Unravelling the history of biodiversity in mountain ranges through integrating geology and biogeography

Shan Huang1 | Maud J. M. Meijers1 | Alison Eyres1,2 | Andreas Mulch1,3 | Susanne A. Fritz1,2

1Senckenberg Biodiversity and Climate Research Centre, Frankfurt, Germany
2Institute of Ecology, Evolution and Diversity, Goethe-University Frankfurt, Frankfurt, Germany
3Institute of Geosciences, Goethe-University Frankfurt, Frankfurt, Germany

Correspondence
Shan Huang, Senckenberg Biodiversity and Climate Research Centre, 60325 Frankfurt, Germany.
Email: shan.huang@senckenberg.de

Funding information
Alexander von Humboldt Foundation; German Science Foundation (DFG), Grant/Award Number: HU 2748/1-1 and FR 3246/2-1

Handling Editor: Carina Hoorn

Abstract

Aim: We advocate an interdisciplinary approach to biogeography, integrating geology and paleobiology to examine how biodiversity dynamics evolved as mountain ranges formed through (geological) time.

Location: Global; case study: Anatolia (Turkey).

Methods: We discuss the links between surface uplift and biodiversity dynamics and review recent developments for reconstructing the history of geography and biodiversity. To illustrate an integrative approach to biogeography, we present a case study of Neogene Anatolia. In particular, we reconstruct Anatolian paleogeography based on a synthesis of both quantitative and qualitative evidence, and review the fossil record of the regional flora and fauna, to identify changes in compositions that might be induced by surface uplift and associated environmental changes.

Results: The Central Anatolian Plateau and its mountainous margins display different histories of surface uplift during the late Miocene to Pliocene, which are detectable in the regional fossil record of large mammals. Overall changes in vegetation and climatic conditions for the whole region also align with the general time frame of surface uplift.

Main conclusions: Our discussion and case study highlight the value of an integrative biogeographic framework, by combining knowledge and techniques from geology and paleobiology to simultaneously consider the biotic and environmental dynamics in space and time. Neogene surface uplift in Anatolia has affected the regional biota, particularly the diversity of plants and large mammals, along with well-known global and regional changes in climate and other environmental factors. To disentangle the effects of different, but most likely interactive environmental changes at various scales, we call for rigorous examination of the geological record in a biogeographic framework, using innovative methods to uncover how environmental and biotic processes have shaped mountain biodiversity.

KEYWORDS

Anatolia, biogeographic history, compositional turnover, mountain biodiversity, paleobiology, paleofauna, paleoflora, paleogeography, surface uplift, terrestrial mammals
Mountain ranges are one of the most fascinating systems in biogeography, well-recognized since the celebrated work of Alexander von Humboldt (von Humboldt & Bonpland, 1805, 2010). The disproportionate concentration of present-day biodiversity in mountain ranges (Körner, 2000) has inspired ever-growing interest in understanding the origin and maintenance of biodiversity in relation to mountain building and its associated environmental history. The current biodiversity crisis and projected global changes make it increasingly urgent that we understand the fundamental principles governing biotic responses to environmental changes. In particular, mountainous regions with their large environmental gradients are prime locations to help anticipate future scenarios (Barnosky et al., 2017; Finnegan et al., 2015).

Exciting advances have been made in the past decade in reconstructing surface uplift in mountain ranges (e.g. Rowley & Garzione, 2007; Mulch, 2016; Hoorn, Perrigo, & Antonelli, 2018a), particularly in those that cover a wide range of climate zones such as the Andes (Garzione et al., 2008; Hoorn et al., 2010). However, the response of regional biotas to both gradual and abrupt environmental changes that accompany mountain building remains inherently difficult to grasp. A large body of literature on mountain biodiversity has inferred the role of surface uplift and other environmental factors in driving biodiversity dynamics based on the present-day spatial patterns (the space for time approach, e.g. Kessler, Herzog, Fjeldså, & Bach, 2001; McCain, 2009; Antonelli et al., 2018), thereby not accounting for potential time-lags in different biotic responses such as extinction and niche evolution (e.g. Ivory, Early, Sax, & Russell, 2016; Rowan, Kamilar, Beaudrot, & Reed, 2016; Svenning, Eiserhardt, Normand, Ordonez, & Sandel, 2015). Further disconnect between temporal and spatial patterns of biodiversity arises as the spatial dynamics of biodiversity are not solely constrained by physical environment, but also driven by biotic interactions and dispersal ability (Fortelius et al., 2014; Jablonski, Huang, Roy, & Valentine, 2017; Linder, Lehmann, Archibald, Osborne, & Richardson, 2018). To fully understand how mountain biodiversity has been shaped, we join recent advocates (e.g. Hoorn, Mosbrugger, Mulch, & Antonelli, 2013) of an interdisciplinary approach, synthesizing geology and paleobiology in a biogeographic framework. Furthermore, we emphasize the importance of looking beyond simple measures of biodiversity like taxon counts.

Disentangling the roles of different but interactive processes is the key in understanding the origin and maintenance of mountain biodiversity. The formation of a mountain range can last several to tens of million years, with interaction with atmospheric processes (e.g. rainfall, moisture transport) often characterized by threshold behaviour where once a certain height and width is attained by the mountain range, moisture transport may be re-routed (e.g. Rohrmann et al., 2016; Vera et al., 2006). Mountain building hence may have profound and complex impacts on the regional biota on various time-scales (illustrated in Figure 1). In addition to comparing different environmental factors in predicting the number of extant taxa (e.g. Antonelli et al., 2018), we propose that investigating the temporal relationship between diversity dynamics and environmental changes is crucial for understanding how mountain biodiversity has been shaped at various time-scales (also see discussion in Badgley et al., 2017; Favre et al., 2015; Fortelius et al., 2014). This temporal perspective is thus highly relevant in predicting the biotic responses to future changes.

Furthermore, we discuss methodological challenges that can best be tackled through combining interdisciplinary information and tools. In particular, we highlight the pivotal role of the fossil record for

**FIGURE 1** A hypothetical network for illustrating the complex interactions among a selection of geological (left) and biological (right) processes which might have underlain the evolution of regional biota during the time of surface uplift. The processes are illustrated as nodes, connected by arrows which indicate potential influences (double arrows for reciprocal impacts) broadly based on discussions by Badgley and Finarelli (2013); Hoorn et al. (2010); Hoorn et al. (2013); Mulch (2016); Hoorn, Perrigo, and Antonelli (2018b)
reconstructing historical dynamics (see also Edie, Huang, Collins, Roy, & Jablonski, 2018; Fritz et al., 2013; Hagen, Andermann, Antonelli, Silvestro, & Quental, 2017; Huang, Roy, Valentine, & Jablonski, 2015; Quental & Marshall, 2010; Silvestro, Zsika, et al., 2018) and thus complementing investigations of the present-day biogeography in illuminating mechanisms that underlie the biota-environment relationship. To demonstrate the value and relevance of fossil evidence, we present a case study on paleoflora and paleofauna in relation to Neogene surface uplift in Anatolia (Turkey), where both the fossil record and the surface uplift history of a continental plateau (and its margins) have been intensively studied (e.g. Eronen et al., 2009; Fritz et al., 2016; Huang et al., 2017; Meijers et al., 2018; Schildgen et al., 2012).

2 | UNDERSTANDING BIOTIC RESPONSES TO SURFACE UPLIFT

2.1 | Reconstructing paleotopography

A realistic reconstruction of paleoenvironments is essential for understanding past biodiversity dynamics, and the transformation of topography, such as the rise of plateaus and mountain ranges, is a key component of past environmental change. In recent years, much effort has been dedicated to reconstructing the history of surface uplift based on the combined evidence from quantitative geochemical analyses and qualitative geological observations (e.g. Hoorn et al., 2018a; Rowley & Garzione, 2007).

The most commonly applied technique to quantitatively reconstruct paleoelevation is stable isotope paleoaltimetry (e.g. Mulch, 2016; Rowley & Garzione, 2007). The method is based on the systematic decrease of δ18O (i.e. the ratio between 18O and 16O with respect to a standard) in precipitation as a function of elevation, due to the cooling of rising air masses upon their rise across a mountain range and resulting distillation (Dansgaard, 1964). In many present-day mountain ranges, this systematic decrease averages ~2.8% for each km of elevation gain (Chamberlain & Poag, 2000). As precipitation forms one of the building blocks of authigenic carbonate in the continental rock record, δ18O values of past precipitation can be recovered from carbonates that formed in lakes and soils (Chamberlain & Poag, 2000). However, stable isotope paleoaltimetry requires knowledge on the temperature of carbonate formation (Rowley & Garzione, 2007), which may not only be subject to changes as a result of surface uplift, but also follow regional and global temperature trends. Other factors that influence paleoelevation estimates based on oxygen stable isotopes include: (a) heterogeneity in evaporation of lake or soil water during carbonate precipitation, as evaporation preferentially removes the light isotope 16O (i.e. increasing δ18O) and thus obscures the systematic decrease of δ18O resulting from surface uplift (Poag & Chamberlain, 2001; Quade, Garzione, & Eiler, 2007), (b) the relative abundance of grasslands, which promote seasonal atmospheric vapour recycling (Mix, Winnick, Mulch, & Chamberlain, 2013), and (c) climatic variation that changes the rate of δ18O decrease with elevation (Botsyun et al., 2019; van Hinsbergen & Boschman, 2019; Poulsen & Jeffery, 2011).

Quantitative paleoelevation reconstructions can be tested against geological observations that provide circumstantial evidence for surface uplift. For instance, a switch from marine to continental sedimentation in a large region provides a maximum age for the onset of surface uplift. The presence of large volumes of conglomerates (whose formation requires significant erosional forces) provides evidence for the presence of significant erodible relief, such as the conglomerates within the Siwalik Group to the south of the Himalayas (e.g. Chauvel et al., 2013). Similarly, the spatio-temporal distribution of lake systems may provide insight into lake connectivity, depositional environments and ultimately elevation structure of a region (e.g. DeCelles et al., 2018). Additional evidence for the presence of topographic features may come from the fossil floral and faunal records, as some taxa may only be found at specific elevations (Hoorn et al., 2010).

2.2 | Environmental changes associated with surface uplift

The rise of a mountain range can have a significant impact on climate across continents as a result of altered atmospheric circulation (Barnes, Ehlers, Insel, McQuarrie, & Poulsen, 2012; Ruddiman & Kutzbach, 1989). Surface uplift to a specific threshold elevation can dramatically shift atmospheric circulation patterns and associated teleconnections, which rather rapidly affects moisture transport, precipitation seasonality, and ultimately moisture availability to flora and fauna (e.g. Mulch, 2016; Mulch, Uba, Strecker, Schoenberg, & Chamberlain, 2010; Poulsen, Ehlers, & Insel, 2010; Rohrmann et al., 2016). For instance, models for late Miocene Andean plateau uplift have shown a shift in convective rainfall patterns and dramatic changes in water balance for certain South American regions once a threshold plateau elevation of 2 km was reached (Poulsen et al., 2010). Similarly, the position and elevation of the Andes presently dictates the location of the intertropical convergence zone in the eastern Pacific (Takahashi & Battisti, 2007) and promotes the development of convective storms (Rohrmann et al., 2014). The regional effects of plateau and mountain range formation are even more profound. Within a relatively small area, mountain ranges exhibit different climatic zones along an altitudinal gradient as air masses cool with elevation, providing a complex environmental template for local communities. The presence of a mountain range typically also leads to rainout on the windward side of a mountain range and drier conditions on its leeward side. The resultant contrasting climatic conditions on each side of a mountain range select for different soil and vegetation systems, which directly influence erosion rates and consequently topographic relief. Such changes in the environment can have a strong impact on biogeography, leading to habitat heterogeneity and restructured regional biodiversity (Favre et al., 2015; Mulch, 2016).

Besides geological techniques such as stable isotope geochemistry (Sharp, 2017), the plant fossil record is also useful for reconstructing paleoenvironmental dynamics, particularly changes in climatic conditions, biomes and vegetation structures. Climatic parameters can be quantitatively estimated from plant fossils, either from specific physiognomy like leaf or wood anatomy (e.g. Wiemann, Manchester, Dilcher, Hinojosa, & Wheeler, 1998) or from
the taxonomic composition of leaf and pollen assemblages using the Coexistence Approach, based on the climatic requirements of the nearest living relatives (Mosbrugger & Utescher, 1997). Fossil plant communities can therefore provide a useful tool for estimating local (terrestrial) temperature and precipitation (Utescher et al., 2014).

Furthermore, the presence of vegetation types, as well as the overall vegetation composition (e.g. providing open or closed habitats) form an important component of the paleoenvironment for animals (e.g. as food or nest resources) and thus play important roles in driving animal diversity dynamics (Albrecht et al., 2018; Foronor, Klein, Blüthgen, & Staab, 2019). The presence of different vegetation types can be inferred from the fossil leaf and pollen record, e.g. through Integrated Plant Record vegetation analysis (Kovar-Eder, Jechorek, Kvaček, & Parashiv, 2008). In addition, phytolith analyses can infer closed versus open habitats through proportions of different forest indicators and grass types (Strömborg, 2005). Note that plants are also a central component of biodiversity (discussed below), and regional floras are thus shaped through ecological and evolutionary processes like dispersal and extinction in relation to the abiotic and biotic environment, including the composition of herbivore communities (Figure 1).

2.3 | Biodiversity dynamics during surface uplift

Complexity of environmental conditions has long been hypothesized to be one of the key drivers of biodiversity (Macarthur, 1965; MacArthur, Recher, & Cody, 1966; Ricklefs, 1977). The vast majority of studies on this subject are based on spatial correlation among present-day patterns (e.g. Cramer & Verboom, 2017; Pianka, 1966; Qian & Ricklefs, 2008), limiting the inference of underlying processes which rarely act instantaneously (Preston, 1966; Ricklefs, Latham, & Qian, 1999). Recent developments in reconstructing the geological history of surface uplift (e.g. Hoorn et al., 2018a; Mulch, 2016; Rowley & Garzione, 2007) thus provide exciting opportunities for examining the temporal patterns of biodiversity in relation to the increase in topographic complexity and changes in related environmental factors (Badgley, 2010; Badgley et al., 2017; Baker et al., 2014; Lagomarsino, Condamine, Antonelli, Mulch, & Davis, 2016).

The exceptional biodiversity in mountain ranges is likely generated by topographic barriers that promote speciation to levels far exceeding local extinction, and maintained by the environmental heterogeneity that accommodates lineages with diverse niches (Badgley et al., 2017; Finarelli & Badgley, 2010). At the same time, increasing environmental gradients tend to intensify local extinction (Huang et al., 2015; Jablonski et al., 2017), but the gradual process of surface uplift might have allowed some lineages to adapt and persist through these topographic changes (Sandel et al., 2011; Svenning et al., 2015). In addition to selecting existing taxa, the newly emergent environments might also invite colonization of new species from nearby regions (e.g. Eronen, Janis, Chamberlain, & Mulch, 2015; Janis, 1993). The combined effects of these processes not only resulted in a rich biota holding more taxa, but probably also re-sorted the faunal composition based on ecological properties. Examination of molecular phylogenies of mountainous (and nearby) lineages has begun to distinguish the relative contribution of different processes to shaping the regional biota during surface uplift (e.g. Antonelli, Nylander, Persson, & Sanmartín, 2009; Esquerre, Brennan, Catullo, Torres-Pérez, & Keogh, 2019; Fjeldså, 2018; Lagomarsino et al., 2016; Merckx et al., 2015; Santos et al., 2009). However, because the phylogeny of extant lineages allows very limited inferences about extinct lineages and dispersal events in the past, revealing the full picture of past dynamics requires incorporating fossil evidence (Hagen et al., 2017; Huang et al., 2015; Quental & Marshall, 2010; Silvestro, Zitka, et al., 2018).

The first-order expectation for the fossil record is that the temporal trajectory of mountain biodiversity, e.g. in terms of taxonomic richness, reflects the timing of surface uplift (Badgley, 2010). However, the apparent pattern of taxonomic richness often masks the change in faunal composition, which may be more revealing about underlying processes than variation in taxon count (Huang et al., 2015; Korhonen, Soininen, & Hillebrand, 2010; MacArthur & Wilson, 1963). The change of a fauna through time can be a result of either removal or addition of species without affecting the remainder of the fauna (i.e. nestedness), thus a mere change in the total number of species (S). However, any combination of removal and addition leads to a less apparent change in S but also changes in the faunal composition (e.g. taxon replacement, or turnover). Many β-diversity metrics developed in community ecology (e.g. Koleff, Gaston, & Lennon, 2003) can be adopted for measuring the change (or continuity) in faunal composition through time in the fossil record. For example, Baselga (2010) demonstrated the advantage of using Sørensen’s index ($I_{SS}$) for overall change in the composition, thus including the change in S, in combination with Simpson’s index ($I_{SD}$) for turnover: the difference between the two ($I_{SS} - I_{SD}$) effectively reflects composition nestedness (i.e. faunal change due to the net change in S).

Even more valuable is to know the replacement in forms and functional groups (many only observable in the fossil record), because the appearance and disappearance of species in a region is likely selective with regard to the ecology of the lineages (Alfaro et al., 2009; Alroy, 2010; Cardillo et al., 2008; Huang et al., 2017; Pimiento et al., 2017). Understanding the temporal dynamics of the morphological and functional space in relation to environmental transitions will shed greater light onto the mechanisms that underly the assembly and disassembly of the (regional) biota (Edie, Jablonski, & Valentine, 2018; Eronen et al., 2015; Fortelius et al., 2014; Orzechowski et al., 2015; Strömborg, 2005).

3 | A CASE STUDY: LANDSCAPES AND LIFE IN ANATOLIA (TURKEY)

To demonstrate an integrative approach to biogeography, we present a case study of Anatolia, the region positioned between the Eastern Mediterranean and the Black Sea basins with diverse landscapes and living forms. The present-day Anatolian plateau is bordered by the Pontide Mountains (Mts) to its north and the Tauride Mts to its south (Figure 2a) (GTOP030 elevation dataset from USGS, 1996, downloaded from http://edc.usgs.gov in March 2007). Elevations of the
The average elevation of the plateau region increases from ~1.0–1.5 km in the Central Anatolian Plateau (CAP) to ~2 km in the Eastern Anatolian Plateau (EAP, east of ~38°E). The variations in absolute elevation and relief (Figure 2b) provide a highly heterogeneous environment, the development of which is expected to have promoted species diversification and accumulation. Indeed, Anatolia is a region containing high diversity of plants and animals, including many endemic species (reviewed in Şekerçioğlu et al., 2011), and thus provides an excellent and important system for investigating how the regional fauna has been shaped by environmental changes including surface uplift.

Here, we take the example of terrestrial mammals, which have been a model system in biodiversity research because their present-day distribution as well as their fossil occurrence have been intensively studied (e.g., Fritz et al., 2016; Schipper et al., 2008). Today’s mammalian fauna in Anatolia comprises 145 native species of land mammals (based on range maps from Schipper et al., 2008; downloaded from https://www.iucnredlist.org in July 2018), after excluding marine species and areas where current presence was unlikely (records classified as possibly extant, possibly extinct and extinct). Of these, 29 species are large mammals in the orders Artiodactyla (Cetartiodactyla) and Carnivora, but the fossil record (see below) shows that three other orders of large mammals (Primates, Perissodactyla, and Proboscidea) were once present in this region during the Neogene (though not today).

The present-day distribution of terrestrial mammals in Anatolia reflects the contemporary spatial variation in elevation, supporting a link between topographic complexity and diversification (reviewed in Badgley, 2010; Badgley, Smiley, & Cable, 2018, 2017). The highest species richness (SR, i.e. number of species whose ranges overlap with a grid cell) of mammals is found in mountainous areas (Figure 2c,d). In particular, a simple comparison shows that relief (i.e. range of elevation in a grid cell as a measure of topographic complexity) shows a stronger link with large mammal SR (based on Generalized linear models [GLM] with a Poisson error distribution, \( R^2 = 0.27, \ p < 0.001 \)) than with total SR (\( R^2 = 0.07, \ p < 0.001 \); see bivariate plots in Figure S1; all data were processed and analysed in ArcGIS 10.5 and R 3.4.4 by R Development Core Team, 2018, and \( R^2 \) for GLM was calculated using the rsq package by Zhang, 2018). Even a more comprehensive model accounting for variation in several contemporary climatic and geological factors only explained 50%–70% of the spatial variation of SR in mountain tetrapods across the world (Antonelli et al., 2018). These findings invite further investigation of mountain biodiversity from a different perspective: combining information from paleogeography and paleobiology to identify the role of surface uplift and associated environmental change in shaping biodiversity patterns through time, especially comparing the relatively flat Anatolian plateau interior to its high-relief margins.

3.1 | Windows to the past: The geological record of paleogeography and paleobiology

In this case study, we synthesize recent findings in geology and paleobiology to illustrate the Anatolian history of landscapes and life during the Neogene (~23–2.6 Ma) from three perspectives: paleogeography, paleovegetation and mammalian diversity dynamics.

3.1.1 | Paleogeography

To reconstruct the paleogeography of Anatolia, we reviewed geological evidence of the former physical landscape (references listed

![Image](48x336 to 286x733)

**FIGURE 2** Present-day distribution of (a) elevation and (b) relief (range in elevation) compared to species richness distribution of (c) all mammals and (d) large mammals in Anatolia. The extent large mammals only include the orders Carnivora and Artiodactyla; Perissodactyla, Primates and Proboscidea are no longer present in Anatolia today but persisted throughout the Neogene (Figure S10–11). The elevation map was annotated with major geographic features: CAP and EAP refer to the Central and Eastern Anatolian Plateaus, respectively. All other maps are in an equal area grid with a 25 km resolution as a compromise between the precision of IUCN range map data (see arguments against finer resolutions by Graham & Hijmans, 2006; Hurlbert & Jetz, 2007) and our need for capturing spatial variation in topography with a sufficient sample size. All maps are based on the Eckert IV projection.
in Appendix 1). To produce the paleogeographic sketches, we define five paleoenvironmental categories: (a) marine and restricted basins, (b) fluvio-lacustrine depocenters (i.e. fluvial and lake environments), (c) lowlands (elevations below ca. 500 m), (d) highlands (elevations of ca. 500–1500 m) and (e) alpine regions (elevations exceeding ca. 1500 m). We provide brief summaries of the studies that we consulted in the Supporting information (references also listed in Appendix 1 at the end of the paper). Synthesizing multiple types of evidence, both quantitative and qualitative, is particularly important for our case study of Anatolia, as stable-isotope based paleoaltimetry estimates are currently only available for the CAP interior and its southern margin, the Tauride Mts (Meijers et al., 2018).

### 3.1.2 | Paleovegetation

Vegetation serves as the primary energy source for animals and can thus contribute to connecting changes in the physical environment and the regional fauna. To explore changes in paleovegetation and paleoclimate during the Neogene, we combine a phytolith dataset of 21 sample locations (Strömberg, Werdelin, Friis, & Sarac, 2007) with a paleobotanical dataset of 74 leaf and pollen locations (Akgün, Kayseri, & Akkiraz, 2007; Akkiraz, Akgün, Utescher, Bruch, & Mosbrugger, 2011; Kayseri-Özer, 2013, 2017; Kayseri-Özer, Akgün, Mayda, & Kaya, 2014; Kayseri-Özer, Özberk, & Akgün, 2014; Yavuz-İsink, Sarac, Ünyal, & Brüjin, 2011). We excluded data for the EAP to match the mammalian data extent (see below). Anatolia’s rich paleobotanical record allows the reconstruction of vegetation types and regional climate, particularly during the late early and middle Miocene (~20–12 Ma; e.g. Akgün et al., 2007; Jiménez-Moreno, Altıçek, Altıçek, Hoek Ostende, & Wesselingh, 2015; Kayseri-Özer, 2017; Kayseri-Özer, Akgün, et al., 2014). In most of the paleobotanical studies cited above, climatic parameters were also estimated from leaf and pollen floras using the Coexistence Approach (CA) following the nearest living relative principle (Utescher et al., 2014). Additionally, phytolith assemblages from the fossil record allow quantification of habitat openness and are documented particularly well for the late Miocene (Strömberg et al., 2007).

To reflect the relevant periods of surface uplift while accommodating the variation in spatio-temporal resolution and sampling coverage among sources, we first classified all data into discrete time bins (Figure S2–S5) based on the original studies (Kayseri-Özer, 2017; Strömberg et al., 2007). We then weighted the contribution of each original location to the regional composition by the density of sample locations in an area (Figure S2). Lastly, we follow Fritz et al. (2016) to incorporate the full local climatic range (i.e. accounting for confidence intervals, Utescher et al., 2014) in the regional climatic estimates (Figure S5). We provide additional details about these processes in Supporting information and the combined dataset in Appendix S1.

### 3.1.3 | Mammalian diversity dynamics

To explore the compositional change of fossil faunas through time in Anatolia, we examined an extensive Neogene fossil mammal dataset comprising 868 fossil samples for 247 species in the orders of Artiodactyla and Carnivora, as well as in three more orders that are no longer present in Anatolia today: Perissodactyla, Primates and Proboscidea (Fritz et al., 2016; The NOW Community, 2015; see data distributions in Figure S6–S9). The current record of mammalian fossils are concentrated in west and central Anatolia, so we excluded the EAP in this study. All samples were dated biostatigraphically and resolved to the Mammal Neogene (MN) zones following the time-scale by Hilgen et al. (2012).

For each mammal species, we searched for the first and last appearances (FA and LA) in the Anatolian region as a whole, as well as in the respective plateau interior and margin areas (data provided in Appendix S2). We assumed that the species persisted in the region throughout the time between its FA and LA (the “range-through” approach for reducing sampling effect), thus ignoring the finer scale range dynamics of the species. We then calculated the number of species (S) in each MN zone and species turnover (Jturn) between adjacent MN zones for the same geographic divisions as for FA and LA (see additional details about these indices in Supporting information; Figure S9). We acknowledge that both indices illustrated here are still subject to sampling bias, although we found consistent patterns at the genus levels (Figure S10) and no apparent effect of the time bin duration on the patterns (Table S1). In addition, we applied the method by Foote (2000) to the current fossil dataset and found increases in both origination and extinction rates near the times of increased turnover rates (Figure S11), although we do not have sufficient data to examine the diversification dynamics in the plateau interior and margin areas separately. We suggest that rigorous quantification of the relationship between environmental and faunal dynamics must incorporate robust models of sampling effects that do not sacrifice data abundance (e.g. Silvestro et al., 2016; Starrfelt & Liow, 2016; 2019).

To further connect faunal changes and environmental dynamics in Anatolia, we explored temporal patterns of one key species trait that has been widely accepted as a useful proxy of species ecology: average adult body mass (e.g. see Agnarsson, Kuntner, & May-Collado, 2010; Peters, 1983; Roy, Jablonski, & Valentine, 2001; Smith, Elliott Smith, Lyons, & Payne, 2018). Species body mass has been documented for 186 species (>75% coverage, see Figure S12) in our fossil occurrence dataset, compiled by Huang et al. (2017) as an extension of the NOW database (The NOW Community, 2015). We considered changes in the frequency distributions of body size as an indicator of ecological change in regional faunas (Calder, 1984; Peters, 1983; Smith et al., 2016). For the body size distribution of mammal species present in each MN zone (illustrated in Figure S12 using the package vioplot by Adler & Kelly, 2018), we calculated kurtosis and skewness (using the R package moments by Komsta & Novomestky, 2015), two commonly used parameters to summarize the distribution of trait values among taxa in a local community or a regional assemblage for large-scale comparisons (e.g. Smith et al., 2004; Wieczynski et al., 2019). Kurtosis indicates the evenness of the trait values and skewness reflects symmetry around the median value.

### 3.2 | The history of surface uplift

Anatolia was likely near sea level until the middle Miocene (~16–12 Ma), with occurrences of marine sedimentary rocks as young as ~13 Ma
(Çoriç, Harzhauser, Rögl, İslamoğlu, & Landau, 2012; Hüsing et al., 2009; Ocakoğlu, 2002; Palcu, Tulbure, Bartol, Kouwenhoven, & Krijgsman, 2015; Poisson et al., 2016). However, local relief already existed, such as in south-central Anatolia where thick sequences of middle Miocene continental rocks filled in paleovalleys, indicating locally rugged topography (Figure 3a) (Ocakoğlu, 2002). Mountain forest elements are also abundant in the central Anatolian pollen and spore records from the middle to late Miocene (Akgün et al., 2007; Yavuz-Isik et al., 2011), suggesting higher elevation than western Anatolia (Akgün et al., 2007).

Surface uplift of the Anatolian plateau (interior) started after ~11 Ma based on stable isotope paleoaltimetry (Meijers et al., 2018). In comparison, southern margin uplift postdates ~8–7 Ma, as indicated by the occurrence of marine limestones of that age presently exposed at high elevations in the Tauride Mts (1.5–2 km; Figure 3b; e.g. Cosentino et al., 2012). The southern plateau margin reached similar-to-present elevations (~2 km) by 5 Ma (Figure 3c), based on stable isotope paleoaltimetry data from late Miocene continental sedimentary rocks (Meijers et al., 2018). Nearby high and erodible relief around that time is also evident from up to 2.2 km thick sedimentary deposits in the Mediterranean Basin south of the Tauride Mts (Figure 3c) (e.g. Walsh-Kennedy et al., 2014). The northern plateau margin (Pontide Mts) probably experienced >1 km uplift since the late Miocene or early Pliocene (~8–5 Ma) as suggested by the type of sedimentary rocks exposed and their deformation (i.e. type of faulting) (Yıldırım, Schildgen, Echtler, Melnick, & Strecker, 2011).

Surface uplift can greatly increase heterogeneity in relief, climate, vegetation system and habitat type (e.g. see Schemmel, Mikes, Rojay, & Mulch, 2013; Şekerçioğlu et al., 2011), and thus result in a complex environment as a platform for diversification and range dynamics in the regional fauna (Badgley & Finarelli, 2013; Finarelli & Badgley, 2010). Well-dated sedimentary basins indicate that large areas in Anatolia were occupied by fluvial and lake systems throughout the Miocene (~23–5 Ma; Meijers et al., 2018), allowing preservation of a rich fossil flora and fauna record. Cautious interpretation of the fossil record will provide most informative clues on how Anatolian biota reacted to surface uplift. Here, we take an initial step of examining the Anatolian fossil record by identifying changes in paleovegetation and faunal compositions at times corresponding to the surface uplift of the plateau interior and margins. In particular, we expect earlier changes in vegetation, climate and mammalian diversity in the plateau interior (starting ~11 Ma) than in the margin regions (starting ~8–7 Ma).

3.3 The history of vegetation and climate changes

A warm subtropical and humid climate prevailed over Anatolia during the late Oligocene and early Miocene (~27–16 Ma), with low proportions of open habitats and predominance of mixed mesophytic and broad-leaved evergreen forests in the late early to late middle Miocene (ca. 20–12.6 Ma, Figure 4a-b) (see also Akgün et al., 2007; Kayseri-Özer, 2017). Around 12 Ma (late middle Miocene), the proportions of subtropical evergreen forests slightly increased whereas the warm-temperate to subtropical mixed mesophytic forests decreased (ca. 12.6–11.9 Ma, Figure 4b). Phytolith data from the early and middle Miocene are sparse, but an early increase of open habitats may be observed at ~12 Ma (ca. 12.6–11.2 Ma, Figure 4a).

After the middle Miocene, subhumid sclerophyllous and xeric vegetation components started to dominate Anatolia, in accordance with global and local cooling and aridification trends that intensified at the Miocene-Pliocene transition (~5 Ma; Jiménez-Moreno et al., 2015; Kayseri-Özer, 2017; Kayseri-Özer, Akgün, et al., 2014). Phytolith assemblages show a continuous presence of open habitats in the late Miocene (ca. 11.2–5.3 Ma, Figure 4a). The few paleobotanical sites for the late Miocene (aggregated in the 11.9–2.6 Ma time interval due

---

**FIGURE 3** Paleogeographic sketches of Anatolia with present-day coastlines at (a) ~13 Ma, (b) ~8 Ma and (c) ~5 Ma, based on a synthesis of multiple publications (references listed in Appendix 1). Lowlands: elevations below ca. 500 m, highlands: elevations of ca. 500–1500 m, alpine: elevations exceeding ca. 1,500 m. The areas with predominantly fluviolacustrine sedimentation do not necessarily represent connected lake basins.
to their low number) are in line with a pronounced transition from widespread mesophytic and evergreen forests to subhumid sclerophyllous forests and xeric open wood- and grasslands (Figure 4b), suggesting climatic conditions were changing from warm and wet to colder and drier (Figure 4c; note that despite high local heterogeneity, this is supported by most locations with data from multiple time intervals; also see Denk, Zohner, Grimm, & Renner, 2018).

It remains difficult to link the vegetation and climatic changes directly to surface uplift processes with the temporal resolution of current data, although their timings could conceivably match. As data on local climatic conditions inferred from the paleobotanical record in consecutive time intervals are limited, we could not explicitly test the expectation of different timing in the plateau interior versus margin regions (see Figure S13 and results in Supplementary Information). However, both the paleofloral composition and the inferred climatic conditions show spatial variation in their temporal patterns (Figure 4c and Figure S3–S5). Although current data coverage is insufficient for a finer-scale assessment, a rigorous comparison of vegetation and climate patterns between plateau interior and margins may unravel the impact of surface uplift. Further samples of the paleobotanical record, particularly for the late Miocene and after, will thus be most helpful for identifying links among changes of topography, vegetation, climate and animal diversity.

Overall, the combined effect of the appearance of new habitats (e.g., the drier and more open wood- and grasslands in the late Miocene and Pliocene) and an increased spatial heterogeneity in climatic conditions and habitat type might have selected for animal lineages with different ecological traits. This is expected to result in higher rates of compositional turnover in regional faunas during strong environmental changes.

### 3.4 The history of mammalian diversity

Coinciding with the onset of CAP surface uplift, compositional turnover as quantified by \( J_{sim} \) for the whole Anatolian fauna (Figure 5a) reached its first peak during the mid- to late Miocene (MN07-09; Mammal Neogene zones following Hilgen et al., 2012). High faunal turnover during this time might be due to the transition in vegetation openness and climatic conditions as indicated by the paleobotanical data. The second turnover peak (MN13-15) coincided with the full establishment of the Anatolian plateau and its margins (Figure 2c) (Meijers et al., 2018), as well as with several other events likely to have re-sorted lineages in many regions: the rapid cooling during and after the Miocene-Pliocene transition (Hansen, Sato, Russell, & Kharecha, 2013; Jablonski et al., 2017; Zachos, Pagani, Sloan, Thomas, & Billups, 2001) and possibly the Messinian Salinity Crisis, during which a reduced basin connectivity of the Mediterranean Sea and the Atlantic Ocean led to dramatic environmental changes in surrounding regions (Flecker et al., 2015). In comparison, signals of the topographic change are less obvious in the trend of taxonomic diversity (S), which rose to its peak during the late Miocene (MN11) and declined rapidly during the early Pliocene (MN 14–15; Figure 5a).

Surprisingly, the respective timing of elevated turnover in the faunas occupying the plateau interior and its margins (Figure 5b,c; Figure S9) seems more related to surface uplift in the neighbouring region, suggesting a significant role of geographic range dynamics in biotic responses (see similar patterns of individual orders in Figure S14–S15). When we examined the plateau interior and margin areas separately, the margin areas apparently experienced a turnover peak coinciding with the earlier rise of the plateau interior (MN9), while
uplift in the interior fauna might also be related to the lack of relief emerging of new conditions (as suggested by Badgley & Finarelli, 2013; Finarelli & Badgley, 2010), because the interior S remained relatively high. In comparison, S in the margin areas did not rise up to its peak until the MN11 stage when surface uplift also started here (also see comparisons in Figure S6–S7), but the signal of the initiation of uplift is not obvious in faunal turnover possibly due to limited fossil data from locations within the rising mountain range. A more robust account for fossil occurrences is also required for the reconstruction of the evolutionary history at finer spatiotemporal scales, especially for separating the processes of speciation, extinction and range shift (Silvestro et al., 2016; Valentine, Jablonski, Krug, & Berke, 2013).

To understand the selectivity in faunal turnover, we thus suggest future investigations not only need to expand the current data coverage to allow finer-scale analyses but also include traits that more directly reflect the interactions between animals and their environment, such as the dietary preference and locomotion mechanism.

The temporal patterns of species richness (S) and species turnover (Jsim for adjacent time intervals) in large mammals of Anatolia (a), as well as separately in the plateau interior (b) and margin areas (c). The Mammal Neogene (MN) zones are indicated by grey vertical lines (labels at the top) following Hilgen et al. (2012); MN07 short for MN07-08. Shaded background indicates the onset of surface uplift in the plateau interior and margin areas. See Figure S14–S15 for patterns of individual orders.

Jsim in the interior fauna did not peak until after the marginal mountains started to rise (MN11-12). These patterns suggest that the initial surface uplift (i.e. interior) and associated environmental changes might have driven local species to invade surrounding areas at lower elevations (especially the southwestern margin), and the influx of new species and any environmental changes induced by CAP uplift might have resulted in local extinction of original margin species. Further knowledge of the landscape and faunal history, especially at a finer resolution of both geography and time, will substantially improve our understanding of regional biodiversity dynamics by, for example, pinpointing the formation of geographic barriers that promoted speciation in lineages with dispersal constraints.

The weaker signal of a biotic response (in terms of turnover) to CAP uplift in the interior fauna might also be related to the lack of relief within the interior (similar to today, see Figure 2b) and thus lower climatic and vegetation variation. In contrast, surface uplift should have generated steeper environmental gradients near the edge of the plateau, affecting nearby faunas (i.e. in the margin areas). Meanwhile, new species must have entered the interior fauna, or originated in situ due to emergences of new conditions (as suggested by Badgley & Finarelli, 2013; Finarelli & Badgley, 2010), because the interior S remained relatively high. In comparison, S in the margin areas did not rise up to its peak until the MN11 stage when surface uplift also started here (also see comparisons in Figure S6–S7), but the signal of the initiation of uplift is not obvious in faunal turnover possibly due to limited fossil data from locations within the rising mountain range. A more robust account for fossil occurrences is also required for the reconstruction of the evolutionary history at finer spatiotemporal scales, especially for separating the processes of speciation, extinction and range shift (Silvestro et al., 2016; Valentine, Jablonski, Krug, & Berke, 2013).

The kurtosis of the body size distribution (see Figure S12) increased through time (i.e. an increasingly taller and thinner, thus more clustered body size distribution; MN9-13) except for right after initial surface uplift. In comparison, most species in the fauna initially had smaller bodies than the fauna-wide average (thus a positively skewed distribution), but this skewness disappeared during the time corresponding to the initial uplift of the plateau interior. This can be due to disappearance of relatively small-bodied taxa and/or appearance of larger-bodied taxa which tend to have higher dispersal ability and tolerance for colder and less nutritious environments (Lindstedt & Boyce, 1985; Millar & Hickling, 1990; Peters, 1983; Pyron, 1999). As argued in many studies on body size evolution, it remains unclear whether body size was indeed the trait under selection or simply an effective proxy for key traits that played fundamental roles in lineage persistence through time (e.g. Finarelli, 2007; Jablonski, 2017).

To understand the selectivity in faunal turnover, we thus suggest future investigations not only need to expand the current data coverage to allow finer-scale analyses but also include traits that more directly reflect the interactions between animals and their environment, such as the dietary preference and locomotion mechanism.

3.5 Integrating geological and biological dynamics across scales for Anatolia

We detected a difference between the turnover patterns in the plateau interior and margin areas in the mammalian fossil record, although local vegetation changes were less clear. The pattern of faunal turnover indicates that the effect of surface uplift was non-trivial compared to possible impacts of the concurrent changes in the regional to global environment. Coinciding with the formation of the Anatolian plateau (and its margins) were a series of changes at a variety of geographical scales, including global cooling since the mid-Miocene (Hansen et al., 2013; Zachos et al., 2001), the rise and fall of the Pikermian paleobiome (seasonal sclerophyllous evergreen woodland to grassland, i.e. savanna) in the Old World during the late Miocene (Eronen et al., 2009; Kaya et al., 2018; but see Denk et al., 2018; Fortelius et al., 2019) and an increasing dominance of open grassland habitats in Anatolia (Strömberg et al., 2007). Evaluating the relative contribution of these changes to driving dynamics of
regional biodiversity is thus crucial for understanding the ecology and evolution of our biota.

During the time when initial surface uplift induced a series of environmental changes, we found that large-bodied species might have been favoured at least temporarily because they are more tolerant to harsh environments. This phase of reduced skewness of body size distribution (i.e. MN9-11) also coincided with the hypothesized rise and fall of the Pikermian paleobiome during the middle to late Miocene (Kaya et al., 2018). This paleobiome has been characterized by mammals with high-crowned, wear-tolerant teeth adapted to (partially) open environments, but the openness of the habitat might have varied across space based on the fossil plant record (Denk et al., 2018; Fortelius et al., 2019). The confluences and potential interactions among changes at various spatiotemporal scales thus call for novel analytical tools to distinguish the effects of surface uplift from other environmental transitions on regional biota. For example, further investigation of traits that reflect specific interactions between organisms and different environmental components will be valuable for distinguishing the effects of various factors including temperature, habitat openness and relief. In addition, given the complex system of interactive processes that generated and maintained mountain biodiversity (see Figure 1), a potentially fruitful approach is through innovative simulations of mechanistic models, which take advantage of the explosive computational power today (e.g. see Servedio et al., 2014).

Overall, our finding of coinciding surface uplift, habitat transition and faunal turnover in Anatolia highlights reconstructions of the history, both of the geography and the biota (including plants, animals and any other forms of life), as key for identifying processes that shaped the regional biota. However, such reconstructions are largely hindered by the limited record preserved in the natural system. We propose that a more effective approach to unravelling the biodiversity history will be for the traditionally separate fields, such as geology and paleobiology, to jointly generate comparable datasets that provide a solid base for testing ecological and evolutionary hypotheses.

4 | FINAL REMARKS

Our case study of Anatolia demonstrates a powerful approach to biogeography: integrating knowledge from geology and paleobiology to examine the history of regional biota and identify mechanistic links among geological and biological processes. In particular, we found that geographic range dynamics might be an important response of large mammals facing drastic changes in the physical and biological Anatolian environment. However, range dynamics are often neglected in studies on mountain biodiversity (but see Esquerré et al., 2019; Merckx et al., 2015). This is partly because past changes in geographic ranges of lineages, as well as dynamics of speciation and extinction, are difficult to infer from molecular phylogenies alone (e.g. Hagen et al., 2017; Huang et al., 2015; Rabosky, 2010), but variation in sampling across space, taxa and time also makes interpreting the fossil record a persistent challenge (Ezard, Quental, & Benton, 2016; Valentine, Jablonski, Kidwell, & Roy, 2006; Warnock, Yang, & Donoghue, 2017). Comparing the relative importance of range dynamics and diversification processes in response to environmental changes is critical for identifying the general principles shaping regional to global biogeography. For this, the most effective tool may be an integration of paleontological and present-day data (Fritz et al., 2013; Hopkins, Bapst, Simpson, & Warnock, 2018; Hunt & Slater, 2016; Silvestro, Warnock, Gavryushkina, & Starl, 2018). A particularly promising direction is to reconstruct the phylogeny of both living and fossil lineages, which will then allow us to examine the temporal patterns of phylogenetic diversity as a measure of overall genetic and ecological diversity (e.g. Davis, Fairby, & Svenning, 2018).

Knowledge of past biodiversity dynamics in relation to changes in the abiotic and biotic environment can provide valuable insight for anticipating future changes in our biota, especially after accounting for human impact (Fritz et al., 2016; Rowe & Terry, 2014; Smith et al., 2018). In particular, comparative analyses of how lineages of different lifestyles persisted through changes like habitat transition and climate change can provide a baseline of vulnerability and thus inform conservation strategies (e.g. Collins, Edie, Hunt, Roy, & Jablonski, 2018; Finnegan et al., 2015; Tietje & Rödel, 2018). Furthermore, given the interaction between the terrestrial and marine environments as well as between their biotas, synthesizing across systems will be a particularly fruitful research direction for biodiversity and conservation (e.g. Jaramillo, 2018; Tomášových et al., 2016).

ACKNOWLEDGEMENTS

We thank P. Linder, C. Hoorn and two anonymous reviewers for their constructive comments, and thank the Alexander von Humboldt Foundation (postdoctoral fellowship) and the German Science Foundation (DFG) for supporting S.H. (HU 2748/1-1); DFG for supporting A.E. and S.A.F. (FR 3246/2-1).

DATA AVAILABILITY STATEMENT

In our case study, the paleogeography reconstruction is based on a series of quantitative and qualitative findings, which are briefly summarized in Supporting information (references listed in Appendix 1). The paleobotany dataset reviewed in the case study is provided in Appendix S1 and the fossil mammal dataset in Appendix S2.

ORCID

Shan Huang https://orcid.org/0000-0002-5055-1308
Maud J. M. Meijers https://orcid.org/0000-0003-2724-4980
Alison Eyres https://orcid.org/0000-0001-7866-7559
Andreas Mulch https://orcid.org/0000-0002-9141-7535
Susanne A. Fritz https://orcid.org/0000-0002-4085-636X
Lagomarsino, L. P., Condamine, F. L., Antonelli, A., Mulch, A., & Davis, C. C. (2016). The abiotic and biotic drivers of rapid diversification in Andean bellflowers (Campanulaceae). New Phytologist, 210, 1430–1442. https://doi.org/10.1111/nph.13920

Linder, H. P., Lehmann, C. E. R., Archibald, S., Osborne, C. P., & Richardson, D. M. (2018). Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat transformation. Biological Reviews, 93, 1125–1144. https://doi.org/10.1111/brv.12388

Lindstedt, S. L., & Boyce, M. S. (1985). Seasonality, fasting endurance, and body size in mammals. The American Naturalist, 125, 873–878. https://doi.org/10.1086/284385

MacArthur, R. H. (1965). Patterns of species diversity. Biological Reviews, 40, 510–533. https://doi.org/10.1111/j.1469-185X.1965.tb00815.x

MacArthur, R., Recher, H., & Cody, M. (1966). On the relation between habitat selection and species diversity. The American Naturalist, 100, 319–332. https://doi.org/10.1086/282425

MacArthur, R. H., & Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. Evolution, 17, 373–387. https://doi.org/10.1111/j.1558-5646.1963.tb03295.x

McCaI, C. M. (2009). Global analysis of bird elevational diversity. Global Ecology and Biogeography, 18, 346–360. https://doi.org/10.1111/j.1466-8238.2008.00443.x

Meijers, J. M., Brocard, G. Y., Cosca, M. A., Lüdecke, T., Teyssier, C., Whitney, D. L., & Mulch, A. (2018). Rapid late Miocene surface uplift of the Central Anatolian Plateau margin. Earth and Planetary Science Letters, 497, 29–41. https://doi.org/10.1016/j.epsl.2018.05.040

Merckx, V. S. F. T., Hendriks, K. P., Beentjies, K. K., Menes, C. B., Becking, L. E., Peijnenburg, K. T. C. A., ... Schiltzuizhen, M. (2015). Evolution of endemism on a young tropical mountain. Nature, 524, 347. https://doi.org/10.1038/nature14949

Millar, J. S., & Hickling, G. J. (1990). Fasting endurance and the evolution of mammalian body size. Functional Ecology, 4, 5–12. https://doi.org/10.2307/2389646

Mix, H. T., Winnick, M. J., Mulch, A., & Chamberlain, C. P. (2013). Grassland expansion as an ins truncate of hydrologic change in Neogene western North America. Earth and Planetary Science Letters, 377–378, 73–83. https://doi.org/10.1016/j.epsl.2013.07.032

Mosbrugger, V., & Utescher, T. (1997). The coexistence approach—a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. Palaeogeography, Palaeoclimatology, Palaeoecology, 134, 61–86. https://doi.org/10.1016/S0031-0182(96)00154-X

Mulch, A. (2016). Stable isotope paleoalimetry and the evolution of landscapes and life. Earth and Planetary Science Letters, 433, 180–191. https://doi.org/10.1016/j.epsl.2015.10.034

Mulch, A., Uba, C. E., Strecker, M. R., Schoenberg, R., & Chamberlain, C. P. (2010). Late Miocene climate variability and surface elevation in the central Andes. Earth and Planetary Science Letters, 290, 173–182. https://doi.org/10.1016/j.epsl.2009.12.019

Ocaño-Jul, F. (2002). Palaeoenvironmental analysis of a Miocene basin in the high Taurus Mountains (southern Turkey) and its palaeo-geographical and structural significance. Geological Magazine, 139, 473–487.

Orzechowski, E. A., Lockwood, R., Byrnes, J. E. K., Anderson, S. C., Finnegan, S., Finkel, Z. V., ... Tittensor, D. P. (2015). Marine extinction risk shaped by trait-environment interactions over 500 million years. Global Change Biology, 21, 3595–3607. https://doi.org/10.1111/gcb.12963

Palcu, D. V., Tulbure, M., Bartoi, M., Kouwenhoven, T. J., & Krijgsman, W. (2015). The Badenian-Sarmatian Extinction Event in the Carpathian foredeep basin of Romania: Paleogeographic changes in the Paratethys domain. Global and Planetary Change, 133, 346–358. https://doi.org/10.1016/j.gloplacha.2015.08.014

Peters, R. H. (1983). The ecological implications of body size. Cambridge, UK: Cambridge University Press.

Planka, E. R. (1966). Latitudinal gradients in species diversity: A review of concepts. The American Naturalist, 100, 33. https://doi.org/10.1086/282398

Pimiento, C., Griffin, J. N., Clements, C. F., Silvestro, D., Varella, S., Uhen, M. D., & Jaramillo, C. (2017). The Pliocene marine mega fauna extinction and its impact on functional diversity. Nature Ecology & Evolution, 1, 1100–1106. https://doi.org/10.1038/s41559-017-0223-6

Poage, M. A., & Chamberlain, C. P. (2001). Empirical relationships between elevation and the stable isotope composition of precipitation and surface
Warnock, R. C. M., Yang, Z., & Donoghue, P. C. J. (2017). Testing the molecular clock using mechanistic models of fossil preservation and molecular evolution. Proceedings of the Royal Society B: Biological Sciences, 284. https://doi.org/10.1098/rspb.2017.0227

Wieczynski, D. J., Boyle, B., Buzzard, V., Duran, S. M., Henderson, A. N., Hulshof, C. M., ... Savage, V. M. (2019). Climate shapes and shifts functional biodiversity in forests worldwide. Proceedings of the National Academy of Sciences, 116, 587-592. https://doi.org/10.1073/pnas.1813723116

Wiemann, M. C., Manchester, S. R., Dílcher, D. L., Hinojosa, L. F., & Wheeler, E. A. (1998). Estimation of temperature and precipitation from morphological characters of dicotyledonous leaves. American Journal of Botany, 85, 1796–1802. https://doi.org/10.2307/2446514

Yavuz-İsik, N., Sarac, G., Unay, E., & Bruijn, H. (2011). Palynological analysis of Neogene mammal sites of Turkey-vegetational and climatic implications. Yerbillimleri, 32, 105–120.

Yıldırım, C., Schildgen, T. F., Echtler, H., Melnick, D., & Strecker, M. R. (2011). Late Neogene and active orogenic uplift in the Central Pontides associated with the North Anatolian Fault: Implications for the northern margin of the Central Anatolian Plateau, Turkey, Tectonics, 30, TC5005.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. Science, 292, 686–693. https://doi.org/10.1126/science.1059412

Zhang, D. (2018). rsq: R-Squared and related measures. R package version 1.1. Retrieved from https://CRAN.R-project.org/package=rsq

**BIOSKETCHES**

This paper is a product of discussion and collaboration between biologists and geologists at the Senckenberg Biodiversity and Climate Research Centre (SBiK-F). S.H., A.E. and S.A.F. are biologists interested in macroecology and macroevolution of biodiversity in relation to environmental variations and M.J.M.M. and A.M. are geologists interested in the interactions among surface uplift, biodiversity and changes in paleoclimate.

Author contributions: M.J.M.M., S.H., S.A.F. and A.M. conceived the ideas; M.J.M.M. compiled the paleogeographic reconstructions and S.H., S.A.F. and A.E. conducted data analyses in the case study; all authors contributed to writing the manuscript.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Huang S, Meijers MJM, Eyres A, Mulch A, Fritz SA. Unravelling the history of biodiversity in mountain ranges through integrating geology and biogeography. *J Biogeogr*. 2019;46:1777–1791. https://doi.org/10.1111/jbi.13622