Title: Environmental variables that influence resource temporal variability and abundance drive trophic diversity in mammals

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Running Title: Drivers of mammal trophic diversity

Keywords: mammal diversity; trophic diversity; trophic levels; global biodiversity; species richness

Article Type: Letter

Abstract Word Count: 150

Main Text Word Count: 5020

Number of References: 55

Number of Figures: 4

Number of Tables: 2

Number of Supplementary Figures: 1

Number of Supplementary Tables: 1

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Statement of Authorship: TA conceived the study, and all authors contributed substantially to data collection and preparation. JA, EH, and UA performed statistical analysis and prepared figures. JA wrote the first draft of the manuscript and all authors contributed substantially to revisions.

Data Accessibility Statement: The authors confirm that, should the manuscript be accepted, associated data will be archived in a public repository and DOI included at end of article.

Abstract

Understanding environmental drivers of species diversity has become increasingly important under climate change. Different trophic groups (predators, omnivores, herbivores) interact with their environments in fundamentally different ways, and may therefore be influenced by different environmental drivers. Using random forest models, we identified drivers of terrestrial mammals' total and proportional species richness within trophic groups at a global scale. Precipitation seasonality was the most important predictor of richness for all trophic groups. Richness peaked at intermediate precipitation seasonality, indicating that moderate levels of environmental heterogeneity promote mammal richness. Gross primary production (GPP) was the most important correlate of the relative contribution of each trophic group to total species richness. The strong relationship with GPP demonstrates that basal-level resource availability influences how diversity is structured among trophic groups. Our findings suggest that environmental characteristics that influence resource temporal variability and abundance are important predictors of terrestrial mammal richness at a global scale.

Introduction

Global geographic patterns in species richness have been studied since the 19th century (Hawkins 2001). Although we have posited a host of explanations, there is no consensus regarding the mechanisms that drive geographic patterns of biodiversity. This lack of consensus is perhaps because no single mechanism dictates diversity at such a broad geographic scale, and because different drivers may underly patterns for different organismal groups (Richardson & Pennington 2016).

Several mechanisms hypothesized to underpin the global richness gradient are related to energy and resource acquisition, which are also integral to understanding ecological food webs. Despite the overlap between diversity and food web theories, how diversity gradients vary among different trophic groups (i.e., herbivores, omnivores, and predators) has only been described at the global scale for arthropods (Castagneyrol & Jactel 2012) and coral reef fishes (Siqueira *et al.* 2023), and at a very coarse spatial scale for the role of trophic interactions in shaping mammalian diversity patterns (Zhang *et al.* 2018a). Our study helps identify drivers that underly species richness patterns in different mammalian trophic groups, shedding new light on drivers of ecological patterns in species and providing valuable information for biodiversity conservation in an era of global change.

Broadly, two major categories of mechanisms have been invoked to explain latitudinal patterns of species richness: evolutionary mechanisms and ecological mechanisms. Evolutionary mechanisms focus on the processes that promote speciation and extinction, whereas ecological mechanisms focus on the current and historical abiotic and biotic interactions that help shape diversity patterns (Mittelbach *et al.* 2007). Although evolutionary processes are ultimately responsible for creating diversity, ecological conditions can affect speciation (e.g., diversification rate), extinction, and dispersal processes to influence spatial patterns in species and trait-based richness (Graham *et al.* 2014; Wiens 2023). Furthermore, because diversity is rapidly declining in response to changing ecological conditions, identifying the ecological mechanisms that help drive richness patterns may provide better insight for managing and predicting diversity under global change.

Recent increases in the availability of animal diet and climate data now allow scientists to examine patterns and ecological drivers in an understudied area of diversity, trophic diversity. In this study, we focus on three longstanding ecological-diversity hypotheses that can be tested using global-scale climate data to explain patterns in trophic richness in mammals: the species-energy hypothesis (Willig *et al.* 2003), the environmental heterogeneity hypothesis (Stein *et al.* 2014), and the environmental harshness hypothesis (Chesson & Huntly 1997).

The species-energy hypothesis posits that species richness increases with the amount of energy and resources available to species (Willig *et al.* 2003) and has previously been assessed using plant productivity [e.g., gross primary production (GPP), net primary production (NPP), normalized difference vegetation index (NDVI)], solar radiation, or temperature data. The species-energy hypothesis implies that richness increases with the quantity and quality of biomass available lower on the food web, and species richness should decrease sequentially with increasing trophic levels (Hawkins *et al.* 2003). Therefore, if the species-energy hypothesis holds, herbivore richness would be more tightly coupled to plant productivity than other trophic groups due to their position on the food web. Studies have demonstrated that, among arthropods, positive relationships between plant and consumer diversity are dampened at higher trophic positions (Haddad *et al.* 2009; Scherber *et al.* 2010). This effect could be due to a positive relationship between plant diversity and productivity, leading to greater resource availability for herbivores (Tilman *et al.* 1996, Zhang *et al.* 2018b). A second, non-exclusive explanation is that plant diversity increases the number of ecological niches for all trophic groups by increasing habitat complexity (Castagneyrol & Jactel 2012).

The environmental heterogeneity hypothesis suggests that environmental variability (here proxied by precipitation seasonality, temperature seasonality, and isothermality) affects diversity by influencing niche specialization and competition. Environmental heterogeneity operates on both a spatial and temporal scale, and climate data lends itself particularly well to testing the temporal component. The impact of temporal environmental fluctuations on diversity can be tested on a daily, seasonal, or annual scale using temperature and precipitation data, two of the most important environmental filters that influence terrestrial species distributions.

Predictions about the direction of the effects of heterogeneity on richness are varied. Some have suggested that stable environments promote greater diversity through increased specialization, as species can focus on a narrow, but predictable resource to reduce competition. Meanwhile, unstable environments could limit diversity by imposing physiological constraints on organisms (Klopfer 1959; Luo *et al.* 2012). Conversely, others have posited that some environmental fluctuation or disturbance promotes species co-existence by preventing competitive exclusion (e.g., the intermediate disturbance hypothesis; Hutchinson 1961; Connell 1978). This dichotomy of the impact of environmental stability on species richness may be due to the temporal scale considered. For example, short-term (i.e., seasonal) environmental fluctuations may promote biodiversity by allowing for predictable variation (i.e., variability that recurs reliably), whereas longer-term fluctuations may negatively impact biodiversity by forcing species to endure sub-optimal conditions for extended periods (Liu *et al.* 2021).

Due to their generalist lifestyle, omnivores may better tolerate fluctuations in environmental conditions and food availability due to flexibility in the types of resources they exploit, and may rely on environmental fluctuations to balance competitive abilities (Wootton 2017). Environmental fluctuations that alter food quality and quantity may improve omnivores' fitness relative to predators and herbivores because they can change their feeding habits to tolerate a wider range of environmental conditions (Kondoh 2008). For example, omnivorous fish in environments with fluctuating water levels consume different amounts of plant vs. animal tissue during wet seasons compared to dry seasons (McMeans *et al.* 2019). In contrast, in stable systems, omnivores are often inferior competitors compared to herbivores and predators due to trade-offs associated with maintaining the ability to consume multiple food types (Diehl 2003).

The environmental harshness hypothesis also predicts that the environment operates on diversity by influencing niche differentiation and competition (Chesson & Huntly 1997), and could be assessed using extremes in mean annual temperature and precipitation. Similar to the effects of environmental variability on trophic structure diversity, omnivores may be more tolerant of harsh environments than herbivores and predators. For example, omnivores can adjust their degree of herbivory or carnivory in response to temperature-induced changes in food quality and quantity (Boersma *et al.* 2016; Zhang *et al.* 2018b).

This study aims to determine whether the three ecological mechanisms outlined above operate differently at different trophic levels of mammals. Here, we posit that global patterns of mammal species richness will differ among trophic groups (herbivores, omnivores, and predators) due to different dominant environmental mechanisms influencing their diversity. Specifically, we hypothesize that 1) plant production will be the dominant driver of herbivore diversity and be less important for other trophic groups, and 2) that the negative impacts of environmental harshness and temporal heterogeneity will be greater for herbivores and predators than omnivores. We assessed these hypotheses by leveraging multiple global-scale, spatial datasets that characterize mammal species richness and ecological properties.

Methods

Trophic Categories and Environmental Variables

We used and updated a database by Atwood *et al.* (2020) to assess global, extant terrestrial mammal biodiversity across trophic levels. The original database contained trophic group classifications (predator, omnivore, and herbivore) and geographical data on all extant mammals assessed on the 2019-2 IUCN Red List of Threatened Species (IUCN 2019). We augmented the database by adding previously unincluded extant mammals assessed on the 2021-1 IUCN Red List of Threatened Species (IUCN 2021). We characterized the diets and trophic groups of species following an approach described in detail by Atwood *et al.* (2020). Briefly, we searched published literature and reference texts for diet information from wild populations (see supplementary table 1 for diet source references). For ~5% of species, diet information was not available in published resources; for these species, we extrapolated a diet from the most closely related taxonomic group with published diet information, typically congeners or confamilials. Atwood *et al.* (2020) used this extrapolation approach in their study and found it predicted coarse trophic groups of mammals with 94% accuracy. We classified species as either predators, omnivores, or herbivores based on the contribution of plant vs. animal material to a species' diet: we defined predators as species that consume ≥80% animal-based diets, herbivores as species that consume ≥80% plant-based diets, and all other species as omnivores.

To reduce overall uncertainty in diet classifications and trophic diversity patterns, we did not classify species' diets further than predator, herbivore, or omnivore. Past quantifications of more refined diet categories, such as those in EltonTraits 1.0, only provide semiquantitative information on the importance of different diet categories, and taxonomic extrapolations were used to fill in missing species' diets (Wilman *et al.* 2014; Atwood *et al.* 2020). While extrapolating diets from related taxa performs well for coarse diet categories (i.e., herbivore, omnivore, predator), it is less accurate for more refined diets (Gainsbury *et al.* 2018). Finally, grouping species into more refined diet categories (frugivore, insectivore, etc.) can obscure global diversity patterns because, unlike coarse categorizations, most species are not confined to a single category, and diets may vary spatially, seasonally, and temporally for a single species.

Without quantitative information that captures spatial and temporal variation in the importance of different diet items to a species, it becomes difficult to ascertain global patterns and their drivers for more refined diet categories.

We used gross GPP as an indicator of plant production and resource availability. We used isothermality and seasonal variations in temperature and precipitation as proxies for temporal environmental heterogeneity. Finally, we characterized environmental harshness based on mean annual temperature (MAT) and mean annual precipitation (MAP).

We leveraged published geographic environmental databases as sources for environmental variables. We extracted MAT (°C), temperature seasonality (standard deviation × 100), isothermality (diurnal range/annual range), MAP (cm), and precipitation seasonality (coefficient of variation) from the WorldClim v. 2 global climate database at a resolution of 30 arc seconds (0.083 degrees; ~85 km^2); values were annual means from 1970-2000 (Fick & Hijmans 2017). We used annual GPP (g C m^{-2} y^{-1}) at a 0.05 degree resolution (~30 km^2) (Zhang *et al.* 2017).

There has been great debate about the implications of spatial scale on species distribution data, with some arguing that analyses using a finer resolution than 200 km x 200 km overestimates occupancies (Hurlbert & Jetz 2007). Yet others have suggested that such a coarse grain resolution degrades the data and obscures important diversity patterns driven by finer-scale changes in climatic variables, such as those imposed by changes in elevation (Jenkins *et al.* 2013). Acknowledging that some species distributions could be overestimated, we gridded the terrestrial surface of the globe into 30 km × 30 km pixels to better capture relevant variability in climatic variables. We calculated the average of each environmental variable, total mammal species richness, species richness for each trophic group within each pixel. We also calculated the relative contribution of each trophic group to total richness in each pixel, and we identified pixels where a particular trophic group is overrepresented. We considered a trophic group to be overrepresented if its relative contribution to total diversity in each pixel was greater than its global upper quartile value. For example, the global upper quartile for relative predator richness is 52.17%. Thus, they are overrepresented in pixels where they contribute to more than 52.17% of relative diversity. In this interpretation, overrepresentation indicates that a geographic region is more favorable to a certain trophic lifestyle than others.

Random Forest Modelling

We used random forest modeling to identify environmental drivers of total mammal richness, the richness of each trophic group, and the relative contribution of each trophic group to total richness. We opted to use random forest modeling due to its robustness in dealing with non-linear responses and because it allowed us to determine the relative importance of different environmental variables (Cutler *et al.* 2007). To balance the distribution of mammal richness for our analyses, we performed stratified sampling of 30 × 30 km geographic pixels based on total mammal richness. We grouped pixels into 19 bins at richness intervals of ten (i.e., 0-10 species, 10-20 species, etc.) except for richness levels greater than 180 (max=228), which we grouped into a single bin. We randomly sampled 1500 pixels from each bin for a total of 28,500 pixels. Our stratified sampling approach also mitigates spatial autocorrelation, reducing the number of adjacent or nearby pixels used in the data set (Chevalier *et al.* 2021).

Each random forest model initially included latitude coordinate, MAT, temperature seasonality, isothermality, MAP, precipitation seasonality, and GPP as explanatory variables. We performed reverse-fold cross-validation to determine the optimal number of variables for each model and eliminated non-useful variables based on a measure of variable importance (increase in MSE) and on variance inflation factors (VIF). We assessed the marginal effects of each predictor variable using random forest partial dependency plots (Breiman 2001). Random forest models were constructed using the *randomForest* package (Liaw & Wiener 2002) in the R statistical computing environment (R Core Team 2022).

Results

Our final dataset included 5713 unique mammal species, with 2024 species classified as predators, 2268 species classified as herbivores, and 1421 classified as omnivores. The global average of terrestrial mammal richness is 59.41 ± 44.24 (SD) species per 30 × 30 km pixel. Mean per pixel predator richness is 28.57 ± 22.31 species, mean herbivore richness is 18.13 ± 14.40 species, and mean omnivore richness is 12.72 ± 9.34 species. Predator, herbivore, and omnivore mammal diversity all peak near the equator and decrease poleward (Figs. 1 and 2a). Across most regions of the globe, predator richness is higher than the other trophic groups, followed by herbivore richness and omnivore richness. However, from ~15-30 °N, omnivore richness is slightly higher than herbivore richness. At the northernmost latitudes (>65 °N), herbivore richness tends to be similar or slightly higher than predator richness (Fig. 2). On average, predator species represent 46.75 ± 11.93% of per pixel richness. In contrast, herbivore species represent 30.16 ± 11.64%, and omnivore species represent 22.72 ± 9.69%. The relative contribution of each trophic group to total richness varies with latitude (Fig. 2b). Predator relative richness exhibits local maxima at ~25 °S and ~10 °N. Herbivore relative richness exhibits local maxima at ~5 °S and ~60 °N, and omnivore relative richness exhibits local maxima at ~10 °S and ~25 °N.

Each trophic group exhibits different patterns of over-representation across the globe (Fig. 3). Over much of the tropics and subtropics, omnivory is overrepresented. In the temperate zones, particularly the northernmost parts of the temperate zone, herbivory tends to be overrepresented. Predators do not exhibit clear latitudinal patterns in overrepresentation, but are overrepresented in portions of tropical Africa, temperate humid regions of Europe and northern Africa, and Greenland tundra (Fig. 3).

Random Forest Models – Raw Species Richness

Based on reverse fold cross-validation and percent increase in mean square error (increase in MSE), we included the following five parameters in all trophic models: precipitation seasonality, latitude coordinate, GPP, MAP, and MAT (Table 1). We omitted isothermality and temperature seasonality because they were the least important variables based on increase in MSE. They also exhibited the highest VIFs at 6.82 and 8.90, respectively. All random forest models explained high amounts of variance, ranging from 87.29-91.60% variance explained.

Random forest modeling revealed commonalities in predictors of total mammal richness and richness within trophic groups. For total mammal richness and all three trophic groups, an increase in MSE indicates that precipitation seasonality is, by a large margin, the most important variable explaining global richness patterns (Table 1). Latitude is the second most important explanatory variable for total mammal and herbivore richness. In contrast, GPP is a more important explanatory variable for predator richness than latitude. For omnivore richness, MAT and MAP are more important than latitude.

Although the relative importance of the explanatory variables differed among trophic groups, partial dependency plots indicate that species richness of different trophic groups tends to respond similarly to the explanatory variables, except for the response to MAT (Fig 4). Predator richness increases with MAT to ~15 °C and then exhibits fairly consistent diversity levels at higher temperatures. Herbivore richness also increases to a maximum at ~15 °C, whereas omnivore richness achieves a maximum at a lower temperature of ~12 °C. In contrast to predator richness, herbivore and omnivore richness decrease at higher temperatures.

Random Forest Models – Relative Contribution to Richness

Because patterns in species richness across trophic levels can be masked by the disproportionate number of species in different regions, we also investigated the mechanisms controlling diversity across different trophic groups by using their relative contribution to richness. Reverse-fold cross-validation indicated that the best model configuration included five explanatory variables. However, variable importance measures based on increase in MSE indicated different top predictors for the three trophic groups. To facilitate comparisons among trophic groups, we retained the six most important variables in all models (GPP, precipitation seasonality, temperature seasonality, MAT, MAP, and latitude coordinate) according to their increase in MSE (Table 2). We omitted isothermality because it was the least important variable in all models. For predators and herbivores, GPP was the most important predictor explaining the relative contributions of trophic groups to total richness. Precipitation seasonality and temperature seasonality were the next most important predictors for predator relative richness and were of similar importance. Temperature seasonality, MAP, and latitude were the next most important variables explaining herbivore relative richness and were all of similar importance. The top three most important variables for omnivore relative richness (precipitation seasonality, MAP, and GPP) were equally important. The individual models for predator, omnivore, and herbivore relative richness explained 79.91%, 73.40%, and 76.30% of the variance, respectively.

Partial dependency plots indicate that for any given variable, trophic groups varied in their response (Fig. 4). Here, we focus on the responses of relative richness to GPP and precipitation seasonality, which tended to be among the most important predictors for all trophic groups (Table 2). The relative richness of omnivores was negatively related to GPP between 100-1500 g C m^{-2} y^{-1}, decreasing by ~5% between these values. In contrast, relative richness for predators and herbivores increased by ~3.5% and ~1%, respectively, between these GPP values. At GPP values above 1500 g C m^{-2} y^{-1}, the relative richness of all three trophic groups remained fairly consistent. Predator relative richness was positively related to precipitation seasonality between 0-125 (CV), increasing by ~4.5% between these values. Omnivore relative richness decreased by ~4% between the same precipitation values, while herbivore relative richness decreased by ~0.5%.

Discussion

The objective of our study was to determine whether environmental conditions differentially impact mammal species richness at different trophic levels. Our results support the hypothesis that species richness spatially varies across trophic groups, with mammalian predators, herbivores, and omnivores dominating different regions of the globe. A combination of climate and productivity variables helps predict the global patterns in total mammal richness, richness within trophic groups, and the relative contribution of trophic groups to total richness. However, the relative importance of different environmental characteristics and their relationship with richness varied among predators, omnivores, and herbivores. These differences suggest that the interplay between a mammal's environment and its trophic strategy influences how mammalian diversity is structured.

We did not find support for our hypothesis that GPP would be a more important predictor for herbivores and omnivores than predators. Although GPP emerged as an important predictor of total mammal richness, when segregated by trophic groups, it was a more important predictor for total predator richness than herbivore or omnivore richness. Varied responses by the different trophic groups to GPP indicate that future changes in this variable could alter how diversity is structured among trophic levels, with predators experiencing the most dramatic effects with changes to GPP.

When considering the relative contribution of trophic groups to diversity, GPP was again an important predictor for predators, herbivores, and omnivores. However, in contrast to predators and herbivores, which increased in proportion with GPP, the proportion of omnivores slightly declined with increasing GPP. Studies on the tempo of lineage diversification and trophic transition in mammals show that omnivore diversity primarily evolves through transitions into that strategy from herbivores and carnivores (Price *et al.* 2012). Additionally, herbivores and carnivores have developed greater diversity than omnivores through specialization and subdivision of niches (Price *et al*. 2012). Thus, one might expect that under higher GPP, more specialized trophic niches would develop for herbivores and, subsequently, carnivores, suppressing the need to transition to omnivory. Simulation models support this hypothesis by showing that the evolution of omnivory decreases with increased plant production (Chubaty *et al.* 2014).

Our findings that GPP is the most important variable predicting the relative contribution of trophic groups to total diversity and the generally positive relationship between GPP and species richness for all trophic groups indicates that total energy and basal resource availability are key correlates of diversity. These results support the species-energy hypothesis, which posits that overall diversity is positively correlated with the energy available in an ecosystem (Wright 1983). Our finding that the magnitude of the effect of GPP on species diversity is greatest at the highest trophic level (i.e., for predators) provides an interesting new context to the version of the species-energy hypothesis asserting that productivity exerts bottom-up controls on diversity.

The bottom-up formulation of the species-energy hypothesis suggests that the number of trophic levels is regulated by the energy available at the base of the food chain, and that in areas of high productivity, longer food chains promote greater predator richness (Evans *et al.* 2005a, b). However, in this explanation, herbivores and omnivores are expected to have a stronger positive relationship with productivity than predators (Hawkins *et al.* 2003; Jetz *et al.* 2009). Yet, we observed the opposite: the rate of increase of species richness with GPP is greater for predators than for herbivores and omnivores. Furthermore, when considering simple bivariate correlations between GPP and predator, herbivore, or omnivore richness in our global dataset (n=134,491), GPP is more strongly correlated with predator richness (Spearman's ρ= 0.74) than herbivore or omnivore richness (ρ= 0.70 and ρ= 0.65, respectively). Together, this indicates that the influence of GPP on mammal diversity is not necessarily dampened in higher trophic groups. However, our findings do not entirely refute the bottom-up hypothesis. Although we did not assess diet specialization within trophic groups in this study (i.e., classifying mammals as insectivores, frugivores, granivores, etc.), Atwood *et al*. (2020) found that the diets of >90% of extant mammalian predators included insects. Thus, we cannot conclude that predator diversity is not driven by bottom-up processes acting on lower taxa, as Zhang et al. (2018b) found.

Another formulation of the species-energy hypothesis suggests that highly productive ecosystems contain abundant resources that increase the number of available niches, thereby allowing species to specialize on a few resource types and leading to increased species co-existence and richness (Evans *et al.* 2005a, b; Pautasso & Gaston 2005). If this hypothesis holds, we would expect positive correlations between GPP and raw species richness for all trophic groups, positive correlations between GPP and the relative contribution of diet specialists to richness, and negative correlations between GPP and diet generalist relative richness. If we consider trophic grouping as a coarse scale indicator of diet specialization, with predators and herbivores representing specialists because they feed on only plant or animal tissue and omnivores as generalists because they feed on both, we indeed observe these trends in our data. Additionally, at very low GPP, the relative contribution of omnivores to diversity is similar to that of herbivores, but then declines as GPP increases. However, we recognize substantial variation in the degree of diet specialization within trophic groups, and more refined diet specialization analyses are required to test this hypothesis thoroughly.

Alternative versions of the species-energy hypothesis suggest that temperature should be the strongest correlate with diversity because, at higher temperatures, species can switch energy investments from thermoregulation to reproduction, thereby maintaining larger populations and decreasing extinction risk (Evans *et al.* 2005b). Our findings do not necessarily refute this version of the species-energy hypothesis, as we found a positive relationship between mammal richness and MAT between temperatures of -10 and 20 °C. While GPP was more important than MAT for explaining total mammal richness, predator richness, and herbivore richness, the opposite was true for omnivore richness. Furthermore, the relative contribution of omnivores to diversity generally increased with MAT, suggesting that some temperature-driven effect other than productivity is important for driving omnivore richness.

We did not find support for our hypothesis that omnivore richness is more tolerant to environmental harshness and heterogeneity than predator and herbivore richness. We considered harsh environments to be areas with very high or very low MAT (i.e., extreme heat or extreme cold) and/or low MAP (drought stricken). There was no indication that omnivore richness benefited in harsh conditions; instead, they appeared less tolerant. Omnivore richness peaked at milder MAT levels than herbivores and predators, and their relative contribution to diversity was lowest where annual precipitation was minimal. In contrast, predators appear to be reasonably tolerant of harsh temperature conditions as they maintained high richness levels at MAT exceeding 25 °C, and the relative contribution of predators to diversity increased at extreme temperatures. Additionally, predators accounted for 35.4% of the mammals in our data set, representing 46.75% of per pixel richness on average. The overrepresentation of predators indicates they are more cosmopolitan than herbivores and omnivores, potentially due to an ability to tolerate a broader range of environmental conditions.

We considered precipitation seasonality, temperature seasonality, and isothermality to represent temporal environmental heterogeneity. We found that environmental heterogeneity in the form of precipitation seasonality, an uncommonly explored predictor variable in mammal diversity studies, was very important for predicting mammal richness as a whole. Precipitation seasonality emerged as the most important explanatory variable for the richness of all trophic groups, with maximum richness at intermediate seasonality values. Intermediate levels of precipitation seasonality correspond to regions that receive precipitation seasonally with a defined, but often short dry season (Walsh & Lawler 1981; O'Donnell & Ignizio 2012). Total mammal richness was lowest in regions of low seasonality (i.e., precipitation evenly distributed throughout the year) and high seasonality (i.e., areas with long dry/short wet seasons). Again, we found no evidence that omnivore richness disproportionately benefited from more heterogenous conditions. However, we did find evidence that predators benefit from intermediate levels of precipitation and that omnivores appeared to be replaced by predators as precipitation seasonality increased from low to intermediate values.

The peaking of mammal richness in regions with seasonal precipitation supports the theory that intermediate levels of environmental heterogeneity promote species diversity (Adler

& Drake 2008; Tonkin *et al.* 2017). Ecological theory and modeling studies have indicated that temporal fluctuations in environmental conditions promote more species co-existence than stable environments as long as the oscillations occur with intermediate and predictable frequency (Liu *et al.* 2021). Seasonal variability satisfies these criteria and likely promotes species co-existence by creating temporal niches and minimizing fitness differences between species with different competitive abilities, particularly in predators and herbivores (Chesson 2000; White *et al.* 2010).

In contrast, low temporal environmental variability may limit species co-existence by promoting competitive exclusion of inferior competitors, while high variability limits diversity by forcing species to endure long periods of suboptimal conditions that could increase extinction risk (Adler & Drake 2008; Liu *et al.* 2021). There is empirical support for the positive impact of seasonal fluctuations of various environmental conditions, including precipitation seasonality, on species diversity among stream invertebrates, waterfowl, and small mammals (Asher & Thomas 1984; Dalby *et al.* 2014), an effect that appears to be driven by seasonal turnover in species assemblages. Our results indicate that this phenomenon influences mammal diversity globally and likely affects how diversity is structured among trophic groups by favoring predators at the expense of omnivores. Under climate change, drought frequency, severity, and spatial extent are projected to increase in many regions, including areas that currently experience intermediate precipitation seasonality (Parmesan *et al.* 2022). Such changes will shift these regions to higher values of the precipitation seasonality index, potentially making these regions more vulnerable to biodiversity loss.

Conclusions

Past studies on latitudinal gradients in species diversity have largely overlooked the role of trophic ecology on the distribution of species. Our results show that diversity patterns in mammal trophic groups are not randomly distributed and that different ecological drivers influence predators, omnivores, and herbivore diversity patterns. Overall, our results suggest that temporal environmental heterogeneity (particularly in precipitation) and basal energy availability (e.g., GPP) are important drivers of total mammal richness, the richness within trophic groups, and the relative contribution of each trophic group to total richness.

Although our models accounted for 73-92% of the variability in mammalian richness across trophic groups, the best-performing models always included latitude, indicating that environmental heterogeneity and basal energy availability do not fully explain the observed patterns in trophic diversity. As a result, we cannot discount other hypotheses that attempt to explain diversity patterns with evolutionary (e.g., cradle hypothesis), anthropogenic, or other ecological causes. In particular, anthropogenic activities have led to non-random species extinctions and invasions, and can also modify the environmental variables we found to be associated with richness patterns (Pacifici *et al.* 2020). Thus, the diversity patterns we identify here may reflect natural processes and human impacts.

The most important drivers of total mammal richness were precipitation seasonality and GPP, which are both predicted to shift under climate change. Furthermore, we found that areas experiencing intermediate levels of environmental heterogeneity expressed the highest trophic richness. However, climate projections and recent weather phenomena indicate that the intensity and duration of extreme weather events will increase (Diffenbaugh *et al.* 2017), likely resulting in higher environmental heterogeneity in many systems. Such changes could negatively impact terrestrial mammal richness and potentially increase the relative contribution of predators to mammal diversity.

Given the strong relationship between precipitation seasonality and terrestrial mammal richness, our findings indicate the need for additional research on the impacts of precipitation seasonality on local and global biodiversity. Precipitation seasonality is expected to shift in many ecosystems under climate change (Pascale *et al.* 2016; Breinl *et al.* 2020). However, projected changes to precipitation seasonality have been understudied compared to other potential impacts of climate change (Parmesan *et al.* 2022), making it difficult to predict how trophic richness could vary geographically under changing precipitation regimes. Therefore, better projections of precipitation seasonality and concomitant changes to biodiversity are paramount for conservation and resource management.

Acknowledgments

Support for this paper was provided by an OPP NSF grant (1932889) and an Early Career Research Fellowship from the Gulf Research Program of the National Academies of Sciences, Engineering, and Medicine grant to TBA (The content is solely the responsibility of the authors and does not necessarily represent the official views of the Gulf Research Program of the National Academies of Sciences, Engineering, and Medicine). We would also like to thank the Utah State University Ecology Center for supporting this research. We thank Dr. Richard Cutler for his advice on random forest modeling.

Data Availability

The compiled dataset used for analysis in this study can be found in an online repository at http://dx.doi.org/10.17632/pw8r7jh8kw.1

Figure Captions

Figure 1. Global geographic patterns of species richness for a) herbivores, b) omnivores, and c) predators. Richness was assessed at a pixel resolution of 30 × 30 km.

Figure 2. Distribution of terrestrial mammal species richness by latitude a) and relative contribution to the richness of each trophic group b). Richness was assessed at a pixel resolution of 30 × 30 km, and distributions were fit using the GAM function within the ggplot2 package in the R statistical computing environment.

Figure 3. Global geographic patterns of species richness overrepresentation for herbivores, omnivores, and predators. In some regions, two trophic groups are overrepresented. A trophic group is considered to be overrepresented if its richness within a pixel is greater than the value of its global upper quartile of richness.

Figure 4. Partial dependency plots depicting marginal effects of random forest models for total richness of all mammals (first column), species richness within trophic groups (second column), and relative contribution of each trophic group to total richness (third column). Only environmental variables retained in the final models are presented. Temperature seasonality was only retained in models of relative richness contribution and so is not presented for total mammal richness or within trophic group richness.

Figure S1. Bivariate correlations between explanatory variables used in random forest models. Correlations are based on all data points in the global dataset (n=134,491), and presented coefficients are Spearman's ρ.

Tables

Table 1. Importance of five predictor variables retained in final random forest models for raw species diversity. Importance is measured as percent increase in mean square error.

	All Mammals	Predators	Omnivores	Herbivores
Precipitation Seasonality	133.7	126.3	132.9	130.8
Latitude Coordinate	99.8	87.6	86.0	98.1
Gross Primary Production	91.7	102.4	85.1	88.1
Mean Annual Temperature	70.1	75.1	109.1	68.8
Mean Annual Precipitation	60.7	72.6	91.9	60.9

Table 2. Importance of six predictor variables retained in final random forest models explaining relative contribution (%) of each trophic group to total mammal richness. Importance is measured as percent increase in mean square error.

	Predators	Omnivores	Herbivores
Gross Primary Production	97.3	50.7	74.8
Precipitation Seasonality	81.4	57.0	56.4
Temperature Seasonality	78.5	27.4	64.1
Mean Annual Temperature	64.6	41.7	36.8
Mean Annual Precipitation	63.1	52.3	62.7
Latitude Coordinate	66.9	33.7	62.3

Figure 1

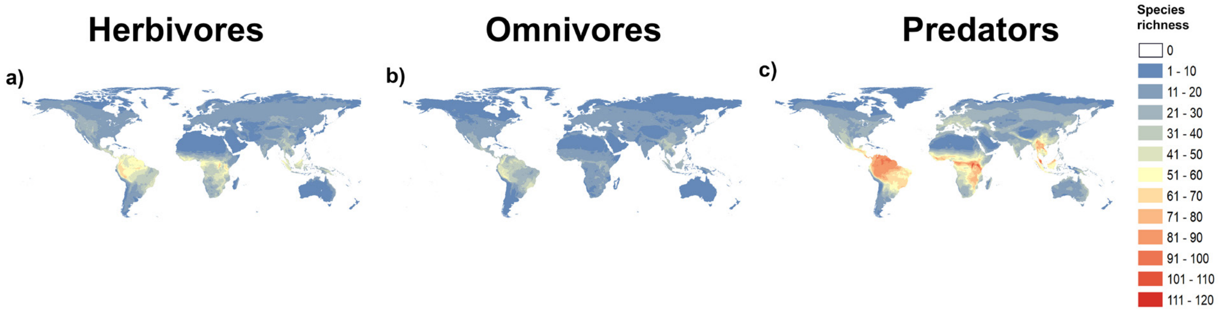


Figure 2

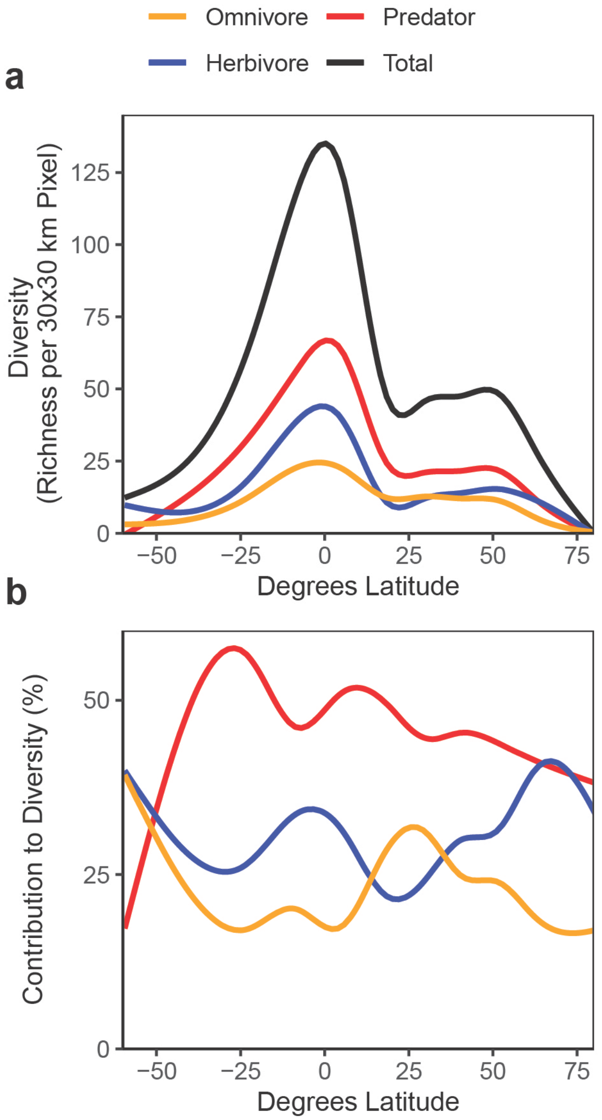


Figure 3

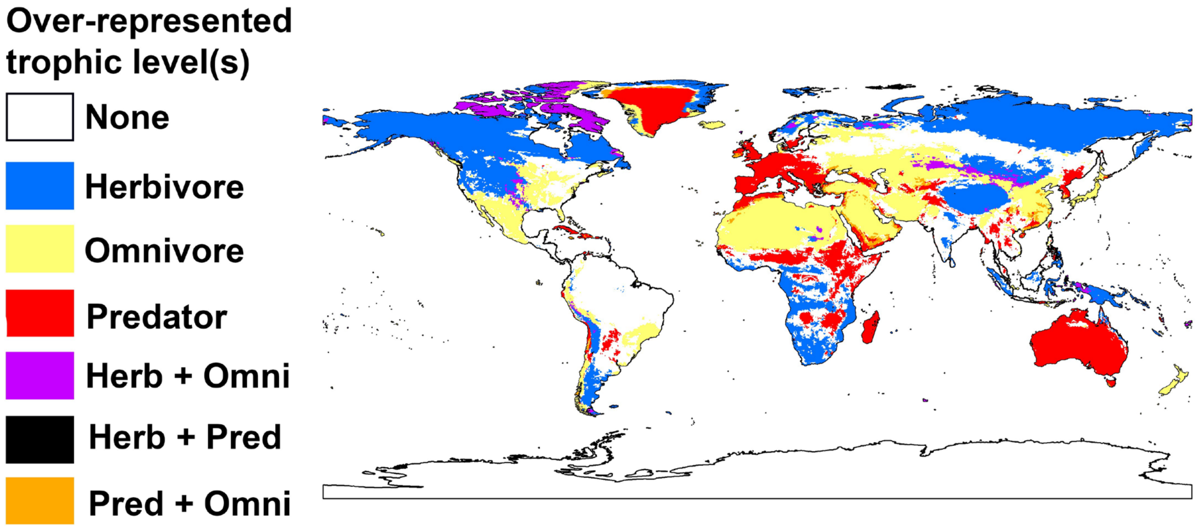
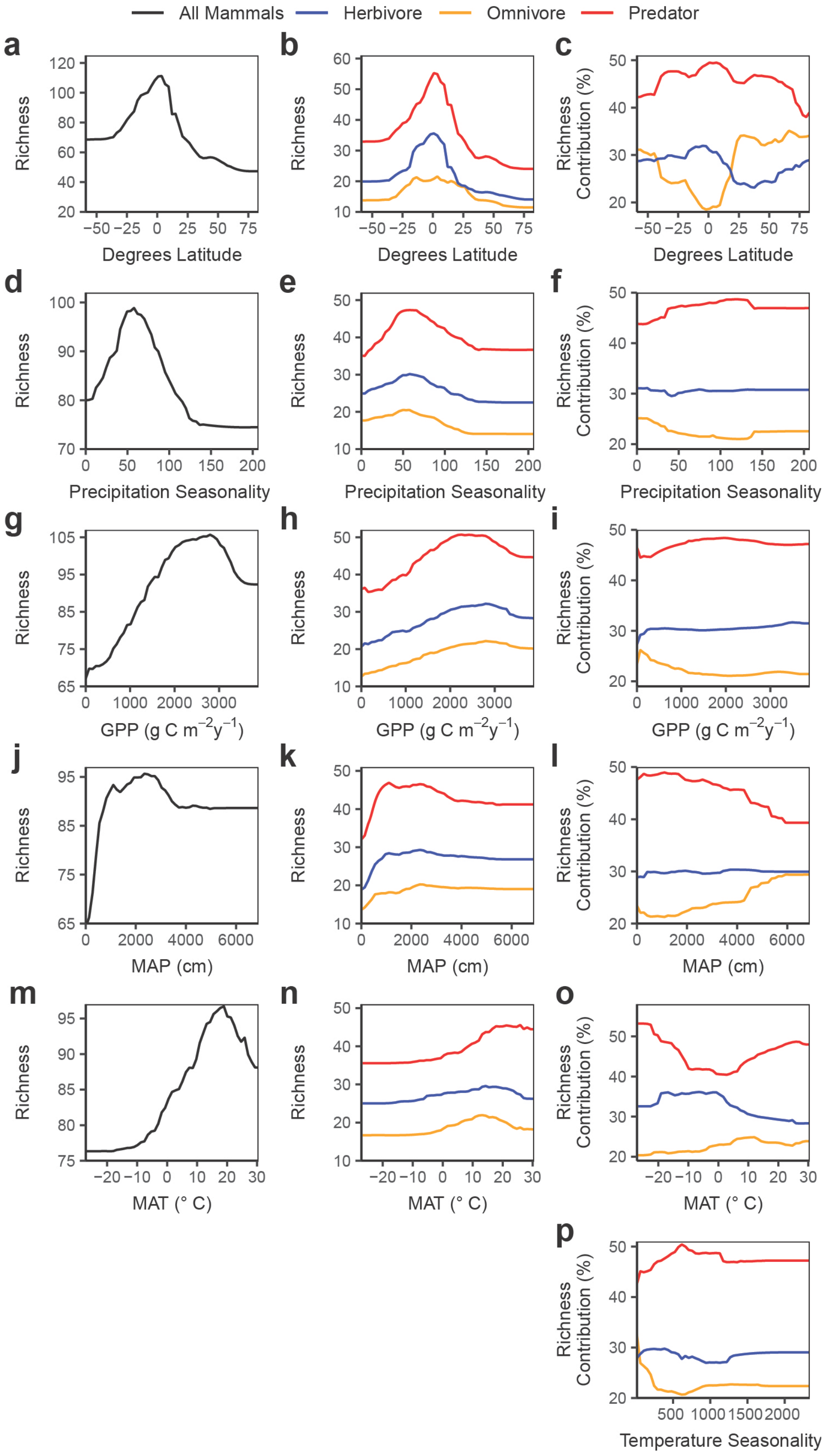

Over-represented trophic level(s)
None
Herbivore
Omnivore
Predator
Herb + Omni
Herb + Pred
Pred + Omni

Figure 4


All Mammals
Herbivore
Omnivore
Predator
a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
Richness
Richness Contribution (%)
Degrees Latitude
Precipitation Seasonality
GPP (g C m^{-2}y^{-1})
MAP (cm)
MAT (° C)
Temperature Seasonality
−50 −25 0 25 50 75
0 50 100 150 200
0 1000 2000 3000
0 2000 4000 6000
−20 −10 0 10 20 30
500 1000 1500 2000

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