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Investigating the Biotic and Abiotic Drivers of Body Size Disparity in Communities of Non-Volant Terrestrial Mammals

William Gearty[1,2] | Lawrence H. Uricchio[3] | S. Kathleen Lyons[1]

[1]School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, Nebraska, USA | [2]Division of Paleontology, American Museum of Natural History, New York, New York, USA | [3]Department of Biology, Tufts University, Medford, Massachusetts, USA

Correspondence: William Gearty (willgearty@gmail.com)

ABSTRACT

Aim: The species that compose local communities possess unique sets of functional and ecological traits that can be used as indicators of biotic and abiotic variation across space and time. Body size is a particularly relevant trait because species with different body sizes typically have different life history strategies and occupy distinct niches. Here we used the body sizes of non-volant (i.e., non-flying) terrestrial mammals to quantify and compare the body size disparity of mammal communities across the globe.

Location: Global.

Time Period: Present.

Major Taxa Studied: Non-volant terrestrial mammals.

Methods: We used IUCN range maps of 3982 terrestrial mammals to identify 1876 communities. We then combined diet data with data on climate, elevation and anthropogenic pressures to evaluate these variables' relative importance on the observed body size dispersion of these communities and its deviation from a null model.

Results: Dispersion for these communities is significantly greater than expected in 54% of communities and significantly less than expected in 30% of communities. The number of very large species, continent, range sizes, diet disparity and annual temperature collectively explain > 50% of the variation in observed dispersion, whereas continent, the number of very large species, and precipitation collectively explain > 30% of the deviation from the null model.

Main Conclusions: Climate and elevation have minimal predictive power, suggesting that biotic factors may be more important for explaining community body size distributions. However, continent is consistently a strong predictor of dispersion, likely due to it capturing the combined effects of climate, size-selective human-induced extinctions and more. Overall, our results are consistent with several plausible explanations, including, but not limited to, competitive exclusion, unequal distribution of resources, within-community environmental heterogeneity, habitat filtering and ecosystem engineering. Further work focusing on other confounding variables, at finer spatial scales and/or within more causal frameworks is required to better understand the driver(s) of these patterns.

1 | Introduction

Communities are complex biological units, which are made up of disparate species that fulfil a variety of ecological roles. Collectively, this local biodiversity produces an interactive network whose membership and interactions fluctuate across time and space. Physical geographic features, evolutionary history, life history, climate and many other factors result in the inclusion of different collections of species from the continental species pools across space (Vellend 2010; Götzenberger et al. 2012). Meanwhile, events on short (e.g., drought and monsoons) and long (e.g., glaciation and climate change) timescales result in local extirpations and global extinctions, producing further alteration of community dynamics (Lyons and Smith 2013). All of this results in the potential for communities to be highly taxonomically and functionally heterogeneous across the globe. However, the relative contributions of abiotic and biotic processes to this heterogeneity remain poorly understood (Ricklefs 1987). Furthermore, we do not yet understand whether local (e.g., competition) or regional (e.g., climate) processes dominate the assembly of species into communities (i.e., community assembly), with the former predicting that nearby communities would be highly heterogeneous (Terborgh and Faaborg 1980), and the latter predicting that local communities merely reflect the regional diversity (Cornell 1985). Finally, the degree to which the activities of humans have reduced this heterogeneity, if at all, remains understudied (although see Dornelas et al. 2014; Fraser et al. 2022).

Many previous studies have addressed questions regarding heterogeneity among and between communities within a taxonomic framework; here we address them within a functional framework. In order to accomplish this, we need to assess the ecological niches that are occupied within individual communities and how the distributions of these niches vary from one community to another. Body size, while by no means a comprehensive measure of a species' niche, is inextricably associated with many other life history traits, including population size and density, home range size, diet and metabolic rate (Peters 1983). Furthermore, body size is an easily measured trait and has been exhaustively recorded for many extant and extinct taxa (e.g., Alroy 1999; Smith et al. 2003; Faurby et al. 2018; Gearty, McClain, and Payne 2018; Gearty, Carrillo, and Payne 2021; Gearty and Payne 2020; Cooke et al. 2022). Body size, therefore, serves as a reasonable and convenient proxy for an individual species' fundamental niche. Consequently, the distribution of body sizes of species within a community can be used to assess the disparity of the niches that are occupied within that community (Brown and Nicoletto 1991; Marquet and Cofre 1999; Bakker and Kelt 2000; Kelt and Meyer 2009; Smith and Lyons 2013; Fraser and Lyons 2020). Specifically, the properties of the distribution of body sizes within a community, particularly dispersion, can be used to identify the relative niche breadth and density of communities (Fraser and Lyons 2020).

Mammalia is an extremely diverse and well-documented clade that is ideal for such a community-level assessment. Extant non-volant terrestrial mammals span a wide range of body sizes, ranging from less than 2 g (Remy's pygmy shrew) to greater than 5000 kg (African bush elephant). Beyond this body size diversity, they also occupy a wide range of diets and life histories, resulting in a large and disparate array of occupied ecological niches (Cooke, Eigenbrod, and Bates 2019; Smith et al. 2022). The body size distributions of mammalian communities have been shown to be highly conserved within individual biomes and geographic regions (Brown and Nicoletto 1991; Marquet and Cofre 1999; Bakker and Kelt 2000; Kelt and Meyer 2009). Furthermore, continental body size distributions of mammals tend to be quite similar to one another, especially prior to the Late Pleistocene extinction (Bakker and Kelt 2000; Lyons, Smith, and Brown 2004; Smith and Lyons 2011; Lyons and Smith 2013). However, despite the similarities of mammalian body size distributions at these different geographic scales, the distributions of body sizes in local mammalian communities indeed vary dramatically across space (Marquet and Cofre 1999; Lyons and Smith 2013; Lyons, Smith, and Ernest 2019). Further, limited work has investigated how these distributions globally vary at the community level (however, see Lyons and Smith 2013 for a sample of communities across different continents). Finally, to our knowledge, the biotic and abiotic factors that govern these body size distributions have never been investigated.

To this end, we used IUCN mammal range maps (IUCN 2023) to identify the species that compose individual non-volant terrestrial mammal communities across the globe. Using these community assemblages and existing mammal body size data, we quantified the body size distributions (as a proxy for niche distribution) of these individual communities. We then combined existing mammal diet data (Wilman et al. 2014) with global data on modern climate (Fick and Hijmans 2017), elevation (Danielson and Gesch 2011) and anthropogenic disturbances (Sanderson et al. 2002; Millennium Ecosystem Assessment 2005; Lepers et al. 2005; Venter et al. 2016) to investigate the comparative effects of community species composition, regional climate and human impacts on the body size dispersion of mammal communities. In addition to investigating the relative impacts of these variables on the observed body size dispersion values, we also developed a null model based on observed home ranges, trophic body size relationships and continental species pools to investigate the relative impacts of these variables on the deviation of the observed dispersion values from a null expectation.

2 | Methods and Materials

We assembled a biogeographic database consisting of 3982 non-volant terrestrial mammal species (hereafter referred to as mammals). Extant geographic ranges were obtained from the IUCN Red List (IUCN 2023). Trait data, including diet and body mass, were obtained from the Elton Traits database (Wilman et al. 2014). Diet in this database is reported as percentages of various food sources (e.g., 10% invertebrate, 10% fruit, 20% seed and 60% other plant). To simplify this for our analyses, we derived two diet codings, one continuous and one discrete. First, we calculated the total percentage of any plants (fruit, nectar, seeds and other plants) in each species' diet. Second, we coded each species as one of three discrete trophic group based on the plant composition of their diet: Carnivore ($<5\%$ plant), Omnivore ($>5\%$ plant and $<95\%$ plant) and Herbivore ($>95\%$ plant). Body mass in the Elton Traits database is reported in grams. We $\log_{10}$-transformed this body mass to fit the assumptions of the regressions described below. We also derived a discrete body mass

coding, consisting of three size classes: small (< 1 kg), medium (> 1 kg and < 10 kg) and large (> 10 kg) (Smith and Lyons 2011). We used synonymy data from the IUCN Red List (https://www.iucnredlist.org/search?dl=true&permalink=6da36cdc-5f19-46e7-b980-aeb06b2b6208) to match species in the Elton Traits database to their IUCN geographic ranges.

We assembled global abiotic and anthropogenic impacts data from various sources. We obtained elevation data at 30s resolution from the Global Multi-resolution Terrain Elevation Data model (Danielson and Gesch 2011). We collected various climate variables at 30s resolution from the WorldClim 2 database (Fick and Hijmans 2017), including mean annual temperature (BIO1), temperature seasonality (BIO4), maximum temperature (BIO5), minimum temperature (BIO6), mean annual precipitation (BIO12) and precipitation seasonality (BIO15). We utilised deforestation data at 0.1° resolution from the Millennium Assessment (Millennium Ecosystem Assessment 2005; Lepers et al. 2005). Finally, we obtained a measure of human pressures on ecological systems, termed the Human Footprint, at 1 km resolution (Sanderson et al. 2002; Venter et al. 2016). This metric is based on a model that incorporates data from 2009 on human population density, croplands, pasturelands, navigable waterways and human-constructed infrastructure such as buildings, roads and railways.

We used the *dggridR* R package (Barnes and Sahr 2017) to establish 7292 equal-area hexagonal cells across the surface of the Earth (*res* = 6), each with an area of about 70,000 km². The centroids of the cells are, on average, 285 km away from their nearest neighbours. This is in line with recommended spatial resolutions of > 200 km when dealing with range maps to avoid overestimation of species occupancy area and mischaracterisation of spatial patterns of species richness (Hurlbert and Jetz 2007; Hawkins, Rueda, and Rodríguez 2008). We then removed all hexagonal cells whose midpoints were over the ocean (5204 cells) or Antarctica (178 cells), resulting in 1910 terrestrial cells. Using the *raster* R package (Hijmans 2022), we calculated the average of the Human Footprint and Deforestation measurements for each of these cells. We also calculated the mean of each climate variable and elevation for each cell. We assembled mammal communities by identifying which mammal species' ranges overlap with each cell. For statistical purposes, we discarded 34 communities that had fewer than 5 species (Iceland, Svalbard, New Zealand, the Caribbean, the Falkland Islands and most of Greenland). We then used the remaining 1876 communities to calculate a range of community statistics for each cell: species richness, dispersion of body mass, body mass skewness, body mass kurtosis, minimum and maximum body mass, proportion of species in each body size class (small, medium and large), number of species larger than 100 kg (i.e., those with increased ecosystem engineering potential (Naiman 1988)), mean percent of plant in the species' diets, dispersion of percent of plant in the species' diets, proportion of species in each trophic group (herbivore, omnivore and carnivore), mean range size and dispersion of range size. To calculate dispersion, we took the average pairwise difference of all co-occurring species as introduced by Fraser and Lyons (2017):

$$\frac{1}{n(n-1)} \sum_{i=1}^{n} \sum_{j=i+1}^{n} \left| x_i - x_j \right| \qquad (1)$$

where x_i denotes the trait value (e.g., body mass) of the *i*th species, and *n* represents the total number of mammal species in a community.

To assess how mammal community assembly and development have impacted community body mass dispersion across the globe, we developed a null model to quantify what body mass dispersion would be if species were randomly assigned to communities. A key prediction of competitive exclusion models is that co-occurring species may have overdispersed trait distributions with respect to a null model that considers all species that could possibly be sampled from the regional species pool. However, since there are well-known associations between trophic levels, range size and body mass that may be driven by processes independent of competitive exclusion (Brown and Maurer 1987; Cooke et al. 2022), simply permuting body mass without considering these other factors would generate an anti-conservative null. Therefore, in developing our null model, we conserved the geographic range of each species but associated it with a randomly chosen body mass from another species that shares its trophic group and body size class and that lives on the same continent. In other words, we took all small carnivore species in North America and randomly shuffled their body masses, then took all medium carnivores in North America and shuffled their body masses, and so on. This process accounts for the aforementioned well-known associations between trophic group, body mass and range size. For example, a null model in which an elephant-sized mammal has the range size of a mouse or vice versa would be physiologically unrealistic. The null model also maintains the proportion of species in each of the three trophic groups and the proportion of species in each of the three size classes within individual communities, both of which are critical to the functioning of ecosystems (Cooke et al. 2022). A null model without these constraints would be ecologically unrealistic. Finally, this also accounts for the known differences in body size distributions in different continental species pools (Bakker and Kelt 2000; Lyons, Smith, and Brown 2004; Lyons and Smith 2013). Other functional traits could be used to further parameterise the null model (e.g., diurnal/nocturnal or habitat tiering), but we decided to balance the accuracy of the null model with its simplicity. We performed this simulation 100 times and calculated the body mass dispersion for each community each time to provide a range of expected community body mass dispersions across modern mammal communities given the geographic ranges of species, the different species that inhabit each continent, and the trophic and body size compositions of communities. For each community, we then calculated the average difference between these simulated body mass dispersions and the observed body mass dispersion, henceforth referred to as the deviation from the null. We used a one-sample Wilcoxon test to calculate the probability that the observed dispersion is from the same distribution as that of the null model. We used the FDR correction to adjust the p-values for multiple (1876) comparisons (Benjamini and Hochberg 1995).

Ecological data that are observed across geographical space often exhibit spatial autocorrelation where data that are observed closer to one another often exhibit similar values (Legendre 1993). Due to this phenomenon, such observations are no longer statistically independent, violating the assumptions of most parametric statistical tests, resulting in more

significant results than are merited if not addressed (Dale and Fortin 2002). We used the *spdep* R package to calculate the global version of Moran's I for our entire dataset (Cliff and Ord 1981; Bivand 2022). This metric ranges from −1 (perfectly dispersed) to 1 (perfectly clustered). Values of zero indicate that observations have no spatial autocorrelation and are statistically independent. With the dependent variable set to the observed body size dispersion, we calculated a Moran's I value of 0.64. With the dependent variable set to the deviation of the observed body size dispersion from the null model, we calculated a Moran's I value of 0.58. Both values indicate very strong spatial autocorrelation, as expected. Therefore, given the large number of observations, we implemented a spatial subsampling routine to ensure independence of the data, as is common in geospatial ecology (Dale and Fortin 2002). First, we used the *dggridR* R package to establish 272 equal-area hexagonal cells across the surface of the Earth ($res = 3$), each with an area of about $1,900,000\,km^2$. We then identified which one of these large cells corresponded to each mammal community hexagon's centroid. We filtered out 146 large hexagonal cells that did not cover any mammal communities, leaving 126 large cells which contained between 1 and 37 mammal community hexagons (median = 14). We then sampled one mammal community for each of the large hexagon cells (Figure S1). With this subsample of 126 mammal communities, Moran's I dropped to between −0.06 and 0.21, indicating that this spatial subsampling indeed results in more independent observations. Given this, we then used this subsampling routine to conduct the statistical analyses described below. For each statistical analysis, we generated 100 random spatial subsamples of 126 mammal communities and averaged the statistical results across all 100 iterations (described for each analysis below).

First, we estimated the relative importance of various abiotic and biotic factors in predicting both the observed mass dispersion and the deviation from the null. The biotic predictors included continent, proportion small-sized, proportion large-sized, mean percent plant in diet, dispersion of percent plant in diet, proportion of herbivores, proportion of carnivores, mean range size, range size dispersion, human footprint index and deforestation index. The abiotic predictors included measures of a mammal community's habitat and were mean elevation, mean annual temperature, mean temperature seasonality, mean maximum temperature, mean minimum temperature, mean annual precipitation and mean precipitation seasonality. Species richness was also included as a predictor to account for any sampling biases. We used the *cor* function in R to calculate the correlations between all pairwise independent variables (Table S1). Positive correlations ($N = 77$) ranged from 0.01 to 0.97, with a mean of 0.26, and negative correlations ($N = 94$) ranged from −0.01 to −0.95, with a mean of −0.24. Given the high correlation between several of the variables (21 correlations with an absolute value greater than 0.5), we prioritised methods that account for such variable intercorrelation. We used the *relaimpo* R package (Grömping 2006) to calculate the LMG metric (Lindeman, Merenda, and Gold 1980) for each of these variables as predictors of both the observed size dispersion and the deviation from the null. The LMG metric decomposes the R^2 value of a full regression into individual contributions for each predictor. While similar to a standard partial R^2 value which is calculated

from the sequential sums of squares, the LMG metric takes into account potential variable intercorrelation by averaging these partial R^2 values over all possible orderings of the variables in the regression equation, taking into account the dependence of partial R^2 values on the order of predictors (Grömping 2006). Therefore, if a variable consistently has strong predictive power regardless of its order in the regression equation, it will have a large LMG value, whereas a variable that often does not contribute to the R^2 will have a low LMG value. We calculated the minimum, mean and maximum LMG values for each predictor across the 100 spatial subsampling iterations. For the analyses where the observed mass dispersion was the response variable, we excluded minimum and maximum mass, proportion small-sized and proportion large-sized as predictors because of their direct dependence in the calculation of mass dispersion.

Finally, we performed an exhaustive suite of regressions with any predictors that had a mean LMG value greater than 0.01, explaining more than 1%, on average, of the variance. We used the dredge() function from the *MuMIn* package in R (Bartoń 2022) to run a set of linear regressions with all combinations of these important predictors against each of the response variables. The predictors were ordered within the regression equations based on their LMG values. The model coefficients were standardised using their partial standard deviations (using the 'beta = "partial.sd"' option), which has the same effect as scaling and centring the input variables while also adjusting for the multiple correlation of each variable to the other variables (Bring 1994; Cade 2015). This ensures that the effect sizes are comparable across all the variables and that the strong correlations between the variables (Table S1) are accounted for when calculating the effect sizes. For each of these sets of dredge regressions, we then performed model averaging based on the AICc support values of each individual regression using the model.avg() function from the *MuMIn* R package (Burnham and Anderson 2002; Bartoń 2022). This process produced a model-averaged coefficient and a standard error for each predictor. We then used the *Hmisc* R package (Harrell 2023) to calculate a weighted mean and weighted standard deviation for each predictor across the 100 spatial subsampling iterations using the inverses of the squared standard errors as the reliability weights.

We performed all data manipulation and statistical analyses using version 4.3.3 of the R programming language (R Core Team 2024). We used the *tidyverse* suite of R packages to manipulate data (Wickham et al. 2019). We used the *sf* (Pebesma 2018; Pebesma and Bivand 2023) and *terra* (Hijmans 2023) R packages to perform geospatial analyses. Finally, we used the *ggplot2* (Wickham 2016), *deeptime* (Gearty 2023), *patchwork* (Pedersen 2022) and *viridis* (Garnier et al. 2021) R packages to visualise the results of all of the above analyses.

3 | Results

We recover a familiar species richness latitudinal gradient, with the communities with the highest species richness between 30°S and 30°N, including Southeast Asia, northern South America and central Africa (Figure 1). However, not all communities within this latitudinal zone have high species richness, such as northern Africa, eastern South America and Australia.
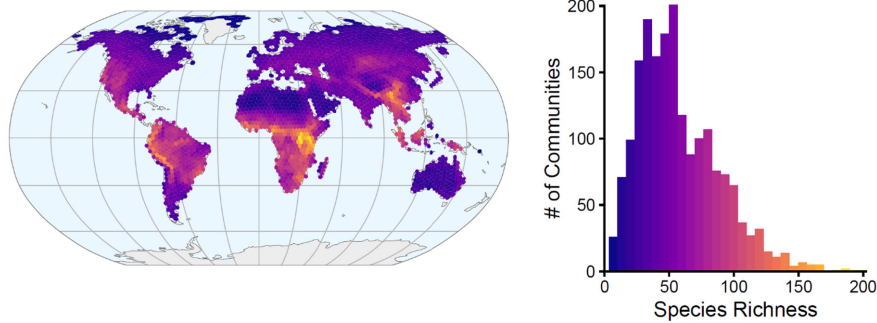
FIGURE 1 | Mammal community species richness as a function of geography. The left panel shows richness values plotted geographically for individual hexagonal communities, and the right panel shows a histogram of all the community richness values. The right panel provides a colour scale for the left panel.

Communities outside of this latitudinal zone consistently have lower species richness, with richness generally decreasing towards the poles.

Mass dispersion, however, shows a dramatically different pattern (Figure 2a). The overall distribution is normally distributed with a mean of about 1.5 $\log_{10}$g. Notable regions with communities with elevated mass dispersion include many parts of Africa, South Asia and parts of the Arctic. The lowest mass dispersions occur in Madagascar, parts of South America and parts of Southeast Asia. North America and Asia (outside of South Asia) have an apparent inverse latitudinal gradient with mass dispersion generally increasing towards the poles. There is a significant negative relationship ($p < 0.001$) between species richness and mass dispersion, although this only accounts for a very small proportion of the variance ($R^2 = 0.035$) (Figure 2a). The most extreme mass dispersion values occur only at extremely low species richness (< 40 species). Furthermore, in the lower end of richness (0–100 species), mass dispersion appears to converge on moderate values with increasing number of species. However, at higher richness (100–350 species), it diverges to two separate regions of dispersion space (roughly 1.0–1.3 and 1.5–1.8 $\log_{10}$g).

Mass kurtosis describes the relative height of a distribution compared to its standard deviation. We find that mass kurtosis is generally uniform across the globe with all communities having kurtosis greater than 1 (Figure 2b) indicating that most of the community body mass distributions are normally distributed (Lyons and Smith 2013). However, there are some communities with extremely elevated kurtosis (> 3) indicating distributions with high peaks and long tails. This includes parts of Indonesia, the Philippines and Australia. The communities with the lowest kurtosis occur in Greenland and other parts of the Arctic and northern Africa. There is a significant positive relationship between kurtosis and species richness ($p < 0.001$), but again, this explains relatively little of the community variance of kurtosis ($R^2 = 0.067$) (Figure 2b). As with mass dispersion, the most extreme community values occur only for communities with low species richness, with kurtosis converging with increasing richness.

Mass skewness describes the length and direction of the tail of the distribution. We find that skewness across the globe is normally distributed, with a mean of about 0.3 (Figure 2c). Most communities ($> 84\%$) have positive skewness, indicating that larger mammals make up the long tail of the distribution, likely reflecting the overall skewness of mammalian body masses (Brown and Maurer 1989). The communities with the highest skewness values, and therefore the longest right tails, occur in Australia, South America, Indonesia and the Philippines. The communities with the lowest skewness values, often with negative values indicating long left tails made up of smaller mammals, occur in northernmost Canada and Greenland, Tibet, Nepal and parts of Africa. There is a barely significant negative relationship between skewness and species richness ($p = 0.01$), but again, this explains little of the community variance of skewness ($R^2 = 0.003$) (Figure 2c). As with the other metrics, extreme values of community skewness occur only in communities with very low species richness and skewness converges with increasing richness.

The average community consists of about 58% small species (< 1 kg), 23% medium species (1 kg-10 kg) and 19% large species (> 10 kg), although there is a great deal of variation from community to community (Figure 3). The proportion of large species within communities is elevated in many parts of Africa, Nepal, Tibet and the arctic (including Greenland and northernmost Canada). Other communities, like those in parts of Australia, most of South America, Central America and central and southern North America have very reduced proportions of large species and inflated proportions of small and medium species. Most islands, such as those in Oceania and Madagascar have no large species whatsoever.

Community mass dispersion estimates from the null model vary globally, with a mean of 1.43 $\log_{10}$g (Figure 4a). At the continental scale, South America and Australia have the lowest expected mass dispersions; North America, Europe and Asia have intermediate null expectations; and Africa has the highest average null dispersion. Despite the broad continental differences in null model estimates resulting in a multimodal distribution (Figure 4a), the degree to which observed dispersions deviate from the null model follows a normal distribution (Figure 4b). Furthermore, regions such as northern North America and Madagascar, deviate from this continental pattern. Mass dispersion estimates for communities with lower species richness can fluctuate dramatically between
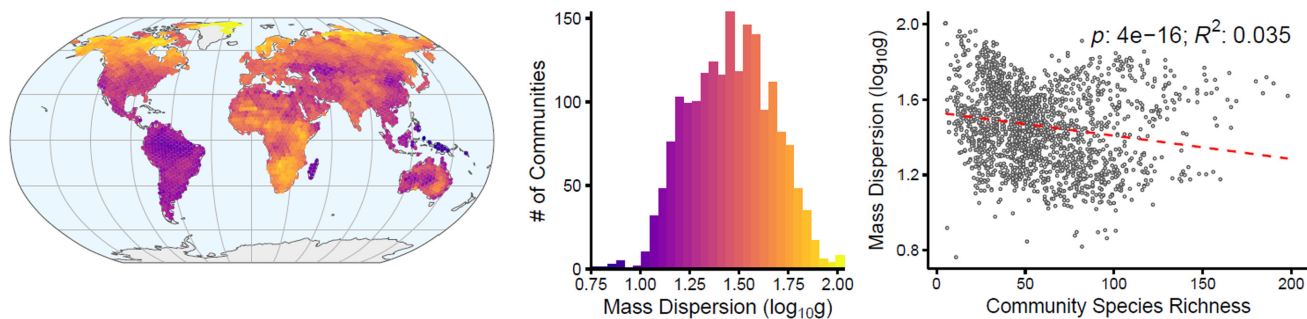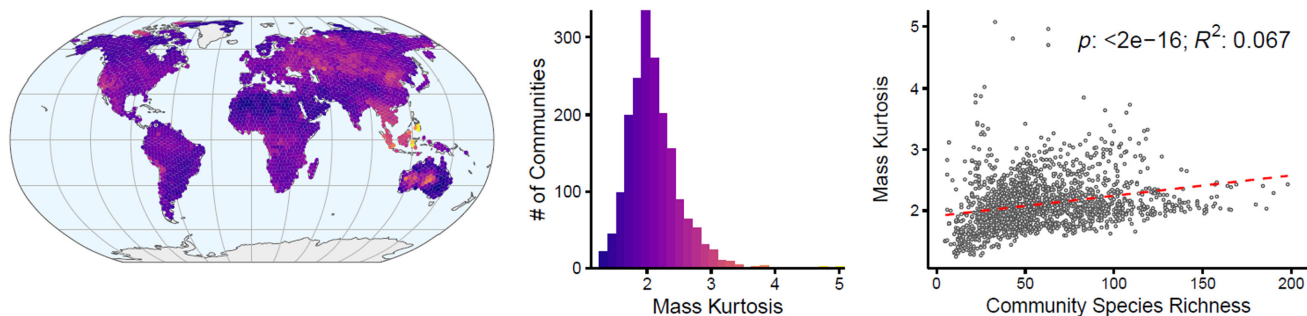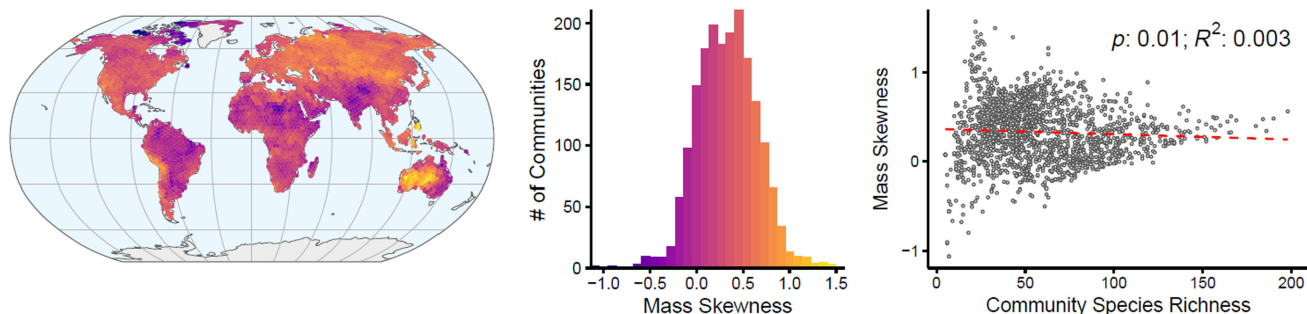
FIGURE 2 | Mammal community body mass dispersion (a), kurtosis (b) and skewness (c) as functions of geography and species richness. The left panels show metrics plotted geographically for individual hexagonal communities. The middle panels show histograms of metrics across all communities. The middle panels provide colour scales for their respective left panels. The right panels show the metrics as functions of community taxonomic size. Each point represents a geographic community. Red dashed lines represent linear regressions with p-values and r-squared values reported in the top-right corner of each panel. Note that the p-values are anti-conservative due to spatial autocorrelation.

individual simulations, resulting in large errors (standard deviations of up to 0.29 $\log_{10}$g; Figure 5a). The average estimates from the null model broadly appear to match the observed mass dispersion. However, upon closer inspection, 56% of the observed mass dispersions for communities are significantly greater than their respective estimates from the null model and 29% of communities have significantly lower observed dispersion than their respective null model estimates (Figures 4 and 5; one-sided Wilcoxon signed rank test, $p < 0.05$ with FDR adjustment (Benjamini and Hochberg 1995)).

When assessing the relative importance of all 20 variables, the number of very large species, mean range size and continent are the most important predictors of raw dispersion, collectively accounting for 40% of the variance (Figure 6). The dispersion of the proportion of plants in diets, the mean annual temperature and the mean minimum temperature are the next most important

predictors. When predicting the deviation of the observed body mass dispersion from our null model, the continent, mean annual precipitation and number of very large species in the community are the most important predictors. Other important predictors include mean minimum temperature and mean annual temperature. Of the two human impact variables, only deforestation was above the cut-off of 0.01, albeit marginally.

The dredge regressions covered 15 predictor variables for raw dispersion and 17 predictor variables for the deviation from the null model (Figure 7). Being on Asia or South America has a significant negative relationship with raw dispersion (compared to Africa), whereas being on Oceania, Europe, North America or South America has a significant positive relationship with the deviation from the null model. With regards to biotic predictors, the number of very large species, the mean and dispersion of range size, and the mean and dispersion of plant
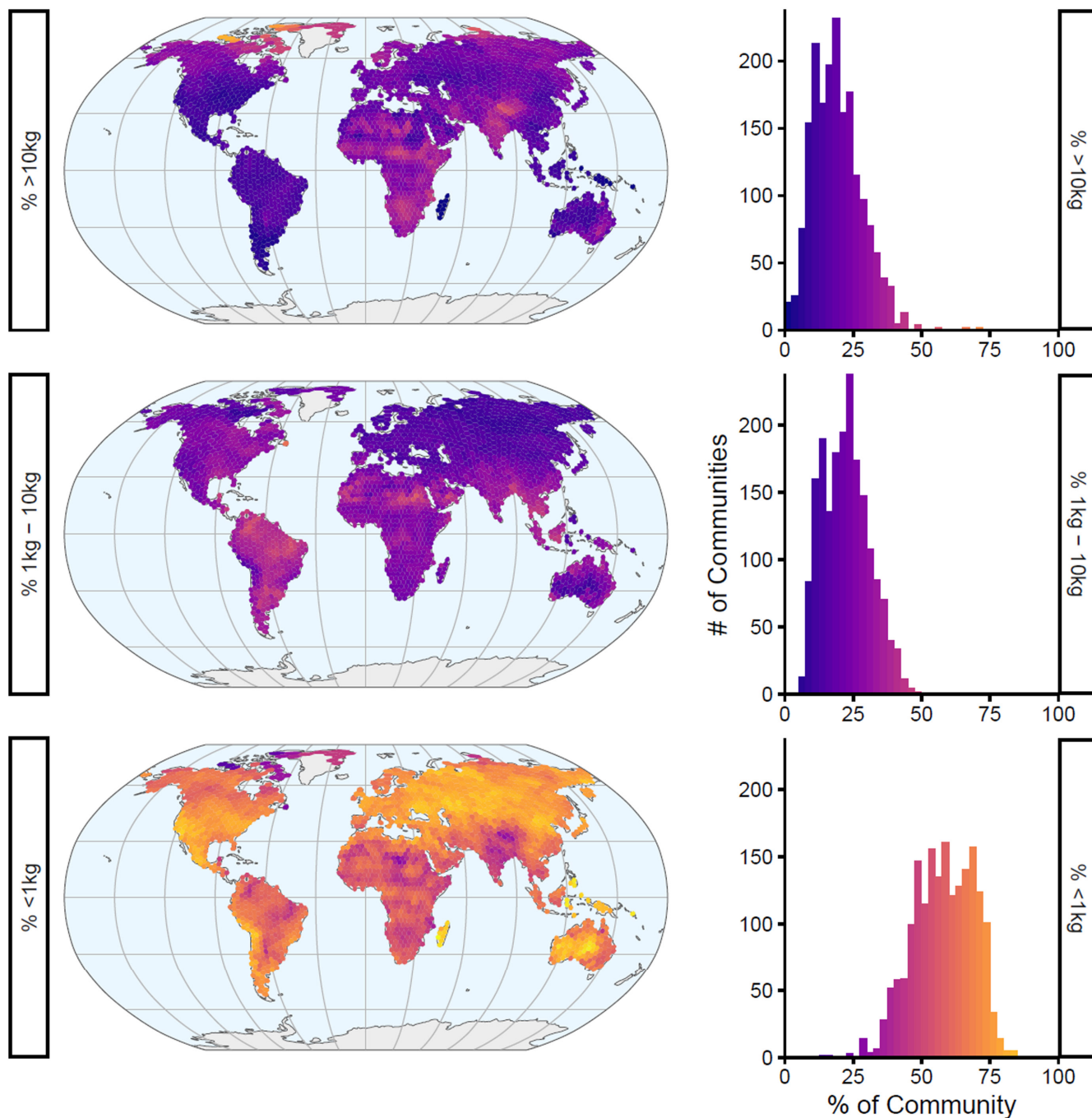
FIGURE 3 | Size composition of mammal communities as a function of geography. The left panels show the proportions of small (< 100 g), medium (100 g to 10 kg) and large (> 10 kg) species with individual hexagonal communities. The distributions of these proportions are summarised as histograms in the right panels. The right panels provide colour scales for their respective left panels.

in diet have positive relationships with the observed mass dispersion of communities, whereas species richness has a negative relationship with observed mass dispersion. The number of very large species and the dispersion of range size have positive relationships with the null deviation, whereas species richness has a negative relationship with the deviation. With regards to abiotic predictors, no variables had a significant relationship with observed dispersion. Mean precipitation seasonality has a positive relationship with deviation from the null model, whereas mean minimum temperature and mean annual precipitation have a negative relationship with it.
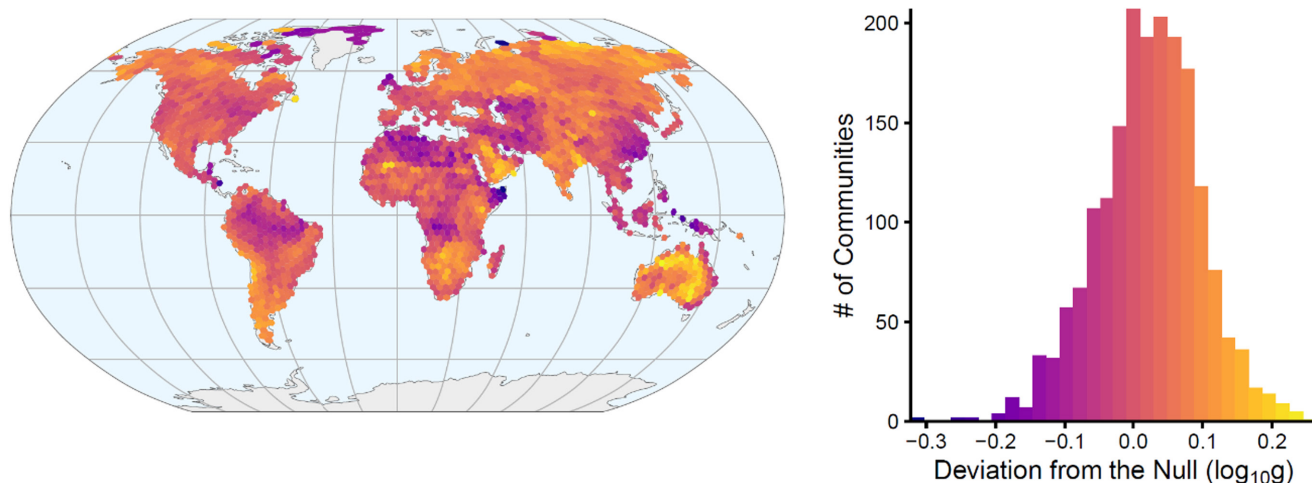
4 | Discussion

Mammal communities across the globe exhibit a wide variety of body size distributions (Brown and Nicoletto 1991; Marquet and Cofre 1999; Bakker and Kelt 2000; Kelt and Meyer 2009; Lyons

(a) Null Model Mean Mass Dispersion
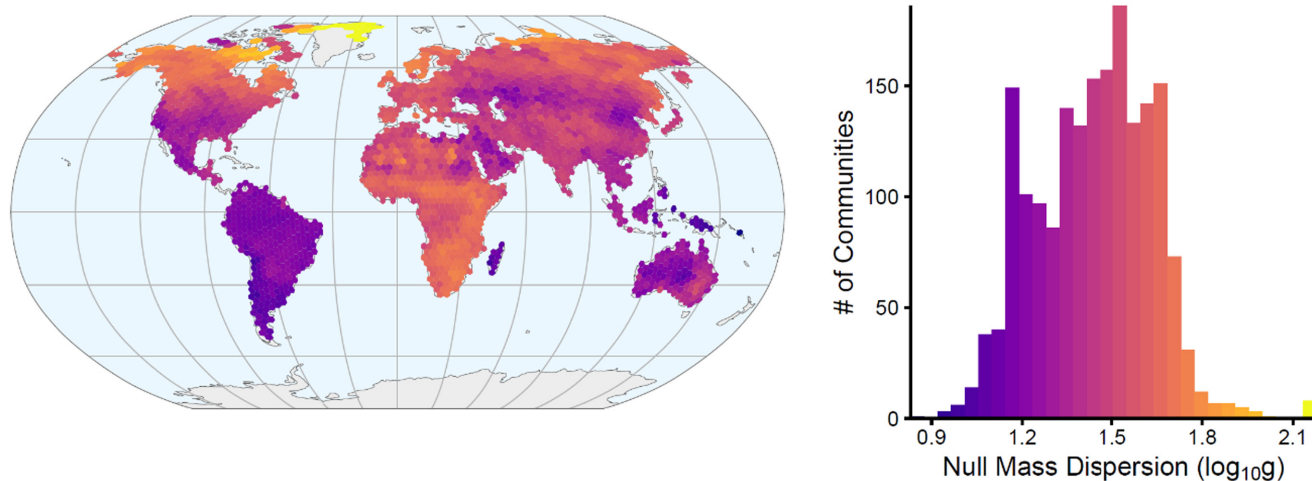
(b) Observed Mass Dispersion − Null Model Mean Mass Dispersion


FIGURE 4 | Null model results for mammal communities as a function of geography. (a) The average mass dispersion from all null model iterations. (b) The difference between the observed mass dispersion (Figure 2a) and the average null model mass dispersion (a). Left panels show metrics plotted for individual hexagonal communities; right panels show histograms of metrics. The right panels provide colour scales for their respective left panels.

and Smith 2013). The complex overlapping of mammalian home ranges produces highly taxonomically and functionally unique communities that have body size distribution characteristics that are distinctive from one another, including dispersion, skewness, kurtosis and composition (Figures 2 and 3). Often these characteristics also deviate quite dramatically from those of the body size distribution of mammals as a whole. For example, some communities have negative body size skewness, which greatly contrasts with the positive skewness consistently found at the continental level (Lyons, Smith, and Brown 2004; Lyons and Smith 2013) (Figure 2c). There is also notable variation in the size composition of modern mammal communities, with some communities having almost exclusively small mammals while others having equal proportions of small, medium and large mammals (Figure 3). While particular regions may have higher or lower community body size metrics than others, such as many Southeast Asian communities having highly elevated kurtosis or many African communities having elevated dispersion, there does not appear to be any broadly generalisable geographic

pattern (e.g., latitudinal gradient) for mass dispersion, kurtosis or skewness (Figure 2). Species richness does not account for much of the variation of these metrics either (Figures 1, 2 and 6). However, the variance of these metrics does decrease at higher species richness as communities have more overlapping species and thus body size distributions of communities with high species richness tend to reflect the distributions of the continental species pool (Figure 2).

Here we find that the observed body mass dispersion of communities tends to reflect the varying biotic and abiotic factors of these communities, even at high species richness (Figure 6). In fact, the 18 variables that we included in our regressions accounted for a total of 87.5% of the variance. In terms of biotic variables, we find that the number of very large species, range size, continent and trophic composition are the most important predictors of observed dispersion. A community's continent explains, on average, 13% of the total variance (Figure 6), reflecting the large differences in species pools from one continent to
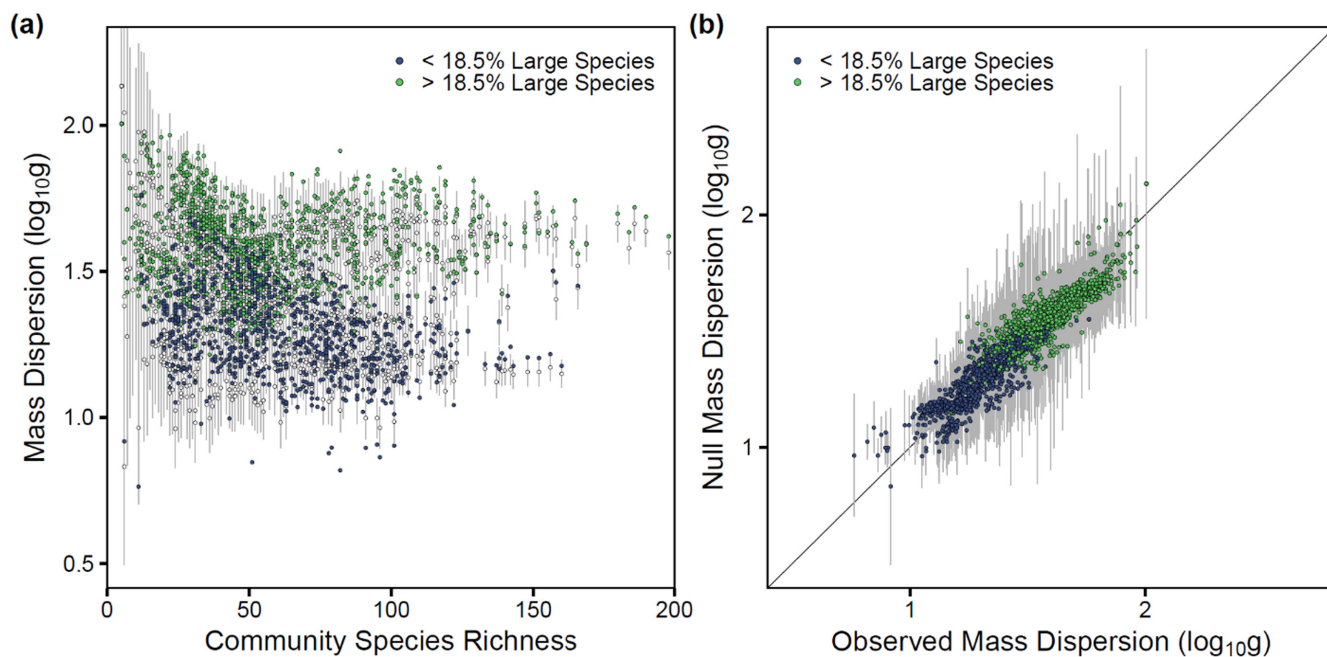
FIGURE 5 | Relationships between observed mass dispersion and community richness and null model mass dispersion. The left panel (a) shows the results of the null model compared to the observed mass dispersion with respect to community species richness. The right panel (b) shows the null model mass dispersion with respect to observed mass dispersion. The grey diagonal line is the line of equality (1:1). Communities are coloured based on their proportions of large species (blue, less than the global community mean of 18.5%; green, more than 18.5%). White points and grey lines represent mean values and two standard deviations, respectively, for mass dispersion values across all null model iterations.

another (Smith and Lyons 2011), which is strongly influenced by the intensity of the megafaunal extinction on continents (Lyons, Smith, and Brown 2004; Smith et al. 2018, 2019). The average and variation of species' range sizes also appear to play a major role, collectively explaining 17% of the variation in observed mass dispersion across communities (Figure 6). Communities with larger average range sizes tend to have larger size dispersion (Figure 7). Range size is correlated with body size (Brown and Maurer 1987; Lyons and Smith 2013; Lyons, Smith, and Ernest 2019), so this may indicate an expected influence of body size composition on body size dispersion. Maximum size, minimum size and the proportions of small- and large-sized species were explicitly not included in this analysis but are indirectly included because of the relationship between body size and range size. However, species with larger range sizes may also have decreased regional competition and redundancy, which may also lead to increased dispersion. The average and variation of % plant in species diets collectively explain about 10% of the variation (Figure 6). Specifically, communities with higher means or dispersions also tend to have larger observed dispersion values (Figure 7). While herbivory may also be tied to body size (Price and Hopkins 2015; Pineda-Munoz, Evans, and Alroy 2016; Cooke et al. 2022), this may also indicate stronger competition among species that are more herbivorous due to limited plant resources, resulting in higher body size and niche compartmentalisation. Finally, the number of species with body masses greater than 100 kg within a community single-handedly accounts for about 14% of the variation of observed dispersion (Figure 6). An excess of large species within a community likely drives an increased body size range, which would cause an increased pairwise distance between all species pairs, resulting in an overall increase in the body mass dispersion metric. However, it appears that

this is a much more important factor than the percentage of any particular size class, even the small size class (Figure 6). This seems understandable given that mammal community body size distributions tend to have positive skewness (Figure 2); a raw increase in the number of very large species has a much higher chance of increasing the body size range than a raw increase in the number of small species.
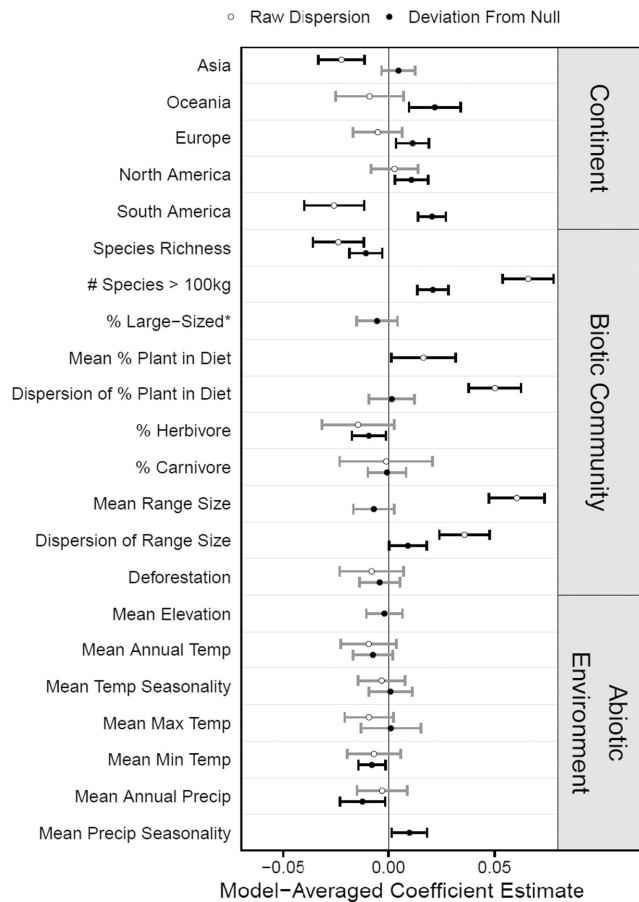
In terms of abiotic factors, temperature (annual average, minimum, maximum and seasonality) collectively accounts for about 18% of the variation of observed dispersion and precipitation, whereas precipitation (annual and seasonality) explains 5% (Figure 6). These variables all exhibit slightly negative effect sizes with respect to body size dispersion, perhaps suggesting that niche disparity is decreased in colder and/or dryer habitats; however, it should be noted that none of these effect sizes are significantly different from zero (Figure 7). This aligns with observations of decreased functional richness in birds and mammals in cold or dry regions (Oliveira et al. 2016; Schumm et al. 2019). Elevation also shows little relationship with observed dispersion. Taken together, this suggests that ecological structure and interactions may be more important than these abiotic factors for structuring the disparity of body sizes in local communities. In fact, previous studies agree that communities with high resource availability, such as tropical rainforests, have low competition for those resources, resulting in relatively low niche variability, whereas communities with low resource availability, such as temperate regions, have high degrees of competition and relatively high niche variability (Oliveira et al. 2016).

Overall, even when accounting for home ranges (Tucker, Ord, and Rogers 2014), trophic levels and body size classes
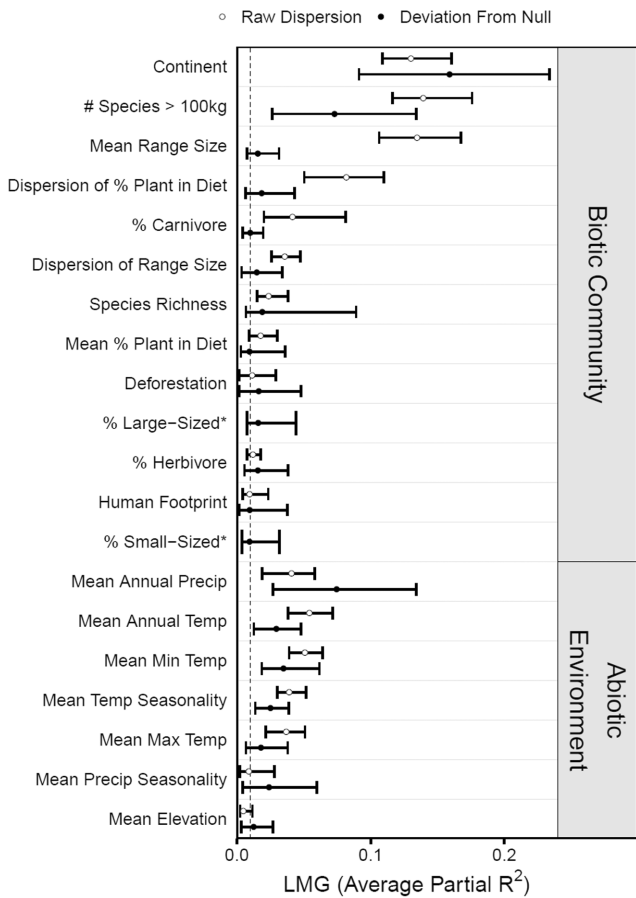
FIGURE 6 | Relative importance of abiotic and biotic variables as predictors. Values indicate the LMG or average partial R^2 for each variable (see Section 2). Points represent the mean values across all spatial subsampling replicates (see Section 2). Error bars represent the minimum and maximum values across all spatial subsampling replicates. White points are for the model where the dependent variable is the observed body mass dispersion. Black points are for the model where the dependent variable is the observed body mass dispersion deviation from the null model. Asterisks indicate variables that were excluded from the raw dispersion analysis. The dashed line indicates the 0.01 cut-off.

FIGURE 7 | Regression coefficient estimates from model averaging. Only variables with more than 0.01 LMG were included (see Figure 6). White points represent coefficients for models where the dependent variable is the observed body mass dispersion. Black points represent coefficients for models where the dependent variable is the deviation of the observed body mass dispersion from the null model. Asterisks indicate variables that were excluded from the raw dispersion analysis. Error bars represent 95% confidence intervals (error bars that overlap with zero are faded). Continental coefficients are based on differences with respect to Africa.

(Price and Hopkins 2015; Cooke et al. 2022) and different continental species pools (Bakker and Kelt 2000; Lyons and Smith 2013), there is a strongly non-random association of species to communities. These results are largely consistent with many different potential drivers. First, strongly competing species must live in largely non-overlapping geographic ranges (i.e., competitive exclusion) (Hardin 1960). Similarly sized species, which likely share similar diets (Carbone et al. 1999, 199; Price and Hopkins 2015; Pineda-Munoz, Evans, and Alroy 2016; Cooke et al. 2022), should therefore tend to occupy different communities, and we would expect greater body size variation within individual communities than expected by chance. Second, the unequal distribution of energy across communities predicts that some communities should have lower dispersion than others due to varying numbers of supported niches (Brown and Nicoletto 1991; Marquet and Cofre 1999). Further, an increase in the spatial variety of food resources within individual communities would also

be expected to support a larger number of niches through the creation of microhabitats (Stauffer et al. 1996; Jones, Szyska, and Kessler 2011). We would, therefore, expect some communities within a continent to have more size dispersion than expected by chance while others are expected to have less size dispersion than expected based on the amount of energy available in those communities, the heterogeneity of within-community energy availability or the degree of environmental filtering (Suárez-Tangil and Rodríguez 2023). Third, very large species of mammals are known to indirectly create more open niches via ecosystem engineering (Naiman 1988; Erwin 2008). For example, elephants and other large mammals can cause vegetation changes, modify fire regimes, impact soil formation and transfer sediment and nutrients, all of which have monumental impacts on niche availability for and occupation by other mammals (Naiman 1988; Haynes 2012; Doughty et al. 2016; Geremia et al. 2019). We would expect communities with more large-bodied species would result in higher body size dispersion among other size classes. Fourth,

the potential seasonal migration of species into and out of communities with high precipitation seasonality due to the seasonal viability of particular niches may artificially inflate our calculation of body size dispersion, whereas the calculation of body size dispersion in any single season would possibly be much lower (and in line with the expectations from the null model) (Ochoa-Ochoa et al. 2019; Parolari et al. 2020). As a result, there is likely to be significant variation in the degree to which these different mechanisms are important for different communities.

Ultimately, we acknowledge that the approach we have taken here prevents us from fully distinguishing between these different drivers. First, range maps are notorious for not reflecting heterogeneity and porosity within ranges, not accounting for seasonal migration and lacking abundance information (Hurlbert and White 2005; Hawkins, Rueda, and Rodríguez 2008; Qian 2020; Higino et al. 2023). The use of range maps, particularly at the scale we have elected to use, may therefore reduce the amount of community-level and regional variation, weakening any possible signal related to spatial biotic or abiotic variation. It's possible that future analyses at finer spatial scales or of only small mammals, which have much smaller ranges and would therefore be less impacted by the lack of porosity and, would be better suited to test the expectations of the mechanisms discussed above. Second, we only covered a small subset of all possible abiotic variables in this study. Future studies would benefit from expanding this to other abiotic variables, including, but not limited to, soil characteristics, hydrology and geological history. Beyond this, quantifying the degree to which abiotic factors vary within communities would be valuable, although this would also likely require a much finer spatial resolution.

Finally, neither of the human impact metrics that we investigated—deforestation and the human footprint—directly explained appreciable amounts of variance in the observed mass dispersion nor the deviation from the null model. Humans have most certainly had a profound impact on mammal communities across the globe, with anthropogenic global change recorded since the Pleistocene (Lyons and Smith 2013; Smith et al. 2018; Tóth et al. 2019; Cooke et al. 2022). However, here we find no evidence that humans have directly impacted the density and/or disparity of mammal body size within individual communities in so far as we can detect it through this body mass dispersion metric. Given that human impacts have been highly biased against larger sized mammals (Smith et al. 2018) and have had differential effects on different continents (Lyons, Smith, and Brown 2004), it is extremely likely that human impacts are highly correlated with other variables that we included in our analyses, such as continent and number of extra-large species. Furthermore, communities with below average proportions of large species (< 18.5%) converge on mass dispersion values much lower than those of communities with above average proportions (> 18.5%) (Figure 5). Therefore, we propose that these communities with larger proportions of large species and higher mass dispersion represent more natural, undisturbed communities (green in Figure 5), whereas communities with lower proportions of larger species and lower mass dispersion represent more disturbed communities (blue in Figure 5).

5 | Conclusion

Numerous abiotic and biotic factors interact to produce a complex set of interactions in mammal communities, resulting in highly heterogeneous body size distributions, even at this coarse spatial scale. Continental species pools, trophic levels, range sizes and regional climate appear to have varying effects on these distributions, specifically the dispersion of body mass. However, when continental differences, home ranges and trophic and body size composition are accounted for, many mammal communities still have higher body mass disparity than would be expected by chance whereas a minority of communities have lower mass disparity than expected. Overall, our results are consistent with many different plausible mechanisms including, but not limited to, competitive exclusion, unequal distribution of resources, within-community environmental heterogeneity, habitat filtering and ecosystem engineering. The relative importance of these mechanisms is likely to differ among communities. Future work including other confounding biotic and abiotic variables, at final spatial scales and/or within more causal frameworks is required to better understand how these patterns have arisen over time.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All code and publically available data are archived on Dryad at https://doi.org/10.5061/dryad.gqnk98sxg.

References

Alroy, J. 1999. "The Fossil Record of North American Mammals: Evidence for a Paleocene Evolutionary Radiation." *Systematic Biology* 48: 107–118.

Bakker, V. J., and D. A. Kelt. 2000. "Scale-Dependent Patterns in Body Size Distributions of Neotropical Mammals." *Ecology* 81: 3530–3547.

Barnes, R., and K. Sahr. 2017. "dggridR: Discrete Global Grids for R." R Package Version 2.0.4.

Bartoń, K. 2022. "MuMIn: Multi-Model Inference." R Package Version 1.47.1.

Benjamini, Y., and Y. Hochberg. 1995. "Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing." *Journal of the Royal Statistical Society: Series B (Methodological)* 57: 289–300.

Bivand, R. 2022. "R Packages for Analyzing Spatial Data: A Comparative Case Study With Areal Data." *Geographical Analysis* 54: 488–518.

Bring, J. 1994. "How to Standardize Regression Coefficients." *American Statistician* 48: 209–213.

Brown, J. H., and B. A. Maurer. 1987. "Evolution of Species Assemblages: Effects of Energetic Constraints and Species Dynamics on the Diversification of the North American Avifauna." *American Naturalist* 130: 1–17.

Brown, J. H., and B. A. Maurer. 1989. "Macroecology: The Division of Food and Space Among Species on Continents." *Science* 243: 1145–1150.

Brown, J. H., and P. F. Nicoletto. 1991. "Spatial Scaling of Species Composition: Body Masses of North American Land Mammals." *American Naturalist* 138: 1478–1512.

Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference*. New York, NY: Springer New York.

Cade, B. S. 2015. "Model Averaging and Muddled Multimodel Inferences." *Ecology* 96: 2370–2382.

Carbone, C., G. M. Mace, S. C. Roberts, and D. W. Macdonald. 1999. "Energetic Constraints on the Diet of Terrestrial Carnivores." *Nature* 402: 286–288.

Cliff, A. D., and J. K. Ord. 1981. *Spatial Processes: Models & Applications*. London, UK: Pion.

Cooke, R., W. Gearty, A. S. A. Chapman, et al. 2022. "Anthropogenic Disruptions to Longstanding Patterns of Trophic-Size Structure in Vertebrates." *Nature Ecology & Evolution* 6: 684–692.

Cooke, R. S. C., F. Eigenbrod, and A. E. Bates. 2019. "Projected Losses of Global Mammal and Bird Ecological Strategies." *Nature Communications* 10: 2279.

Cornell, H. V. 1985. "Species Assemblages of Cynipid Gall Wasps Are Not Saturated." *American Naturalist* 126: 565–569.

Dale, M. R. T., and M.-J. Fortin. 2002. "Spatial Autocorrelation and Statistical Tests in Ecology." *Écoscience* 9: 162–167.

Danielson, J. J., and D. B. Gesch. 2011. "*Global Multi-Resolution Terrain Elevation Data 2010 (GMTED2010)*."

Dornelas, M., N. J. Gotelli, B. McGill, et al. 2014. "Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss." *Science* 344: 296–299.

Doughty, C. E., J. Roman, S. Faurby, et al. 2016. "Global Nutrient Transport in a World of Giants." *Proceedings of the National Academy of Sciences of the United States of America* 113: 868–873.

Erwin, D. H. 2008. "Macroevolution of Ecosystem Engineering, Niche Construction and Diversity." *Trends in Ecology & Evolution* 23: 304–310.

Faurby, S., M. Davis, R. Pedersen, S. D. Schowanek, A. Antonelli, and J. C. Svenning. 2018. "PHYLACINE 1.2: The Phylogenetic Atlas of Mammal Macroecology." *Ecology* 99: 2626.

Fick, S. E., and R. J. Hijmans. 2017. "WorldClim 2: New 1-Km Spatial Resolution Climate Surfaces for Global Land Areas." *International Journal of Climatology* 37: 4302–4315.

Fraser, D., and S. K. Lyons. 2017. "Biotic Interchange Has Structured Western Hemisphere Mammal Communities." *Global Ecology and Biogeography* 26: 1408–1422.

Fraser, D., and S. K. Lyons. 2020. "Mammal Community Structure Through the Paleocene-Eocene Thermal Maximum." *American Naturalist* 196: 271–290.

Fraser, D., A. Villaseñor, A. B. Tóth, et al. 2022. "Late Quaternary Biotic Homogenization of North American Mammalian Faunas." *Nature Communications* 13: 1–11.

Garnier, S., N. Ross, R. Rudis, A. P. Camargo, M. Sciaini, and C. Scherer. 2021. "viridis(Lite) – Colorblind-Friendly Color Maps for R."

Gearty, W. 2023. "deeptime: Plotting Tools for Anyone Working in Deep Time."

Gearty, W., E. Carrillo, and J. L. Payne. 2021. "Ecological Filtering and Exaptation in the Evolution of Marine Snakes." *American Naturalist* 198: 506–521. https://doi.org/10.1086/716015.

Gearty, W., C. R. McClain, and J. L. Payne. 2018. "Energetic Tradeoffs Control the Size Distribution of Aquatic Mammals." *Proceedings of the National Academy of Sciences* 115: 4194–4199.

Gearty, W., and J. L. Payne. 2020. "Physiological Constraints on Body Size Distributions in Crocodyliformes." *Evolution* 74: 245–255.

Geremia, C., J. A. Merkle, D. R. Eacker, et al. 2019. "Migrating Bison Engineer the Green Wave." *Proceedings of the National Academy of Sciences of the United States of America* 116: 25707–25713.

Götzenberger, L., F. de Bello, K. A. Bråthen, et al. 2012. "Ecological Assembly Rules in Plant Communities—Approaches, Patterns and Prospects." *Biological Reviews* 87: 111–127.

Grömping, U. 2006. "Relative Importance for Linear Regression in R: The Package relaimpo." *Journal of Statistical Software* 17: 1–27.

Hardin, G. 1960. "The Competitive Exclusion Principle." *Science* 131: 1292–1297.

Harrell, F. E. 2023. "*Hmisc: Harrell Miscellaneous*."

Hawkins, B. A., M. Rueda, and M. Á. Rodríguez. 2008. "What Do Range Maps and Surveys Tell Us About Diversity Patterns?" *Folia Geobotanica* 43: 345–355.

Haynes, G. 2012. "Elephants (And Extinct Relatives) as Earth-Movers and Ecosystem Engineers." *Geomorphology* 157–158: 99–107.

Higino, G. T., F. Banville, G. Dansereau, N. R. F. Muñoz, F. Windsor, and T. Poisot. 2023. "Mismatch Between IUCN Range Maps and Species Interactions Data Illustrated Using the Serengeti Food web." *PeerJ* 11: e14620.

Hijmans, R. J. 2022. "raster: Geographic Data Analysis and Modeling." R Package Version 3.6-3.

Hijmans, R. J. 2023. "terra: Spatial Data Analysis."

Hurlbert, A. H., and W. Jetz. 2007. "Species Richness, Hotspots, and the Scale Dependence of Range Maps in Ecology and Conservation." *Proceedings of the National Academy of Sciences of the United States of America* 104: 13384–13389.

Hurlbert, A. H., and E. P. White. 2005. "Disparity Between Range Map- and Survey-Based Analyses of Species Richness: Patterns, Processes and Implications." *Ecology Letters* 8: 319–327.

IUCN. 2023. "*The IUCN Red List of Threatened Species. Version 2023-1.*"

Jones, M. M., B. Szyska, and M. Kessler. 2011. "Microhabitat Partitioning Promotes Plant Diversity in a Tropical Montane Forest." *Global Ecology and Biogeography* 20: 558–569.

Kelt, D. A., and M. D. Meyer. 2009. "Body Size Frequency Distributions in African Mammals Are Bimodal at all Spatial Scales." *Global Ecology and Biogeography* 18: 19–29.

Legendre, P. 1993. "Spatial Autocorrelation: Trouble or New Paradigm?" *Ecology* 74: 1659–1673.

Lepers, E., E. F. Lambin, A. C. Janetos, et al. 2005. "A Synthesis of Information on Rapid Land-Cover Change for the Period 1981-2000." *Bioscience* 55: 115–124.

Lindeman, R. H., P. F. Merenda, and R. Z. Gold. 1980. *Introduction to Bivariate and Multivariate Analysis*. Glenview, IL: Scott, Foresman.

Lyons, S. K., and F. A. Smith. 2013. "Macroecological Patterns of Body Size in Mammals Across Time and Space." In *Animal Body Size*, 116–144. Chicago, IL: University of Chicago Press.

Lyons, S. K., F. A. Smith, and J. H. Brown. 2004. "Of Mice, Mastodons and men: Human-Mediated Extinctions on Four Continents." *Evolutionary Ecology Research* 6: 339–358.

Lyons, S. K., F. A. Smith, and S. K. M. Ernest. 2019. "Macroecological Patterns of Mammals Across Taxonomic, Spatial, and Temporal Scales." *Journal of Mammalogy* 100: 1087–1104.

Marquet, P. A., and H. Cofre. 1999. "Large Temporal and Spatial Scales in the Structure of Mammalian Assemblages in South America: A Macroecological Approach." *Oikos* 85: 299.

Millennium Ecosystem Assessment. 2005. "Millennium Ecosystem Assessment: MA Rapid Land Cover Change."

Naiman, R. J. 1988. "Animal Influences on Ecosystem Dynamics." *Bioscience* 38: 750–752.

Ochoa-Ochoa, L. M., N. R. Mejía-Domínguez, J. A. Velasco, K. A. Marske, and C. Rahbek. 2019. "Amphibian Functional Diversity is Related to High Annual Precipitation and low Precipitation Seasonality in the New World." *Global Ecology and Biogeography* 28: 1219–1229.

Oliveira, B. F., A. Machac, G. C. Costa, et al. 2016. "Species and Functional Diversity Accumulate Differently in Mammals." *Global Ecology and Biogeography* 25: 1119–1130.

Parolari, A. J., K. Paul, A. Griffing, et al. 2020. "Liana Abundance and Diversity Increase With Rainfall Seasonality Along a Precipitation Gradient in Panama." *Ecography* 43: 25–33.

Pebesma, E. 2018. "Simple Features for R: Standardized Support for Spatial Vector Data." *R Journal* 10: 439–446.

Pebesma, E., and R. Bivand. 2023. *Spatial Data Science: With Applications in R*. New York, NY: Chapman and Hall/CRC. https://doi.org/10.1201/9780429459016.

Pedersen, T. L. 2022. "patchwork: The Composer of Plots."

Peters, R. 1983. *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.

Pineda-Munoz, S., A. R. Evans, and J. Alroy. 2016. "The Relationship Between Diet and Body Mass in Terrestrial Mammals." *Paleobiology* 42: 659–669.

Price, S. A., and S. S. B. Hopkins. 2015. "The Macroevolutionary Relationship Between Diet and Body Mass Across Mammals." *Biological Journal of the Linnean Society* 115: 173–184.

Qian, H. 2020. "Are Species Lists Derived From Modeled Species Range Maps Appropriate for Macroecological Studies? A Case Study on Data From BIEN." *Basic and Applied Ecology* 48: 146–156.

R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Ricklefs, R. E. 1987. "Community Diversity: Relative Roles of Local and Regional Processes." *Science* 235: 167–171.

Sanderson, E. W., M. Jaiteh, M. A. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002. "The Human Footprint and the Last of the Wild." *Bioscience* 52: 891–904.

Schumm, M., S. M. Edie, K. S. Collins, et al. 2019. "Common Latitudinal Gradients in Functional Richness and Functional Evenness Across Marine and Terrestrial Systems." *Proceedings of the Royal Society B: Biological Sciences* 286: 20190745.

Smith, F. A., E. A. Elliott Smith, A. Villaseñor, C. P. Tomé, S. K. Lyons, and S. D. Newsome. 2022. "Late Pleistocene Megafauna Extinction Leads to Missing Pieces of Ecological Space in a North American Mammal Community." *Proceedings of the National Academy of Sciences of the United States of America* 119: e2115015119.

Smith, F. A., R. E. Elliott Smith, S. K. Lyons, J. L. Payne, and A. Villaseñor. 2019. "The Accelerating Influence of Humans on Mammalian Macroecological Patterns Over the Late Quaternary." *Quaternary Science Reviews* 211: 1–16.

Smith, F. A., and S. K. Lyons. 2011. "How big Should a Mammal Be? A Macroecological Look at Mammalian Body Size Over Space and Time." *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 366: 2364–2378.

Smith, F. A., and S. K. Lyons. 2013. "Animal Body Size: linking Pattern and Process Across Space, Time, and Taxonomic Group."

Smith, F. A., S. K. Lyons, S. K. M. Ernest, et al. 2003. "Body Mass of Late Quaternary Mammals." *Ecology* 84: 3403.

Smith, F. A., R. E. E. Smith, S. K. Lyons, and J. L. Payne. 2018. "Body Size Downgrading of Mammals Over the Late Quaternary." *Science* 360: 310–313.

Stauffer, J. R., J. M. Boltz, K. A. Kellogg, and E. S. van Snik. 1996. "Microhabitat Partitioning in a Diverse Assemblage of Darters in the Allegheny River System." *Environmental Biology of Fishes* 46: 37–44.

Suárez-Tangil, B. D., and A. Rodríguez. 2023. "Environmental Filtering Drives the Assembly of Mammal Communities in a Heterogeneous Mediterranean Region." *Ecological Applications* 33: e2801.

Terborgh, J. W., and J. Faaborg. 1980. "Saturation of Bird Communities in the West Indies." *American Naturalist* 116: 178–195.

Tóth, A. B., S. K. Lyons, W. A. Barr, et al. 2019. "Reorganization of Surviving Mammal Communities After the end-Pleistocene Megafaunal Extinction." *Science* 365: 1305–1308.

Tucker, M. A., T. J. Ord, and T. L. Rogers. 2014. "Evolutionary Predictors of Mammalian Home Range Size: Body Mass, Diet and the Environment." *Global Ecology and Biogeography* 23: 1105–1114.

Vellend, M. 2010. "Conceptual Synthesis in Community Ecology." *Quarterly Review of Biology* 85: 183–206.

Venter, O., E. W. Sanderson, A. Magrach, et al. 2016. "Global Terrestrial Human Footprint Maps for 1993 and 2009." *Scientific Data* 3: 1–10.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer International Publishing.

Wickham, H., M. Averick, J. Bryan, et al. 2019. "Welcome to the Tidyverse." *Journal of Open Source Software* 4: 1686.

Wilman, H., J. Belmaker, J. Simpson, C. de la Rosa, M. M. Rivadeneira, and W. Jetz. 2014. "EltonTraits 1.0: Species-Level Foraging Attributes of the world's Birds and Mammals." *Ecology* 95: 2027.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.