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Mammalian body size evolution was shaped by habitat transitions as an indirect effect of climate change

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Abstract

Aim: Body size evolution has long been hypothesized to have been driven by factors linked to climate change, but the specific mechanisms are difficult to disentangle due to the wide range of functional traits that covary with body size. In this study, we investigated the impact of regional habitat changes as a potential indirect effect of climate change on body size evolution.

Location: Europe and North America.

Time period: The Neogene (~23–2 million years ago).

Major taxa: Five orders of terrestrial mammals: Artiodactyla, Carnivora, Perissodactyla, Proboscidea and Primates.

Methods: We compared the two continental faunas, which have exceptional fossil records of terrestrial mammals and underwent different processes of habitat transition during the Neogene. Using Bayesian multilevel regression models, we assessed the variation in the temporal dynamics of body size diversity among ecographic groups, defined by their continent of occurrence and dietary preference.

Results: Model comparisons unanimously supported a combined effect of diet and continent on all metrics of body size frequency distributions, rejecting the shared energetic advantage of larger bodies in colder climates as a dominant mechanism of body size evolution. Rather, the diet-specific dynamics on each continent pinpointed an indirect effect of climate change – change in habitat availability, and thus the resource landscape as a key driver of mammalian evolution.

Main conclusions: Our study highlights dietary preference as a mechanistic link between mammalian evolution and habitat transition mediating an indirect climate-change effect and demonstrates the complexity of climatic influence on biodiversity. Our findings suggest that the intensified habitat modification today likely poses a bigger threat than climate change in itself to living mammals, and perhaps all endotherms.

KEYWORDS
fossil diversity, habitat change, macroevolution, palaeobiome, regional fauna, trophic niche

1 | INTRODUCTION

Both the present-day biota and its evolutionary history show an incredible diversity of taxon-specific body size (Berke et al., 2013; Heim et al., 2015; Jones et al., 2009; Smith et al., 2016; Wilman et al., 2014), which might suffer reduction under ongoing and impending global changes (Gardner et al., 2011; Jirinec et al., 2021; McCain & King, 2014). For clades of vastly different organisms, larger body sizes tend to be absent during warmer times in the past (Finkel et al., 2005; Huang et al., 2017; Hunt & Roy, 2006). As taxon body size covaries with a variety of physiological and ecological traits (Brown et al., 1993; Downs et al., 2019; Eisenberg, 1981; Huang et al., 2015; Peters, 1983; Sibly & Brown, 2007), the spatial and temporal variation of body size among taxa reflect complex ecological and evolutionary processes of how communities and regional assemblages have been shaped by environmental changes (Brown & Nicoletto, 1991; Heim et al., 2017; Olson et al., 2009; Pigot et al., 2016; Saarinen et al., 2014; Spanbauer et al., 2016). Therefore, identifying the dominant mechanism that links body size evolution to environmental changes can help us better understand the environmental pressures for the global biota and strategize conservation effort. In this study, we compare the evolutionary histories in two continental faunas through 20 million years of climate change to demonstrate that for terrestrial mammals, the direct impact of climatic change was limited but strong indirect effects, mediated through habitat changes, shaped the evolution of body size.

Much of the previous work has been focused on the direct impact of climate, mostly temperature change on body size evolution (Huang et al., 2022; Jirinec et al., 2021; McCain & King, 2014). For endotherms like mammals, larger bodies are expected to have energetic advantage over smaller bodies during colder times, with larger volume-to-surface ratios for efficient heat conservation (Gardner et al., 2011; Peters, 1983). When compared globally, terrestrial mammals generally showed a trend of increasing body size as climate became colder (Alroy, 1998; Raia et al., 2012; Westerhold et al., 2020; Zachos et al., 2008). However, the extent of climate change was never homogenous across space (Dowsett et al., 2013; Hagen et al., 2019) and complexity in its effect on evolution was revealed by regional and clade comparisons (Berke et al., 2013; Gorczynski et al., 2021; Huang et al., 2017; Olson et al., 2009; Rodríguez et al., 2004). If an energetic advantage is the dominant mechanism of selection, lineages on the same continent, experiencing the same regional climates, should display similar evolutionary patterns. The difference in evolutionary patterns between mammalian clades on the same continent (Huang et al., 2017) thus suggested complex environmental effects during the Neogene Period [~23–1.9 million years ago (Ma)].

Global climate during the Neogene showed a general cooling trend (Hansen et al., 2013; Zachos et al., 2001) with spatial variation in the rate of change experienced by regional biotas (Hagen et al., 2019). In the Northern Hemisphere, changes in climatic condition caused large areas of forests to transition into open, drier habitats (e.g., savanna and grasslands) with dry-adapted, tough vegetation (Eronen et al., 2012; Pound et al., 2012; Ulrich et al., 2011). The open habitats appeared in larger extents in North America, increasing the spatial heterogeneity in habitat type (Lintulaakso et al., 2019), while more forests persisted in Europe (Denk et al., 2018; Fortelius et al., 2019; Pound et al., 2012). These changes presumably have differential consequences in animal evolution (Figueirido et al., 2015; Fritz et al., 2016; Jetz et al., 2009). Reconstructions of regional environmental histories at high temporal resolution over large geological time-scales are currently limited, hindering direct evaluations of their effects on body size evolution, but the dominant environmental drivers could be illuminated by comparing taxa of different ecological functions.

In separate investigations, the loss of forests and associated primary productivity in North America has been suggested as an important cause of the decline in North American browsers (Janis et al., 2000), while the diversification of carnivores on the same continent seemed to have been primarily driven by lineage competition (Pires et al., 2017; Silvestro et al., 2015). How these factors and the patterns of taxonomic diversity are linked to the diversity and trends of body size is still unclear and needs to be elucidated from tracking the diversity of body size through time. For example, following climate change and habitat loss, extinction can be induced by strong selection of body size (Huang et al., 2017; Smith et al., 2016), niche contraction (i.e., reduction in size range) and/or niche thinning (i.e., a flattening frequency distribution of body size) due to a decrease in resource availability, while taxa more adaptive to the new environment could be accumulated through expanding the overall niche space and/or partitioning the niche space more finely (Huang et al., 2019; Pigot et al., 2016).

Here, we compare the evolutionary histories of mammals with different dietary preferences, living in different continental regions, to investigate the impact of habitat changes as a potential indirect effect of climate change on body size evolution. Dietary preference is an important ecological trait, reflecting the resource requirements of animals from their biotic environment (Fortelius et al., 2006; Janis, 1993, 2008; Jernvall et al., 1996) and highly relevant to the evolution of body size (Cooke et al., 2022; Esmaeili et al., 2021; Huang et al., 2021; McNab, 2010; Price & Hopkins, 2015; Smith et al., 2010). The different dietary groups should display similar trends in their body size variation if evolution was primarily driven by a direct climatic effect experienced by all taxa on the same continent. If an indirect effect of climate change through transition of vegetation systems (i.e., biomes, as habitats to animals) was the dominant driver of body size evolution, we expect such changes to affect herbivorous mammals more directly than they affect carnivores, leading to different temporal trends in body size variation among trophic levels. Smaller-bodied mammals in the new habitats generally suffered from lower fasting endurance (Lindstedt & Boyce, 1985; Millar & Hickling, 1990) while also losing their advantage in manoeuvrability (Bro-Jørgensen, 2008). However, small-bodied herbivores also have a digestive disadvantage (Clauss et al., 2003) while the body size of carnivores might be relevant to their prey sizes and hunting strategies (Donadio &

Buskirk, 2006; Gittleman, 1985). In addition, the North American faunas should have experienced larger changes during this period (Huang et al., 2017; Janis, 1993, 2008), and more importantly, shown differential selection pressures for mammals that primarily feed on dicotyledonous plants such as leaves and shoots of trees and shrubs (browsers) versus on grass (grazers) (reviewed in Huang et al., 2022).

2 | MATERIALS AND METHODS

2.1 | Mammal fossil data

We used the New and Old World (NOW) mammal fossil database (The NOW Community, 2022) to compare evolutionary patterns of body size among dietary groups during the Neogene (data downloaded on 3 February 2022; an earlier version was also described in Huang et al., 2022 and other chapters in the book). We extracted 19,286 fossil occurrences of large land mammals in five extant orders: Artiodactyla, Carnivora, Perissodactyla, Primates and Proboscidea in Europe and North America, two continental faunas that can serve as two natural experiments of macroevolution (Fritz et al., 2016; Huang et al., 2017).

We used genus as our analytical unit, which is generally robust to taxonomic revision (as commonly demonstrated in macroevolutionary studies using the fossil record, e.g., Fritz et al., 2016). We only included records that have been taxonomically resolved to the genus level or below in the NOW database (actively curated by the NOW Community). The geological age (reported in Ma) of each record was based on the continental biostratigraphical zones for each continent: the Mammal Neogene (MN) units for European occurrences (Steininger, 1999), and the North American Land Mammal Ages (NALMAs) for the North American occurrences (Woodburne, 2004). We assumed that a genus persisted on the continent between its first and last appearances in the database (a 'range-through' approach to reduce potential effect of sampling variation). The large majority of the fossil occurrences extracted from the NOW database were dated to the Neogene (n = 15,685, Supporting Information Figure S1). The remaining records extended the duration of genera to reduce the edge-effect due to incomplete sampling of genus diversity near the beginning and the end of the Neogene. We only included genera that were inferred to have lived during the Neogene in our further analyses. The resulting dataset includes a total of 488 genera living in Europe and 352 in North America. The median genus duration was 4.5 million years (Myr) in Europe and 6.4 Myr in North America (illustrated in Supporting Information Figures S2 and S3).

The body size data in the NOW database currently cover 482 of the 721 Neogene genera (~67%) based on the literature and inferences from measurements of museum specimens (see data coverage of different faunas in Supporting Information Figure S4). When size data were available for more than one species of the same genus, we considered the largest size as the genus body size under the assumption that the larger-sized fossils tend to be discovered and studied before smaller ones. In general, smaller-bodied animals are more likely to be underrepresented in older, less complete and more under-sampled fossil compilations (Behrensmeyer & Chapman, 1993; Carrillo et al., 2015; Plotnick et al., 2016), and so the previous finding of an increase in body size using the same database indicated robustness of this particular fossil record (Huang et al., 2017) (see the temporal distribution of body size in Supporting Information Figures S2 and S3).

We compared body size diversity among four major dietary groups on each of the two continents, as eight ecographic groups, which were sampled across the continents and time bins (Supporting Information Figures S2–S12). This comparative framework allows us to test whether body size diversity among the different dietary groups on the same continent displays similar trends as expected from a direct climatic effect, or different trends under the influence of palaeobiome transitions. Each genus was categorized in the NOW database as carnivores (genera primarily eating animals), omnivores (eating similar proportions of animal and plant materials), and two types of herbivores (primarily eating plants): grazers (herbivores at least partially eating grass) and browsers (herbivores exclusively eating leaves), following Huang et al. (2022). We expect genera that can at least partially rely on grass for nutrition to have a better chance of persistence in open, grass-dominated habitats than strict browsers.

2.2 | Statistical analyses

To assess the indirect impact of climate change through habitat changes on mammalian evolution, we compared the temporal dynamics of body size variation and taxonomic richness among ecographic groups.

For each ecographic group in each (continental) time bin, we summarized the frequency distribution of genus body size based on eight metrics: the minimum, median, maximum, range, and the four moments – mean, variance, skewness (asymmetry) and kurtosis (weight of the tails capturing outliers) – to quantify the shape of the distribution. We compared four linear models of each summary metric (as the response variable, y):

- Model 1: $y \sim t + (1 \mid diet) + (1 \mid continent)$
- Model 2: $y \sim t + (t \mid diet) + (t \mid continent)$
- Model 3: $y \sim t + (1 \mid diet:continent)$
- Model 4: $y \sim t + (t \mid diet:continent)$

where t is the age of the mid-point in each time bin as an overall temporal effect (i.e., the 'population-level effect' in a multilevel modelling framework) to identify any general trend through time, diet is the dietary category, and continent is the continent identity (see below). We acknowledge that the evolutionary trajectory of body size was unlikely to be linear throughout an extensive period at the geological time-scale, but linear models represent simplifications that are useful for comparing the first-order patterns among ecographic groups and avoiding overfitting. We then included the continent and diet type as

group-level effects to compare their influences on the evolution of body size.

In all models, we quantified the variation in the response variable due to continental and dietary effects (i.e., the group-level effects on the intercepts). Additionally, in Models 2 & 4, we quantified differences in how the response variable changed through time (i.e., the group-level effects on the slopes) to assess how climate and habitat changes affected the evolution of body size. If regional climate was the dominant driver of body size evolution, the slope of body size should only vary between continents but not among dietary groups. Therefore, we assessed two models that included the continent and diet as two separate (group-level) effects on the intercepts (Model 1) or on both the intercepts and the slopes (Model 2), and two models with the combined effects of continent and diet type (i.e., as a joint group-level effect) on the intercepts (Model 3) or on both the intercepts and the slopes (Model 4).

To further investigate the impact of habitat changes on the different ecographic groups, we also compared their temporal patterns of genus richness. We calculated total genus richness and its standard deviation for each ecographic group in each time bin using the Chao 2 estimator, which is based on observed richness and samples of rarely observed (low-incident) species (Chao, 1984, 1987). We then used the same modelling framework as above to compare the temporal trends of taxonomic diversity among ecographic groups. In addition, we evaluated the associations between body size patterns and genus diversity (Chao 2 estimate, S) in a separate model, including the combined ecographic effect: $y \sim S + (S \mid \text{diet:continent})$. We also calculated sampling rates based on the ratio of observed to estimated genus richness in each time bin for each ecographic group to identify systematic bias in sampling coverage.

We repeated our analyses of the best model on patterns starting from the middle Miocene, because the global climatic condition was relatively stable during the early Miocene, whereas global cooling trends started in the middle Miocene (Hansen et al., 2013; Zachos et al., 2001). Although the detected trends are often weaker with smaller sample sizes, large variation remained among ecographic groups and the main patterns are qualitatively consistent with those from the full dataset (Figure 1 in comparison with Supporting Information Figure S13). Therefore, we focus on discussing the variation of Neogene patterns.

We fit all the models in a Bayesian framework and compared them based on leave-one-out (loo) cross validations and the expected log pointwise predictive density (ELPD). Each model was run for five chains of 15,000 iterations, discarding the first 5,000 iterations as burn-ins and sampling every 10th interval to produce 5,000 posterior samples. We processed the data and conducted all analyses in R 4.1.2 (R Development Core Team, 2021), with the packages 'brms' (Bürkner, 2017, 2018) for Bayesian multilevel regression analyses with the default priors, 'fossil' (Vavrek, 2011) for applying diversity estimators, 'moments' (Komsta & Novomestky, 2022) for calculating moments of frequency distributions and 'tidyr' (Wickham et al., 2019), 'tidybayes' (Kay, 2021), 'RColorBrewer'

(Neuwirth, 2014), 'cowplot' (Wilke, 2020) and 'egg' (Auguie, 2019) for data visualization and transformation.

3 | RESULTS

For Neogene large mammals, the temporal trends in all summary metrics of their body size diversity were best explained by Model 4, which quantified the combined effect of continent and diet type (ΔELPD >> 2, see model comparisons in Supporting Information Table S1). The ecographic groups showed significant variation in their evolutionary patterns, including opposite directions of change for some metrics (Figure 1; see temporal ranges of all genera and their body sizes in Supporting Information Figures S2 and S3). In particular, the carnivores and omnivores differed from the herbivores on the same continent in many aspects of their size distributions. Therefore, when all taxa were considered together, we could not detect a general trend in most aspects of the body size distributions (the temporal effects in all models, except for the median body size in Model 4; Supporting Information Tables S2–S4).

Several ecographic groups of terrestrial mammals showed increasing trends in mean or median body size towards Recent. Specifically, the European carnivores and the North American browsers and grazers showed increases in both their mean and minimum body size (Figure 2; see median and maximum body size in Supporting Information Figure S14), indicating selection against smaller bodies during the Neogene. In contrast, the European browsers, and the grazers to a lesser extent (inner 95% quantiles: [−0.0001, 0.05]), only showed increases in mean body size but did not change their minimum or maximum sizes. The North American omnivores were the only group showing a decrease in mean body size, but this is unlikely an artifact from sampling bias because their minimum body size did not decrease significantly towards Recent. Their decreasing maximum body size also suggests selection against larger bodies in this group. Moreover, the trends in minimum body size in all other ecographic groups were relatively flat (but not maintained by any single long-lived genus along the entire period investigated, see Supporting Information Figures S2 and S3) and the sampling rates based on Chao 2 estimates did not show bias towards recent times (Supporting Information Figure S15), both suggesting robustness in our results against sampling variation.

In addition to the ecographic difference in body size trends, the shapes of size frequency distributions also changed in various ways during the Neogene (Figure 1). Between the two groups with increasing body sizes in North America, the grazers maintained a relatively stable distribution of body size through time, while the browsers showed reduction in their size range but increased size variance, thus flattening their size distribution (Supporting Information Figure S16; also indicated by the decreasing kurtosis in Supporting Information Figure S17). In comparison, the European browsers maintained a relatively stable distribution like the North American grazers, while the size distribution of European grazers became increasingly centralized through time,
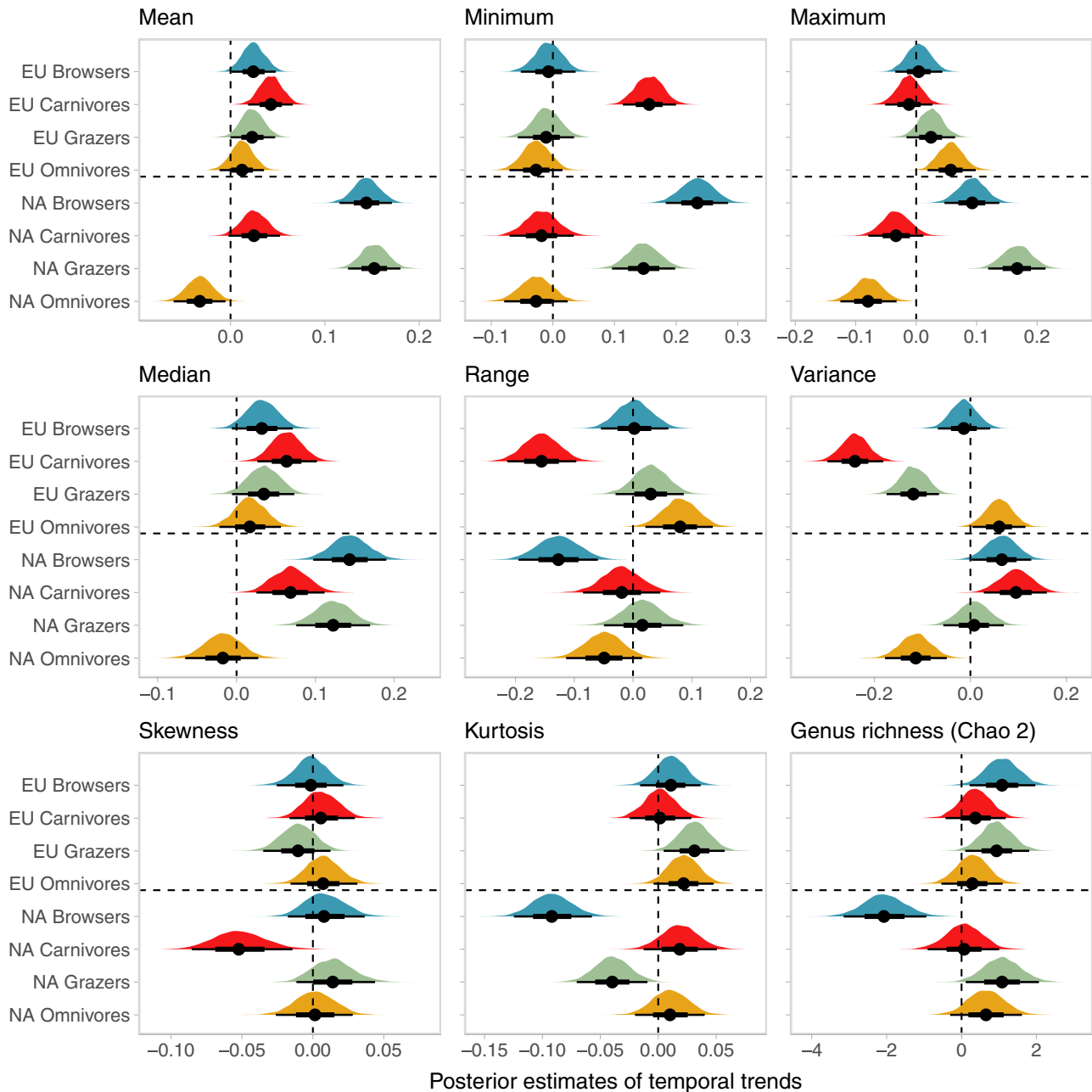
FIGURE 1 The temporal trends of all summary metrics for Neogene mammal body size and genus richness varied across ecographic groups, indicating combined effects of the continental environment and dietary preference on mammalian evolution (EU = European; NA = North American). The posterior estimates of temporal trends (x axis) were based on Model 4 (see model setup in Supporting Information Table S1), with positive estimates indicating increases through time (note that an increase in skewness indicates a shift of the peak towards smaller body sizes, such as in European carnivores). The shapes coloured by different dietary preferences (see y axis labels) represent density distributions of the posterior estimates, which are also summarized by the black points for the median, thick bars for the inner 67% quantiles and thin lines for the inner 95% quantiles

with a decreasing variance and increasing kurtosis. In contrast to the herbivores, the European carnivores showed a reduction in body size diversity (both in the range and the variance) but maintained the shape (skewness and kurtosis) of their size distribution around a higher mean.

Similarly, the temporal trends of taxonomic diversity, measured in estimated genus richness, as well as their associations with body size patterns, also varied among the ecographic groups, further suggesting a strong impact of habitat change on Neogene mammals (Figure 1, Supporting Information Figures S18 and S19). The estimated genus richness in several groups (e.g., carnivores on both continents) peaked close to the middle of the Neogene (Figure 3), which diminished the slope that could be estimated in a linear model (used here as a simplification of the temporal patterns to detect their first-order variation). Yet, our model was able to identify the dramatic taxonomic loss in North American browsers, and the increasing
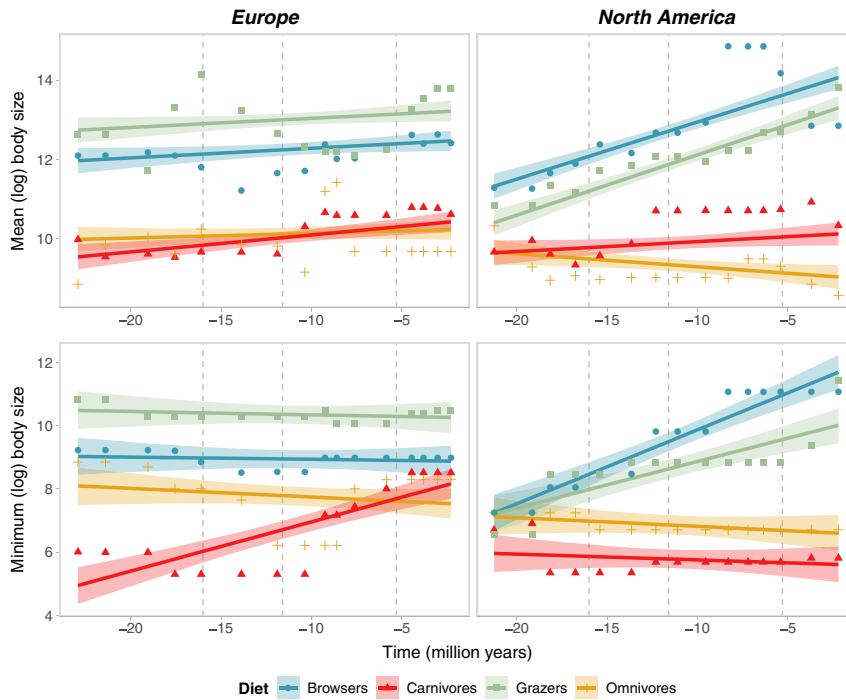
FIGURE 2 The temporal trend of body size (with natural logarithm transformation) varied among ecographic groups based on Model 4 (see model setup in Supporting Information Table S1). The shaded areas represent the 95% posterior estimates of the trends and the dashed vertical lines indicate the ends of the early, middle and late Miocene following Hilgen et al. (2012). The increasing mean body sizes in North American herbivores (upper right) were echoed by similar trends in minimum body sizes (lower right) to indicate active evolution (see median and maximum body size in Supporting Information Figure S14)
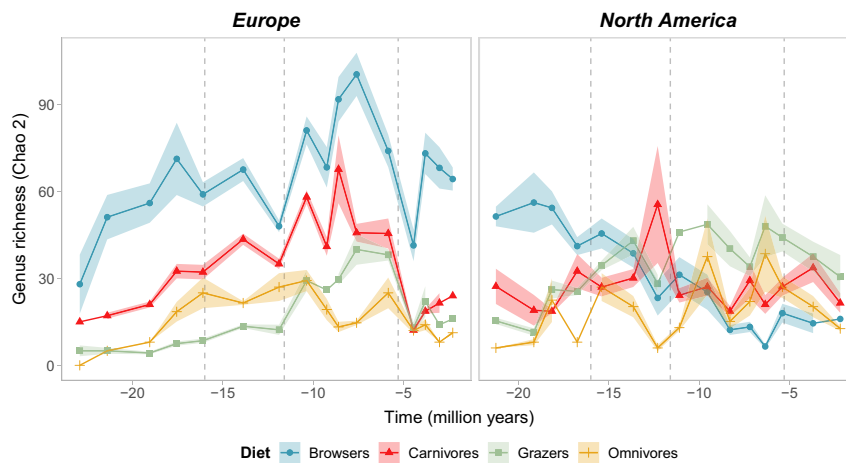

FIGURE 3 Estimated genus richness in the eight ecographic groups of Neogene mammals based on the Chao 2 estimator (Chao, 1984, 1987), with the standard deviation represented by the shaded areas. The dashed vertical lines indicate the ends of the early, middle and late Miocene following Hilgen et al. (2012). Variation of their temporal trends (Figure 1) indicates a combined effect of continental environment and dietary preference. The sampling rates (the ratio of raw to estimated genus richness) are shown in Supporting Information Figure S15

genus richness in the other three groups of herbivores (i.e., North American grazers, European browsers and European grazers).

4 | DISCUSSION

Our findings of most ecographic groups showing slight to large increases in mean and median body sizes are consistent with previous reports (Alroy, 1998; Huang et al., 2017; Raia et al., 2012; Smith et al., 2016). However, in all the other aspects of body size distributions, we found large variation in their temporal dynamics, including opposite directions of change on the same continent, which indicate

a strong influence of habitat change on mammalian body size evolution during the Neogene. The often-discussed direct effect of climate change would be unlikely to differentiate mammalian taxa with different dietary preferences. As an indirect effect of climate change, the large-scale habitat changes in the Northern Hemisphere (Pound et al., 2012; also see Supporting Information Figure S20) altered the resource landscape for animals. The change in vegetation systems was probably experienced by the herbivores more directly through their diet than by the carnivores. This was supported by our finding that the evolutionary patterns of carnivores and herbivores on the same continent differed in many ways. Further, the North American herbivores showed more dramatic changes in their body

size distributions than the European herbivores, likely in response to the more substantial habitat changes in North America than in Europe (Denk et al., 2018; Fortelius et al., 2019; Pound et al., 2012).

The transition into more open, drier habitats in North America affected the two groups of herbivores (grazers and browsers) heavily, reflected in their evolution towards larger bodies. Larger bodies can provide fasting endurance (Lindstedt & Boyce, 1985; Millar & Hickling, 1990) and digestive advantage (Clauss et al., 2003) in the new environment with less nutritious plant materials but more space for manoeuvrability [an advantage of small bodies in forests (Bro-Jørgensen, 2008)]. In addition, we found significant taxon loss in browsers (also in Janis et al., 2000), reduction in their range of body size, and flattening of their size distribution (see also Supporting Information Figure S19). As taxa with different body sizes likely occupied different positions in the general niche space of browsers (Huang et al., 2019; Pigot et al., 2016), our results suggest both a contracting niche space and a thinning process of niche partition, possibly due to increasing competition among taxa in their shrinking habitats. The increase in the number of North American grazer genera in the increasingly open habitats did not fully compensate the loss of browser diversity (see Supporting Information Figure S21), probably as a result of the reduction in primary productivity during the middle to late Miocene (Fritz et al., 2016; Janis et al., 2000) even with increasing habitat heterogeneity across space – an often-suggested promoter of biodiversity (Stein et al., 2014). However, the regional fauna also failed to recover (except for carnivores, see Figure 3) despite the Pliocene peak of net primary productivity (Fritz et al., 2016), suggesting that the effects of environmental changes on the regional fauna might last long beyond the time frame of the changes. To further disentangle the diversity dynamics, region-specific climatic dynamics should also be considered, especially directly compared with habitat changes as detailed palaeoenvironment reconstructions (e.g., Edwards et al., 2010; Hagen et al., 2019; Huang et al., 2019; Strömberg et al., 2007) become available at matching spatial and temporal scales.

The strong effects of habitat availability on mammalian faunas are also reflected in the striking similarity between the European browsers and North American grazers. Both groups gained more genera and yet, displayed stable distribution of body size diversity through time, likely owing to their prefered habitats being (or becoming) dominant in their respective continents. Therefore, their size distribution might reflect an optimal partition of ecological niche space without a strong restriction of resources. A key difference was that only the North American grazers shifted their entire size distribution and evolved to have larger bodies as their regional habitats changed. Open habitats such as savannas also occurred on the European continent during the Miocene (Fortelius et al., 2019; Kaya et al., 2018) but large areas continued to be dominated by forests (see also Pound et al., 2012) offering a relatively stable, widespread environment for the browsers. Such (relative) stability in the European environment through time and across space allowed not only the browsers, but also the grazers to increase in genus-level diversity, at least until the migration of African taxa became impossible after

the Messinian Salinity Crisis (~6 Ma; Krijgsman et al., 1999; Meijers et al., 2018), despite a continuous, albeit slow, reduction in net primary productivity during the Neogene (Fritz et al., 2016). Possibly owing to the mildness in environmental changes, the relatively small-scaled open habitats in Europe also provided resources for the grazers to accumulate near the centre of their niche space without elevating competition. More generally, today's European mammals of different ecological functions are well mixed across space to compose one continental faunal cluster while the North American fauna shows several smaller regional clusters – a contrast also tracible in the fossil record (Lintulaakso et al., 2019), suggesting long-lasting influence from a history of stable environment.

The lack of apparent selection against smaller bodies in European herbivores (even after the onset of global cooling during the middle Miocene, see Supporting Information Figure S13) is in contrast to the higher origination rates for larger-bodied European artiodactyl species (order: Artiodactyla) found in a clade-level analysis (Huang et al., 2017) and the overall size increases at larger taxonomic scales (Alroy, 1998; Smith et al., 2016). The Neogene artiodactyls included both herbivorous and omnivorous (e.g., in the family Suidae) taxa, which showed different dynamics both in taxon richness and body size evolution (Huang et al., 2017, 2022; Raia et al., 2012). Yet, from a functional (trophic) perspective, later-emerging genera in European grazers were mostly of intermediate sizes, leading to an increasingly centralized body size distribution, while the omnivores expanded their size range following a bounded diffusion process (see Gould, 1988; McShea, 1994, 2000). These results, in combination with the stable shapes of size distributions in European browsers and North American grazers, reflect a large degree of stability in their respective niche space under Neogene climate change (see also Lintulaakso et al., 2019). However, changes in the environments affected lineage survivorship (Eronen et al., 2015; Fritz et al., 2016; Janis et al., 2000) and positioned emerging taxa to continuously fill the niche space. The different patterns from previous lineage comparisons versus our assemblage comparison might reflect independent evolutionary dynamics at different taxonomic scales (Jablonski, 2007; McGill, 2010), but within-genus size variation alone cannot explain our findings, as the minimum size of neither European browsers nor grazers was maintained by one long-lived genus (Supporting Information Figure S2), and the order of origination within a genus has been found unrelated to ungulate body size (Huang et al., 2017). The disconnect between lineage replacement and ecological niche dynamics highlights the challenge as well as the importance in reconciling the clade-level versus guild-level perspectives on biodiversity dynamics to reach a deep understanding of ecology and evolution (Blanco et al., 2021; Edie et al., 2018; Griffith et al., 2020).

The increase in carnivore body sizes also invites further investigations on the evolutionary mechanisms. For the North American carnivores (with an increasing median), we did not find selection for larger sizes, in contrast to such selection for larger sizes in the herbivores (also in Huang et al., 2017), and an expected link between prey and predator mass (Cuyper et al., 2019; Tucker et al., 2016). Previous

findings also rejected a link between body size and diversification dynamics in the order Carnivora (not exclusively with a carnivorous diet; Pires et al., 2017; Silvestro et al., 2015). Meanwhile, the European carnivores experienced large contraction of their niche space, especially around the time of the Vallesian Crisis (~9.8 Ma; Agustí et al., 2013; Morales et al., 2015; see Supporting Information Figure S16), despite the increases in herbivore diversity (Supporting Information Figure S21) within stable size ranges. Many of the carnivores presumably preyed on small mammals not included in our dataset or on animals other than mammals, and it is unclear to what extent body sizes covary between trophic levels (see discussions on extant carnivores in Gittleman, 1985; Tucker & Rogers, 2014). As more comprehensive data of fossil communities become available, reconstructions of their food webs might provide valuable insights on how environmental impacts cascade through trophic links (e.g., Dunne et al., 2014; Roopnarine et al., 2007) and why direct comparisons found mixed signals of climatic influences in carnivore evolution (e.g., Morales et al., 2015; Pires et al., 2017; Silvestro et al., 2015). Because hunting can involve complex strategies and interactions in mammalian carnivores, the evolution of locomotor abilities and social structures (both in the predators and the prey) might also be important factors to consider (Bailey et al., 2013; Donadio & Buskirk, 2006; Figueirido et al., 2015; Hirt et al., 2020) under environmental changes.

5 | SUMMARY

Collectively, our results show that climate change has more complex and stronger impacts than just its direct effect on biodiversity. Mammalian body size evolution was strongly influenced by transitions of habitats and associated resource landscapes as an indirect effect of climate change. The large variation in evolutionary trajectories among ecographic groups also demonstrates that terrestrial mammals experience environmental changes largely through their diet and are thus highly sensitive to change in the biotic environment. At present, modification of the world's habitats is intensified by the combined effects of climate change and human activities (Felipe-Lucia et al., 2020; Magioli et al., 2019; Peters et al., 2019). As more comprehensive data on the characteristics of fossil communities and palaeoenvironments become available, further investigations on the mechanisms driving assembly of regional faunas will offer invaluable insights on the future of the living biota (Barnosky et al., 2017; David & John, 1996; Janis, 1993). In particular, our findings highlight the importance of an ecographic perspective, integrating taxonomic diversity with trait evolution and functional ecology in biodiversity research. Given the wide range of covariates with taxon body size (Brown et al., 1993; Downs et al., 2019; Huang et al., 2015; Peters, 1983; Sibly & Brown, 2007), considerations of additional ecological properties (e.g., social structure and population density, Saarinen et al., 2016, 2021), as well as their interactions and trade-offs, should also be fruitful directions to further illuminate the mechanisms of body size evolution (Janis et al., 2020; Sibly & Brown, 2007; Smith & Lyons, 2011) and faunal turnover through environmental changes (Figueirido et al., 2019; Polly, 2020; Weiher et al., 2011).

CONFLICT OF INTEREST

The authors have declared no conflicts of interest for this article.

DATA AVAILABILITY STATEMENT

All fossil data are available on the NOW database (https://nowdatabase.org). The summary datasets of body size diversity and genus richness in ecographic groups by time bin, the R scripts for filtering the data and analysing the Bayesian linear models and the posterior samples from all the models are archived at https://doi.org/10.6084/m9.figshare.21119359.v1.

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BIOSKETCH

The authors collaborate on studying the evolution of land mammals in relation to environmental changes at geological timescales and are broadly interested in macroevolution, macroecology, biogeography, palaeobiology and paleoenvironment.

SUPPORTING INFORMATION

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