



# Geographically divergent evolutionary and ecological legacies shape mammal biodiversity in the global tropics and subtropics

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**Studies of the factors governing global patterns of biodiversity are key to predicting community responses to ongoing and future abiotic and biotic changes. Although most research has focused on present-day climate, a growing body of evidence indicates that modern ecological communities may be significantly shaped by paleoclimatic change and past anthropogenic factors. However, the generality of this pattern is unknown, as global analyses are lacking. Here we quantify the phylogenetic and functional trait structure of 515 tropical and subtropical large mammal communities and predict their structure from past and present climatic and anthropogenic factors. We find that the effects of Quaternary paleoclimatic change are strongest in the Afrotropics, with communities in the Indomalayan realm showing mixed effects of modern climate and paleoclimate. Malagasy communities are poorly predicted by any single factor, likely due to the atypical history of the island compared with continental regions. Neotropical communities are mainly codetermined by modern climate and prehistoric and historical human impacts. Overall, our results indicate that the factors governing tropical and subtropical mammalian biodiversity are complex, with the importance of past and present factors varying based on the divergent histories of the world's biogeographic realms and their native biotas. Consideration of the evolutionary and ecological legacies of both the recent and ancient past are key to understanding the forces shaping global patterns of present-day biodiversity and its response to ongoing and future abiotic and biotic changes in the 21st century.**

biogeography | functional ecology | human impacts | paleoclimate legacies | phylogenetic diversity

A central goal of community ecology and biogeography is to understand the relative importance of different factors governing patterns of biodiversity (1, 2). Research on this topic has both theoretical and applied importance. For example, understanding how abiotic vs. biotic drivers (e.g., climate vs. competition) shape diversity sheds light on the processes of community assembly and disassembly (3), as well as on the temporal dynamics and plasticity of species geographic ranges and their ecological niches (4). Such studies, in turn, feed directly into efforts to mitigate the effects of ongoing and future human-driven abiotic and biotic changes on global biodiversity (5) in the face of a potential sixth mass extinction (6, 7).

To date, many studies investigating the drivers of biodiversity patterns have focused on present-day climatic factors, as climate is well known to be correlated with global aspects of species distributions (8) and community diversity (9), and because anthropogenic climate change remains a present threat (10, 11). Despite this focus on modern climate, a growing body of evidence from geographically and taxonomically diverse studies, including tropical palms (12), European ectothermic vertebrates (13), and African mammals (14), suggests that paleoclimate legacies may be

as important as contemporary climate in structuring patterns of community diversity today (15). Many of these studies found that Quaternary glacial-interglacial climate changes and related effects (e.g., glaciation extent) were the primary drivers of present-day species distributions (16), community phylogenetic and functional trait structure (14), and species endemism (17), highlighting a critical need to consider paleoclimatic effects on contemporary biodiversity.

Likewise, studies of the relationship between biodiversity and current human activities, such as land use intensification (18), are critical for projecting community responses to human population growth and concomitant ecosystem transformation in the 21st century, but potentially overlook the importance of past human impacts. Anthropogenic transformation of the world's ecosystems since the Industrial Revolution has been extensive (19) and is well known to have reshaped patterns of biodiversity over the last several hundred years (20). Indeed, extensive human impacts extend into prehistory, as the diaspora of humans (*Homo sapiens*) over the last ~100,000 y is linked to extirpations and extinctions of large-bodied vertebrates worldwide (21), with legacies that continue to shape patterns of community diversity today (22–24).

## Significance

Research in ecology and biogeography often assumes that ecological communities are shaped primarily by recent drivers, such as current climate and human activity. Here we analyze a comprehensive dataset of 515 large mammal communities across the Earth's tropics and subtropics and show that present-day diversity patterns are codetermined by both past and present factors. Although current climate is important, paleoclimatic influences are strong. Likewise, while post-Industrial Revolution human impacts have affected mammal diversity patterns, imprints of prehistoric human-driven extinctions over the last ~100,000 y are also evident. The influence of past versus present climate and human impacts varies markedly around the world, highlighting the importance of regionally unique evolutionary and ecological histories in shaping global patterns of biodiversity.

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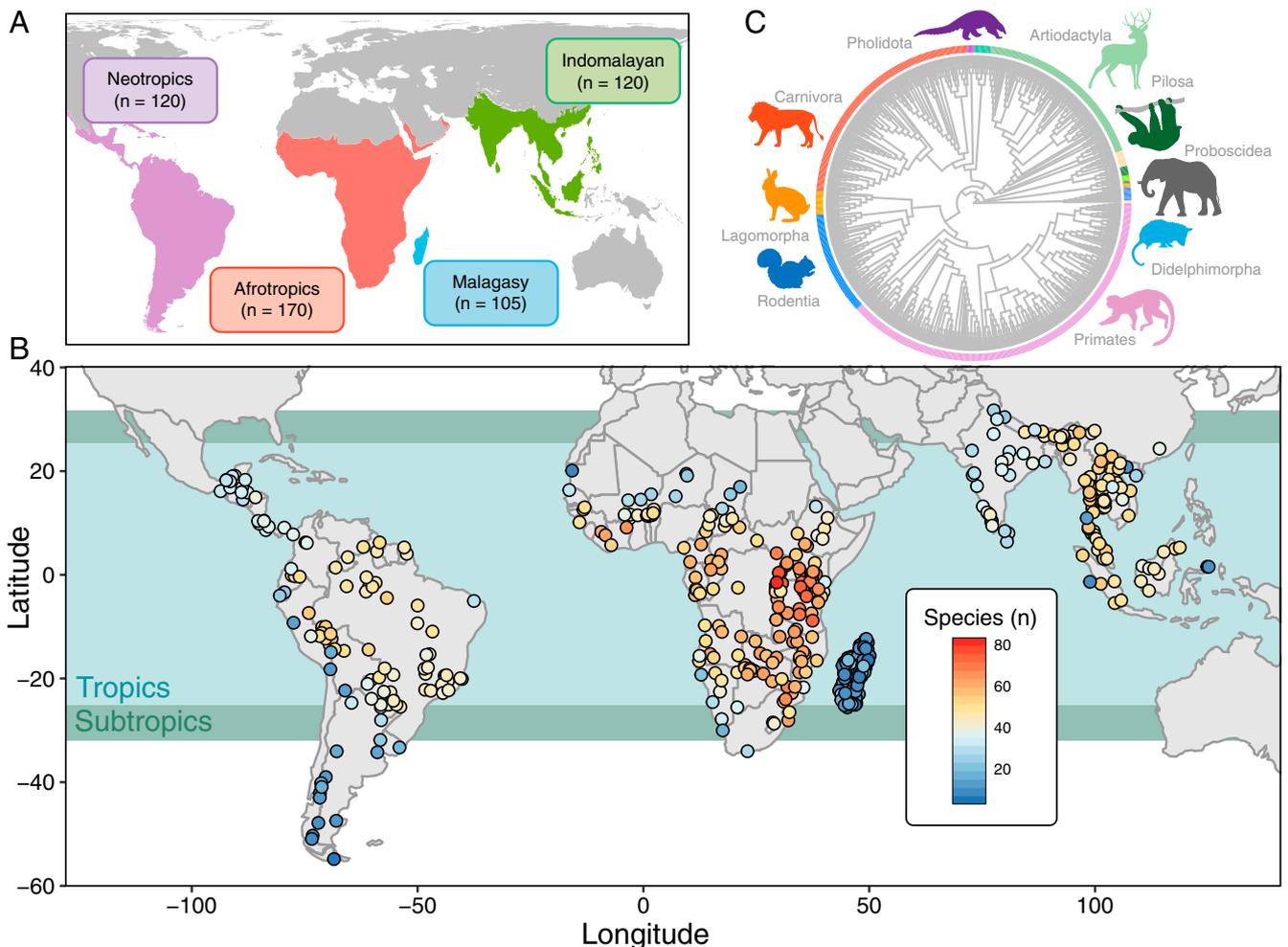
Thus, the emerging picture is one in which contemporary patterns of global biodiversity are strongly shaped by both past and present climate and human impacts, though we have little knowledge of how the influence of these factors varies worldwide. Deciphering their relative influence has the potential to shed light on a number of critical issues. For example, if paleoclimate has a stronger influence than modern climate on species geographic distributions today, this might suggest significant time lags in species responses to climate change and indicate that community disequilibrium dynamics are common (25). Nevertheless, analytical differences and limits on the spatial and taxonomic scope of existing studies effectively hamper our ability to assess the global generality of past vs. present climatic and human impacts within a single clade, which could be used to address this question.

Here we analyze the relative importance of modern climate, Quaternary paleoclimatic change, recent human land use change (1700 AD to present), and prehistoric human-driven extinctions on mammal diversity in the global tropics and subtropics. Using a checklist-compiled dataset of 515 large mammal (species weighing >500 g) communities, we quantify patterns of community phylogenetic and functional trait structure across four biogeographic realms (Fig. 1 A and B) and predict their structure from past and present climate and human impact variables. Our focus on tropical and subtropical large mammals is threefold. First, large mammals are one of the most intensively studied groups of organisms, and there is a great amount of available data on their geographic

distributions, functional traits, and phylogeny (26). Second, the tropics and subtropics are global hotspots of biodiversity (27), and patterns of mammalian diversity are correlated with those of other vertebrate groups (28), meaning that our study bears on issues of global biodiversity more broadly. Finally, large-bodied mammals are among the most threatened groups of vertebrates (29) due mainly to human activities, including climate change (30, 31). Our study therefore provides direct knowledge of the relative influence of anthropogenic and climatic factors on mammalian diversity today and its future in the 21st century.

## Results

We quantified community phylogenetic and functional trait structure for 515 large mammal communities across the Afrotropical, Indomalayan, Malagasy, and Neotropical biogeographic realms. Phylogenetic structure was measured using the net relatedness index (NRI) and nearest taxon index (NTI), which measure the evolutionary breadth and depth of species present in a community, respectively (32). Functional trait structure was measured using the overall trait range (Range) and SD of trait distances among species in a community divided by the overall trait range (SDNDR). Range measures the overall trait diversity of a community, whereas SDNDR measures how evenly spaced species are in terms of their traits (33). Body mass and two dietary axes (Diet1 and Diet2) were used as functional traits. We predicted community phylogenetic and functional trait structure from modern mean annual temperature



**Fig. 1.** (A) Terrestrial biogeographic realms in the tropics and subtropics used in this study. (B) Map of 515 mammal communities analyzed in this study, colored by overall community species richness. (C) Phylogeny of 852 mammal species, with major clades denoted by silhouettes of representative taxa.

and annual precipitation, temperature and precipitation change from the Last Glacial Maximum (LGM; ~22,000 y ago) and mid-Holocene warm period (~6,000 y ago), recent anthropogenic impacts (land use change from 1700 AD to the present), and prehistoric anthropogenic impacts (late Quaternary extinction debt) using simultaneous autoregressive models (*Materials and Methods*).

We found that the relative influence of past and present climatic and anthropogenic factors on the structure of communities varies greatly across realms (Fig. 2). We summarize the principal findings below and provide complete results in *SI Appendix, Tables S6–S9 and Figs. S5–S9*. In the Afrotropics, we found that modern temperature and precipitation were the overall most important variables and had a significant influence on all aspects of community structure. NRI was negatively related to modern precipitation, while NTI declined with temperature. On the other hand, body mass Range was positively related to both modern temperature and precipitation, whereas body mass SDNDR was positively related to precipitation. Effects of modern climate on dietary structure were mixed, with Diet1 Range being negatively related and Diet1 SDNDR positively related to precipitation. Diet2 Range was positively related to temperature, but Diet2 SDNDR declined with precipitation. Paleoclimate effects on Afrotropical communities were mainly concentrated on dietary structure, with LGM temperature change being negatively related to Diet1 Range and Holocene and LGM precipitation change negatively related to Diet 2 Range. Diet1 SDNDR was positively related to precipitation change since the mid-Holocene. Human impacts were weak compared with other continental regions and had no significant influence on any community structure metric.

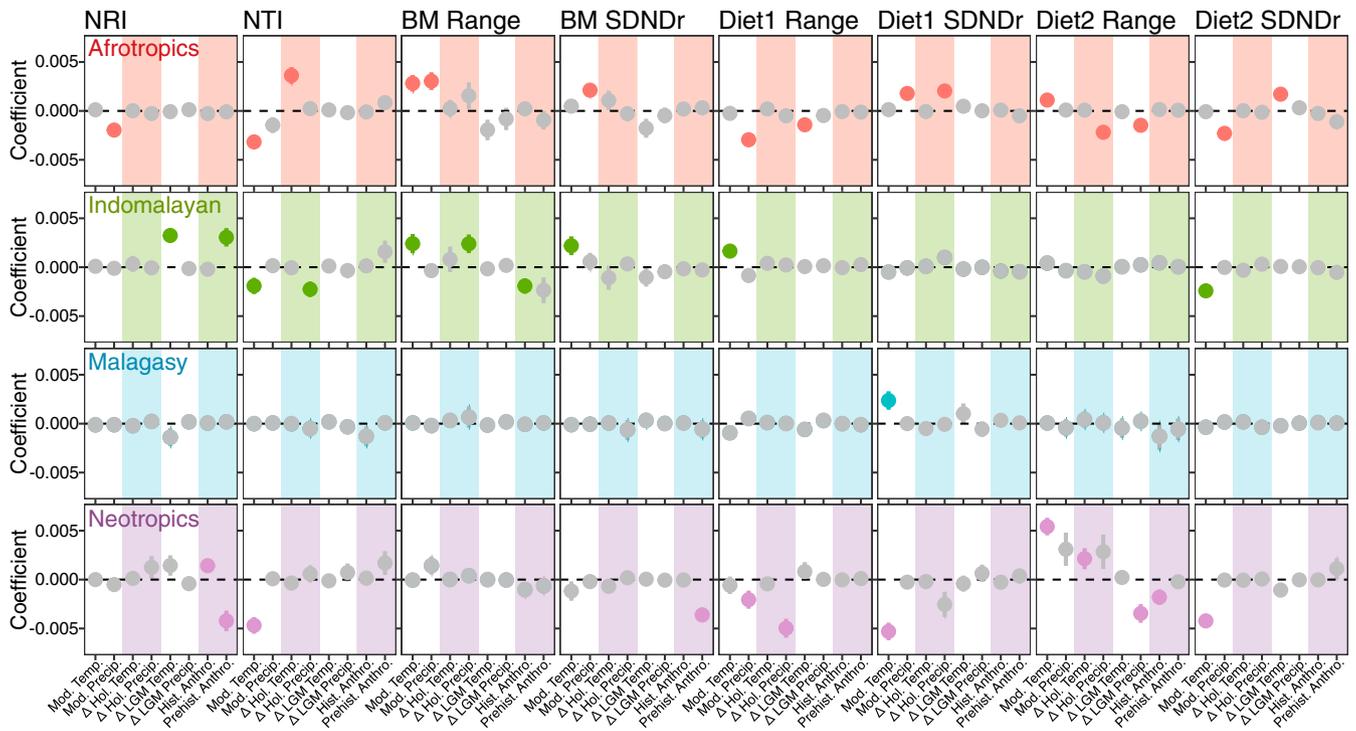
In the Indomalayan realm, modern temperature was overwhelmingly the most important variable, being positively related to body mass Range and SDNDR and Diet1 Range but negatively related to NTI and Diet2 SDNDR. Unlike the Afrotropics, modern precipitation was relatively unimportant and did not significantly

predict any metric. Among paleoclimate variables, precipitation change since the mid-Holocene positively influenced body mass Range but negatively influenced NTI, and temperature change since the LGM was positively related to NRI. Body mass Range declined with the magnitude of historical anthropogenic impacts, while NRI increased with prehistoric anthropogenic impacts.

Malagasy communities were poorly predicted by any factor measured. The only community metric with a significant predictor was Diet1 SDNDR, which was positively related to modern temperature. Conversely, Neotropical communities had several significant climatic and human impact predictors. As in the Indomalayan realm, modern temperature outweighed precipitation in importance, being negatively related to NTI and Diet1 and Diet2 SDNDR, but positively related to Diet2 Range. Diet1 Range declined with modern precipitation. Paleoclimate influences were generally weak in the Neotropics. Precipitation change since the mid-Holocene negatively influenced Diet1 Range, whereas Diet2 Range was positively related to Holocene temperature change and negatively related to LGM precipitation change. Finally, anthropogenic impacts were stronger in the Neotropics than elsewhere and generally had negative effects. NRI and body mass SDNDR declined with the magnitude of prehistoric human impacts, whereas Diet2 Range declined with more recent human activity. NRI was positively related to historical anthropogenic impacts.

### Discussion

Though the tropics and subtropics cradle the vast majority of the world's remaining large mammals (27), we have much to learn about the factors governing global patterns of mammalian biodiversity. Here we show that similar climatic and anthropogenic factors have regionally specific effects on mammal community structure across biogeographic realms. We propose that the unique evolutionary and ecological histories of each realm play key roles in explaining global patterns of mammal biodiversity. By focusing on phylogenetic and functional trait structure, we characterized



**Fig. 2.** Coefficient plots showing the effects of past and present climate and human impacts on mammal community structure. Significant predictors are shown in color; nonsignificant predictors, in gray.

communities by the breadth and depth of the “tree of life” they sample, as well the range and patterning of key ecological traits—body mass and diet—within them. Our community structure measures thus shed light on multiple dimensions of mammalian biodiversity and permit investigations of the past and present-day factors, namely climate and human impacts, shaping them.

Previous studies aiming to explain global patterns of biodiversity have focused on climate (34), habitat heterogeneity (35), or a number of other present-day factors, such as energy and water availability (36, 37) or interactions across trophic levels (38). Our results bear directly on such studies in two key ways. First, we found that present-day drivers alone are insufficient to account for diversity patterns, as legacies of Quaternary paleoclimatic change are detectable across contemporary communities worldwide. Second, we found that the relative importance and directionality of past and present climate and human impacts vary markedly across realms, meaning that there is unlikely to be a “catch-all” explanation for global patterns of mammalian biodiversity.

**Past Climate Shapes Biodiversity Patterns Today.** Quaternary climate changes over the last several million years (Myr) are an interval of Earth’s recent history characterized by marked oscillations between cool and arid glacial and warm and wet interglacial phases following the onset of Northern Hemisphere glaciation just after ~3 Myr (39). We show that Quaternary climate changes in three of the four realms in our study (the Afrotropics, Indomalayan, and Neotropics) influence all aspects of phylogenetic and functional trait community structure (Fig. 2). Importantly, our study reveals that paleoclimatic effects are strong on communities of tropical large-bodied endotherms and that this is a worldwide pattern, a finding that is potentially surprising for two primary reasons. First, previous studies of the effects of Quaternary climate change have mainly focused on ectothermic vertebrates (13), invertebrates (40), or flora (12, 16), all of which, for physiological reasons, are strongly influenced both directly and indirectly by climate (41, 42). Likewise, although micromammals (<500 g) are characterized by the same degree of endothermy as their large-bodied counterparts, their small size and corresponding thermoregulatory constraints make them susceptible to the effects of climate change, particularly the temperature minima (43) characterizing the dominant glacial phases of the Quaternary. In contrast, endothermic large-bodied mammals are relatively free of such constraints (44, 45) and tend to be most limited by extreme temperature maxima—an uncommon feature of Quaternary paleoclimatic change—although they have wider thermoneutral zones than smaller-bodied species overall (43). Indeed, many comparative studies have found weak evidence for phylogenetic conservatism of climatic niches across large mammals (46–48), meaning that closely related species have plastic climatic requirements and/or broad climatic tolerances despite sharing highly conserved similarities in body size and physiology (48, 49). For these reasons, it might be expected that Quaternary paleoclimatic changes had only a limited impact on the structure of large mammal communities, although we find that this is not the case.

The second reason why our results are potentially surprising is that, because the magnitude and velocity of both past and present climate change increase as a function of latitude (50, 51), low-latitude tropical biotas might be expected to exhibit relatively muted responses to Quaternary paleoclimatic oscillations. This prediction is consistent with expectations derived from Rapoport’s Rule and the related Climatic Variability Hypothesis (52), which propose that low species richness and large range sizes at high latitudes reflect the long-term interactions of temperate biotas with changing climates, whereas comparatively speciose and small-ranged tropical taxa reflect long-term climatic stability (53). Indeed, many previous studies documenting Quaternary paleoclimatic impacts have done so through analysis of communities in

temperate regions of the Northern Hemisphere (15). For example, Araújo et al. (13) identified climate stability from the LGM to the present day as the best predictor of species richness patterns in western European reptiles and amphibians. Likewise, functional diversity patterns across North American (54) and northern Eurasian (55) plant communities are codetermined by LGM climate change and dispersal accessibility to ice-free refugia. Because the tropics were never subject to continental glaciation (56), access to ice-free refugia during intervals of even the most extreme Quaternary glacial phases would have little influence on tropical biodiversity.

Thus, in contrast to expectations derived from the climatic requirements and tolerance of large-bodied mammals and the geographically mediated effects of climate change, we found that phylogenetic and functional diversity patterns across most tropical large mammal communities are strongly shaped by Quaternary paleoclimatic legacies. This result reinforces recent evidence that paleoclimatic legacies may override contemporary climates in structuring present-day biotas (15) in what is, for reasons of physiology and geography, an otherwise unexpected group.

**Unique Histories Underlie Realm Biodiversity Patterns.** The search for generalizable explanations of global biodiversity patterns has long been a focus of ecological and biogeographic research (1, 2, 57). In contrast, our study suggests that the factors governing large mammal diversity in the global tropics and subtropics are realm-specific, and that there are unlikely to be universal explanations for patterns of phylogenetic and functional trait community structure (Fig. 2). Specifically, our findings stand in contrast to the recognition of community similarities among the world’s mammalian faunas. For example, Mazel et al. (58) documented striking convergence in community functional trait structure across the globe. Using body mass, diet, activity cycle, and foraging strata as functional traits, they showed that Australasian mammal faunas have structural similarities to those in nearly all other continental realms, particularly the Afrotropics, Palearctic, and Nearctic. They proposed that this pattern emerges from selection for similar functional traits in akin environments, as well as similarities in the dominant assembly processes shaping community composition (58). In contrast to the findings of Mazel et al. and others (e.g., ref. 59), we show that although communities may converge in overall structure, the factors responsible for this structure differ markedly across realms (Fig. 2). We propose that such dissimilarities stem from the divergent evolutionary, ecological, and anthropogenic impact histories of the world’s tropical regions.

In the Afrotropics, mammal communities occur across a wide breadth of biomes, ranging from true desert (e.g., the Namib) to semidesert, savanna, woodland, and dense equatorial forests (60). Because climate’s direct effects on large mammals are weak, Quaternary paleoclimatic effects on Afrotropical communities were likely mediated indirectly through well-documented biome shifts (e.g., refs. 61 and 62). Rowan et al. (14) showed that the strength of both modern climatic and paleoclimatic effects on African mammal communities varies as a function of diet and trophic level. Communities of specialized frugivorous and stenotopic primates are influenced mainly by modern climate, suggesting that they have closely tracked shifts in forest distribution across glacial-interglacial cycles (63). On the other hand, large-bodied and savanna-dwelling ungulate communities show strong paleoclimatic influences, whereas carnivore community structure is unrelated to climate in general. These results suggest that larger body size, dietary flexibility, and/or higher trophic levels confer a degree of ecological resilience to the effects of climate change (see also refs. 64 and 65). Such dietary and trophic stratification of climatic influence may explain our finding of mixed effects of modern climates and paleoclimates in the Afrotropics, although an in-depth analysis is outside the scope of the present study.

As both the Indomalayan and Neotropical realms contain a similar breadth of biomes and mammal dietary and trophic strategies (*SI Appendix, Tables S1–S4*), the question then arises of why paleoclimatic legacies are most influential in the Afrotropics (Fig. 2). We propose that differences in paleoclimatic effects across these realms stem from their decisively different histories of human impacts. Unlike Asia and South America, sub-Saharan Africa was relatively unscathed by extinctions over the last ~100,000 y, during which the vast majority of Earth's large-bodied vertebrates disappeared (24). For example, examining terrestrial herbivores weighing  $\geq 10$  kg, we find that the Indomalayan and Neotropical realms lost 27% and 75% of these species, respectively, over the last ~100,000 y, compared with a milder extinction of 15% of Afrotropical species (*SI Appendix, Fig. S10*). Furthermore, while Indomalayan and Neotropical extinctions were almost certainly driven by humans (21), evidence from the Afrotropics is equivocal. Extinctions of browsing eastern African megaherbivores (species weighing  $\geq 1,000$  kg) were in motion by at least ~4.5 Myr and occurred gradually throughout the Plio-Pleistocene in response to CO<sub>2</sub> decline and regional grassland expansion (66). Similar patterns of long-term extinctions are unknown elsewhere, as most large mammals abruptly disappeared over the last ~100,000 y in a spatiotemporally staggered pattern tracking the global diaspora of *H. sapiens* (21). Because predator novelty was likely key to human-driven extinctions (67) it is highly unlikely to account for those in the Afrotropics, a region in which humans had been evolving in and interacting with mammalian faunas for ~7 Myr (68). Instead, the handful of late Quaternary extinctions that did occur in the Afrotropics seem to have preferentially targeted ungulate grazers near the Pleistocene–Holocene boundary as grasslands gave way to woody vegetation, suggesting a climatic driver of these extinctions decoupled from human activities (69).

A more in-depth look at the among-realm differences in specific community structure metrics predicted by paleoclimatic change vs. prehistoric human impacts sheds further light on their distinct histories. For example, that Afrotropical mammal extinctions were driven by Quaternary paleoclimate change is consistent with our finding that paleoclimate variables predict all aspects of diet (Diet1 and Diet2 Range and SDNDR) but predict neither body mass metric (Fig. 2). As noted above, paleontological records show that Afrotropical extinctions preferentially targeted particular dietary groups (browsers in the long-term, grazers more recently) but were not overly size-selective (66, 69). On the other hand, extreme size-selectivity is a hallmark of human-driven extinctions (68) and explains the strong negative effect that we found for prehistoric human impacts on body mass spacing (SDNDR) in the Neotropics and historical human impacts on body mass Range in the Indomalayan realm. Because body mass is one of the most phylogenetically conserved traits across mammals (48, 49), this also accounts for why NRI (i.e., phylogenetic structure) is significantly predicted by anthropogenic impacts in the Indomalayan and Neotropical realms but not in the Afrotropics (Fig. 2). Thus, we propose that extensive prehistoric and historical impacts have overridden paleoclimatic legacies in the Indomalayan and Neotropical realms, but that those legacies remain evident in the Afrotropics due to a far weaker history of human impacts that thus allow for their detection.

The most unusual region is Madagascar, as Malagasy communities are poorly predicted by any single past or present climatic or anthropogenic factor (Fig. 2). Some of the differences between Malagasy communities and those of the continental realms are likely due to the island's atypical Quaternary history in terms of human impacts. Although humans arrived in Madagascar ~10,000 y ago (70), widespread extinctions of the island's mammals did not occur until far later, just under ~1,000 y ago (71). Such an extinction pattern would obscure all previous influences of Quaternary climate change on community patterns but would fall outside of our two windows of human impact variables,

occurring neither during the Late Pleistocene and early Holocene, when most of the world's continental large mammals disappeared, nor more recently (1700 AD to present).

Finally, although the main focus of our study is on the influence of relatively recent Quaternary history on mammal communities, deep time drivers also shape contemporary biodiversity patterns. *SI Appendix, Fig. S11* presents the first two axes of a principal components analysis of species trait data revealing major differences in overall functional trait composition at the realm level. The Malagasy realm occupies the smallest portion of functional trait space, suggesting a high degree of functional redundancy despite having community richness values overlapping with those of the Afrotropical, Indomalayan, and Neotropical realms (*SI Appendix, Tables S1–S4*). Malagasy functional redundancy is likely related to the realm's low phylogenetic diversity as an island isolated by deep water currents that has been colonized by only a handful of mammalian clades, primarily strepsirrhine primates, euplerid carnivores, and tenrecs (72).

A similar explanation may apply to the Neotropics, which exhibits far less functional diversity than the Afrotropical and Indomalayan realms (*SI Appendix, Fig. S11*). The history of the Neotropics is divergent from that of the other continents, characterized by the repeated colonization, radiation, and extinction of mammalian clades after a prolonged period of isolation (73). Neotropical natives from the early Cenozoic, such as xenarthrans and some marsupial lineages, compose a minor proportion of today's faunas, having been largely replaced by northern immigrants during the Great American Biotic Interchange (74). Likewise, immigrant clades to the Neotropics failed to diversify to levels seen in their realms of origin. A classic example of this comes from the radiation of platyrrhine primates, which did not reach levels of ecological diversity seen in Old World primate communities (75). Such deep time factors, coupled with extensive human-driven extinctions in prehistory, results in the markedly different biodiversity patterns seen in the Neotropics compared with the continents of the Old World (Fig. 2).

## Conclusion

Here we present analyses of an extensive community dataset spanning the global tropics and subtropics, regions harboring the vast majority of the world's remaining large mammal diversity. We show that patterns of phylogenetic and functional trait structure are shaped by both present-day climate and, sometimes to a greater extent, legacies of Quaternary paleoclimatic change and prehistoric to historical anthropogenic influences. The markedly different patterns across realms stem from divergent histories of paleoclimatic change and human impacts, as well as differences in deep time. In light of these findings, it follows that consideration of the unique histories of the world's biogeographic realms is critical to unraveling the factors governing the distribution of mammalian biodiversity today and its response to ongoing and future abiotic and biotic changes in the 21st century and beyond.

## Materials and Methods

**Community Structure.** Terrestrial mammal community data were collected from field surveys, species lists, and databases for the Afrotropical, Indomalayan, Malagasy, and Neotropical realms. Community data were cross-checked with multiple sources and standardized to the International Union for Conservation of Nature's Red List taxonomy (29). We focused on species weighing  $\geq 500$  g, because data for smaller taxa are sensitive to detection bias (76). Our final dataset spans 515 communities (Afrotropics,  $n = 170$ ; Indomalayan,  $n = 120$ ; Malagasy,  $n = 105$ ; Neotropics,  $n = 120$ ) and 852 species in 17 orders (*SI Appendix, Tables S1–S4*). We used the phylogeny of Faurby and Svenning (77) to calculate the NRI and NTI of Webb et al. (32). NRI is calculated as the average phylogenetic distance among all species within a community, whereas NTI is calculated as the phylogenetic distance between the two most closely related species in a community. NRI and NTI were calculated using *picante* (78) with 1,000 runs of resampling using the taxa.labels null model. Body mass and diet were used as functional traits, following Rowan et al. (14). Body mass data

were obtained from PHYLACINE (26), and dietary data were obtained from MammalDIET (79). A subset of 13 MammalDIET food types (SI Appendix, Table S5) was used in a Gower distance-based principal coordinates analysis (PCoA) to summarize the overall distribution of diets on a continuous scale. The first and second PCoA axes (Diet1 and Diet2) captured ~83% of the dietary variation across species and were used in subsequent analyses (SI Appendix, Fig. S4). Community functional trait structure was calculated using two metrics described by Kraft and Ackerly (33), Range and SDNDR. Range is calculated as the overall range of trait values across the species present in a community, whereas SDNDR is calculated as the standard deviation of neighbor distances of trait values for species within a community divided by the overall trait range of that community.

**Climatic and Human Impact Predictors.** Each community's central latitude and longitude was used to obtain climate and human impacts data. Mean annual temperature (BIO1) and annual precipitation (BIO12) were collected for the present-day, mid-Holocene (CCSM4), and LGM (CCSM4) at 2.5' resolution from WorldClim (80). We analyzed paleoclimate variables by calculating an anomaly with modern climate (e.g., present precipitation minus LGM precipitation), which measures the magnitude of climate change and has been widely used in biogeographic studies (e.g., refs. 17 and 54). Similarly, anthropogenic impacts were calculated with two anomaly-based measures. For historical impacts, we calculated changes between 1700 AD and 2000 AD with Anthrome maps of human transformation of the world's biomes based on population density and land use data (81). Anthrome classifications were converted to ranks (1, wildlands; 2, seminatural lands; 3, rangelands; 4, croplands; 5, villages; 6, dense settlements), and a 1700 AD to 2000 AD anomaly was calculated for each community. For prehistoric impacts, we subtracted

present-day large mammal richness from counterfactual "present-natural" richness estimates if human-driven late Quaternary extirpations and extinctions had never occurred (24). This prehistoric impact anomaly therefore provides a measure of extinction debt attributable to anthropogenic activity during the late Quaternary as modern humans spread across the globe (21).

**Autoregressive Models.** We used simultaneous autoregressive spatial error models (SAR<sub>err</sub>) (82) and multimodel inference to analyze the relationships between community diversity and climatic and anthropogenic predictor variables. Separate SAR<sub>err</sub> models were run for each realm and each community metric using the full set of predictors. All possible models were then compared using the corrected Akaike information criterion, and the top 95% of model weights were averaged to determine the influence of past and present climates and human impacts on community structure (83). SAR<sub>err</sub> models and multimodel inference analyses were performed using the R packages "Spdep" (84) and "MuMIn" (85) in R (86). All predictor variables were standardized with the scale() function.

**Data Accessibility.** The datasets supporting this work are provided in the SI Appendix.

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