Research Article

Climatic preferences and distribution of 6 evolutionary lineages of *Typhlops vermicularis* Merrem, 1820 in Turkey using ecological niche modeling

Serkan GÜL[1],*, Yusuf KUMLUTAŞ[2], Çetin ILGAZ[2]

[1]Department of Biology, Faculty of Arts and Science, Recep Tayyip Erdoğan University, Rize, Turkey
[2]Department of Biology, Faculty of Science, Dokuz Eylül University, Buca, Izmir, Turkey

Abstract: According to evolutionary biologists, ecology is a very important factor in speciation. Ecology may be effective at driving adaptive divergence between lineages in different environments and climatic conditions. Because Anatolia has major mountain belts, paleogeographic characteristics, and unique climatic traits, it plays an important role in speciation and shows a barrier effect for many terrestrial species. In this study, we investigated the climatic preferences of 6 isolated evolutionary lineages of *Typhlops vermicularis* in Anatolia using ecological niche modeling. Our results revealed that both glacial (Last Glacial Maximum) and interglacial (Last Interglacial) modeling, as well as current modeling, showed the most important climatic variables that potentially limit the spread of 6 major lineages of *T. vermicularis* throughout all of Anatolia. In addition, our results revealed that 6 lineages of *T. vermicularis* could be adapted to different climatic conditions. Finally, our study demonstrates the unique climatic importance of Anatolia as a center for the local diversification of *T. vermicularis*.

Key words: Climate, ecological niche modeling, Last Glacial Maximum, Last Interglacial, Reptilia, Turkey, *Typhlops vermicularis*

1. Introduction

Ecology is an important factor for speciation because divergence between lineages that inhabit different environmental conditions may cause speciation to create new lineages (Wiens, 2004). In order to understand evolutionary processes and patterns, environmental conditions and in particular abiotic elements such as temperature and precipitation are key factors (Kozak et al., 2008) because the abiotic conditions in which a species is able to persist are described by its fundamental niche, according to Hutchinson (1957).

Geographic information system (GIS) data allows the investigation of the effects on genetic lineages of both environmental and climatic factors. The GIS enables the study of phylogeography, speciation, and phenotypic character evolution within and among species (Kozak et al., 2008). In evolutionary biology, the GIS is important for understanding the evolutionary processes that determine gene flow within and between lineages, and to compare genetic diversity between lineages (Pröhl et al., 2010). Ecological niche modeling (ENM) is one of many possible applications of GIS. ENM generates a map of the expected distribution of a species using climatic and geographic conditions based on known locality data (Guisan and

Zimmermann, 2000; Guisan and Thuiller, 2005; Kozak et al., 2008). ENM can be used to interpret the relationship between divergence and speciation mechanisms, as well as to examine deeper lineage nodes in phylogeny using both geographic and environmental space (Graham et al., 2004).

Turkey is a region with vast genetic diversity due to its climatic and topographic characteristics (Çetin et al., 2007) and, according to Conservation International, Turkey covers 3 different biogeographic regions. These regions consist of the Caucasus in the northeast of Turkey; the Irano-Anatolian hotspot, including major parts of central and eastern Anatolia; and the Mediterranean Basin, covering the western and southern portions of the Anatolian peninsula (Myers et al., 2000). Şekercioğlu et al. (2011) reported that Turkey has 4 major mountain belts, including the Yıldız Mountains in the European part of Turkey; the Taurus Mountains, covering southern Anatolia between the Mediterranean coast and eastern Anatolia; the Köroğlu and Kaçkar Mountains in the Northern Anatolian Mountains; and the Anatolian Diagonal, running from the northeast to the Mediterranean. The Anatolian Diagonal, especially, is a barrier for terrestrial species because it has served as a dispersal corridor for many animals from northeastern to southern Anatolia (Nilson et al., 1990).

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* Correspondence: serkan.gul@erdogan.edu.tr

The family Typhlopidae consists of 7 genera and 253 species, and the genus *Typhlops* includes 123 species (http://www.reptile-database.org). *Typhlops vermicularis* has uniformly sized body scales, highly reduced eyes, a small and ventrally placed mouth, and a variably shaped snout. *T. vermicularis*' size can show variation from 5.3 cm to 40 cm (Hutchins et al., 2003; Kornilios et al., 2012). *Typhlops vermicularis* is known in Albania, Bulgaria, Greece, and the former Yugoslavia within the Balkan Peninsula; in Turkey, Syria, Jordan, Cyprus, and Iran in the Middle East, including a majority of West Asia; and in Georgia, Armenia, and Azerbaijan within the Transcaucasus (also known as the southern portion of the Caucasus) (Kornilios et al., 2012; http://www.reptile-database.org). In this paper, we address the climatic preferences of 6 evolutionary lineages of *T. vermicularis* using ENM, because recent phylogenetic studies show that *T. vermicularis* in Turkey is divided by molecular data into 6 fundamental lineages (Kornilios et al., 2012).

This study is the first attempt to investigate the climatic preferences of these 6 lineages of *T. vermicularis*. In this context, we aim to reveal the climatic relationships among the 6 lineages of Anatolian *T. vermicularis* using ENM in order to discern the effect of temperature and precipitation on the 6 lineages and determine the effect of climate on speciation.

2. Material and methods

2.1. Taxon sampling
Locality data for populations of *T. vermicularis* were collected from 59 different localities between 1990 and 2009 while performing fieldwork in several areas of Turkey and were kept in the Biology Laboratories of Dokuz Eylül University (Figure 1; Table 1).

2.2. Ecological niche modeling
The bioclimatic variables result from global land area interpolation of climatic point data (in the period of 1950–2000) at a spatial resolution of 30 arcseconds. The bioclimatic variables are a set of global climate layers with a spatial resolution of 1 km² (Hijmans et al., 2005; available at http://www.worldclim.org). The environmental data for niche modeling consisted of 19 bioclimatic variables (Table 2) obtained from WorldClim (Hijmans and Graham, 2006). Many of these variables appeared redundant. In order to identify potentially redundant variables, we performed correlations between all pairwise combinations of the 19 variables using the Pearson correlation coefficient in ENMTools 1.3 (Warren et al., 2008, 2010). The raw data were the values for all 19 variables at 59 localities for all 6 focal lineages. Pairs of variables with a correlation coefficient ≥0.75 were potentially considered. When variables were highly correlated, we selected the most biologically meaningful variables for the lineages, and 8 temperature and 8 precipitation variables were reserved for analysis (Table 2). According to these 16 bioclimatic variables (Table 2), ENM was conducted for *T. vermicularis* using a total of 59 specimen localities (Figure 1).

We used 2 past climate scenarios: the first for the Last Interglacial (LIG; ~120,000–140,000 years ago; Otto-Bliesner et al., 2006) at a spatial resolution of 30 arcseconds (~1 km) and the second for the Last Glacial Maximum (LGM; ~21,000 years ago). LGM climate data were generated from 2 models: the Community Climate System Model (CCSM; Collins et al., 2004) and the Model for Interdisciplinary Research on Climate (MIROC, version 3.2; Hasumi and Emori, 2004), which were obtained from the WorldClim Global Climate Data at a spatial resolution of 2.5 min. The LGM data set was resampled to a spatial resolution of 30 arcseconds. To produce an ecological niche model depicting the distribution of *T. vermicularis*, we used 59 localities, including present points, and created 51 random points (test points) similar to present points for each lineage using Geospatial Modeling Environment version 0.7.2.0 (http://www.spatialecology.com/gme).
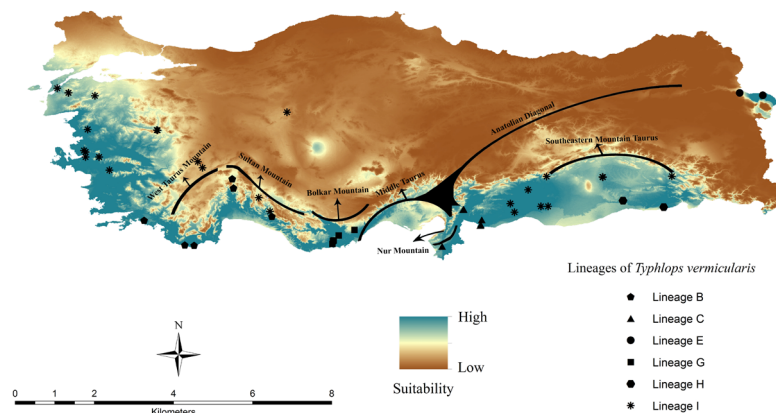

Figure 1. Important mountain chains of Anatolia and ecological niche modeling of *T. vermicularis* in Turkey under current climatic conditions.

Table 1. The locality data of 6 lineages of *T. vermicularis* in Turkey.

Species	Latitude, °N	Longitude, °E	Lineages
T. vermicularis	36.82647	28.61043	B
T. vermicularis	37.64536	30.86927	B
T. vermicularis	37.63884	30.86703	B
T. vermicularis	36.20444	29.63898	B
T. vermicularis	36.19566	29.87569	B
T. vermicularis	37.87442	30.83697	B
T. vermicularis	37.87302	30.83849	B
T. vermicularis	37.87316	30.83498	B
T. vermicularis	36.92355	31.8425	B
T. vermicularis	36.71633	37.11799	C
T. vermicularis	36.84054	37.14395	C
T. vermicularis	36.17027	36.14128	C
T. vermicularis	37.09763	36.67494	C
T. vermicularis	37.10585	36.6849	C
T. vermicularis	36.69879	37.10853	C
T. vermicularis	40.04057	43.66333	E
T. vermicularis	39.98113	44.24684	E
T. vermicularis	36.58488	33.92622	G
T. vermicularis	36.32011	33.39809	G
T. vermicularis	36.30461	33.3823	G
T. vermicularis	36.22877	33.36788	G
T. vermicularis	36.44371	33.52661	G
T. vermicularis	37.15928	41.74251	H
T. vermicularis	37.32294	40.71516	H
T. vermicularis	37.32103	40.71104	H
T. vermicularis	37.93333	41.95	I
T. vermicularis	38.41869	27.47179	I
T. vermicularis	37.17618	38.82174	I
T. vermicularis	37.59139	38.31833	I
T. vermicularis	37.24529	37.86881	I
T. vermicularis	37.17472	38.64119	I
T. vermicularis	37.0293	37.97301	I
T. vermicularis	37.9295	38.78262	I
T. vermicularis	37.91333	40.20636	I
T. vermicularis	37.91035	40.20224	I
T. vermicularis	37.91766	40.19812	I
T. vermicularis	40.15402	26.41555	I
T. vermicularis	39.96307	27.36605	I
T. vermicularis	40.03959	26.70102	I
T. vermicularis	40.03885	26.69605	I
T. vermicularis	38.41885	27.12872	I
T. vermicularis	37.24533	37.86835	I
T. vermicularis	37.17472	38.64119	I
T. vermicularis	38.14955	30.08599	I
T. vermicularis	38.08858	27.73347	I
T. vermicularis	38.41869	27.47179	I
T. vermicularis	38.41957	27.47373	I
T. vermicularis	37.39361	31.5075	I
T. vermicularis	38.3	29.96667	I
T. vermicularis	38.54339	27.13089	I
T. vermicularis	38.54494	27.12621	I
T. vermicularis	38.54753	27.13428	I
T. vermicularis	40.15531	26.41416	I
T. vermicularis	37.04662	31.7922	I
T. vermicularis	39.54971	32.22126	I
T. vermicularis	39.09889	28.93164	I
T. vermicularis	39.09383	28.95395	I
T. vermicularis	39.11667	27.18333	I
T. vermicularis	38.5821	27.0903	I

Since the resulting suitable areas for *T. vermicularis* were compared with the known distribution areas of 6 lineages, 6 lineage models were created as defined by phylogenetic analysis based on 16 variables (Figures 2 and 3).

ENM was performed using Maxent software (version 3.3.3e) for species habitat modeling (Philips et al., 2006). Maxent generates a probability distribution map based on bioclimatic data (Elith et al., 2006; Phillips et al., 2006). The Maxent algorithm (with 0 being the lowest and 1 the highest probability) estimates the habitat suitability of species from locality point data by finding the maximum entropy distribution (Philips et al., 2004, 2006; Kozak et al., 2008; Phillips and Dudik, 2008). Niche models were built independently for 6 lineages of *T. vermicularis*. To develop the model, we used 59 presence points and 51 test points (Figures 2 and 3). To set the cut-off value, we chose a lowest presence threshold associated with any one of the observed presence records (Pearson et al., 2007). Predicted distribution maps and climatic variables were generated using ArcGIS 10.1 software (Esri, 2012).

The fit of each model is defined by a curve that maximizes sensitivity for low values of the false-positive fraction (Hernandez et al., 2006). The area under the receiver operating characteristic curve (AUC) estimates the significance of the model. AUCs usually range from 0.5 to 1.0. Values close to 0.5 do not show an equal correlation with random distribution, whereas values close to 1.0 indicate a perfect fit for potential species distribution. On the contrary, values less than 0.5 may be obtained, but these values show that a model is not better than random (Engler et al., 2004).

3. Results
The distribution model for current climatic conditions covering all of Anatolia was created for *T. vermicularis* as a single model with all presence points (Figure 1). The Aegean region, the west and middle portions of the Mediterranean region, the southwest portion of the Marmara region, the southeast Anatolian region, and the northeast portion of the eastern Anatolian region were identified as suitable, whereas the Black Sea region, the Thrace portion of the Marmara region, and a large part of central and eastern Anatolia region were unsuitable. A single locality in the central Anatolia region (between Polatlı and Haymana, Ankara; Kornilios et al., 2012) was also suitable. The distribution model of *T. vermicularis* had a high mean test AUC value (0.881 ± 1.117). According to current climatic conditions, analyses of ENM for *T. vermicularis* strongly suggested that annual mean temperature (Bio1), mean temperature of the coldest quarter (Bio11), and precipitation seasonality (Bio15) were the most important climatic variables that potentially limit the spread of the major 6 lineages of *T. vermicularis* throughout Anatolia (Table 2).

Table 2. Summary of environmental variables from the WorldClim data set (Hijmans et al., 2005) and contributions of the environmental variables.

Variables	Description	Percent contribution
Bio1*	Annual mean temperature	25.1
Bio2	Mean diurnal temperature range (mean of monthly [max temp–min temp])	-
Bio3	Isothermality (Bio2/Bio7 × 100)	-
Bio4*	Temperature seasonality (standard deviation × 100)	0.1
Bio5*	Minimum temperature of coldest month	0
Bio6*	Maximum temperature of warmest month	1.9
Bio7*	Temperature range (Bio5–Bio6)	1.2
Bio8	Mean temperature of wettest quarter	-
Bio9*	Mean temperature of driest quarter	0
Bio10*	Mean temperature of warmest quarter	2.7
Bio11*	Mean temperature of coldest quarter	20
Bio12*	Annual precipitation	0
Bio13*	Precipitation of wettest month	0.9
Bio14*	Precipitation of driest month	0.9
Bio15*	Precipitation seasonality (standard deviation of monthly precipitation)	39.4
Bio16*	Precipitation of driest quarter	0.3
Bio17*	Precipitation of wettest quarter	0.7
Bio18*	Precipitation of warmest quarter	0
Bio19*	Precipitation of coldest quarter	6.6

*: Environmental variables used for the model.

Based on known occurrences of *T. vermicularis* populations, ENM was developed for 6 lineages based on LIG and LGM models, and distribution maps were generated to predict the possible areas where 6 lineages of *T. vermicularis* populations might occur. Although both LGM and LIG climate models indicated a climate distribution highly suitable for 6 lineages of *T. vermicularis* throughout all of Anatolia (Figures 2 and 3), the models differed partially from current climatic conditions. In addition, 7 climatic parameters (Bio1, Bio4, Bio5, Bio6, Bio14, Bio15, and Bio19) for each lineage contributed more than 10% (Table 3). In lineage B, the AUC of the training data set of 9 records was 0.918 and the AUC of the test data set of 6 records was 0.894. The AUC of lineage C showed the high accuracy of the generated model, with 0.942 for training data and 0.892 for test data. In lineage E, both training and test AUC data showed a high accuracy of 0.999. Similarly, the AUC values of lineages G and H showed much higher accuracy of the generated model, with 0.953–0.961 for training data and 0.995–0.993 for test data, respectively. On the contrary, the AUC of training

data set of 34 records was 0.894 for lineage I, whereas the AUC of test data set of 10 records was 0.661.

4. Discussion

Kornilios et al. (2011) revealed that Anatolian populations of *T. vermicularis* form 5 major lineages. According to this study, Clade A (lineage B in this paper) comprises specimens from the southwestern part of Turkey. Clade B (lineage C in this paper) consists of specimens from the Nur or Amanos Mountain Ridge. Clade C (lineage G in this paper) includes specimens from Mersin Province. Clade D (lineage H in this paper) consists of specimens from Şırnak Province. Finally, Clade E (lineage I in this paper) includes specimens from the northwestern and southeastern parts of Anatolia. However, they did not include the specimens from eastern Anatolia. The next year, Kornilios et al. (2012) did a phylogenetic study including both eastern Anatolia populations of *T. vermicularis* and Georgia, Armenia, Azerbaijan, Iran, Syria, Jordan, and Greece, using mitochondrial and nuclear genes. This study showed similar results to those of the previous study. In
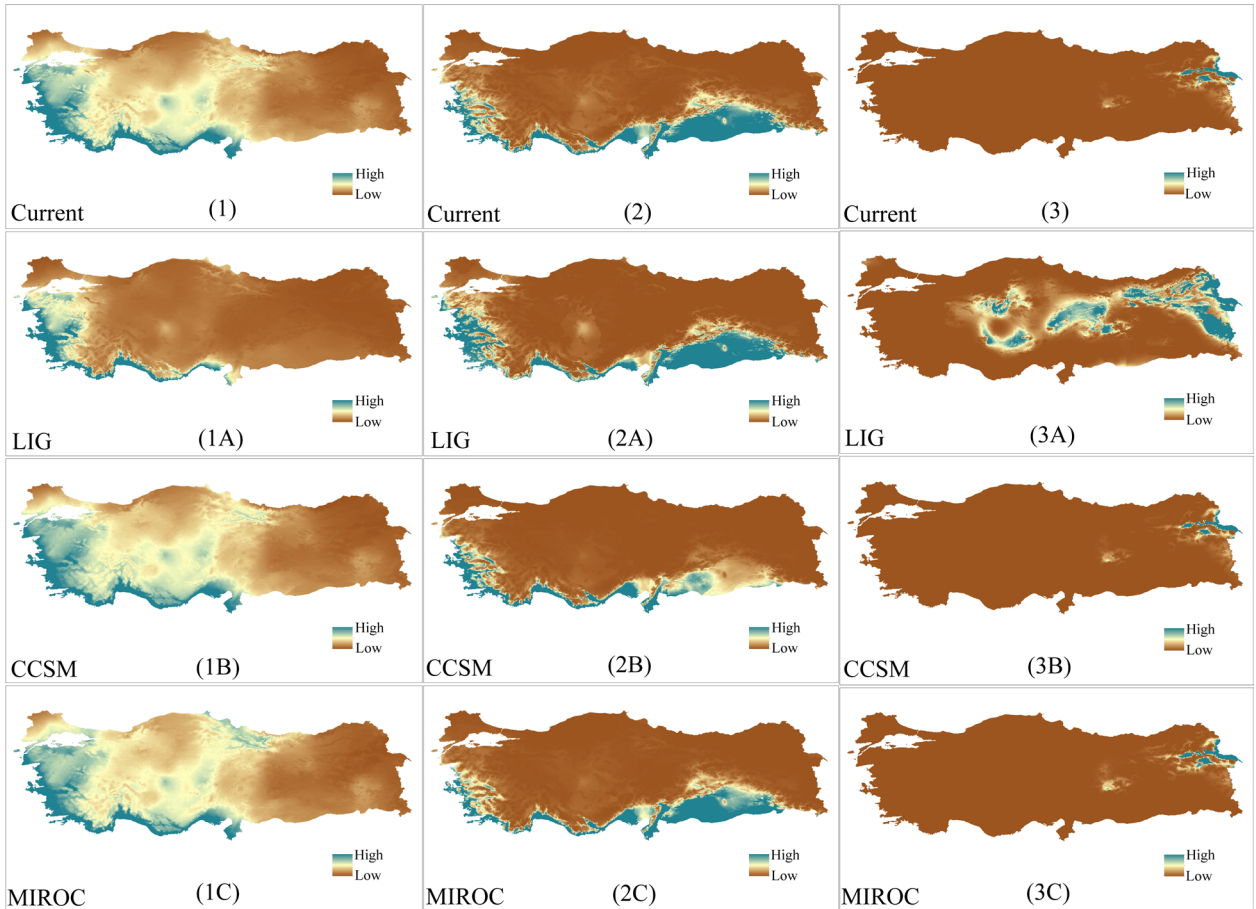
Figure 2. Predicted models of lineages B, C, and E according to Last Interglacial (LIG) and Last Glacial Maximum (LGM; CCSM and MIROC) (1, 1A, 1B, 1C for lineage B; 2, 2A, 2B, 2C for lineage C; 3, 3A, 3B, 3C for lineage E).

addition, in the preceding study, they found 6 major lineages (lineages B, C, E, G, H, and I) for Turkey, and they also disclosed that the oldest split in the *T. vermicularis* phylogeny occurred between 2.0 and 6.4 Mya.

According to ENM of *T. vermicularis* under current climatic conditions (Figure 1), annual mean temperature (Bio1), mean temperature of coldest quarter (Bio11), and precipitation seasonality (Bio15) were the variables that had the largest effect on *T. vermicularis* in Anatolia (Table 2). However, different climatic parameters appeared for each lineage in the models. The models indicate that lineage B prefers wetter habitats with regards to both temperature and precipitation seasonality (Figure 2 (1); Table 3). Lineage C inhabits drier habitats (Figure 2 (2); Table 3). Lineages E and G occur in wetter habitats with higher precipitation with regard to temperature seasonality (Figures 2 (3) and 3 (4); Table 3), whereas lineage H is found in colder and drier habitats with higher temperatures (Figure 3 (5); Table 3). Lineage I occurs in colder and wetter habitats (Figure 3 (6); Table 3). In some cases, this situation appears not only in the actual range

but also in the predicted distributions, although overlap can be seen for lineage I. This probably arises from the characteristic structure of Anatolia, because Anatolia is a western Asian geographic region bounded by the Aegean, the Mediterranean, and the Black Sea to the west, south, and north respectively, while to the northeast and the east it is confined by the Caucasus and the Armenian highlands. It is a predominantly mountainous area whose diverse geomorphology produces many different climatic regions and vegetation types (Sindaco et al., 2000).

Anatolia also played an important role as a refugium during the Quaternary ice ages, holding populations during glacial periods that could migrate during the interglacial periods to Europe via Thrace (the European part of Turkey) and the Caucasus (Hewitt, 2001). Repetitive temperature fluctuations during these periods pushed Anatolian populations from south to north and vice versa (Çıplak, 2003). During the Miocene, Pliocene, and Pleistocene eras, evolutionary lineages of *T. vermicularis* could have originated within populations in habitat refugia. Kornilios et al. (2012) indicated that populations from
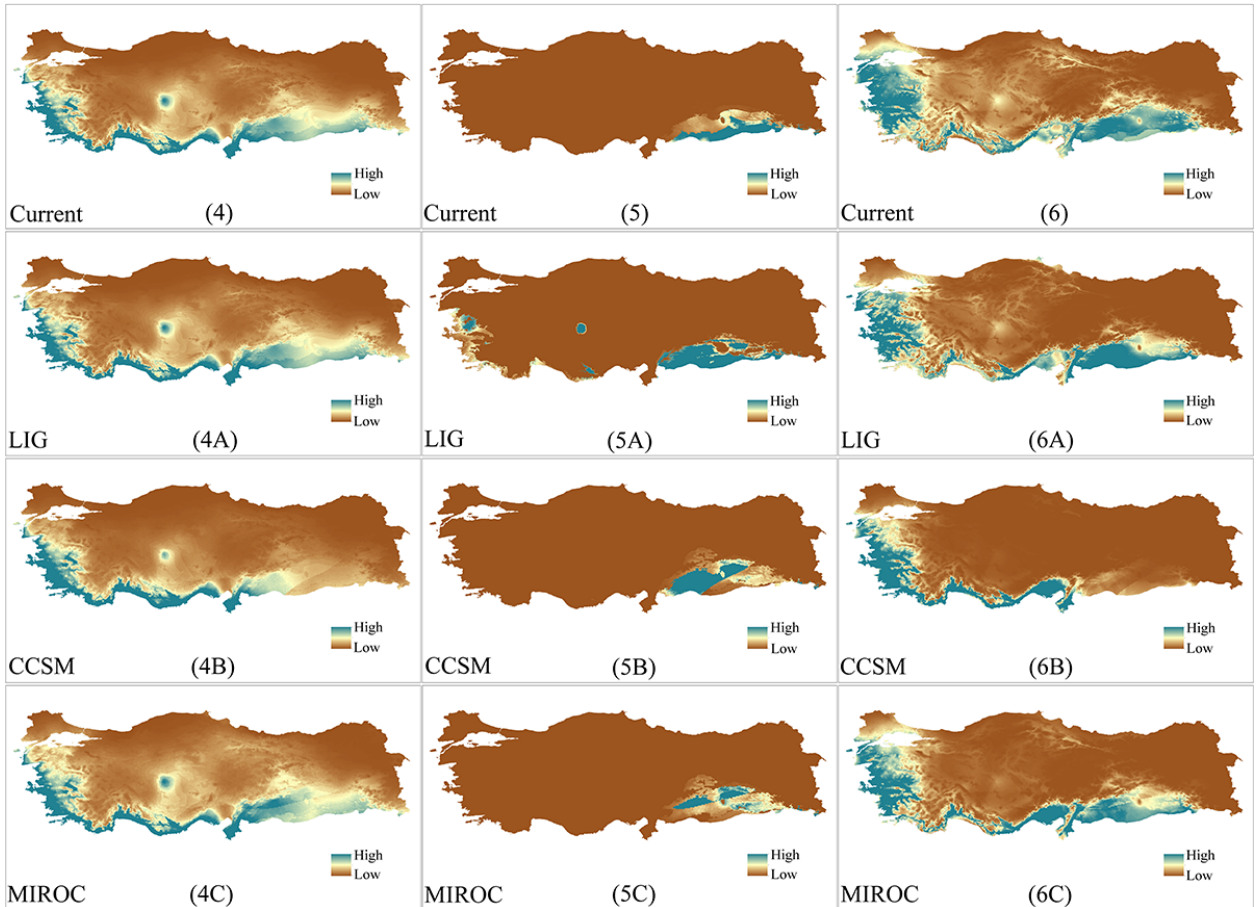
Figure 3. Predicted models of lineages G, H, and I according to Last Interglacial (LIG) and Last Glacial Maximum (LGM; CCSM and MIROC) (4, 4A, 4B, 4C for lineage G; 5, 5A, 5B, 5C for lineage H; 6, 6A, 6B, 6C for lineage I).

southwest Anatolia (lineage B) diverged from the other *T. vermicularis* in the Late Miocene, approximately 6.4 Mya (4.7–8.0 Mya). During this time, there was an increase in summer drought, high evaporation, low rainfall, and lower seasonality. This situation was reported in more arid-adapted fauna in the eastern Mediterranean (Eronen et al., 2009). However, the southwest of Anatolia showed

Table 3. The selected environmental variables for lineages and the variables' relative contributions to the Maxent model.

Lineages	Percent contributions
Lineage B	Bio4 (34.8), Bio15 (11.4), Bio19 (45.9)
Lineage C	Bio1 (64.4), Bio15 (29.8)
Lineage E	Bio4 (47.8), Bio19 (46.2)
Lineage G	Bio15 (86.7)
Lineage H	Bio4 (12.4), Bio5 (49.7), Bio14 (34.4)
Lineage I	Bio1 (18.4), Bio6 (22.6), Bio15 (24.3), Bio19 (17.9)

a higher precipitation rate, indicating wetter conditions during the LGM (Sarıkaya et al., 2008). Our results supported this situation, and both CCSM and MIROC models (Figure 2 (1B and 1C)) indicated a similarity with the current climatic model (Figure 2 (1)). Suitable habitats for lineage B appeared throughout the southwest of Anatolia and toward central Anatolia. Conversely, the LIG model showed suitable habitats along the Mediterranean and Aegean coasts (Figure 2 (1A)).

The first diversification and the split of lineages C and G happened between the Late Miocene and Early Pliocene at approximately 5.6 Mya (4.6–6.5 Mya) and 4.6 Mya (3.3–5.1 Mya), respectively (Kornilios et al., 2012). During this time, the Messinian Salinity Crisis (5.6–5.3 Mya) produced land connections between North Africa and Europe and the drift of Africa toward Europe closed the western end of the Mediterranean (Hewitt, 2011). Our results, based on the current climatic model, were similar to the LGM and LIG models (Figures 2 and 3). These results indicated that both lineages C and G ranged from the coast of the Mediterranean to the coast of the Aegean and to the east

of the Amanos Mountains during the current and glacial periods. The phylogenetic divergence of lineages C and G resulted from vicariance between eastern and western Anatolia (Figure 1). This vicariance likely occurred as a result of the Taurus and Nur Mountains. All models support this vicariance with different climatic preferences for lineages C and G of *T. vermicularis*, because lineage C (Figure 2 (2, 2A, 2B, 2C)) prefers drier habitats than does lineage G (Figure 3 (4, 4A, 4B, 4C)). Similarly, Gül (2013) showed that lineage 1 of *Hyla savignyi* appeared to be confined to warmer and drier habitats in the area east of the Anatolian Diagonal, whereas lineage 2 of *Hyla savignyi* was found in cooler and wetter regions.

Nearly simultaneous phylogenetic splits introducing lineage E occurred during the Late Pliocene or Early Pleistocene at 3.0 Mya (2.4–4.3 Mya) (Kornilios et al., 2012). Populations from western Iran, northeastern Turkey, and Transcaucasia form a monophyletic clade (lineage E). During the Middle Pliocene, i.e. 3.6–2.5 Mya, the climate was hotter and wetter than today (Chandler et al., 1994; Willis et al., 1999; Combourieu-Nebout et al., 2000; Fauquette and Bertini, 2003). This suggests that the range of lineage E is limited by rainy climates, and therefore it inhabits wetter habitats. This case is strongly supported by precipitation during the driest period. In addition, this clearly supports colonization and vicariance occurring in the characteristic structure of the Eastern Anatolian Mountains throughout the Pliocene and Pleistocene (Bilgin, 2011). During both the current time and the LGM, the climatic habitats of lineage E in eastern Anatolia were quite similar to each other (Figure 2 (3, 3B, 3C)). However, this situation did not appear in the interglacial period (Figure 2 (3A)). This may have been due to the effect of the central Anatolian lake system, because mountain chains in Anatolia can be traced back to when the central Anatolian lake system, between the Taurus and the Black Sea Mountains, was also initially formed and persisted cyclically until the end of the Pliocene (Bilgin, 2011).

Lineages H and I split approximately 2.0 Mya (1.4–3.0 Mya) during the Pleistocene (Kornilios et al., 2012). During this time, glacier development within Anatolia was limited to the higher mountain peaks (Atalay, 1996; Ansell et al., 2011). The higher mountain peaks above 2200 m were glaciated (Erinç, 1978; Atalay, 1996). This event provided suitable environmental conditions for local terrestrial species. Moreover, such mountain systems provided moist conditions at higher elevations during the glacial periods (Webb and Bartlein, 1992; Ansell et al., 2011). According to our results, both the LGM and the LIG models, as well as current climatic modeling, indicate similarities in the distributions in Anatolia of lineages H and I (Figure 3). Lineage H appears to be adapting to drier habitats according to the aforementioned results (Figure 3, (5, 5A, 5B, 5C)). The distribution of lineage H may have been limited by the southeastern Taurus Mountains (Figure 1). However, this case does not appear for lineage I because lineage I ranges from the western to the southeastern parts of Anatolia. When viewed generally, lineage I prefers climatically wetter habitats than lineage H.

Consequently, the present study demonstrates the different climatic characteristics of Anatolia as the center for local diversification for *T. vermicularis*. Our paper confirms the importance of climatic variations on the study of how new species originate (speciation) and the study within and among species genetic variation over space and time (phylogeography).

Acknowledgments

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