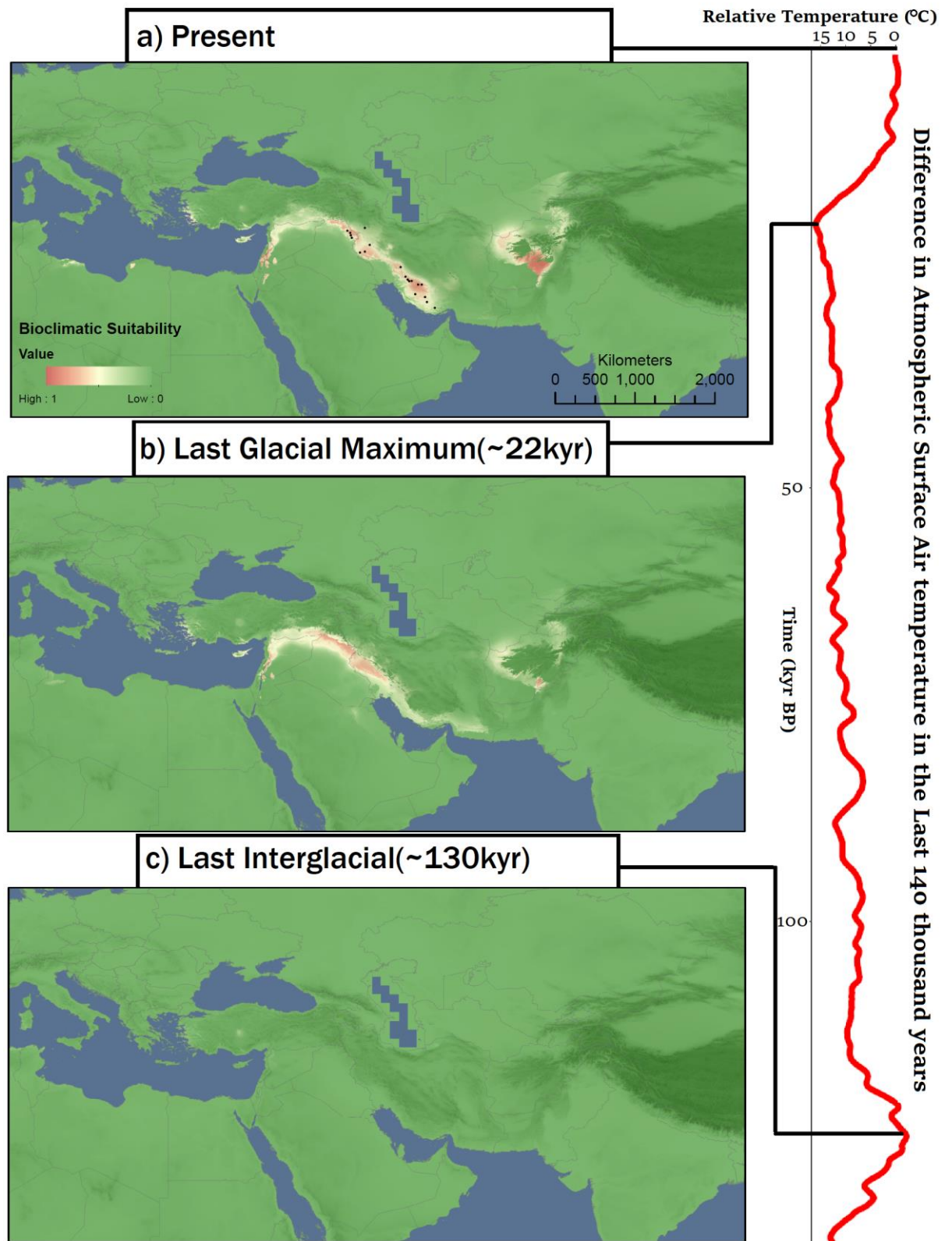
Figure 30 ENM showing the suitable conditions for *S. tephronota*'s Zagros population for present(~1960-1990) and the reconstructed past bioclimatic conditions. Here LGM is obtained by combining CCSM4, MIROC-ESM and MPI-ESM-P GCMs.

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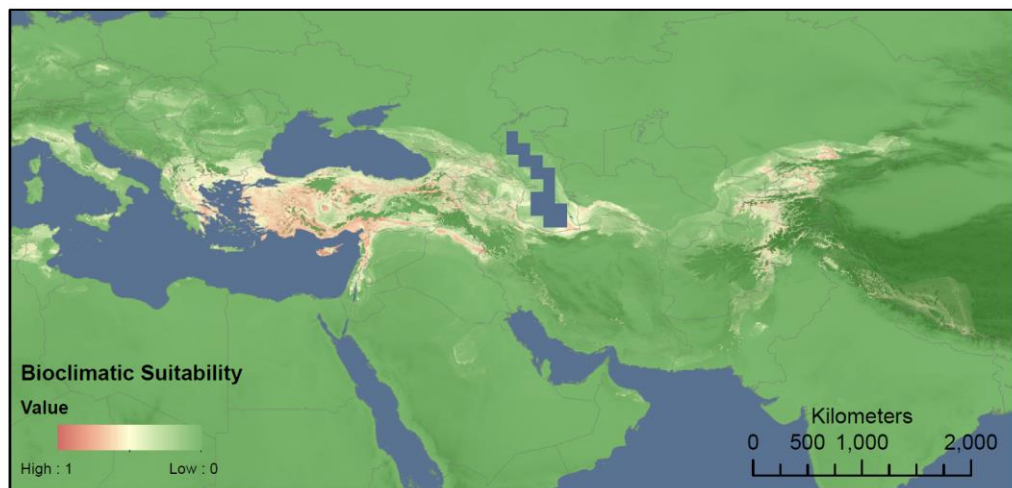
a) CCSM4 Model
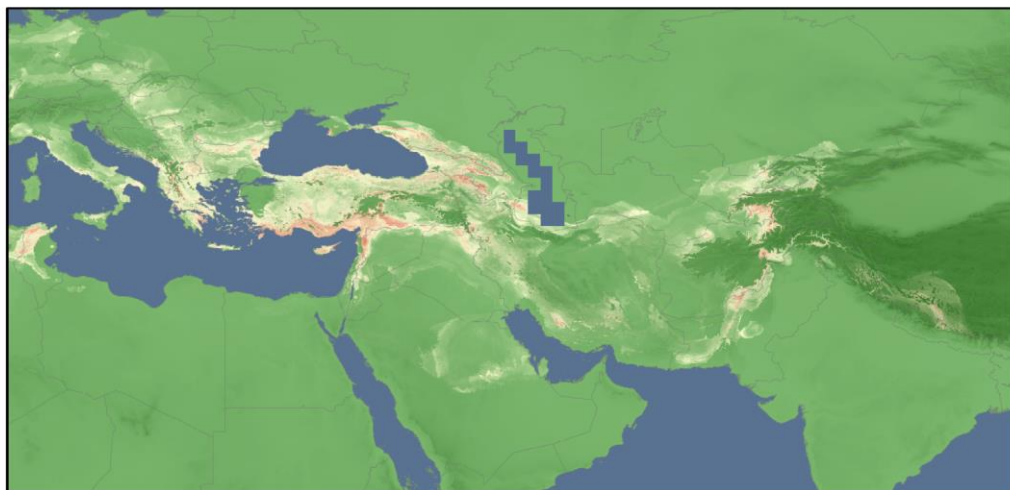
b) MIROC-ESM Model
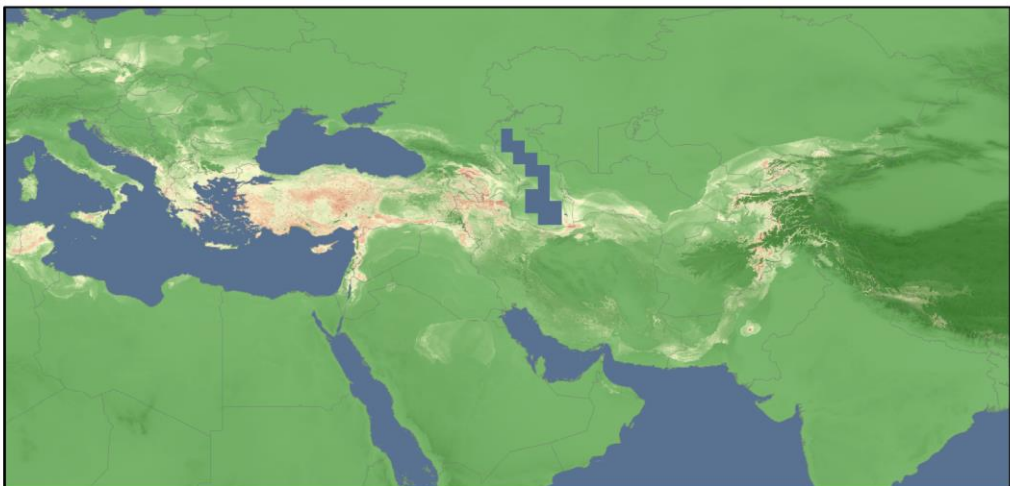
c) MPI-ESM-P Model

Figure 31 LGM results for *S. neumayer* (all occurrences). Results of 3 different GCM models can be seen in a,b and c.

a) CCSM4 Model

Bioclimatic Suitability
Value
High : 1   Low : 0

Kilometers
0   500 1,000   2,000
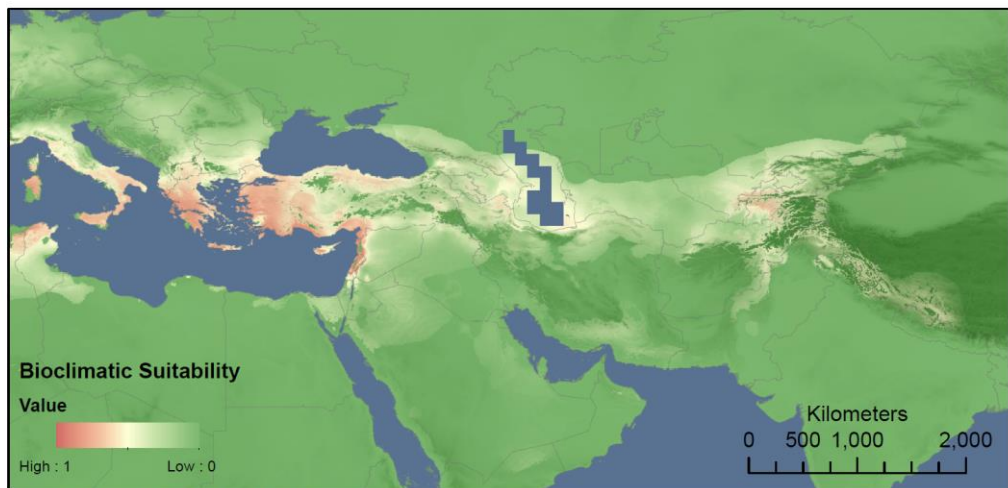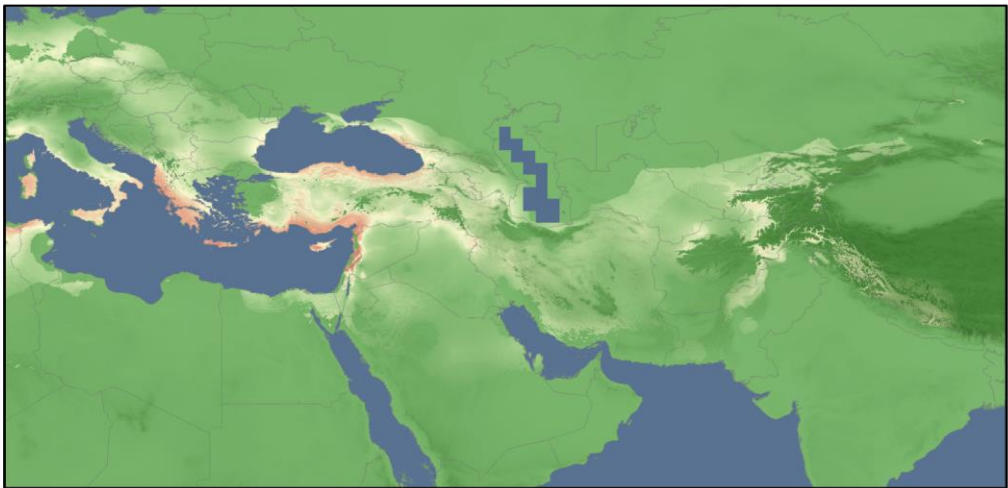
b) MIROC-ESM Model
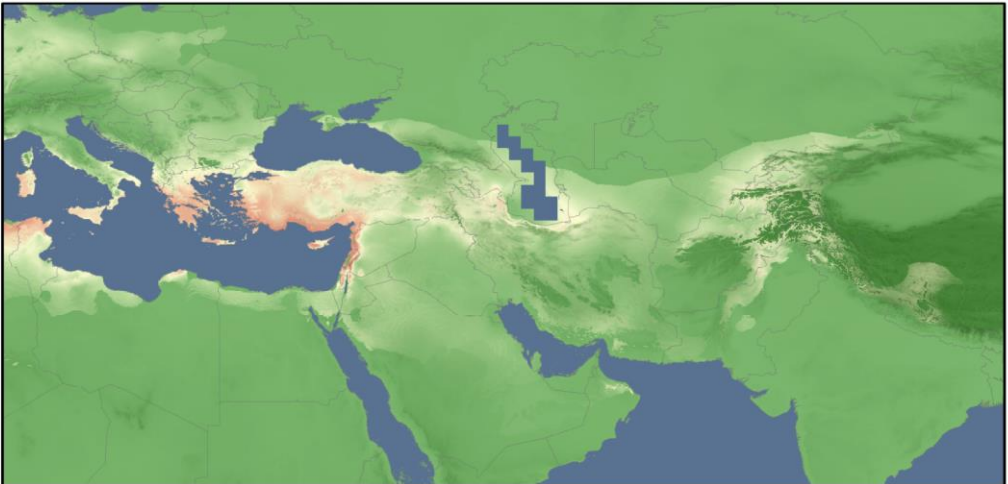
c) MPI-ESM-P Model

Figure 32 LGM results for *S. neumayer* without Zagros population. Results of 3 different GCM models can be seen in a,b and c.
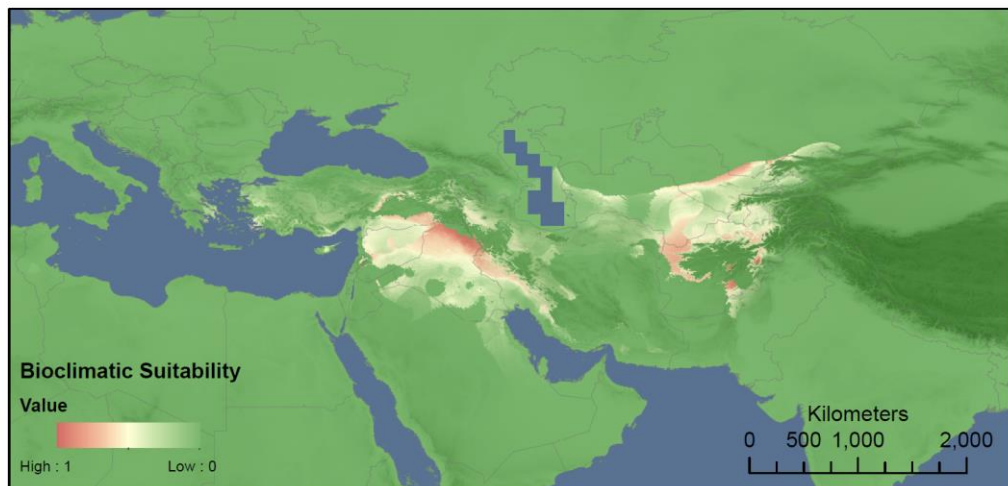
a) CCSM4 Model
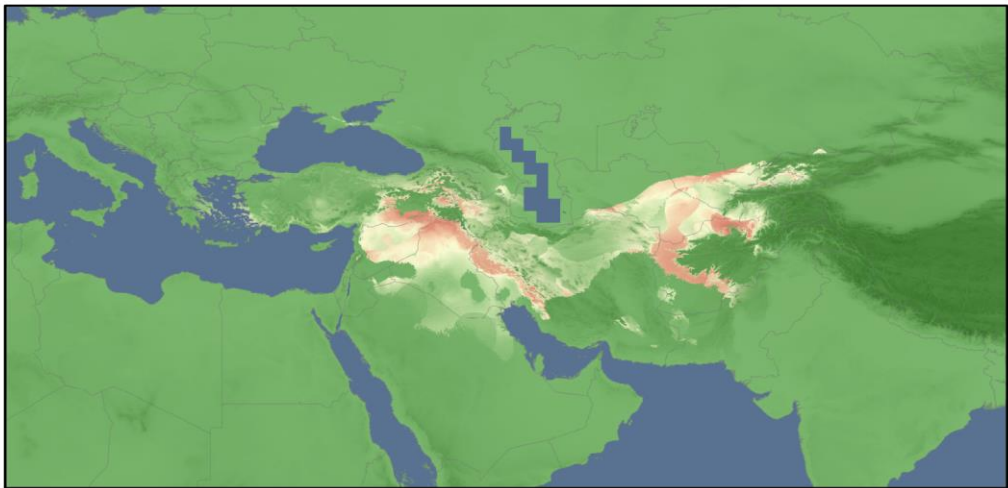
b) MIROC-ESM Model
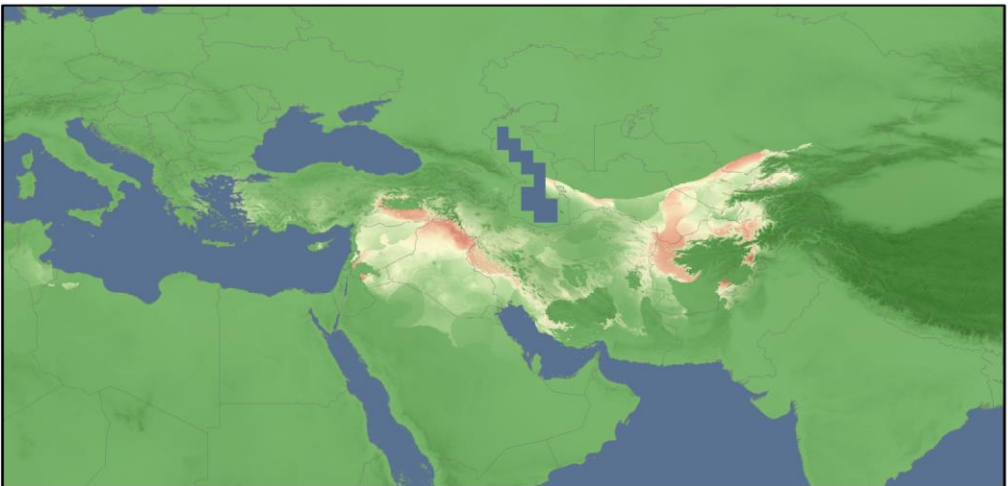
c) MPI-ESM-P Model

Figure 33 LGM results for *S. neumayer*'s Zagros population. Results of 3 different GCM models can be seen in a,b and c.
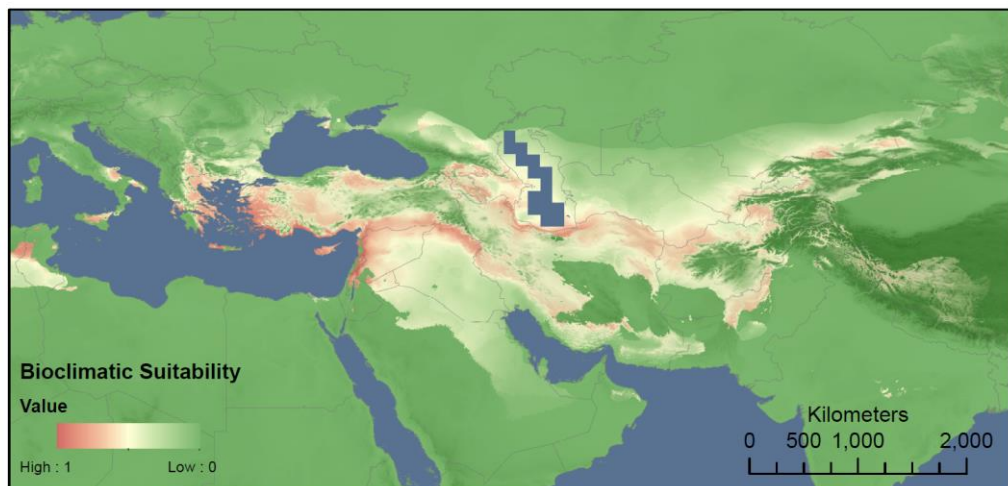
a) CCSM4 Model
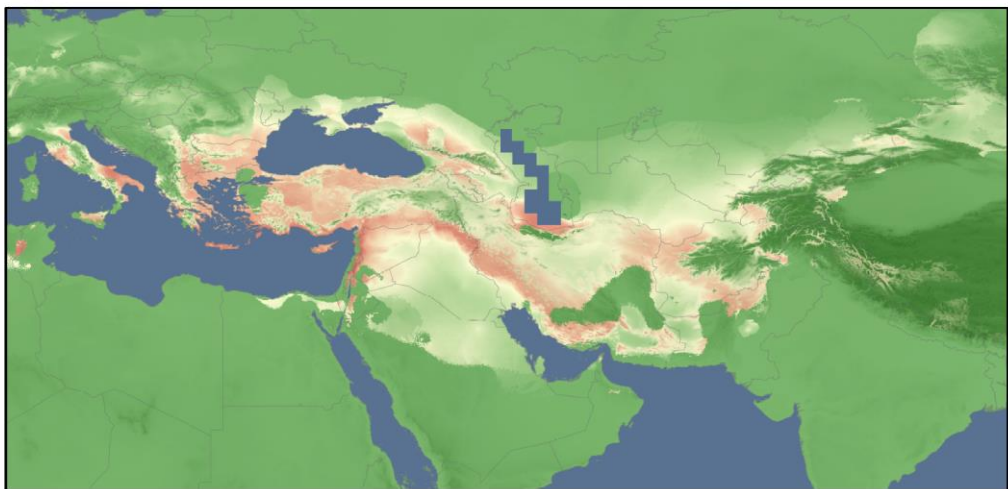
b) MIROC-ESM Model
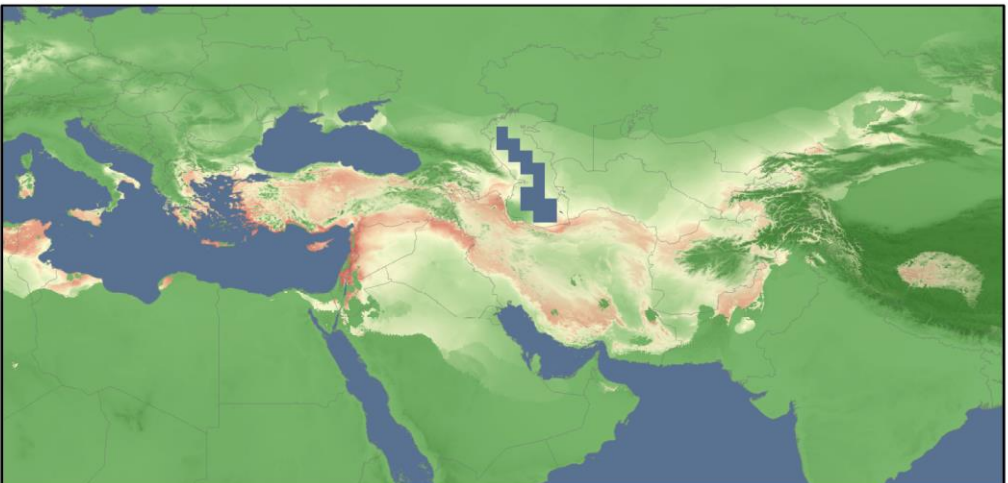
c) MPI-ESM-P Model

Figure 34 LGM results for *S. tephronota* (all occurrences). Results of 3 different GCM models can be seen in a,b and c.

a) CCSM4 Model

Bioclimatic Suitability
Value
High : 1   Low : 0

Kilometers
0   500 1,000   2,000
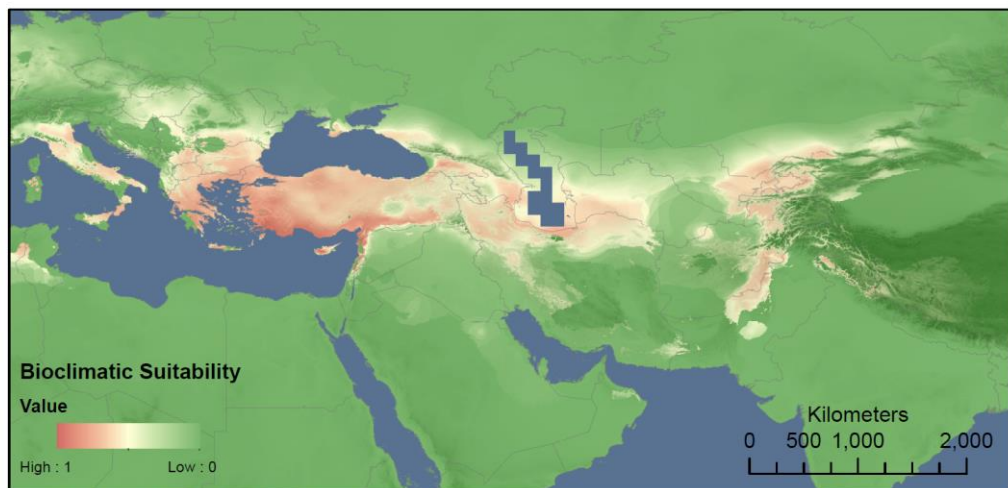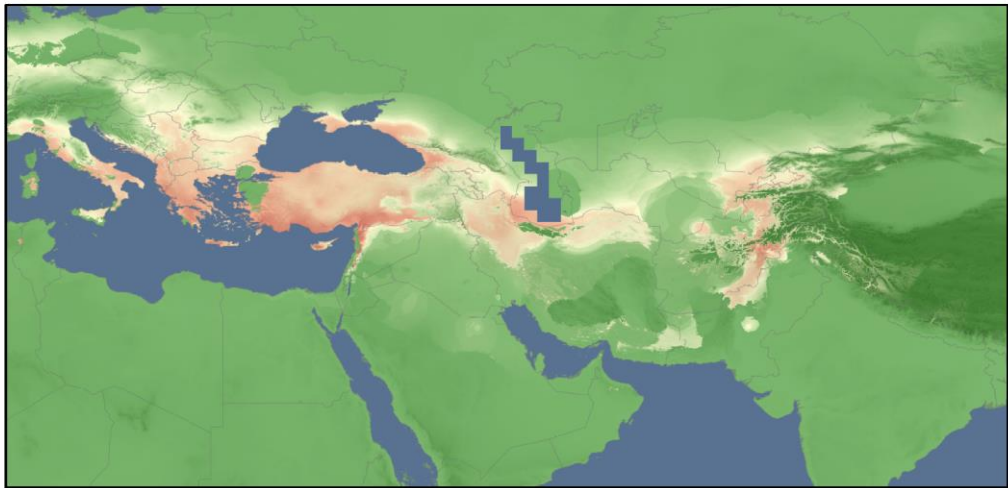
b) MIROC-ESM Model
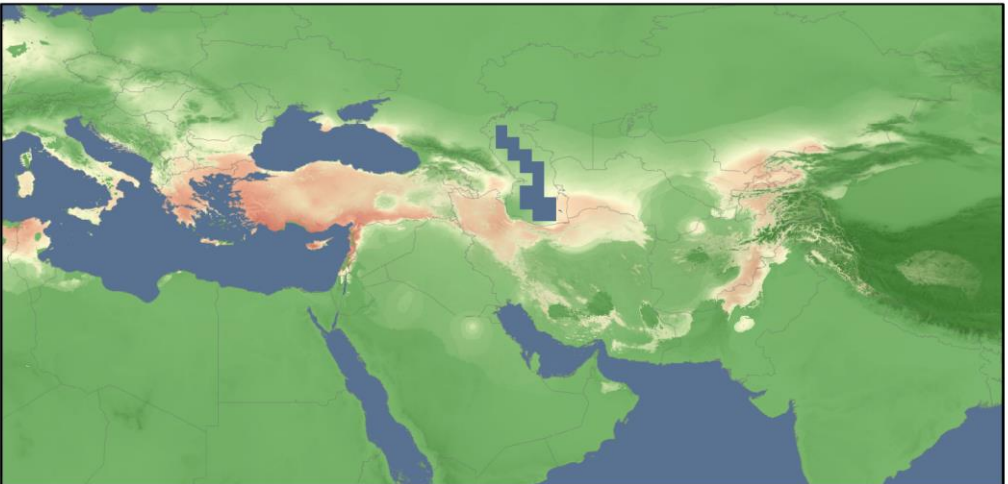
c) MPI-ESM-P Model

Figure 35 LGM results for *S. tephronota* without Zagros population. Results of 3 different GCM models can be seen in a,b and c.

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a) CCSM4 Model
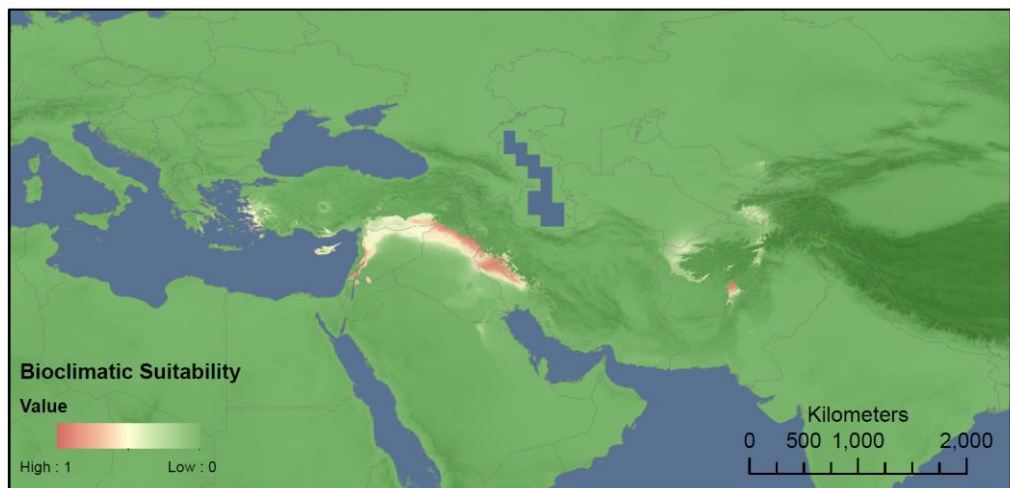
b) MIROC-ESM Model
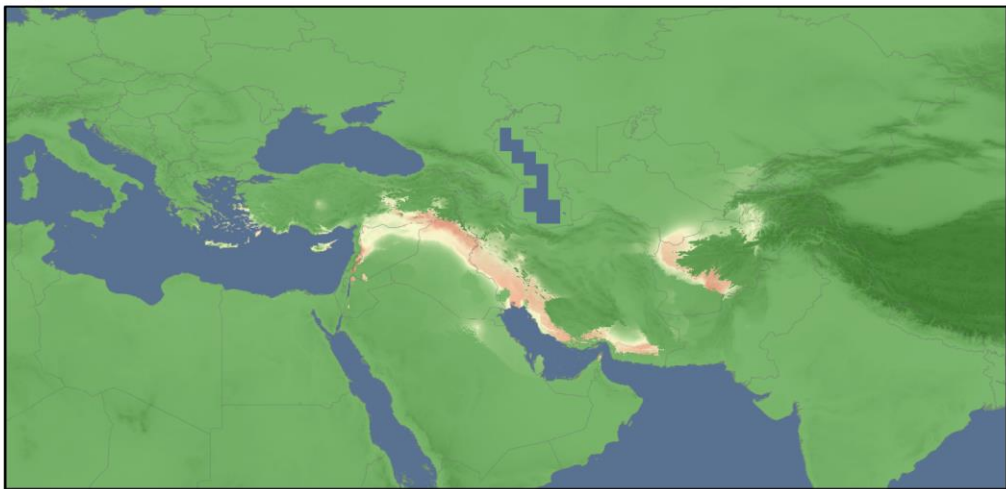
c) MPI-ESM-P Model
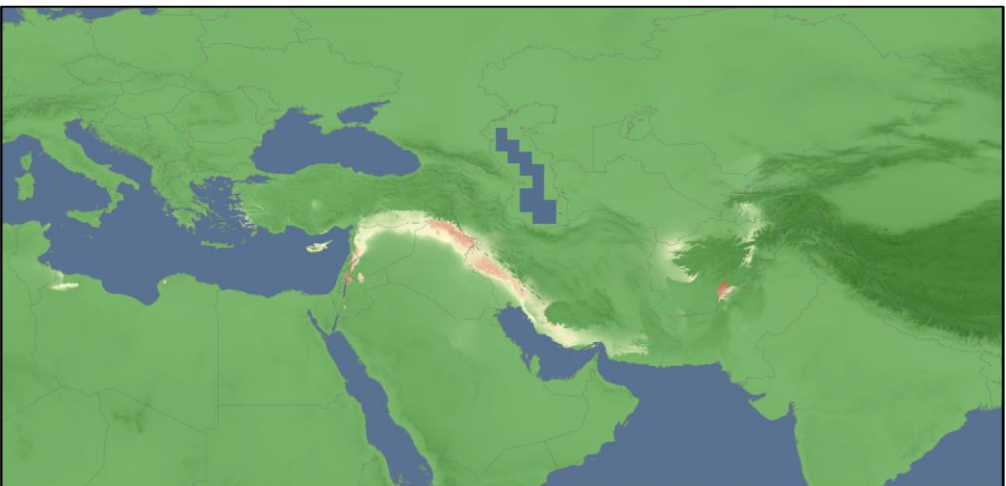
Figure 36 LGM results for *S. tephronota*'s Zagros population. Results of 3 different GCM models can be seen in a,b and c.

4. DISCUSSION

In this thesis morphology, phylogeography and ENM approaches were used to study the evolutionary histories of two bird species almost endemic to the Middle East. Phylogenetic results have pointed out a cryptic genetic diversity in their distribution range. In addition, it has been found that the distribution of both species contracted in the LIG which happened approximately 130,000 years before present.

The phylogeography approach based on mitochondrial DNA data, an important marker to establish neutral genetic variation [87], provides important information on distributional changes in recent histories of species [80, 88, 89]. When sufficient sample size is reached, it is possible to make inferences about the demographic history of species using this data [90].

In support of phylogeograhy approach ENM also evaluates the distribution areas of species for the present and shows whether the current distributions of species are balanced with the climate [91]. If the distributions of species are balanced with climate, it is expected that the model results overlap with the known distributions. If this is confirmed, it is expected that the same coherence will also be seen for the past climatic changes, and the results obtained associated with phylogeography may provide a safe provision for the evolutionary history of species [92]. In this thesis, by integrating these approaches, the evolutionary histories of two Middle Eastern nuthatches were evaluated for the first time and the results were also compared with studies on common species distributed across Western Palearctic. Thus, while the LGM was experienced in the world, the demographic phenomena within a geographic area that hosts many temperate bird species as a refugium have been evaluated in terms of two bird species which are often distributed in this geography.

For bird species in temperate zone expansion-contraction model was proposed for the LGM and present [30]. According to this model, species with broad distribution narrowed their distribution areas when the LGM was experienced and aforesaid species escaped to zones where climate conditions were appropriate or were destroyed in the area they were in [18, 35, 93-96]. Regarding this situation, the glacial refugia hypothesis claimed

refugial areas in Europe (i.e. Iberian Peninsula, Italy and Balkans) located in southern areas and were suitable areas for temperate zone species [19]. However, there is limited number of studies that were condacted for the species that have limited distributions in Mediterranean region or only in proposed refugial areas. Therefore, how have these events happened in a geography known to have hosted suitable conditions for a long time? Gür (2013) stated refugia dating back to the LIG for a mammal species which is almost endemic to Anatolia [88]. Perktaş et al. (2015) found a similar finding for *Sitta krueperi* and defined a refugium in southern Anatolia [80].

While the refugial role of the Middle Eastern geography for the widespread temperate species during the Quaternary period has been discussed in many studies, some important areas within this geography have also been noted [97-100]. Perktaş et al. (2011) described a different genetic diversity pattern in the Zagros Mountains for the green woodpecker and argued that the area hosts a possible independent species of the green woodpecker or a recent refugium for the same species [35]. Nazarizadeh et al. (2016) also found a similar pattern in the area and defined a conservation significant unit for *Sitta europaea* [101].

Obtaining useful georeferenced data is a very important step for developing ecological niche models [102]. Detecting the point coordinates of the museum samples possess an immoderate bias because exact coordinates have never been given in old samples. Producing a point locality can cause a deviation from the real locality within 10 arc minutes [103]. This may effect the results of this study, because the studied climate data is in 2.5 arc minute resolution. Also reading specimen tags are sometimes problematic and may cause wrong deductions. For these reasons museum specimen localities were eliminated and only GPS validated localities, which were obtained from GBIF, were used for *S. neumayer* [104] and *S. tephronota* [105].

Raw occurrence files are biased for many reasons which were discussed in many studies of ENM [103]. Some areas are visited frequently by bird watchers and in some countries their numbers and recording frequencies are significantly higher than others. Some locations are very hard to explore and this causes a bias towards easy to reach locations. Also for sister species

like the subject of this thesis, inexperience of the bird watchers is another problem. Because of these reasons careful examinations of the raw occurrence files were done.

When evidences about glacial refugial role of Anatolia and the Middle East are taken into account and compared with the results of this thesis, they highlight significantly different populations for *S. neumayer* and *S. tephronota* in the Zagros mountains and ENM results supported that LIG distributions were narrower than present and LGM distributions for both species. Sea level changes are debated and because of this their effect was ignored in the resulting maps.

The detailed demographic analysis based on mtDNA were not taken forward due to inadequacy of the sample, but the demographic changes of these two species were briefly discussed in the light of ENM results.

On the phylogenetic tree, there was a reciprocal monophyly which includes evolutionary independent units with good bootstrap support. The most important lineage was the Zagros, and morphological results supported each lineage on the tree. The only problem was the overlap region, Mazandaran, haplotypes from both lineages occurred in same geography. The plausible exaplanation for this geographic pattern was the incomplete lineage sorting [106]. Sarudny (1904) described a species of *S. neumayer* as *S. tschitscherini* [107] and Sarudny and Buturlin (1906) described a species of *S. tephronota* as *S. dresseri* in Zagros Mountains [48, 108] (Later, both were considered subspecies [46, 47]). Therefore, they show a cryptic genetic diversity and this was almost completely in accordance with morphological differentiation (i.e. body size and coloration) for both species. Zagros Mountains are important geographies not only for rock nuthatches, but also for other birds such as *Picus viridis* and *S. europaea* [35, 101]. Taken altogether, based on this study, *S. dresseri* and *S. tschitscherini* are both recognised as species in Zagros. Moist air masses which are coming from Mediterranean Basin and the Persian Gulf cause precipitation in the Zagros Mountains [109] and this feature of the region has a potential to cause population differentiation in some species. By taking this into account these

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properties may cause distinct populations in the area for *S. neumayer* and *S. tephronota*. *S. neumayer*'s Zagros population which represents *S. tschitscherini,* and *S. neumayer* were compared morphologically and showed difference. Comparison of size and shape variables have also shown difference. Phylogenetic results based on ND2 and ND3 sequences have shown different lineages for both species in Zagros Mountains. Mutation numbers and comparison of size and shape variables have shown that *S. t. dresseri* is significantly different than *S. tephronota.* These emphasize the importance of Zagros region for these two species as quite similar pattern found for *S. europaea* by Nazarizadeh et. al. (2016) [101] and *P. viridis* by Perktaş et. al. (2011) [35].

The LIG period is not often studied for palearctic organisms and studies are certainly scarce. It is known that in the LIG climate was warmer than our current climate [110]. Also there was significantly higher seasonality in Middle East which means higher summer and lower winter temperatures [111]. Although there are limited number of studies on the effect of LIG on species, those which was found significant distributional contraction pattern in the Palearctic region [80, 88, 112, 113]. According to the results of this thesis, both *S. neumayer* and *S. tephronota* showed an apparent contraction pattern for the LIG. Also there seems no suitable space for their Zagros populations. This could be due to the lack of enough occurrence records, but their AUC values were good. Therefore, it is possible to say that those populations might have dispersed from Levant. However this needs a confirmation by adding molecular samples from that location.

In conclusion, Zagros Mountains are important regions which hosts unique genetic diversity patterns for studied species and it may harbour unexplored diversities for other organisms. Also the LIG had an impact on studied species and its effect on other species in Middle East and Mediterranean Basin should be investigated in detail.

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SUPPLEMENTARY MATERIALS

Descriptives of *S. neumayer* ♂

Beak Length			Statistic	Std. Error
Beak Length	Mean		23.9943	.14724
	95% Confidence Interval for Mean	Lower Bound	23.7010	
		Upper Bound	24.2875	
	5% Trimmed Mean		23.9703	
	Median		24.0400	
	Variance		1.669	
	Std. Deviation		1.29199	
	Minimum		21.47	
	Maximum		27.51	
	Range		6.04	
	Interquartile Range		1.73	
	Skewness		.303	.274
	Kurtosis		.018	.541
Nostril Length	Mean		15.5330	.12594
	95% Confidence Interval for Mean	Lower Bound	15.2822	
		Upper Bound	15.7838	
	5% Trimmed Mean		15.5811	
	Median		15.7400	
	Variance		1.221	
	Std. Deviation		1.10508	
	Minimum		12.17	
	Maximum		18.20	
	Range		6.03	
	Interquartile Range		1.22	
	Skewness		-.734	.274
	Kurtosis		1.449	.541
Wing Size	Mean		78.82	.257
	95% Confidence Interval for Mean	Lower Bound	78.31	
		Upper Bound	79.33	
	5% Trimmed Mean		78.77	
	Median		78.00	
	Variance		5.072	
	Std. Deviation		2.252	
	Minimum		73	
	Maximum		84	
	Range		11	
	Interquartile Range		3	
	Skewness		.360	.274
	Kurtosis		.401	.541
Tail Size	Mean		46.34	.301
	95% Confidence Interval for Mean	Lower Bound	45.74	
		Upper Bound	46.94	
	5% Trimmed Mean		46.35	
	Median		46.00	
	Variance		6.990	
	Std. Deviation		2.644	
	Minimum		40	
	Maximum		53	
	Range		13	
	Interquartile Range		3	
	Skewness		.053	.274
	Kurtosis		-.120	.541
Tarsus Length	Mean		22.8169	.09265
	95% Confidence Interval for Mean	Lower Bound	22.6324	
		Upper Bound	23.0014	
	5% Trimmed Mean		22.8216	
	Median		22.7200	
	Variance		.661	
	Std. Deviation		.81298	
	Minimum		21.06	
	Maximum		24.63	
	Range		3.57	
	Interquartile Range		1.23	
	Skewness		.107	.274
	Kurtosis		-.522	.541

Descriptives of *S. neumayer* ♀

			Statistic	Std. Error
Beak Length	Mean		24.1042	.14847
	95% Confidence Interval for Mean	Lower Bound	23.8050	
		Upper Bound	24.4035	
	5% Trimmed Mean		24.0784	
	Median		24.3000	
	Variance		.992	
	Std. Deviation		.99600	
	Minimum		22.53	
	Maximum		26.12	
	Range		3.59	
	Interquartile Range		1.61	
	Skewness		.192	.354
	Kurtosis		-.848	.695
Nostril Length	Mean		15.6811	.13548
	95% Confidence Interval for Mean	Lower Bound	15.4081	
		Upper Bound	15.9542	
	5% Trimmed Mean		15.6898	
	Median		15.7800	
	Variance		.826	
	Std. Deviation		.90882	
	Minimum		13.59	
	Maximum		17.45	
	Range		3.86	
	Interquartile Range		1.26	
	Skewness		-.169	.354
	Kurtosis		-.293	.695
Wing Size	Mean		78.09	.341
	95% Confidence Interval for Mean	Lower Bound	77.40	
		Upper Bound	78.78	
	5% Trimmed Mean		78.07	
	Median		78.00	
	Variance		5.219	
	Std. Deviation		2.285	
	Minimum		74	
	Maximum		83	
	Range		9	
	Interquartile Range		4	
	Skewness		.113	.354
	Kurtosis		-.765	.695
Tail Size	Mean		46.20	.356
	95% Confidence Interval for Mean	Lower Bound	45.48	
		Upper Bound	46.92	
	5% Trimmed Mean		46.15	
	Median		46.00	
	Variance		5.709	
	Std. Deviation		2.389	
	Minimum		42	
	Maximum		52	
	Range		10	
	Interquartile Range		4	
	Skewness		.192	.354
	Kurtosis		-.274	.695
Tarsus Length	Mean		22.9249	.11573
	95% Confidence Interval for Mean	Lower Bound	22.6916	
		Upper Bound	23.1581	
	5% Trimmed Mean		22.9522	
	Median		22.9500	
	Variance		.603	
	Std. Deviation		.77635	
	Minimum		20.44	
	Maximum		24.32	
	Range		3.88	
	Interquartile Range		1.00	
	Skewness		-.569	.354
	Kurtosis		1.215	.695

Supplementary Table 1 Descriptives of male and female *S. neumayer*.

Sitta neumayer

MALES   FEMALES
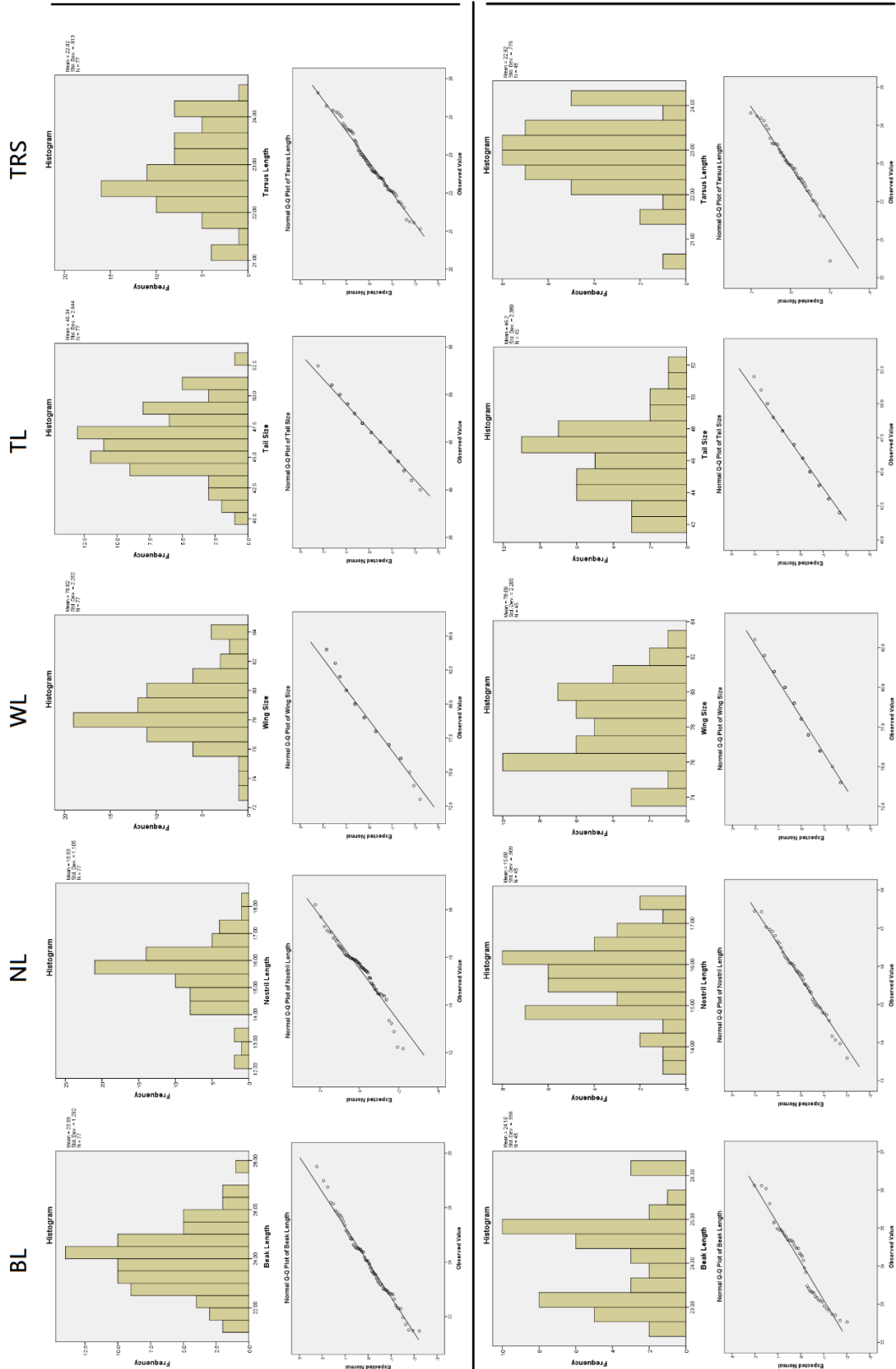
Supplementary Table 2 Histograms and Normal Q-Q plots of each variable of *S. neumayer*.

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Descriptives of *Sitta tephronota* ♂

			Statistic	Std. Error
Beak Length	Mean		27.0165	.18114
	95% Confidence Interval for Mean	Lower Bound	26.6567	
		Upper Bound	27.3763	
	5% Trimmed Mean		27.0361	
	Median		26.9750	
	Variance		3.019	
	Std. Deviation		1.73740	
	Minimum		22.90	
	Maximum		31.01	
	Range		8.11	
	Interquartile Range		2.48	
	Skewness		-.133	.251
	Kurtosis		-.345	.498
Nostril Length	Mean		17.4953	.14954
	95% Confidence Interval for Mean	Lower Bound	17.1983	
		Upper Bound	17.7924	
	5% Trimmed Mean		17.5350	
	Median		17.5500	
	Variance		2.057	
	Std. Deviation		1.43431	
	Minimum		13.14	
	Maximum		20.78	
	Range		7.64	
	Interquartile Range		1.80	
	Skewness		-.431	.251
	Kurtosis		.336	.498
Wing Size	Mean		88.57	.410
	95% Confidence Interval for Mean	Lower Bound	87.75	
		Upper Bound	89.38	
	5% Trimmed Mean		88.50	
	Median		88.00	
	Variance		15.501	
	Std. Deviation		3.937	
	Minimum		81	
	Maximum		98	
	Range		17	
	Interquartile Range		5	
	Skewness		.302	.251
	Kurtosis		-.496	.498
Tail Size	Mean		51.46	.274
	95% Confidence Interval for Mean	Lower Bound	50.91	
		Upper Bound	52.00	
	5% Trimmed Mean		51.44	
	Median		52.00	
	Variance		6.910	
	Std. Deviation		2.629	
	Minimum		45	
	Maximum		58	
	Range		13	
	Interquartile Range		3	
	Skewness		.004	.251
	Kurtosis		-.228	.498
Tarsus Length	Mean		25.5266	.16509
	95% Confidence Interval for Mean	Lower Bound	25.1987	
		Upper Bound	25.8546	
	5% Trimmed Mean		25.4974	
	Median		25.2150	
	Variance		2.507	
	Std. Deviation		1.58347	
	Minimum		22.00	
	Maximum		29.34	
	Range		7.34	
	Interquartile Range		2.66	
	Skewness		.392	.251
	Kurtosis		-.555	.498

Descriptives of *Sitta tephronota* ♀

			Statistic	Std. Error
Beak Length	Mean		26.4700	.22316
	95% Confidence Interval for Mean	Lower Bound	26.0247	
		Upper Bound	26.9153	
	5% Trimmed Mean		26.4214	
	Median		26.4200	
	Variance		3.436	
	Std. Deviation		1.85374	
	Minimum		22.80	
	Maximum		30.91	
	Range		8.11	
	Interquartile Range		2.97	
	Skewness		.366	.289
	Kurtosis		-.476	.570
Nostril Length	Mean		17.2393	.18862
	95% Confidence Interval for Mean	Lower Bound	16.8629	
		Upper Bound	17.6157	
	5% Trimmed Mean		17.2332	
	Median		17.2400	
	Variance		2.455	
	Std. Deviation		1.56682	
	Minimum		13.76	
	Maximum		21.00	
	Range		7.24	
	Interquartile Range		1.98	
	Skewness		.059	.289
	Kurtosis		-.010	.570
Wing Size	Mean		86.96	.447
	95% Confidence Interval for Mean	Lower Bound	86.06	
		Upper Bound	87.85	
	5% Trimmed Mean		86.89	
	Median		86.00	
	Variance		13.777	
	Std. Deviation		3.712	
	Minimum		80	
	Maximum		96	
	Range		16	
	Interquartile Range		6	
	Skewness		.387	.289
	Kurtosis		-.393	.570
Tail Size	Mean		50.29	.347
	95% Confidence Interval for Mean	Lower Bound	49.60	
		Upper Bound	50.98	
	5% Trimmed Mean		50.36	
	Median		50.00	
	Variance		8.327	
	Std. Deviation		2.886	
	Minimum		44	
	Maximum		56	
	Range		12	
	Interquartile Range		4	
	Skewness		-.401	.289
	Kurtosis		-.200	.570
Tarsus Length	Mean		25.1407	.19056
	95% Confidence Interval for Mean	Lower Bound	24.7605	
		Upper Bound	25.5210	
	5% Trimmed Mean		25.0788	
	Median		24.9000	
	Variance		2.506	
	Std. Deviation		1.58293	
	Minimum		22.74	
	Maximum		28.87	
	Range		6.13	
	Interquartile Range		2.73	
	Skewness		.498	.289
	Kurtosis		-.806	.570

Supplementary Table 3 Descriptives of male and female *S. tephronota.*
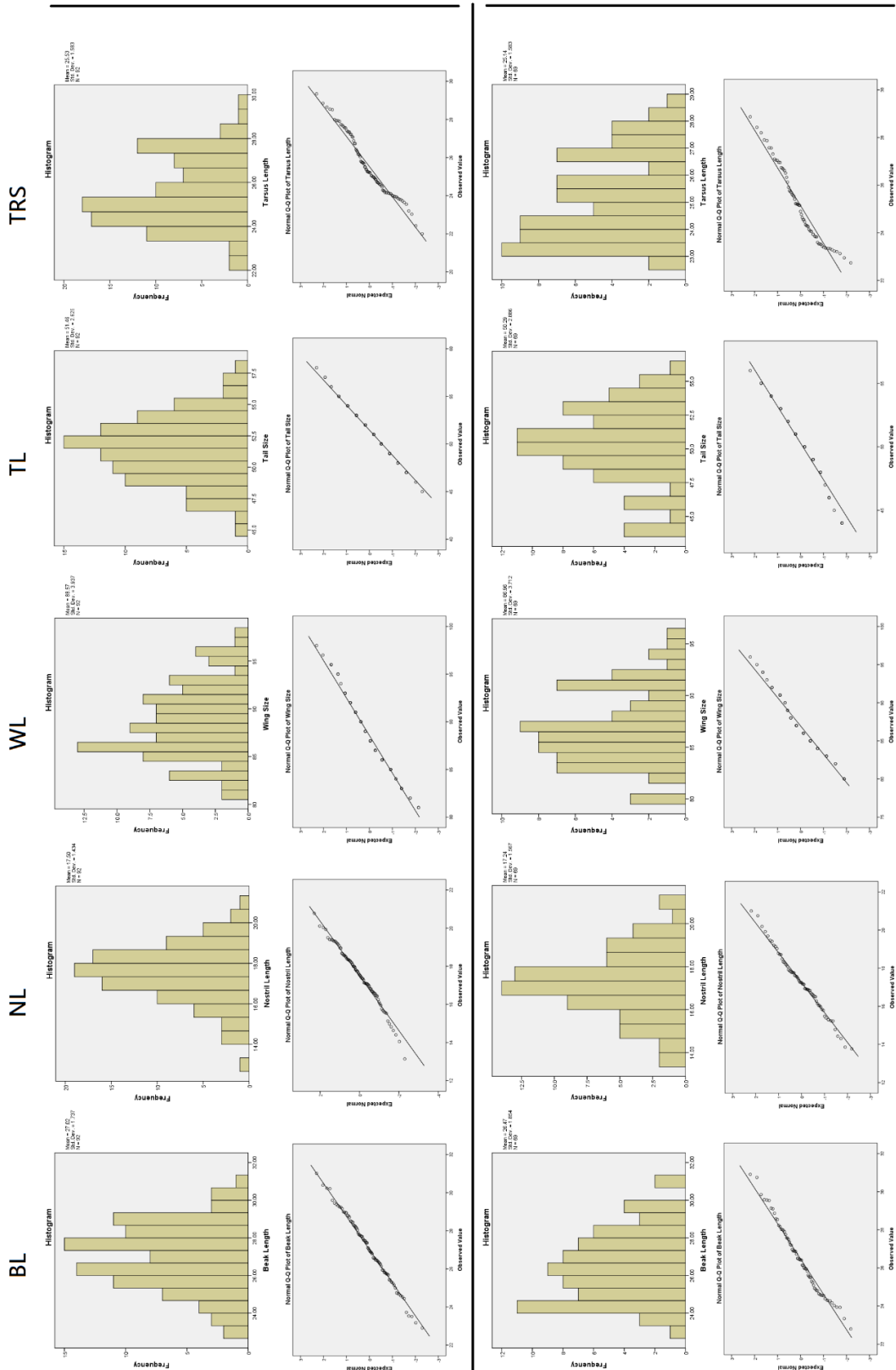
Supplementary Table 4 Histograms and Normal Q-Q plots of each variable of *S. tephronota*

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
							Mean Difference	Std. Error Difference	95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)			Lower	Upper
Wing Size	Equal variances assumed	.501	.480	1.985	130	.049	.817	.412	.003	1.631
	Equal variances not assumed			1.974	90.653	.051	.817	.414	-.005	1.639
Tail Size	Equal variances assumed	.960	.329	-.062	129	.951	-.031	.498	-1.016	.954
	Equal variances not assumed			-.066	109.186	.948	-.031	.469	-.960	.899
Tarsus Length	Equal variances assumed	.672	.414	-.720	120	.473	-.10801	.15006	-.40512	.18911
	Equal variances not assumed			-.729	95.710	.468	-.10801	.14825	-.40229	.18627

Supplementary Table 5 Difference between male and female size variables (WL, TL and TRS) in *S. neumayer*.

Test Statistics[a,b]

	Beak Length	Nostril Length
Chi-Square	.271	.062
df	1	1
Asymp. Sig.	.603	.804

a. Kruskal Wallis Test

b. Grouping Variable: Sex

Supplementary Table 6 Difference between male and female size variables (BL and NL) in *S. neumayer*.

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
							Mean Difference	Std. Error Difference	95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)			Lower	Upper
Beak Length	Equal variances assumed	.556	.457	2.017	169	.045	.55565	.27551	.01177	1.09954
	Equal variances not assumed			1.995	150.495	.048	.55565	.27847	.00543	1.10587
Nostril Length	Equal variances assumed	.721	.397	1.158	169	.249	.26798	.23143	-.18889	.72485
	Equal variances not assumed			1.140	147.212	.256	.26798	.23504	-.19651	.73247
Tail Size	Equal variances assumed	.143	.706	2.727	168	.007	1.134	.416	.313	1.955
	Equal variances not assumed			2.700	150.713	.008	1.134	.420	.304	1.964

Supplementary Table 7 Difference between male and female size variables (BL, NL and TL) in *S. tephronota*.

Test Statistics[a,b]

	Wing Size	Tarsus Length
Chi-Square	6.398	3.102
df	1	1
Asymp. Sig.	.011	.078

a. Kruskal Wallis Test

b. Grouping Variable: Sex

Supplementary Table 8 Difference between male and female size variables (WL and TRS) in *S. tephronota*.

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Correlations

			Beak Length	Nostril Length
Spearman's rho	Beak Length	Correlation Coefficient	1.000	.865[**]
		Sig. (2-tailed)	.	.000
		N	85	85
	Nostril Length	Correlation Coefficient	.865[**]	1.000
		Sig. (2-tailed)	.000	.
		N	85	85

[**]. Correlation is significant at the 0.01 level (2-tailed).

Supplementary Table 9 Spearman test results for BL and NL in males of *S. neumayer*.

Tests of Normality

		Kolmogorov-Smirnov[a]			Shapiro-Wilk		
	Species	Statistic	df	Sig.	Statistic	df	Sig.
Allometric size variable	Sitta neumayer	.050	59	.200[*]	.985	59	.678
	Sitta neumayer Zagros Population	.133	17	.200[*]	.944	17	.371

[*]. This is a lower bound of the true significance.

a. Lilliefors Significance Correction

Supplementary Table 10 Normality test results for *S. neumayer* populations. Allometric size variable is PC1.

Tests of Normality

		Kolmogorov-Smirnov[a]			Shapiro-Wilk		
	Species	Statistic	df	Sig.	Statistic	df	Sig.
Allometric Size Variable	Sitta tephronota	.090	65	.200[*]	.965	65	.062
	Sitta tephronota Zagros Population	.120	23	.200[*]	.927	23	.092

[*]. This is a lower bound of the true significance.

a. Lilliefors Significance Correction

Supplementary Table 11 Normality test results for *S. tephronota* populations. Allometric size variable is PC1.

		Levene's Test for Equality of Variances		t-test for Equality of Means		
		F	Sig.	t	df	Sig. (2-tailed)
Allometric Size Variable	Equal variances assumed	1.252	.267	2.651	74	.010
	Equal variances not assumed			3.072	33.403	.004

Supplementary Table 12 Independent Samples T-Test results for *S. neumayer* and *S. n. tschitscherini* population.

		Levene's Test for Equality of Variances		t-test for Equality of Means		
		F	Sig.	t	df	Sig. (2-tailed)
Allometric Size Variable	Equal variances assumed	3.469	.066	-9.921	86	.000
	Equal variances not assumed			-11.902	57.501	.000

Supplementary Table 13 Independent Samples T-Test results for *S. tephronota* and *S. t. dresseri* population.

Feature Types	Regularization Multipliers	Log Likelihood	Parameters	Sample Size	AICc score
LQP	0.5	-5339.03191	30	455	10742.45061
LQP	1	-5339.03191	30	455	10742.45061
LQP	2	-5339.03191	30	455	10742.45061
LQPH	2	-5320.572458	52	455	10758.85636
LQPH	5	-5348.254497	30	455	10760.89579
LQP	5	-5353.314808	27	455	10764.1706
LQP	10	-5378.065035	18	455	10793.69888
LQPH	10	-5376.327684	22	455	10798.99796
LQPH	1	-5301.039853	84	455	10808.6743
LQ	0.5	-5393.717188	14	455	10816.38892
LQ	1	-5393.717188	14	455	10816.38892
LQ	2	-5393.717188	14	455	10816.38892
LQ	5	-5401.937811	12	455	10828.5815
LQPH	0.5	-5284.863758	107	455	10850.3327
LQ	10	-5414.208673	12	455	10853.12323
L	0.5	-5424.996656	9	455	10868.39781
L	1	-5424.996656	9	455	10868.39781
L	2	-5424.996656	9	455	10868.39781
L	5	-5428.109047	9	455	10874.62259
L	10	-5436.630241	7	455	10887.51104

Supplementary Table 14 Model calibration results for *S. neumayer* (All occurrences). Data is sorted from the smallest AICc score to the largest.

Feature Types	Regularization Multipliers	Log Likelihood	Parameters	Sample Size	AICc score
LQPH	2	-5008.738958	47	433	10123.1974
LQPH	5	-5032.607037	28	433	10125.23388
LQP	0.5	-5046.48255	33	433	10164.58916
LQP	1	-5046.48255	33	433	10164.58916
LQP	2	-5046.48255	33	433	10164.58916
LQP	5	-5059.526953	25	433	10172.24801
LQPH	10	-5064.186977	21	433	10172.62213
LQP	10	-5081.80138	14	433	10192.60754
LQPH	1	-4984.418892	93	433	10206.41301
LQ	0.5	-5093.107415	16	433	10219.52252
LQ	1	-5093.107415	16	433	10219.52252
LQ	2	-5093.107415	16	433	10219.52252
LQPH	0.5	-4969.238084	107	433	10223.59001
LQ	5	-5106.101236	14	433	10241.20726
LQ	10	-5118.715065	12	433	10262.17299
L	0.5	-5127.037242	9	433	10272.50002
L	1	-5127.037242	9	433	10272.50002
L	2	-5127.037242	9	433	10272.50002
L	5	-5130.035543	9	433	10278.49662
L	10	-5138.015639	8	433	10292.3709

Supplementary Table 15 Model calibration results for *S. neumayer* without Zagros population. Data is sorted from the smallest AICc score to the largest.

Feature Types	Regularization Multipliers	Log Likelihood	Parameters	Sample Size	AICc score
L	1	-227.6174768	5	22	468.9849535
LQ	2	-227.6362287	5	22	469.0224574
LQP	1	-226.7122999	6	22	471.0245998
LQP	5	-233.3321448	2	22	471.2958685
LQ	10	-233.5024305	2	22	471.6364399
LQ	5	-230.6960806	4	22	471.7451023
LQP	2	-229.0628035	5	22	471.875607
L	2	-229.8317154	5	22	473.4134308
L	10	-236.8226781	0	22	473.6453561
L	0.5	-226.0728444	7	22	474.1456889
LQ	1	-226.0835392	7	22	474.1670783
LQP	10	-235.9454776	2	22	476.5225342
LQPH	10	-235.9454776	2	22	476.5225342
L	5	-234.7218768	4	22	479.7966948
LQ	0.5	-224.0526468	9	22	481.1052935
LQPH	5	-232.7188456	7	22	487.4376912
LQP	0.5	-224.3531254	10	22	488.7062509
LQPH	2	-227.8586493	11	22	504.1172985
LQPH	0.5	-217.0688594	41	22	x
LQPH	1	-223.3077066	22	22	x

Supplementary Table 16 Model calibration results for *S. neumayer's* Zagros population. Data is sorted from the smallest AICc score to the largest.

Feature Types	Regularization Multipliers	Log Likelihood	Parameters	Sample Size	AICc score
LQP	10	-1314.38476	12	109	2656.019519
LQPH	10	-1314.508379	12	109	2656.266759
LQP	5	-1303.566784	23	109	2666.121803
LQ	0.5	-1315.720507	17	109	2672.166289
LQ	1	-1315.720507	17	109	2672.166289
LQ	2	-1315.889905	17	109	2672.505085
LQPH	5	-1300.777112	28	109	2677.854223
LQ	5	-1326.446041	13	109	2682.723661
LQ	10	-1335.040754	11	109	2694.803158
LQP	2	-1292.479197	37	109	2698.564028
L	0.5	-1347.423078	8	109	2712.286156
L	1	-1347.423078	8	109	2712.286156
L	2	-1347.715821	8	109	2712.871642
LQPH	2	-1284.65407	43	109	2713.523524
L	5	-1350.081065	7	109	2715.271041
LQP	0.5	-1287.204294	43	109	2718.623973
LQP	1	-1287.204294	43	109	2718.623973
L	10	-1353.916795	6	109	2720.65712
LQPH	1	-1271.884479	60	109	2816.268958
LQPH	0.5	-1259.89777	81	109	3173.79554

Supplementary Table 14 Model calibration results for *S. tephronota* (All occurrences). Data is sorted from the smallest AICc score to the largest.

Feature Types	Regularization Multipliers	Log Likelihood	Parameters	Sample Size	AICc score
LQPH	5	-1067.276701	17	90	2177.053402
LQ	1	-1077.921029	16	90	2195.294113
LQP	0.5	-1080.011245	17	90	2202.522489
LQP	5	-1085.081223	14	90	2203.762447
LQP	2	-1067.901695	25	90	2206.115891
LQPH	10	-1090.497954	12	90	2209.047855
LQPH	2	-1043.689939	37	90	2215.456801
LQ	2	-1086.180299	18	90	2217.994401
LQP	10	-1100.060772	10	90	2222.906354
LQ	5	-1099.819794	12	90	2227.691536
LQ	10	-1108.602982	8	90	2234.983742
LQP	0.5	-1045.318699	40	90	2237.576173
LQP	1	-1056.327226	37	90	2240.731376
L	2	-1113.879784	9	90	2248.009568
L	5	-1116.800944	8	90	2251.379666
L	0.5	-1113.015402	11	90	2251.41542
L	1	-1113.095882	11	90	2251.576379
L	10	-1120.84193	7	90	2257.049713
LQPH	1	-1030.566816	53	90	2326.133632
LQPH	0.5	-1020.583209	70	90	2704.324313

Supplementary Table 18 Model calibration results for *S. tephronota* without Zagros population. Data is sorted from the smallest AICc score to the largest.

Feature Types	Regularization Multipliers	Log Likelihood	Parameters	Sample Size	AICc score
L	1	-195.271853	5	19	405.1590906
LQ	1	-193.2045678	6	19	405.4091356
L	5	-203.5413986	0	19	407.0827973
L	10	-203.5413986	0	19	407.0827973
LQP	2	-198.4218777	4	19	407.7008983
LQP	5	-203.1099926	1	19	408.4552793
LQP	1	-194.8641576	6	19	408.7283153
LQP	10	-203.4695332	1	19	409.1743605
LQPH	10	-203.4695332	1	19	409.1743605
L	2	-199.2906361	4	19	409.4384151
LQ	5	-201.1583165	3	19	409.9166329
LQ	10	-203.1621986	2	19	411.0743972
LQ	2	-196.2667856	6	19	411.5335712
LQ	0.5	-190.8933956	8	19	412.1867911
LQPH	2	-191.3299478	8	19	413.0598956
LQPH	5	-199.3199964	5	19	413.2553774
L	0.5	-192.5623241	8	19	415.5246481
LQPH	0.5	-178.7866569	41	19	x
LQPH	1	-186.1868017	22	19	x

Supplementary Table 19 Model calibration results for *S. tephronota*'s Zagros population. Data is sorted from the smallest AICc score to the largest.

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