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Distributional ecology of *Noccaea vesicaria* in relation to the Anatolian Diagonal

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Abstract: Anatolia is located at the intersection of three of the world's 36 biodiversity hotspots (the Caucasus, Irano-Anatolian, and Mediterranean Basin biodiversity hotspots) and has about 10,000 plant species, over 3000 of which are endemic. Among the many reasons for the astonishing biodiversity of Anatolia, one that stands out is the Anatolian Diagonal. Although the Anatolian Diagonal has long been recognized as a biogeographical boundary between Central and Eastern Anatolia, its exact functioning is still not well understood. Thus, in this study, our aims were 1) to assess the environmental barrier function of the Anatolian Diagonal for a plant species, *Noccaea vesicaria*, living on and to the east of it; 2) to evaluate climate-driven range shifts (contractions or expansions), especially through the Quaternary glacial–interglacial cycles; and 3) to contribute to the long-standing debate on the causes of the floral break between the west and east of the Anatolian Diagonal. Accordingly, we used an ecological niche modeling approach with presence records and bioclimatic data. Under the present bioclimatic conditions, areas of more suitable bioclimatic conditions were observed, especially throughout and to the east of the Anatolian Diagonal, therefore largely matching the geographical distribution of *N. vesicaria*. However, areas of high bioclimatic suitability were also observed to the west of the Anatolian Diagonal, especially throughout the Taurus Mountains and Pontic Mountains. Thus, bioclimatic suitability by itself cannot explain the geographical distribution of *N. vesicaria* or the absence of it, especially to the west of the Anatolian Diagonal. Under the past bioclimatic conditions, areas of high bioclimatic suitability contracted during warmer time periods and expanded during colder time periods, suggesting that the geographical distribution of *N. vesicaria* contracted and expanded during warmer and colder time periods, respectively, at least around and in the Anatolian Highlands. There may be two reasons why *N. vesicaria* does not occur to the west of the Anatolian Diagonal: dispersal and/or biotic interactions (e.g., competition and facilitation). Biotic interactions (likely positive plant interaction or facilitation) may have played a significant role in shaping the geographical distribution of *N. vesicaria*, because it seems to be highly associated with the Anatolian Highlands steppe order *Festuco oreophilae-Veronicetalia orientalis* Hamzaoğlu whose range does not extend to Central Anatolia.

Key words: Anatolian diagonal, biotic interactions, climate change, ecological niche modelling, *Noccaea vesicaria*

1. Introduction

Anatolia has a higher level of biodiversity than any other region of its size in the temperate zone (Şekercioğlu et al., 2011). It is located at the intersection of three of the world's 36 biodiversity hotspots (the Caucasus, Irano-Anatolian, and Mediterranean Basin biodiversity hotspots) and has about 10,000 plant species, over 3000 of which are endemic (Güner et al., 2012; Conservation International, 2023). The topographic and climatic features that cause this rich biodiversity are also related to the unique tectonic history of Anatolia. After being under the Tethys Sea for millions of years, Anatolia rose as a landmass from middle Eocene (ca. 41 Ma) to late Miocene (< 8 Ma) (Okay et al., 2020). Thus, it began acting as a bridge between the continents of Asia and Europe (Şengör and Yilmaz, 1981; Tavşanoğlu, 2016). Due to this geographical location, plant and animal species originating from Asia, Europe, and Africa invaded Anatolia (Kosswig, 1955; Davis, 1971). These geological processes also provided the necessary potential for topographic diversity, thus resulting in local climatic variability with altitude differences ranging from 0 to 5000 m within areas of a few hundred kilometers. Consequently, many different vegetation types appeared within short distances (Atalay, 1994). Moreover, this topographical and climatic diversity created opportunities for genetic differentiation, especially for species with limited mobility (Çıplak et al., 1993).

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Among the many reasons for the astonishing biodiversity of Anatolia, one that stands out is the Anatolian Diagonal, which runs from the northeast to the southwest across Turkey and splits into two branches toward the Mediterranean Sea: the Central Taurus Mountains (or the middle part of the Taurus Mountains) and the Nur Mountains (Amanus, or the northern part of the Levant Ranges) (Figure 1). The Anatolian Diagonal was first recognized by Cullen based on the distribution patterns of plant species in the first volume of the *Flora of Turkey and the East Aegean Islands* (hereafter "Flora of Turkey") and was proposed by Davis in 1971 as a biogeographical barrier and corridor at the Symposium on the Plant Life of Southeast Asia (Davis, 1965, 1971). Based on the first volume of the Flora of Turkey, Davis stated that there is a floral break or interruption in the geographical distributions of species in the areas corresponding to the transition between Central and Eastern Anatolia, and he named this line, starting from the Gümüşhane-Bayburt region in the northeast (i.e. the eastern part of the Pontic Mountains) and extending toward the Central Taurus Mountains and the Nur Mountains in the southwest, the Anatolian Diagonal (Davis, 1971; Avcı, 1993). A total of 550 plant species in the first volume of the Flora of Turkey were analyzed and it was found that the geographical distributions of 66% of these plant species are related to the Anatolian Diagonal: 228 species are distributed mainly to the west and 135 species are distributed mainly to the east (Davis, 1971). Subsequently, Ekim and Güner (1986) reexamined the same volume along with the other seven published volumes of the series and confirmed the floral break between Central and Eastern Anatolia and the existence of the Anatolian Diagonal. Based on their results, the geographical distributions of about 33% of the plant species examined are related to the Anatolian Diagonal: 1108 species are distributed in the west, 1138 species in the east, and 390 species on the Anatolian Diagonal (Ekim and Güner, 1986). The fact that most of the 1200 endemic plant species in Turkey are distributed only to the west or east of the Anatolian Diagonal (Conservation International, 2023) and the analyses conducted by Davis (1971) and Ekim and Güner (1986) suggest that the Anatolian Diagonal is a biogeographical boundary.

Although the Anatolian Diagonal has long been recognized as a biogeographical boundary (or more of a floral break) between Central and Eastern Anatolia, exactly how it functions is still not understood. Davis (1971) argued that the floral discontinuity cannot be explained by physical and climatic differences and that it is a consequence of the paleogeological history of Anatolia.

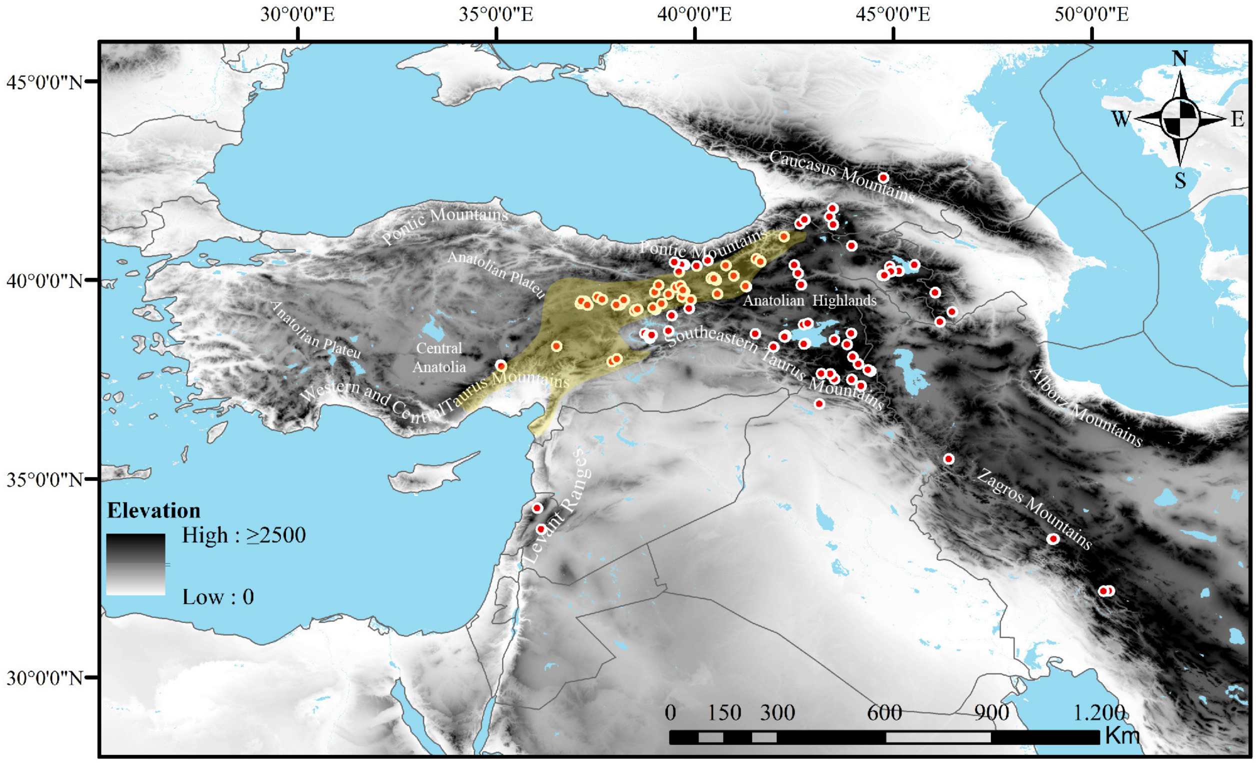

Figure 1. Geographic distribution of *Noccaea vesicaria.* The red dots represent all presence records. The highlighted yellow area shows the Anatolian Diagonal (drawn based on Kuzucuoğlu et al., 2019).

However, Ekim and Güner (1986) argued that ecological and climatic factors are more important. Although there are some studies related to the effect of the Anatolian Diagonal on the geographical distributions of plant or animal species (e.g., Uslu et al., 2011; Mutun and Dinç, 2019; Özüdoğru et al., 2020), to the best of our knowledge, there is no direct study attempting to understand how the Anatolian Diagonal functions, except for that conducted by Gür (2016).

Gür (2016), using an ecological niche modeling approach, examined whether the Anatolian Diagonal is a significant environmental barrier or, in other words, a region where an abrupt environmental change occurs. Accordingly, Gür (2016) created two virtual populations to test this hypothesis, with one to the west and another to the east of the Anatolian Diagonal within the Anatolian part of the Irano-Anatolian hotspot. Gür (2016) found that the western and eastern populations used different environmental spaces and that the Anatolian Diagonal is a region where an abrupt environmental change occurs, mainly regarding temperature seasonality. Therefore, it is a significant environmental barrier. As a result, many populations and taxa are not distributed on both sides of the Anatolian Diagonal for environmental reasons such as changes in temperature seasonality rather than for nonenvironmental reasons such as dispersal and/or biotic interactions (e.g., competition and facilitation). Although these results do not negate the geophysical barrier function of the Anatolian Diagonal, Gür (2016) emphasized that its environmental barrier function is much more important.

In order to test the environmental barrier role of the Anatolian Diagonal, we used *Noccaea vesicaria* (L.) Al-Shehbaz as a model species, which is distributed on and to the east of the Anatolian Diagonal (Figure 1). *N. vesicaria* was long considered a species of the genus *Coluteocarpus* Boiss. until Al-Shahbaz formally transferred it to *Noccaea* Moench (Al-Shehbaz, 2014). This treatment was confirmed in a molecular phylogenetic study of the tribe Coluteocarpeae conducted by Özüdoğru et al. (2019). *N. vesicaria* is a clump-forming perennial herb inhabiting slopes, rocky crevices, and stony slopes of the mountains of the Irano-Turanian phytogeographical region (Figure 1). It is naturally distributed in Georgia, Azerbaijan, Armenia, Turkey, and Iran between 730 and 3200 m (mostly 1500–2500 m), and therefore considered a cold-adaptive species (Hedge, 1965; Shakarishvili and Tchelidze, 2016). There have been few phylogenetic studies on *N. vesicaria* in the literature, with the most comprehensive study conducted by Özüdoğru et al. (2018) despite being based on ITS data. While other studies (Walden et al., 2020 and Hendrix et al., 2022) used high-resolution data, their limited sampling of *Noccaea* species raises suspicion about the phylogenetic position as well as the estimation of divergence time of *N. vesicaria* (Walden et al., 2020 and Hendrix et al., 2022). However, the general diversification seemed to occur through Pliocene in the genus *Noccaea* in these studies. In Özüdoğru et al. (2018), *N. vesicaria* was weakly supported in a clade with *N. pumila* (from Iran, Northern Caucasus, and Transcaucasia), *N. valerionoides* (from Eastern Anatolia), *N. rostrata* (from Transcaucasia), and *N. rubescens* (from the Anatolian Diagonal). Based on the geographical distributions of these plant species, it is possible to infer that they originated on and to the east of the Anatolian Diagonal.

The aim of this study is 1) to test the environmental barrier function of the Anatolian Diagonal, which was previously tested with the virtual populations used by Gür (2016), with a plant species, *N. vesicaria*, living on and to the east of the Anatolian Diagonal; 2) to infer the bioclimatic suitability in the present and past (i.e. from ca. 3.3 Ma to the present), allowing for an evaluation of climate-driven range shifts (expansions or contractions), especially through the Quaternary glacial–interglacial cycles, under the assumption of stability of ecological niche through time (Nogués-Bravo, 2009); and 3) to contribute to the long-standing debate on the causes of the floral break between the west and east of the Anatolian diagonal (Davis, 1971; Ekim and Güner, 1986; Gür, 2016). Accordingly, we used an ecological niche modeling approach with presence records (from different sources) and bioclimatic data (from the PaleoClim database for the present and past; Brown et al., 2018).

2. Materials and methods

2.1. Presence data

Presence data for *Noccaea vesicaria* (119 records, Figure 1) were obtained from the collections of herbariums (ANK, E, GAZI, HUB, ISTE, EGE, KONF, and VANF; 77 records), the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/; 37 records), and field studies (5 records). Presence records with text-only locality descriptions (87 records) were georeferenced with precision of less than 5 km using Google Earth (https://earth.google.com/). The date range of the presence records spanned 1894–2022 (mostly 1950–2022). To reduce the effects of spatial sampling biases (Boria et al., 2014), the presence records were spatially filtered by reducing multiple records to single records within distance of 5 km, resulting in 93 presence records for ecological niche modeling (Table S1).

2.2. Environmental data

Bioclimatic data were downloaded from the PaleoClim database (Brown et al., 2018) at spatial resolution of 2.5 arc-minutes (approximately 4.6 km at the equator) for the present (1979–2013: CHELSA database v1.2b, Karger et al., 2017) and past [*PLEISTOCENE:* Late Holocene, Meghalayan (4.2–0.3 ka); Mid-Holocene, Northgrippian

(8.326–4.2 ka); Early Holocene, Greenlandian (11.7–8.326 ka); Younger Dryas Stadial (12.9–11.7 ka); Bølling-Allerød (14.7–12.9 ka); Heinrich Stadial 1 (17.0–14.7 ka); Last Glacial Maximum (ca. 21 ka); Last Interglacial (ca. 130 ka); and MIS19 (ca. 787 ka); and *PLIOCENE:* Mid-Pliocene warm period (3.205 Ma) and M2 (ca. 3.3 Ma); Otto-Bliesner et al., 2006; Hill, 2015; Dolan et al., 2015; Fordham et al., 2017; CHELSA database v1.2b, Karger et al., 2017; Brown et al., 2018; for more detailed information, see the PaleoClim database]. These data include 19 scenopoetic bioclimatic variables (not affected by the presence of the focal species; Peterson et al., 2011) (for detailed descriptions of the bioclimatic variables, see the CHELSA database and Table S2). A subset of eight bioclimatic variables was selected (for further details, see Table S2): annual mean temperature and precipitation (BIO1 and 12), temperature and precipitation seasonality (BIO4 and 15), and mean temperature and precipitation of the warmest and coldest quarters (BIO10, 11, 18, and 19). To evaluate multicollinearity among these bioclimatic variables, the variance inflation factor (VIF) was used with the usdm package (Naimi, 2017) in R 4.2.1 software (R Core Team, 2013). Bioclimatic variables with VIF of >10 were excluded, resulting in five bioclimatic variables used for ecological niche modeling (Table S2): annual mean temperature and precipitation (BIO1 and 12), temperature and precipitation seasonality (BIO4 and 15), and precipitation of the warmest quarter (BIO18). All of these variables were masked to include only 28°E to 46°E and 23°N to 55°N (i.e. the study area; see Figure 1).

2.3. Ecological niche modeling

To model the Grinnellian niche (Peterson et al., 2011; Anderson, 2013) and to infer bioclimatic suitability throughout the study area in the present and past for *N. vesicaria*, Maxent v3.4.4 software (Phillips et al., 2017) was used. The model settings (Elith et al., 2011; Merow et al., 2013) were selected from WALLACE v1.9.4-5 software (Kass et al., 2018; for detailed methodological descriptions, also see Muscarella et al., 2014; for a Turkish tutorial, see Gür, 2019). To select the background area, a point buffer was created from the presence records, to which a 3-degree buffer was applied (Figure S1). From this area, 10,000 pixels of 2.5 arc-minutes were sampled as the background data. Twenty-five candidate models were tested, using all combinations of (a) five sets of feature classes (linear; linear and quadratic; hinge; linear, quadratic, and hinge; linear, quadratic, hinge, and product) and (b) five values of regularization multiplier (1 to 5 in increments of 1). The model evaluation statistics (for detailed methodological descriptions, see Muscarella et al., 2014; Kass et al., 2018) were calculated as described by Gür (2022), with the presence and background data partitioned into four separate training and testing bins, using a spatial approach (block, k = 4) (Figure S1). The model settings were selected based on the model with the highest value of the conditional Boyce index (Table S3).

A final model was developed using all 93 presence records and 10,000 background points and projected onto the present and past bioclimatic conditions for the study area, with the following settings: extrapolate, do clamping, and fade by clamping. To identify extrapolation risks in model transfers, multivariate environmental similarity surface analysis (Elith et al., 2010) was also used. To evaluate how each variable affected the prediction, response curves were used. The relative contribution of each variable to the final model was determined using a jackknife test. To map the bioclimatic suitability, cloglog output was selected (Phillips et al., 2017). Model performances were evaluated by partial ROC analysis (Peterson et al., 2008) using the software ntbox (NicheToolBox) v0.6.0.1 (Osorio-Olvera et al., 2020), with the following settings: proportion of omission = 0.05, percentage of random points = 50, and number of iterations for bootstrapping = 1000.

3. Results

Twenty-five candidate models were tested based on the model settings. The final model was developed using the input variables of BIO1, 4, 12, 15, and 18; the feature classes of linear and quadratic; and a regularization multiplier of 4 (Table S3). This model used all five input variables (Table S4) and performed better than a random prediction (statistics for AUC ratio, mean ± SD = 1.78 ± 0.03, range = 1.68–1.86, $p < 0.001$).

The variables that contributed most to the final model and therefore most influenced the geographic distribution of *Noccaea vesicaria* were annual mean temperature or BIO1 (having the most useful information both by itself and that is not present in the other variables) and precipitation of the warmest quarter (i.e. summer precipitation) or BIO18 (having the most useful information that is not present in the other variables) (Figure S2). Bioclimatic suitability increased with decreasing annual mean temperature (especially at <10 °C) and precipitation of the warmest quarter (especially at <100 mm, based on marginal response curves) (Figure S3). However, annual mean temperature dominated over precipitation of the warmest quarter, suggesting that temperatures or factors associated with temperature are more important drivers of the distribution patterns of *N. vesicaria* (Figure S2).

Under the present bioclimatic conditions, areas of high bioclimatic suitability were predicted mainly throughout the mountains of Anatolia (Pontic Mountains, Taurus Mountains, and Anatolian Highlands; mainly based on a standardized delineation of the world's mountains, Snethlage et al., 2022) and the adjacent region (Caucasus Mountains, the continuation of the Anatolian Highlands, Alborz Mountains, Zagros Mountains, and the small disjunct area of Jebel Liban and the Anti-Lebanon Mountains in the middle part of the Levant Ranges), with more suitable bioclimatic conditions especially throughout and to the east of the Anatolian Diagonal, which separates the Anatolian Highlands from Central Anatolia and its surrounding Anatolian Plateau. These areas of more suitable bioclimatic conditions largely matched the geographical distribution of *N. vesicaria*. Thus, areas of high bioclimatic suitability outside these areas (and especially to the west of the Anatolian Diagonal) represent areas most likely unoccupied (Figure 2).

Under the past bioclimatic conditions, areas of high bioclimatic suitability contracted during warmer time periods (more pronounced especially in the mid-Pliocene warm period of 3.205 Ma and M2 of ca. 3.3 Ma during the Pliocene) and expanded during colder time periods (more pronounced especially in the Heinrich Stadial 1 of

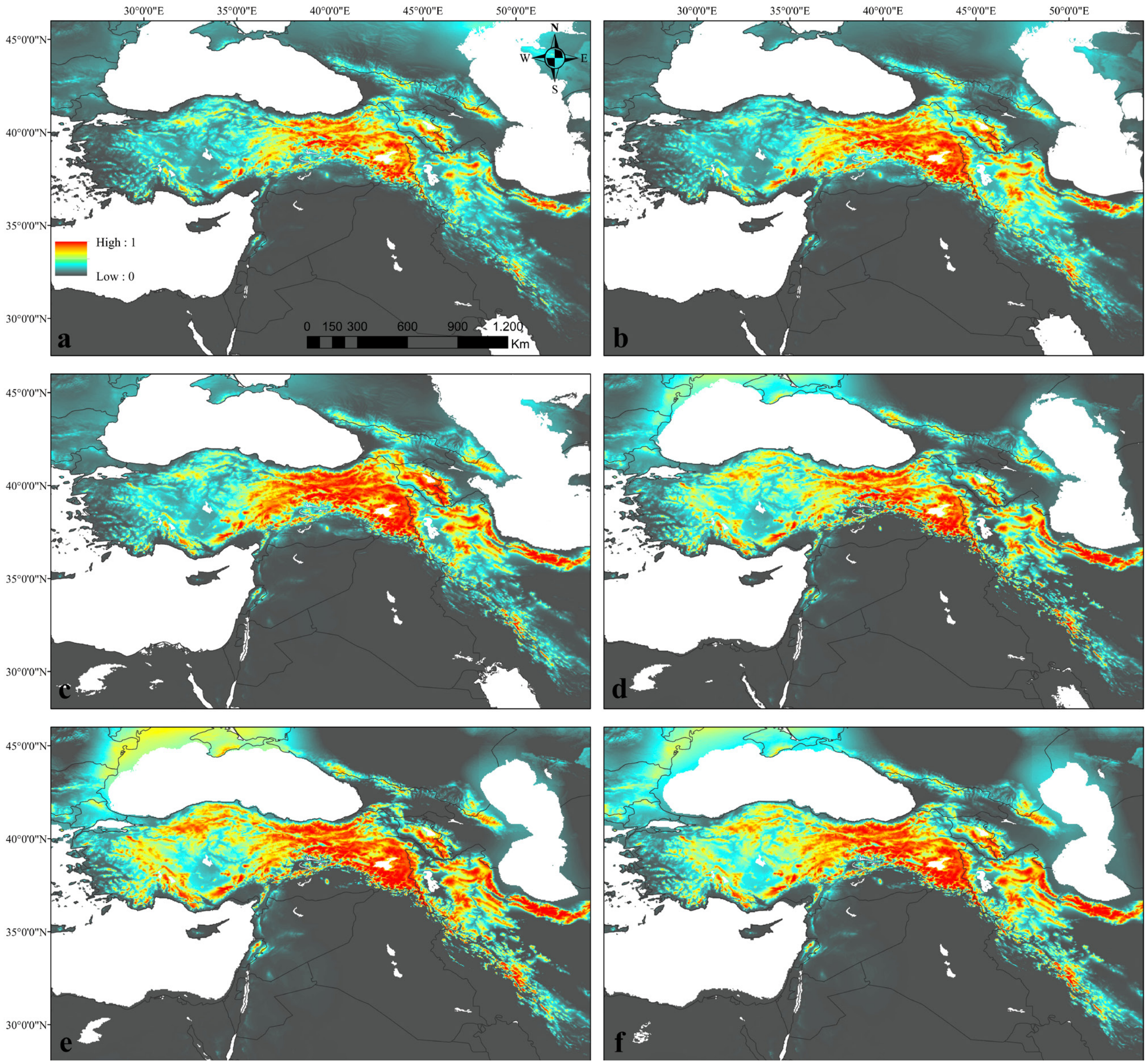

Figure 2. Bioclimatic suitability under the present and past bioclimatic conditions for *Noccaea vesicaria*: a) Present (1979–2013); b) Late Holocene, Meghalayan (4.2–0.3 ka); c) Mid-Holocene, Northgrippian (8.326–4.2 ka); d) Early Holocene, Greenlandian (11.7–8.326 ka); e) Younger Dryas Stadial (12.9–11.7 ka); f) Bølling-Allerød (14.7–12.9 ka). Note that the coastlines for past time periods differ from the present (more pronounced especially during colder time periods, e.g., Last Glacial Maximum) and also that the present borders of lakes are shown for past time periods.

17.0–14.7 ka and the Last Glacial Maximum of ca. 21 ka during the Pleistocene) (Figures 2 and 3), suggesting that the geographical distribution of *N. vesicaria* contracted and expanded during warmer and colder time periods, respectively, at least around and in the Anatolian Highlands.

4. Discussion

In this study, using an ecological niche modeling approach, our first aims were to assess the environmental barrier function of the Anatolian Diagonal for a plant species, *Noccaea vesicaria*, living on and to the east of it and to evaluate climate-driven range shifts (contractions or expansions) especially through the Quaternary glacial–interglacial cycles, under the assumption of stability of ecological niche through time (Nogués-Bravo, 2009). In addition, we aimed to contribute to the long-standing debate on the causes of the floral break (paleogeographic history of Anatolia vs. ecological/climatic differences) between the west and east of the Anatolian Diagonal as

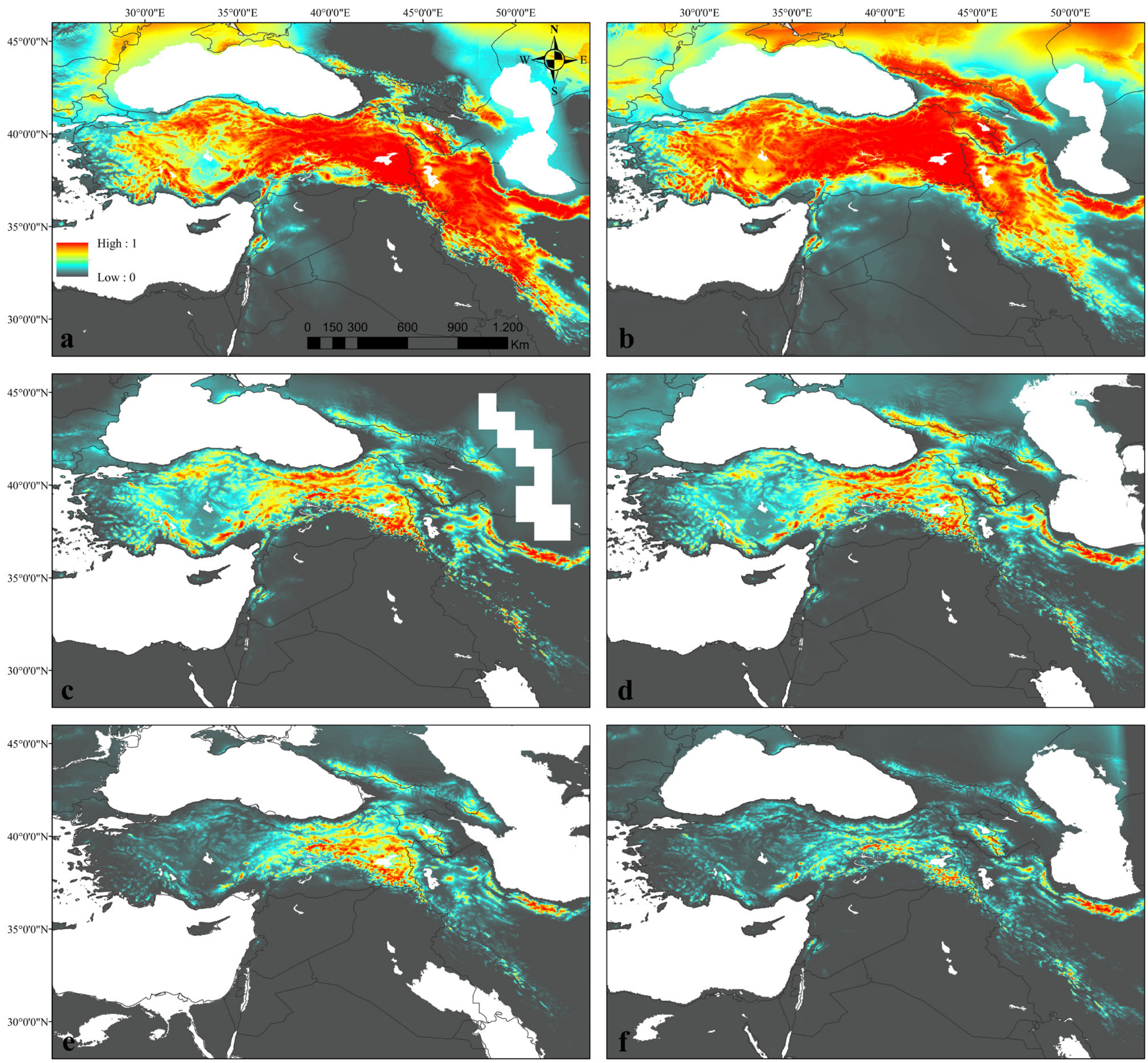

Figure 3. Bioclimatic suitability under the past bioclimatic conditions for *Noccaea vesicaria*. a) Heinrich Stadial 1 (17.0–14.7 ka); b) Last Glacial Maximum (ca. 21 ka); c) Last Interglacial (ca. 130 ka); d) MIS19 (ca. 787 ka); e) Mid-Pliocene warm period (3.205 Ma); f) M2 (ca. 3.3 Ma). Note that the coastlines for past time periods differ from the present (more pronounced especially during colder time periods, e.g., Last Glacial Maximum) and also that the present borders of lakes are shown for past time periods.

well (Davis, 1971; Ekim and Güner, 1986; Gür, 2016). The present study represents the first discussion to comprehensively address the debates on the Anatolian Diagonal by focusing on a plant species whose geographical distribution is associated with it.

Climate is one of the most important factors affecting the growth and reproduction of organisms and it also plays an important role in the geographical distributions of species (Lawler et al., 2009). Understanding the responses of organisms to environmental changes, especially global climate changes, provides an understanding of how they have overcome unfavorable conditions in the past and also gives us clues on how they can potentially respond to future global climate changes (Spence and Tingley, 2020). Thus, it will be possible to make more realistic conservation plans for these species.

The Quaternary period, starting around 2.6 Ma, has been characterized by significant global climate changes, most notably recurring cycles of global cooling and warming, known as glacial and interglacial periods. As a generally accepted pattern, temperate-adapted taxa are in general confined to refugia during glacial periods and expand their ranges from these refugia during interglacial periods (Hewitt, 2004). During glacial periods (e.g., the Last Glacial Maximum), many regions located at higher latitudes and in high mountain ranges (e.g., the European Alps) were covered by ice (Pan et al., 2020), whereas the existence of glaciers in Anatolia was limited only to the peaks of high mountains (e.g., Aladağlar, Kaçkar Mountains) (Atalay, 1996). Although the small number of previous studies restricts our understanding, Anatolia has already been suggested as a refugium for animal and plant species distributed in the northern latitudes, similar to the well-known southern refugia in the Iberian, Italian, and Balkan peninsulas (Hewitt, 1996).

Although the effects of global climate changes through the Late Quaternary glacial–interglacial cycles on the population dynamics of cold-tolerant plants are not yet clear, particularly in temperate regions, it is expected that mountain species generally have larger ranges during glacial periods when they spread to lowland areas (Stewart et al., 2003; Gao et al., 2015). Cold-adaptive plant species have evolved mechanisms to cope with the harsh conditions of glacial periods (e.g., the Last Glacial Maximum), characterized by lower temperatures, increased aridity, and stronger winds. These mechanisms include the development of deep roots, thick cuticles, and smaller leaves to reduce water loss, as well as the accumulation of antifreeze compounds and the ability to undergo freezing without damage (Körner, 2022). However, in certain mountain areas, such as the European Alps, some cold-adapted species may have had a smaller distribution during the cold stages of the Pleistocene due to the movement of glaciers, while this scenario is not expected in Anatolia for the reasons described above (Stewart et al., 2010). Thus, the phenomenon of range contraction and expansion during warmer and colder time periods, respectively, at least around and in the Anatolian Highlands, may also be true for *N. vesicaria* because areas of high bioclimatic suitability contracted during warmer time periods and expanded during colder time periods (Figures 2 and 3). Similarly, an ecological niche modeling approach for two alpine plant species distributed in Anatolia, *Noccaea iberidea* (Boiss.) Al-Shehbaz & Menke and *Vavilovia formosa* (Steven) Fed., suggests that areas of high bioclimatic suitability were larger for these plant species during the Last Glacial Maximum than during the present, as seen for *N. vesicaria* (Smýkal et al., 2017; Özüdoğru et al., 2020).

Under the present bioclimatic conditions, areas of more suitable bioclimatic conditions were observed, especially throughout and to the east of the Anatolian Diagonal, therefore largely matching the geographical distribution of *N. vesicaria*. Peripheral populations in the small disjunct area of Jebel Liban and the Anti-Lebanon Mountains in the middle part of the Levant Ranges may be considered to be glacial relict populations. This area likely hosts glacial relict populations of other species, e.g., *Allactaga williamsi* (Kryštufek et al., 2013). However, areas of high bioclimatic suitability were also observed in the west of the Anatolian Diagonal, especially throughout the Taurus Mountains and Pontic Mountains (Figure 2). These areas represent areas most likely unoccupied, suggested by field studies throughout Anatolia over the past decades, due to nonclimate reasons (nonclimate environmental reasons, e.g., bedrock, topography; dispersal; and/or biotic interactions). Thus, bioclimatic suitability by itself cannot explain the geographical distribution of *N. vesicaria* or the absence of it, especially to the west of the Anatolian Diagonal. Considering that this species does not prefer a particular bedrock type (based on the field observations of the last author), there may be two reasons why *N. vesicaria* does not occur to the west of the Anatolian Diagonal: dispersal and/or biotic interactions.

Dispersal limitation does not seem to be the case for *N. vesicaria* given its relatively wide geographical distribution and its sac-shaped fruits that allow dispersal by wind (Hedge, 1965). Furthermore, the Anatolian Diagonal and the Taurus Mountains form a biogeographical integrity (the Taurus Way; for details, see Kaya and Çıplak, 2017) and there is no physical barrier between these two mountain ranges, especially for alpine species. The migratory corridor role of the Anatolian Diagonal has been shown for the arctic-alpine and widely distributed *Arabis alpina* L., and Ansel et al. (2011) postulated that the Anatolian Diagonal facilitated the connection between the

Mediterranean and Caucasus/Near East Mountain systems and the range expansion of this species out of Anatolia during glacial periods. For species whose geographical distribution is associated with these mountain ranges, this connection can be seen to be relatively uninterrupted, as in the case of the genus *Ricotia* L. or *Heldreichia bupleurifolia* Boiss., or interrupted, as in *Phyllolepidium cyclocarpum* (Boiss) L. Cecchi (Parolly et al., 2010; Özüdoğru et al., 2022). However, the geographical distribution of *N. vesicaria* is not restricted to the Anatolian Diagonal and it extends to the Alborz Mountains throughout the Anatolian Highlands. With the exclusion of the Alborz Mountains and the middle part of the Levant Ranges, this area is more or less congruent with the Anatolian-Armenian areas of endemism, which cover the eastern parts of the Taurus and Pontic Mountains and the Anatolian Highlands, as well as the mountain ranges in Armenia, Northeastern Iraq, Northwestern Iran, and the Talysh Mountains (Noroozi et al., 2021). The Anatolian Highlands, which are higher in elevation with an average altitude of about 2000 m, experience colder temperatures and more precipitation compared to Central Anatolia; therefore, the Anatolian Highlands and the Anatolian Diagonal/Southeastern Taurus Mountains are a biogeographically well-defined region and the vegetation of this region is explicitly different from that of Western Anatolia (Gür, 2016; Parolly, 2020). Phytosociologically, *N. vesicaria* is a characteristic species of the Anatolian Highlands steppe order *Festuco oreophilae-Veronicetalia orientalis* Hamzaoğlu and the range of the order largely matches the geographical distribution of *N. vesicaria* (Hamzaoğlu, 2006). Thus, *N. vesicaria* seems to be highly associated with this phytosociological order and, because the range of this order does not extend to Central Anatolia, one could argue that biotic interactions (likely positive plant interaction or facilitation) may have played a significant role in shaping the geographical distribution of *N. vesicaria*.

The number of studies dealing with associations between climate change and vegetation shift is still inadequate and simple associations may therefore often be unrealistic (Lloret et al., 2012). The contrasting response of populations at the edges of a species' range is due to biotic interactions such as interspecific competition being the primary determinant of the lower range limit, while the upper range limit is determined by abiotic factors like temperature or length of the growing season (Vittoz et al., 2009). Additionally, the ecophysiological and demographic stabilizing mechanisms of the dominant populations and communities, along with various species interactions, appear to compensate for the decline and eventual death of the dominant vegetation (Lloret et al., 2012). Thus, although there are examples of species- or genus-level penetration from the Irano-Turanian region to the Mediterranean region in the literature (Manafzadeh et al., 2014, 2016), a shift of Eastern Anatolian vegetation to the west during colder time periods may be limited, considering the paleogeological history of Eastern Anatolia and its unique vegetation structure.

The environmental barrier function of the Anatolian Diagonal between the Anatolian Highlands and Central Anatolia and the floral break between these two regions has long been under discussion. As explained in the introduction, while Davis (1971) described the reason for this break with the paleogeological history of Anatolia, Ekim and Güner (1986) and Gür (2016) explained it with ecological and climatic variables. It is possible to find supporting evidence from the literature for both hypotheses.

Most of the species of the polyphyletic genus *Grammosciadium* DC. of pre-Quaternary origin are distributed only to the east of the Anatolian Diagonal. Therefore, this region represents a diversification center for this genus and this might be explained by the fact that Eastern Anatolia (the Anatolian Highlands) has a younger age, as Davis claimed (Davis, 1971; Koch et al., 2017). However, the divergence between the two evolutionary lineages (one from the west and one from the east of the Anatolian Diagonal) of the lemon-yellow tree frog *Hyla savignyi* (Audouin, 1827) is explained by climatic variables, supporting the environmental barrier function of the Anatolian Diagonal (Gül, 2013). Alternatively, the geographical distribution of the haplo/ribotypes of *N. iberidea* throughout Anatolia does not show any east-west discontinuity and ecological niche model of this species based on bioclimatic data suggest suitable areas on both the east and west of the Anatolian Diagonal (Özüdoğru et al., 2020). Thus, the Anatolian Diagonal does not act as a physical or ecological barrier for this species.

In conclusion, based on the available data, we might say that neither of these competing hypotheses is right or wrong. It is also important to note that Davis's explanation of the paleogeological history of Anatolia does not actually exclude either the environmental barrier function of the Anatolian Diagonal or the importance of biotic interactions as discussed above. Therefore, given the biology of the species under study, one might conclude that biogeographical inferences about the environmental barrier function of the Anatolian Diagonal should be species-specific rather than general explanations. However, future studies should also focus on niche overlap among populations within species or among taxa with respect to the Anatolian Diagonal.

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Table S1. The presence records for *Noccaea vesicaria*. * indicates the eliminated presence records after the spatially filtering process.

	Longitude	**Latitude**
1	42.682797	39.884845
2	42.650245	41.418006
3	45.142664	40.225677
4	46.175194	38.950064
5	43.95	40.86667
6	44.921841	40.291949
7	44.72306	40.11944
8*	46.05444	39.68694
9	45.533333	40.385833
10	44.914083	40.340133
11	46.482517	39.202112
12	44.950068	40.218945
13 *	44.938829	40.228265
14 *	44.941428	40.218353
15	46.05861	39.68139
16	44.781852	40.119989
17	42.245769	41.09483
18	40.329557	40.496369
19 *	40.50055	40.03361
20 *	42.248054	38.581633
21	42.256803	38.591653
22 *	42.288903	38.609207
23	42.738142	38.88125
24	42.848675	38.911097
25*	42.26083	38.58914
26*	42.269422	38.577439
27	41.985651	38.315708
28*	42.26226	38.571886
29	42.778854	38.408545
30*	42.748437	38.391448
31	38.867724	38.539008
32	38.741916	38.657174
33	38.82994	38.601202
34*	38.884686	38.594101
35	39.341391	38.723792
36	38.917307	38.616455
37	40.570964	39.652883
38	39.68064	39.57834
39	39.524871	39.820142
40*	39.738854	39.720672
41	39.340929	39.648241
42*	38.509003	39.257191

43	38.995338	39.69786
44	38.480897	39.228284
45	38.563069	39.268893
46	39.087931	39.872533
47	39.639637	39.864224
48	39.702798	39.744976
49	41.547087	40.538852
50	41.641171	40.48431
51	40.461823	40.065594
52	40.779999	40.369999
53	40.411342	40.039318
54	41.293299	39.836201
55	40.979608	40.10967
56*	41.659092	40.463264
57*	40.50561	40.04085
58*	41.284787	39.848405
59*	40.53361	40.00083
60*	40.487899	40.038677
61	43.400002	41.599998
62	43.487663	41.398832
63	43.481345	41.802846
64*	43.471933	41.80633
65	44.75275	42.580971
66*	43.471667	41.807778
67 *	43.471545	41.805864
68	39.73621	40.384851
69 *	39.674963	40.38456
70	39.659567	40.389195
71	39.607281	40.208457
72	39.490778	40.451807
73	40.047105	40.360016
74	44.425489	37.709677
75	44.364713	37.740052
76	43.952342	37.500403
77	44.187271	37.343646
78*	44.1876	37.340494
79	43.516953	37.512804
80	43.413118	37.643391
81	43.141289	36.887159
82*	49	33.48333
83	46.4	35.5
84	50.435466	32.181086
85	49.043911	33.488043
86	50.299032	32.170135

87	42.602555	40.172016
88	42.765761	41.525063
89	42.50859	40.380731
90*	42.767905	41.526066
91	36.52042	38.33869
92	36.034863	34.263583
93	37.919113	37.946241
94	38.039265	38.014181
95	41.527322	38.646763
96*	35.108129	37.865672
97	37.239935	39.463439
98	37.553911	39.5737
99	37.113343	39.407938
100	38.124826	39.385078
101	38.0284	39.378448
102	38.21694	39.50055
103	37.146224	39.473271
104	37.30171	39.37424
105	37.66847	39.51609
106	36.13333	33.73333
107	43.188097	37.644732
108	39.900129	39.502518
109	39.011445	39.262799
110	39.166364	39.408339
111	39.41797	39.10986
112	38.94525	39.305102
113	39.856389	39.286111
114	43.833056	38.378333
115	35.1299	37.8298
116	44.119399	37.887951
117	43.939031	38.661867
118	43.977152	38.07085
119	43.514743	38.500071

Table S2. Bioclimatic variables. Highlighted variables were used for ecological niche modeling.

Label	**Variable**	**Units**
BIO1	Annual Mean Temperature	Degrees Celsius
BIO2*	Mean Diurnal Range	Degrees Celsius
BIO3*	Isothermality	Dimensionless
BIO4	Temperature Seasonality	Degrees Celsius
BIO5*	Max Temperature of Warmest Month	Degrees Celsius
BIO6*	Min Temperature of Coldest Month	Degrees Celsius
BIO7*	Temperature Annual Range	Degrees Celsius
BIO8**	Mean Temperature of Wettest Quarter	Degrees Celsius
BIO9**	Mean Temperature of Driest Quarter	Degrees Celsius
BIO10	Mean Temperature of Warmest Quarter	Degrees Celsius
BIO11	Mean Temperature of Coldest Quarter	Degrees Celsius
BIO12	Annual Precipitation	Millimeters
BIO13**	Precipitation of Wettest Month	Millimeters
BIO14**	Precipitation of Driest Month	Millimeters
BIO15	Precipitation Seasonality	Fraction
BIO16**	Precipitation of Wettest Quarter	Millimeters
BIO17**	Precipitation of Driest Quarter	Millimeters
BIO18	Precipitation of Warmest Quarter	Millimeters
BIO19	Precipitation of Coldest Quarter	Millimeters

* These variables are not available for all time periods (for further details, see the PaleoClim database).
** These variables were not considered to focus only on fixed summer and winter three monthly periods.

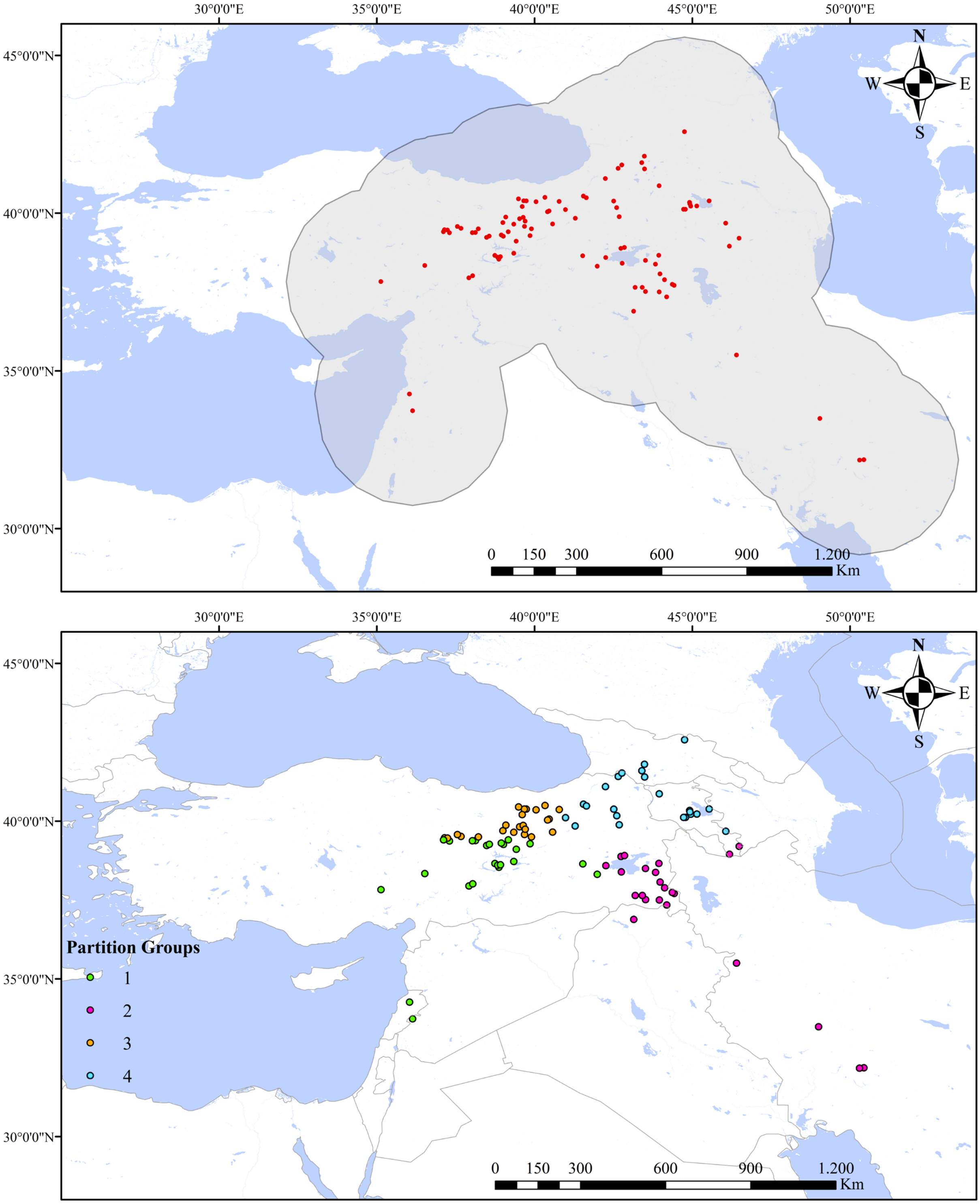


Figure S1. The point buffer created from the presence records (circles) to which a 3-degree buffer was applied (top map) and the presence data (circles) partitioned into four separate training and testing bins using a spatial approach (block, k = 4) (bottom map).

Table S3. Model evaluation statistics of the final model. FC: Feature classes (L = linear, Q = quadratic); RM: regularization multiplier; AUC: value of the area under the curve of the receiver operating characteristic (ROC) plot; CBI: conditional Boyce index; AUC$_{DIFF}$: difference between training and testing AUC; OR$_{10}$: 10% training omission rate; OR$_{MIN}$: minimum training presence omission rate.

FC	**RM**	**AUC$_{TRAIN}$**	**CBI$_{TRAIN}$**	**Mean AUC$_{DIFF}$**	**SD AUC$_{DIFF}$**	**Mean AUC$_{TEST}$**	**SD AUC$_{TEST}$**	**Mean CBI$_{TEST}$**	**SD CBI$_{TEST}$**	**MEAN OR$_{10}$**	**SD OR$_{10}$**	**Mean OR$_{MIN}$**	**SD OR$_{MIN}$**
LQ	4	0.890	0.963	0.034	0.021	8.878	0.033	0.843	0.094	0.130	0.107	0.033	0.065

Table S4. The coefficients of the final model.

The feature type and the bioclimatic variable involved in the feature	**The fitted lambda-value**	**Minimum**	**Maximum**
bio_1	−4.284382737969539	−72.0	272.0
bio_12	4.137592338326543	46.0	2461.0
bio_15	−2.9551718014004646	8.0	135.0
bio_18	−9.148211412009234	0.0	662.0
bio_4	0.0	4943.0	10376.0
bio_1^2	−7.596261981661033	0.0	73984.0
bio_15^2	−0.1417954386295347	64.0	18225.0
bio_4^2	1.1740415702303424	2.4433249E7	1.07661376E8
Linear Predictor Normalizer	−0.36237477970377685		
Density Normalizer	469.9928511604642		
Number Of Background Points	10079		
Entropy	8.2039503113146		

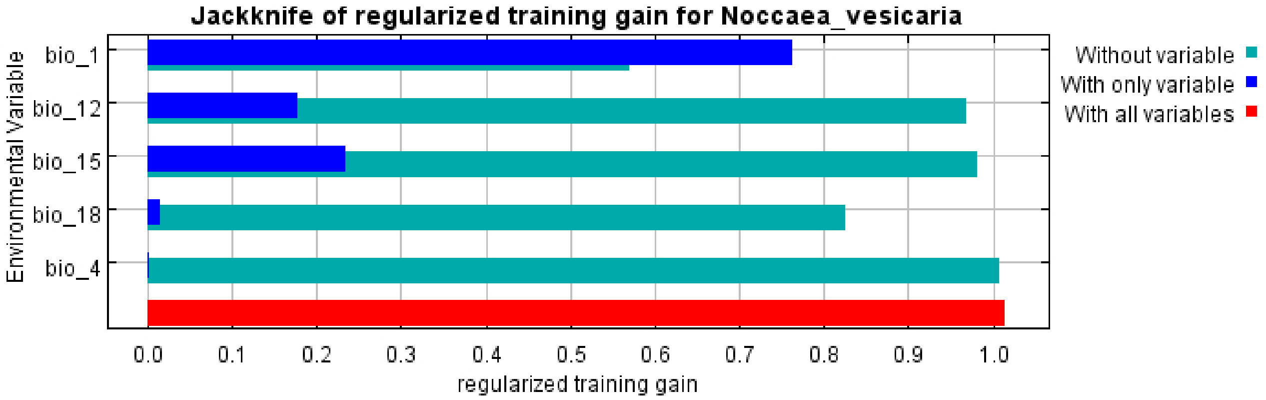
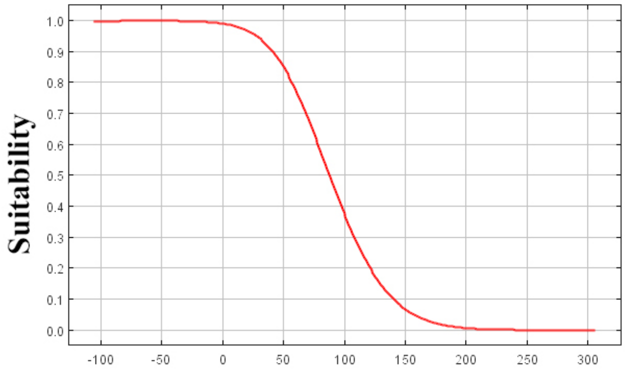
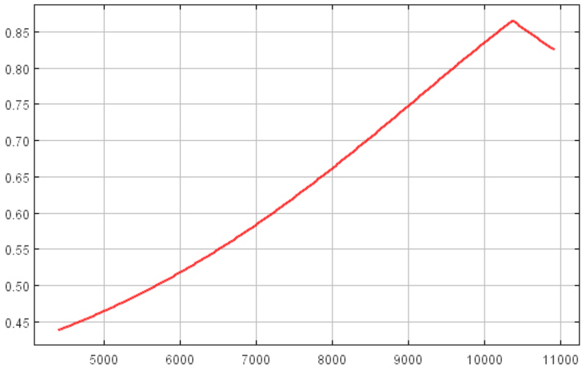


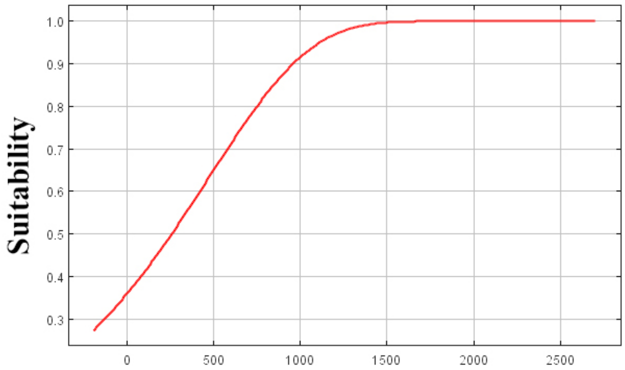
Figure S2. The results of the jackknife test of variable importance. Without variable: Each variable is excluded in turn and a model is created with the remaining variables. With only variable: a model is created using each variable in isolation. With all variables: a model is created using all variables (see for further details, Phillips 2021).



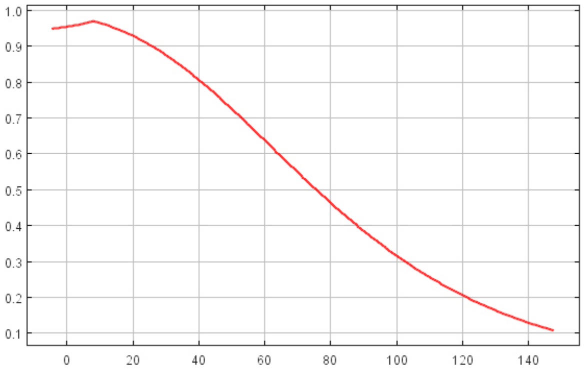
BIO 1



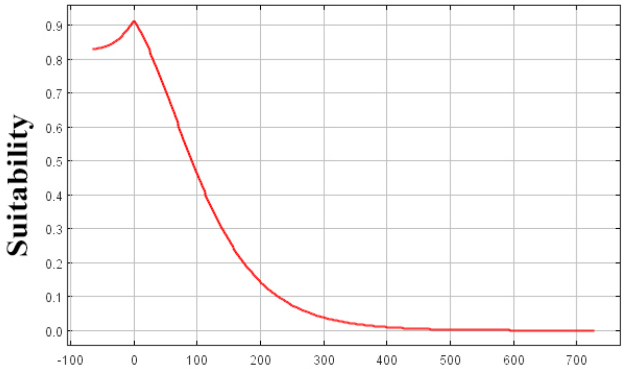
BIO 4



BIO 12



BIO 15



BIO 18

Figure S3. The marginal response curves for the bioclimatic variables used for ecological niche modeling. For detailed descriptions of the bioclimatic variables, see Table S2.