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Research article

The division of food space among mammalian species on biomes

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Understanding how species' ecological partitioning functions across biomes is fundamental to macroecology and conservation biology. Here, we examine the global distribution of dietary strategies in terrestrial mammals, focusing on how biome specialization modulates trophic diversity and structure at a broad geographical scale. Using species-level data from over 3600 terrestrial mammal species, we constructed a multivariate dietary space and quantified the area, redundancy, dispersion, uniqueness, and turnover of trophic strategies across ten major biomes. Species were classified as biome specialists, moderate generalists, or extreme generalists based on their biome breadth. By analysing biome specialists and generalists separately, we show that biome specialists tend to exhibit more constrained and compositionally distinct dietary niches in less productive biomes, while generalists, particularly moderate generalists, dominate functional space occupancy in all biomes, even the harsher ones such as tundra and taiga. This highlights how environmental constraints and ecological roles shape trophic strategies at a global scale. Notably, extreme generalists tended to exhibit more carnivorous or insectivorous diets, suggesting a strategy based on mobile predation or opportunism rather than a highly diversified omnivory. Despite these general patterns, highly productive biomes supported the greatest diversity of dietary strategies, with higher functional redundancy and niche packing. Nestedness and turnover analyses revealed that biome specialists diets are often subsets of generalists diets, but with significant compositional shifts across biomes. These findings underscore the dual role of biome generalists as both functional stabilizers and potential limiters of ecological diversity, and highlight the vulnerability of specialist species to global change. Our study offers a mechanistic framework for understanding how dietary strategies interact with environmental filtering, and for identifying functional risks in changing ecosystems.

Keywords: biome specialization, diet, feeding strategies, generalists, macroecology, specialists

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Introduction

Macroecology and biogeography aim to unveil large-scale biodiversity patterns to find the so-called general 'laws' of life on Earth (Lawton 1999). These disciplines have increasingly adopted the theoretical framework and methods of community ecology, where large spatial units – analogous to ecological plots – summarize species composition. Trait databases and phylogenies are then linked to these assemblages to map average values (e.g. body size, diversification rate) or aggregated metrics (e.g. species richness) (Jetz and Rahbek 2002, Rodríguez et al. 2008). This pixel-based, community-level approach has been pivotal in revealing global patterns (Díaz et al. 2016, Galván et al. 2025), but often collapses within-community variation into single summary values, potentially obscuring internal trait structure within ecological units (Blonder et al. 2014).

A complementary perspective comes from paleobiology, which considers how large-scale environmental dynamics shape trait evolution. In the 1980s and 1990s, palaeontologists explored the role of biomes as macroecological arenas, suggesting that biome dynamics, shaped by past climatic changes, acted as major forces shaping lineage evolution (Vrba 1987, 1992). According to this perspective, large-scale environmental changes result in biome fragmentation, which primarily affects biome-specialist species by resource limitations or population isolation. In contrast, biome-generalist species may be less affected by global changes (Vrba 1992, Hernández Fernández et al. 2022, Gamboa et al. 2024). Despite its relevance, this concept of biome filtering from evolutionary palaeobiology has rarely been integrated into modern trait-based macroecological studies (but see Hernández Fernández and Vrba 2005a, Cours et al. 2025). Bridging insights from palaeobiology and modern trait ecology may clarify species' ecological roles and vulnerabilities.

Among functional traits, dietary strategies represent a critical axis of ecological differentiation, reflecting how species interact with resource availability across environments (Brown and Maurer 1989, Loxdale and Balog 2025). Recent work has shown ecological conditions and geographic context influence mammalian diet breadth (Cruz et al. 2022, Metz et al. 2024). Some studies have linked diet to biome specialization (Fargallo et al. 2022), or explored how trophic generalism may buffer species against environmental disturbances (Cloyed et al. 2021). Yet, most research has emphasized intraspecific or community-level variation; less is known about how biomes shape dietary diversity across species.

Understanding how mammals occupy dietary space across biomes is thus key to linking functional diversity with environmental context. Functional strategies like dietary specialization influence not only species' niches, but also their resilience to disturbance and their evolutionary potential (Devictor et al. 2010, Clavel et al. 2011). Specialist species often occupy functionally unique positions – traits or combinations of traits not shared with other species – which may confer ecological roles that are difficult to replace (Villéger et al. 2008, Mouillot et al. 2013a). Functional uniqueness, redundancy, and dispersion therefore help assess the organization, vulnerability, and resilience of trophic assemblages at large scales (Carmona et al. 2016). Yet, few studies have examined how these functional properties are structured at biome scales or how they differ between biome generalist and specialist species (Losada et al. 2024).

In this study, we investigate how terrestrial mammals partition dietary functional space across the world's biomes, focusing on ecological specialization. We treat biomes as discrete ecological contexts and test whether biome specialist and generalist species differ systematically in their occupation of functional dietary space. Our main hypothesis is that biome specialists exhibit more restricted and unique dietary profiles – particularly in less productive or environmentally extreme biomes such as tundra, taiga, steppe, or subtropical deserts – whereas biome generalists redundantly cover broader regions of the dietary spectrum. We also predict that productive biomes will support greater overall functional richness and functional redundancy due to the energetic support of more diverse trophic strategies (Duffy et al. 2007).

We use dietary data from the EltonTraits 1.0 database (Wilman et al. 2014), which provides quantitative estimates of trophic resource use for thousands of terrestrial mammals. Although these data are not biome-specific, they describe potential dietary strategies, and when combined with species' biome occupancy, allow us to assess how biomes filter dietary diversity. We classify species as biome specialists, moderate generalists, or extreme generalists according to the number of biomes they occupy – an operational definition aligned with previous studies of niche breadth (Gamboa et al. 2022, Hernández Fernández et al. 2022, Thomas et al. 2024). This dual perspective – linking dietary breadth with biome breadth – enables better understanding of functional roles and vulnerabilities under changing environmental conditions.

To avoid information loss from community-level averaging, we adopt a species-level approach, mapping individual dietary profiles in a multivariate trait space. This approach, inspired by methods in functional ecology (Petchey and Gaston 2002, Laliberté and Legendre 2010), allows us to quantify how the area, dispersion, redundancy, and uniqueness of trophic space varies across biomes and specialization. Rather than testing for trait–environment correlations using regression or mean comparisons alone, we explore the internal structure of the functional space, capturing not only how much of it is filled, but also how it is organized.

Ultimately, our goal is to: 1) quantify how mammalian species with different levels of biome specialization (specialists, moderate generalists, and extreme generalists) differ in their occupation of dietary functional space across global biomes, including metrics such as area, dispersion, redundancy, and uniqueness; 2) examine how environmental factors – particularly biome productivity and harshness – influence the structure and composition of trophic strategies, and whether these relationships are modulated by ecological specialization; and 3) identify biome-scale patterns in the overlap and turnover of dietary strategies between specialists and generalists, to evaluate the potential functional consequences of species loss in different ecological contexts.

Material and methods

Diet and biome data

We compiled species-level dietary data for terrestrial mammals from EltonTraits 1.0 (Wilman et al. 2014), which provides standardized estimates of the relative contribution (%) of ten food categories: invertebrates, endothermic vertebrates, ectothermic vertebrates, unknown vertebrates, fish, carrion, fruit, nectar, seeds, and plant matter. The dataset comprises 5400 species, covering all 137 terrestrial mammalian families (Wilson and Reeder 2005). Values reflect average adult diets derived from literature and expert synthesis, and are widely used in macroecological studies (Song et al. 2020, Carlson et al. 2022). We retained terrestrial species with complete dietary data and sources rated as 'highly to somewhat certain'. In some cases, these estimates were inferred from ecologically similar congeners. We ensured proportions summed to 100% per species, and standardized taxonomic names. Species with missing data or unclear taxonomy were excluded.

Biome occupancy data were obtained from Hernández Fernández et al. (2022), who assign mammal species to one or more of the ten biomes defined in Walter's (1970) classification (Fig. 1A). This framework is widely used in biogeographic research and reflects environmental heterogeneity. We validated a representative subset using IUCN distribution maps in QGIS ver. 3.28 (QGIS Development Team 2022).

The combination of both datasets yielded 3696 terrestrial mammal species with reliable, complete information on both diet and biome occupancy. Though not exhaustive, this functionally rich and diverse subset suits macroecological comparison.

From this, we derived a biome specialization index (BSI), defined as the number of biomes a species occupies. Species with BSI = 1 were classified as specialists, BSI 2–4 as moderate generalists, and BSI ≥ 5 as extreme generalists (Hernández

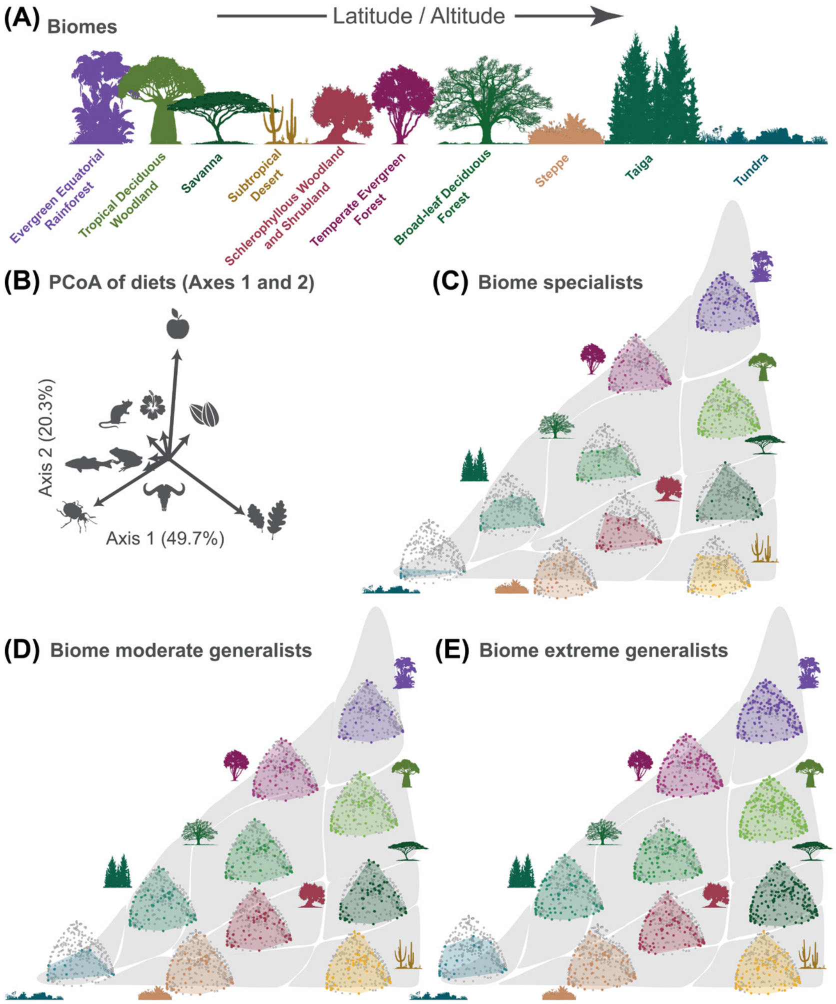

Figure 1. (A) Global biomes considered in this study, classified following Walter (1970). (B) Principal coordinates analysis (PCoA) of mammalian dietary traits showing the first two axes, with vectors indicating diet category loadings. (C–E) Functional dietary space occupied by terrestrial mammals in each biome for three specialization groups: (C) specialists, (D) moderate generalists, and (E) extreme generalists. Colored polygons indicate the convex hulls outlining the dietary trait space of each group within each biome. Points denote individual species. Biomes are ordered by Whittaker's climatic classification (1975), with temperature on the x-axis and precipitation on the y-axis.

Fernández and Vrba 2005b). This index has been used in previous macroevolutionary studies as a proxy for environmental breadth (Cantalapiedra 2011, Menéndez et al. 2021, Gamboa et al. 2022, Hernández Fernández et al. 2022, Thomas et al. 2024).

Construction and analysis of dietary functional space

To analyse how mammals occupy dietary niche space, we constructed a multidimensional functional space using principal coordinates analysis (PCoA). This method summarizes dietary dissimilarities, allowing visualization and quantification of ecological strategies.

Diet proportions were treated as fuzzy variables (percentages summing to 100%). A Gower dissimilarity matrix was computed via the *dist.ktab()* function from the 'ade4' package (Dray and Dufour 2007), and PCoA performed using the *pcoa()* function from the 'ape' package (Paradis and Schliep 2019). The first two axes – explaining 49.3 and 17.6% of total inertia – were retained for subsequent analyses. Axis 1 separated invertebrate-rich from herbivorous diets, while Axis 2 distinguished frugivory and faunivory (Supporting information).

To quantify the portion of dietary space filled by each biome, we calculated the convex hull area encompassing all species in that biome using the *CHullArea()* function from the 'GeoRange' package (Boyle 2017). We expressed this area as a percentage of the total functional space. We repeated this independently for each specialization group – biome specialists, moderate generalists, and extreme generalists – within each biome, allowing us to assess how different ecological strategies contribute to functional space occupancy across environments.

To account for species richness across biomes – particularly the latitudinal diversity gradient (Brown and Lomolino 1998) – we implemented a rarefaction analysis. For each biome, we randomly sampled 100 species (close to the minimum richness observed, in tundra), repeated the sampling 100 times, and calculated convex hull areas. This yielded expected space occupancy under controlled richness. Observed values from specialist species alone ($BSI = 1$) were overlaid for comparison.

Functional nestedness and turnover

To assess whether biome specialists occupy subsets of the functional space filled by generalists or contribute distinct trophic strategies, we quantified nestedness and turnover (Baselga 2010, Keyel and Wiegand 2016) for each biome using convex hull overlap in the two-dimensional dietary space (PCoA axes 1 and 2). For each biome, we computed convex hull for biome specialists ($BSI = 1$), moderate generalists ($1 < BSI < 5$), and extreme generalists ($BSI \geq 5$), using the 'sf' (Pebesma 2018) and 'wk' (Dunnington and Pebesma 2023) R packages.

We then calculated the intersection area (I) between specialists and generalists – i.e. the region of trait space shared by both – and derived two metrics:

$$\text{Nestedness } (N) = \frac{I}{S}$$

$$\text{Turnover}\,(T) = \frac{G - I}{G}$$

where S and G are the areas occupied by specialists and generalists, respectively. Metrics were computed separately for comparisons with moderate and extreme generalists, to assess whether generalists encompass the functional space of specialists or occupy distinct regions. High N indicates nestedness; high T, functional novelty by generalists.

Functional diversity metrics

To assess functional space structure, we calculated two complementary indices. First, functional dispersion (FDis), which quantifies the average distance of species to the centroid of trait space. Higher values indicate greater trait spread. This was calculated using the *dbFD()* function from the 'FD' package (Laliberté et al. 2014).

Second, effective redundancy, defined as the difference between the number of species and the number of unique dietary entities (i.e. species aggregates occupying distinct positions in trait space). To estimate this, we discretized the trait space by rounding the coordinates of each species to two decimal places in both PCoA axes. Species with matching coordinates were considered functionally equivalent (i.e. a unique dietary entity). The number of functionally unique groups was then subtracted from the total number of species in each biome × specialization group, yielding a redundancy score. Lower values indicate higher functional uniqueness, whereas higher values indicate greater overlap in dietary strategies. We computed these metrics by biome and specialization to assess trait space filling.

Functional composition by diet type

To analyse the relative contribution of dietary components across biomes and specialization groups, we computed mean food percentage per group and visualized them in a clustered heatmap using 'ggplot2' (Wickham 2016), and the colourblind-friendly palette 'battus' from the 'lepidochroma' package (Gamboa et al. 2025a). To test group-level dietary differences, we used PERMANOVA with *adonis2()* ('vegan' package; Oksanen et al. 2022), based on Bray–Curtis dissimilarity of diet proportions. Models included biome, specialization, and their interaction, with 999 permutations.

Trophic breadth versus biome breadth

To test whether biome specialization correlates with trophic breadth, trophic breadth was defined as the number of non-zero diet categories per species. We modelled this relationship using linear mixed-effects models (LMMs) with family as a random intercept to account for taxonomic non-independence. Models were fitted using the *lmer()* function from 'lme4' (Bates et al. 2015) and *lme()* from 'nlme' (Pinheiro et al. 2023). Predicted marginal effects were obtained using the 'ggeffects' package (Lüdecke 2018).

Productivity gradient

Biomes were ranked by net primary productivity (NPP), following Whittaker (1975) and Field et al. (1998). The resulting order, from least to most productive, was: subtropical desert, tundra, steppe, sclerophyllous woodland and shrubland, taiga, savanna, broad-leaf deciduous forest, temperate evergreen forest, tropical deciduous woodland, and evergreen equatorial rainforest. This reflects global energy and water availability patterns. We tested productivity–functional space relationships via Spearman, Kruskal–Wallis, and Wilcoxon tests (Benjamini–Hochberg corrected).

Software and reproducibility

All analyses were conducted in R ver. 4.2.3 (www.r-project.org). Scripts and data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.mcvdnckc7.

Results

Structure of mammalian dietary space

The PCoA of dietary profiles showed the first two axes explained 70% of the variance (Axis 1: 49.7%; Axis 2: 20.3%). Axis 1 reflected a gradient from plant-based to animal-based diets, particularly invertebrates and carrion. Axis 2 separated folivore species (feeding on plant matter) from frugivores. (Fig. 1B; Supporting information). These axes reflect main mammalian dietary strategies, from herbivory to invertivory and scavenging (see the Supporting information for loadings).

Patterns of biome specialization across biomes

Biome specialists were never the majority in any biome. The highest proportions were observed in the savanna (44.4%), subtropical desert (40.8%), and sclerophyllous woodland and shrubland (40.1%), and lowest values in the tundra (27.6%) and taiga (30.9%) (Supporting information). Tropical and temperate forests showed intermediate values.

Functional space occupancy by biome

Most biomes exhibited high dietary space occupancy (> 93%), except the tundra (67.3%). Productive biomes like the evergreen rainforest and tropical deciduous woodland reached near-complete occupancy (> 99%; Supporting information). Rarefaction confirmed these patterns were not driven by species richness (Kruskal–Wallis $\chi^2 = 692.44$, df = 9, $p < 0.001$), with significant pairwise differences across most biomes (Fig. 2, Supporting information).

Contributions of specialists and generalists to functional occupancy

When partitioned by specialization, biome generalists, particularly moderate generalists, consistently occupied more dietary space than specialists. In productive biomes like the tropical deciduous woodland and evergreen equatorial rainforest, specialists alone covered more than 97% of space (Fig. 1C; Supporting information), while in harsher biomes like the tundra and taiga, their contribution dropped to 10 and 58%, respectively (Supporting information). In contrast, moderate generalists consistently exceeded 85% occupancy, even in extreme biomes (Fig. 1D); and extreme generalists, although less dominant than moderate ones, often surpassed 90%, except in the tundra, where they occupied only 43% of the dietary space (Fig. 1E; Supporting information).

To further investigate whether biome specialists represent functionally nested subsets of generalist species, we quantified overlap between their occupied regions within the dietary functional space (Supporting information). We found consistently high levels of nestedness across biomes, with specialists occupying at least 98% of their space within

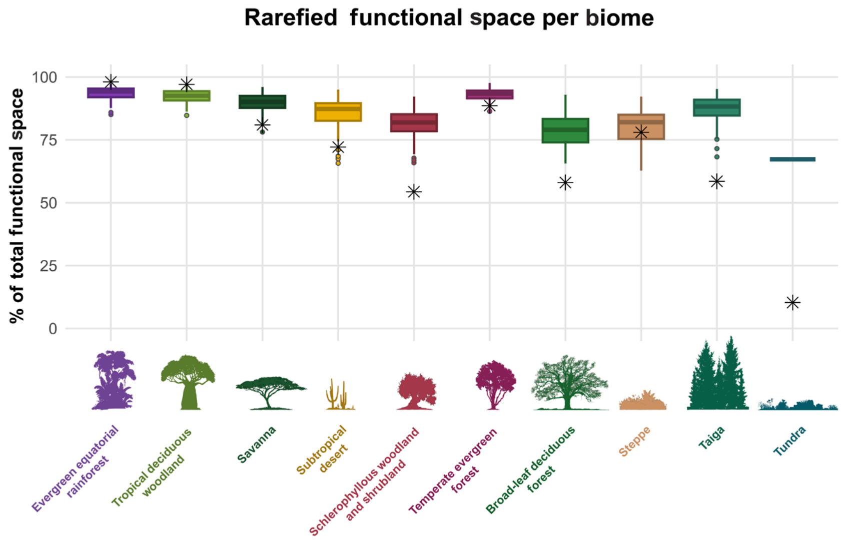

Figure 2. Rarefied functional space occupied by species in each biome, based on 100 iterations of random subsampling of 100 species per biome. Boxplots represent the distribution of rarefied functional space, while black asterisks indicate the observed percentage of dietary space occupied by biome-specialist species.

the bounds of moderate generalists, and slightly lower – but still substantial – overlap with extreme generalists (nestedness $\geq$ 89% in all biomes), indicating that specialists tend to occupy dietary niches already represented by generalist species. In contrast, functional turnover – defined as the proportion of space uniquely occupied by generalists – varied more strongly across biomes. The tundra, taiga, and broad-leaf deciduous forest showed the highest turnover values – up to 0.846 – particularly when comparing specialists with moderate generalists, suggesting that in these environments, generalists occupy distinct trophic roles not filled by specialists. Conversely, productive biomes such as the evergreen equatorial rainforest and tropical deciduous woodland exhibited low turnover (< 0.05), indicating strong functional overlap.

Redundancy and uniqueness

Effective redundancy – quantified as overlapping functional roles – peaked in productive biomes (e.g. tropical deciduous woodland (1202); evergreen equatorial rainforest (923)) and was lowest in the tundra (62) (Supporting information). Moderate generalists drove most redundancy consistently across all biomes. Specialists showed lower values, consistent with their narrower niche overlap and more unique dietary profiles, though exceptions arose in the evergreen equatorial rainforest, tropical deciduous woodland, steppe, and tundra, where specialist redundancy was relatively elevated. In the rainforest and deciduous woodland, this pattern likely reflects the unusually high number of specialists compared to extreme generalists (Supporting information), which increases the probability of functional overlap among them. In contrast, in the steppe and tundra – where the numbers of specialists and extreme generalists are similar – redundancy may arise from convergence in dietary strategies under strong environmental filtering.

Conversely, functional uniqueness – how ecologically distinct a species is – was higher among biome specialists (mean = 0.0019) compared to moderate (0.0011) or extreme generalists (0.0002). This global pattern was strongly supported by statistical tests (Kruskal–Wallis: $\chi^2 = 95.43$, $p < 0.001$; all Wilcoxon pairwise $p < 0.001$). Biome level differences were significant in highly productive environments such as the evergreen equatorial rainforest and tropical deciduous woodland, as well as in the subtropical desert and taiga (Supporting information), but not in the tundra, broad-leaf deciduous forest, steppe, and sclerophyllous woodland. Several tropical species, such as *Poiana leightoni*, *Wyulda squamicaudata*, and *Melursus ursinus* occupied highly peripheral and unique positions in dietary space.

Functional dispersion across specialization groups

Globally, functional dispersion (FDis) – reflecting trait space spread – did not differ significantly across specialization groups (Kruskal–Wallis: $\chi^2 = 3.86$, $p = 0.1449$). Still, specialist species tended to cluster more in biomes like the steppe, broad-leaf forest, and tundra, suggesting environmental filtering or niche convergence (Supporting information).

Relationship between biome breadth and trophic generalism

We compared mixed-effects models treating BSI as either continuous or categorical. The categorical model showed a significantly better fit (ΔAIC = 58.79; $\chi^2 = 74.78$, df = 8, $p < 0.0001$), indicating a non-linear relationship between biome breadth and trophic breadth. In the best-fitting model – including family as a random intercept – trophic breadth increased from specialists (BSI = 1) to moderate generalists (BSI = 2–4), and peaked among extreme generalists with BSI values of 5 to 8. Strongest effects were at BSI = 7 (estimate = 0.48, $p < 0.001$) and BSI = 8 (estimate = 0.42, $p < 0.001$). However, species with the highest biome breadth (BSI = 9) showed a significant decline in trophic breadth (estimate = −0.35, $p < 0.001$). This suggests that trophic generalism increases with biome occupancy up to a threshold, beyond which hyper-generalists may maintain narrow but flexible diets across environments (Fig. 3; Supporting information).

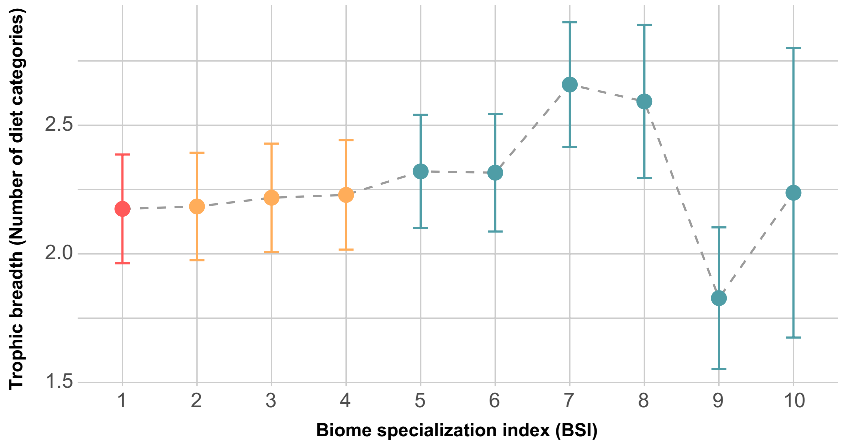

Figure 3. Relationship between biome specialization (BSI) and trophic breadth in terrestrial mammals. Points and error bars show model-predicted trophic breadth and 95% confidence intervals across BSI levels. Colors indicate specialization groups: red = specialists, yellow = moderate generalists, blue = extreme generalists. Dotted line connects marginal means across BSI levels for visual guidance only.

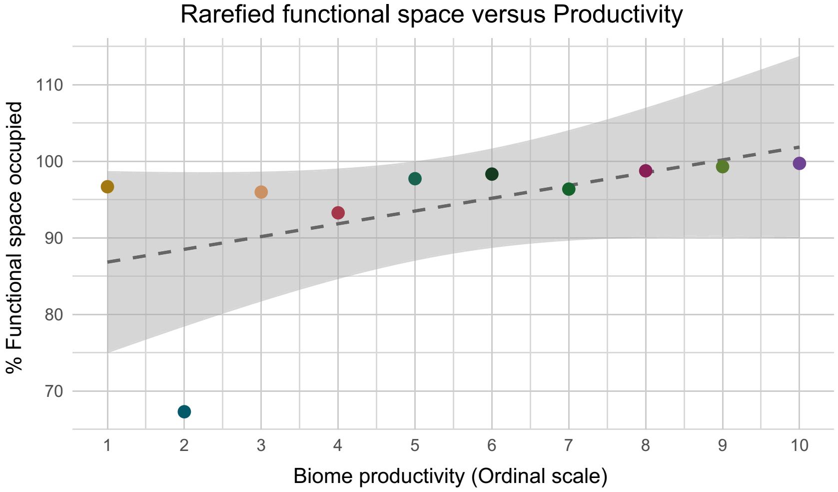

Figure 4. Relationship between biome productivity and functional space occupation. Each point represents a biome, and the y-axis shows the percentage of total functional space occupied after rarefaction (100 iterations of 100 species). A linear regression line (dashed) illustrates the positive association between productivity and functional richness across biomes.

Influence of productivity on functional occupancy

Dietary space occupancy increased with productivity (LM: $\beta = 1.87$, $\rho = 0.72$, $p = 0.024$), supporting the link between energy input and trophic diversity (Fig. 4). This relationship remained significant after controlling for species richness via rarefaction, suggesting a robust link between energy availability and trophic trait diversification across biomes.

Variation in trophic composition across biomes and strategies

A detailed examination of dietary composition revealed contrasting trophic strategies across specialization groups and biomes. Specialists in cold biomes (e.g. tundra and taiga) relied heavily on vegetative matter, which made up over 60–70% of their diets. In contrast, specialists in tropical biomes had more diverse diets, incorporating fruit, seeds, and invertebrates (Fig. 5). This gradient illustrates strong environmental filtering on dietary strategies, where limited resource diversity selects for narrower, more predictable diets in some extreme biomes.

Moderate generalists had plant-dominated intake, with varying fruits, seeds, and invertebrates. Although they exhibited slightly greater trophic diversity than specialists in extreme environments, their reliance on vegetative resources remained strong. Extreme generalists showed consistent profiles across biomes, combining insect and fruit consumption with occasional use of small vertebrates. Patterns were consistent across biomes, likely because the same species occur in several biomes, and suggest a predominance of species with a mobile predatory or opportunistic strategy that allows them to persist in diverse environments without expanding their dietary spectrum.

A PERMANOVA confirmed that both biome ($r^2 = 0.032$) and specialization ($r^2 = 0.011$), as well as their interaction ($r^2 = 0.007$), exert significant effects on dietary composition (Supporting information). Though effect sizes were small – expected in analyses of communities with high species and trait diversity – these results highlight the combined influence of ecological context and specialization on trophic structure.

Discussion

The variation in dietary specialization observed across biomes (Fig. 1C–E) reflects strong environmental filtering driven by resource availability, which in turn is associated with seasonal variations in productivity (Stone 2007). Arid and seasonal environments like the savanna and subtropical desert harboured the highest proportions of dietary specialists (Supporting information), suggesting that temporally predictable but spatially heterogeneous resources may promote specialization (Futuyma and Moreno 1988). In contrast, low-productivity biomes such as tundra and taiga exhibited reduced specialization, highlighting the adaptive advantage of generalist strategies under environmentally extreme, resource-scarce, and highly seasonal conditions (Brown 1984, Futuyma and Moreno 1988).

Our results further demonstrate that terrestrial mammals collectively occupy a substantial portion of the available dietary space in most biomes, exceeding 90% in most environments. The tundra stood out as an exception, with mammals occupying only 67% of the dietary space (Supporting information) – underscoring the ecological limitations imposed by extremely cold climates (Peck et al. 2006, Williams et al. 2015).

One of the most striking findings is the functional dominance of generalist species. Across all biomes, generalists – particularly moderate ones – consistently occupied nearly the entire dietary space, even when controlling for species richness. In some ecosystems – such as the broad-leaf deciduous forest and tundra – generalists accounted for 100% of the space filled. This highlights their role as ecological

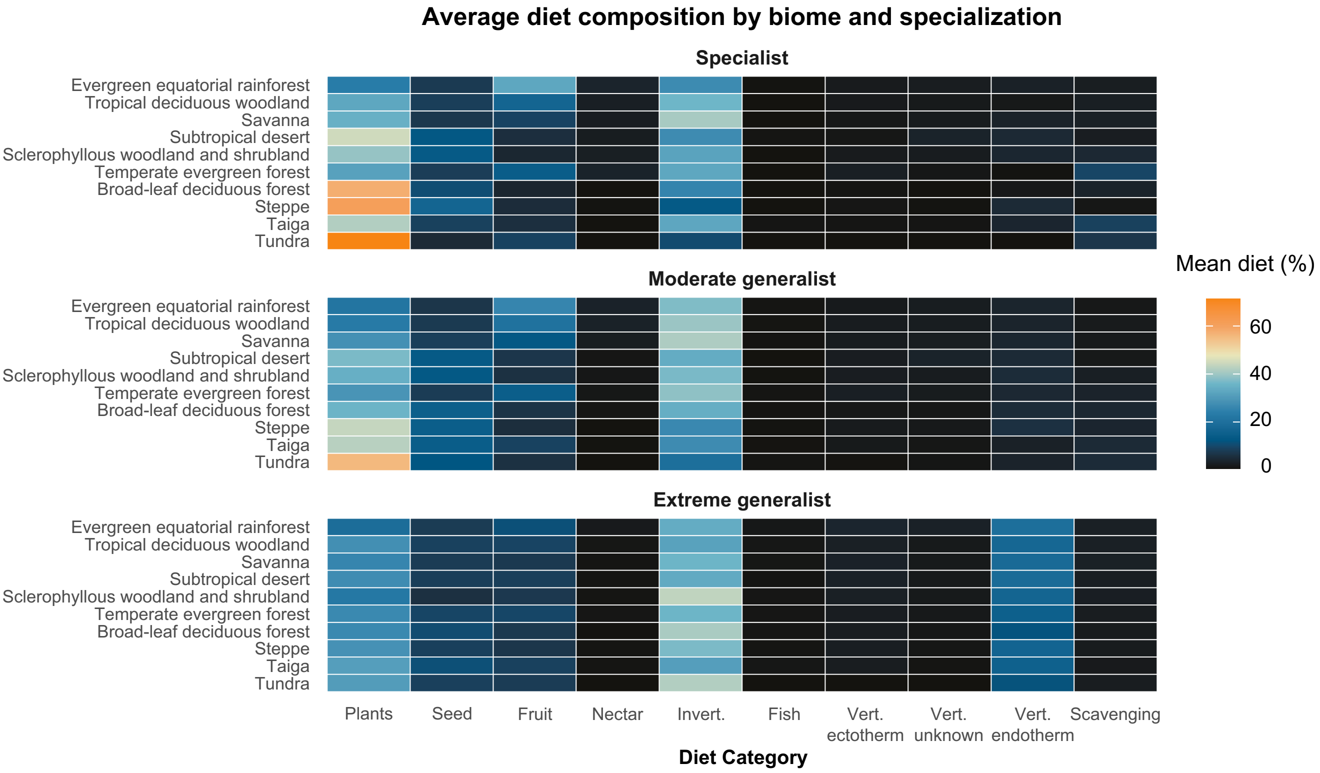

Figure 5. Average diet composition of terrestrial mammal species across biomes and specialization groups. Heatmaps show the mean percentage use of ten dietary resource categories for specialists, moderate generalists, and extreme generalists.

'scaffolders', maintaining trophic structure across environmental gradients. However, generalists' dominance also leads to functional homogenization: although generalists fill much of the dietary space, they contribute less to the total diversity of trophic roles.

In contrast, dietary specialists exhibited more restricted trophic space occupancy – especially in environmentally extreme or seasonal biomes – yet consistently displayed higher functional uniqueness and lower redundancy. This suggests that although biome specialists occupy smaller portions of trophic space, they fill distinct roles that are not replicated by generalists. Examples include species like *Melursus ursinus* (sloth bear), endemic to the tropical deciduous forest, whose myrmecophagous – frugivorous diet (Laurie and Seidensticker 1977) is not mirrored by other sympatric mammals. These patterns reinforce concerns about vulnerability of functionally unique species (Mouillot et al. 2013b), whose extinction implies direct loss of ecological functions (Mouillot et al. 2013a), especially in productive biomes where dietary strategies diversify the most.

Nestedness and turnover analyses refined this interpretation. Specialists often occupied regions nested within the broader dietary space of generalists, especially in productive tropical and temperate biomes. This indicates that specialists refine and specialize pre-existing trophic strategies, rather than introducing entirely novel functions (Devictor et al. 2010, Levis and Pfennig 2019). However, functional turnover strongly varied across biomes: cold ecosystems like tundra and taiga exhibited greater turnover, with specialists occupying peripheral or even exclusive areas of dietary space. In ecologically constrained systems, specialists may functionally innovate by exploiting unique combinations of scarce resources. For instance, tundra specialists adopt limited but distinctive diets, such as herbivory focused on mosses and sedges, or faunivory targeting small invertebrates (Bliss 1962, Hope 2020). These strategies reflect both the scarcity of resources and the energetic demands imposed by extremely cold environments. Thus, while specialists often exist within generalists functional bounds, they may also contribute complementary, non-redundant functions – especially in harsher environments. These findings have direct conservation implications: maintaining biome specialist species is critical for preserving unique trophic roles and ensuring long-term ecological resilience.

The combination of functional dispersion (FDis) and effective redundancy further revealed important differences in functional structure across biomes and strategies. In complex tropical systems, high redundancy and stable FDis suggest dense functional packing and enhanced resilience (Aquilué et al. 2020, Adams et al. 2022). In contrast, in extreme, and less productive, environments like tundra or steppe, specialists exhibited lower redundancy and higher uniqueness, indicating heightened vulnerability to species loss (Fischer and de Bello 2023).

Generalists are considered ecological insurance against environmental change due to flexible resource use and broad distribution (Clavel et al. 2011). Our results support this idea, showing that generalists contribute disproportionately to effective redundancy across all biomes. This ecological redundancy is valuable in variable or disturbed systems, where species loss may not entail immediate functional collapse (Naeem 1998). However, these functional patterns are further modulated by environmental gradients, particularly productivity, which shapes both the breadth and the redundancy of functional space across biomes (Yan et al. 2024). This dominance of generalists, however, can obscure underlying functional vulnerability; when generalists fill a large portion of the trophic space, it may create a false sense of functional richness. This 'averaging effect' can mask the decline of functionally unique species and lead to underestimation of ecological erosion in aggregated trait analyses. Therefore, it is essential to consider trait distributions across ecological strategies, not just overall ecospace occupancy.

The differentiation between productive and extreme environments aligns with broader ecological theory linking resource availability to functional structure. Specifically, the positive correlation we observed between biome productivity and functional space occupation reinforces the hypothesis that energetic richness promotes trophic (Duffy et al. 2007, Adkins et al. 2023) and morphological (Shepherd 1998, Lintulaakso and Kovarovic 2016) diversification. In productive biomes, the abundance and variety of resources likely facilitate the coexistence of more ecologically differentiated species, expanding both the area and complexity of dietary space. Conversely, in harsher environments, resource scarcity restricts both the number of viable trophic strategies and the breadth of functional roles, leading to tighter clustering of species within the ecomorphological space (Shepherd 1998) and increased vulnerability to species loss (Fontaneto et al. 2017).

Environmental gradients further shape these patterns. The reduced use of fruits and nectar in cold or dry biomes reinforces the idea that the resource availability constrains dietary diversity. In extratropical systems, resources associated with reproductive plant structures, such as flowers and fruits, decline markedly due to climatic factors like aridity and seasonality (Bonan and Shugart 1989, Richardson et al. 2013, Hawkins et al. 2018), forcing biome specialists to rely more heavily on more constant or predictable resources like insects or seeds (Herrera 1984). This mirrors patterns observed in frugivorous birds along latitudinal gradients, where frugivory diminishes with increasing latitude and declining primary productivity (Kissling et al. 2009). In contrast, biome generalist species such as *Pteropus scapulatus* and *Bassariscus astutus* can migrate across habitats or adjust their diets seasonally, allowing them to maintain broader functional roles despite local and/or seasonal environmental constraints (Ratcliffe 1932, Poglayen-Neuwall and Toweill 1988). At polar latitudes, in tundra ecosystems, trophic strategies are further constrained by the need for calorically dense and consistently available food sources, such as mosses, lichens, and animal matter (Bliss 1962, Hope 2020). The energetic demands of surviving in cold climates further select for diets high in fat and protein rather than sugars (Young 1976, Marchand 2014), limiting not only the diversity of viable dietary strategies but also the degree of functional overlap among species.

Tundra ecosystems stood out as the most constrained, both in terms of total trophic space and the contribution of specialists. Species in this biome, particularly specialists, exhibited low redundancy, high uniqueness, and minimal functional overlap with generalists – traits strongly associated with high ecological vulnerability (Cloyed et al. 2021). For example, *Lemmus lemmus*, a tundra specialist with a plant-heavy diet (Moen 1990), occupies an exclusive position in trophic space that no other species replicates. As global warming continues to disproportionately affect high-latitude ecosystems (Gonzalez et al. 2010, Kruse et al. 2023), species inhabiting these fragile systems may face compounded risks due to both environmental exposure and functional irreplaceability. These findings underscore the urgency of targeted conservation strategies in polar ecosystems, as their high vulnerability (Li et al. 2018) means even a few species losses may result in irreversible functional collapse (MacDougall et al. 2013).

Our models support the hypothesis that dietary breadth increases with ecological breadth (Brown 1984, Fargallo et al. 2022), but not uniformly. Species occupying a moderate number of biomes (BSI = 3–6) exhibited the highest trophic diversity, whereas those found in all nine biomes – such as *Canis latrans*, *Panthera pardus*, and *Mus musculus* – showed narrower and more faunivorous diets on average. In ecological terms, consuming animals offers a more generalized strategy than consuming plants, which often require highly specialized morpho-physiological adaptations to overcome structural and chemical defences (Brodie and Brodie 1999, Hernández Fernández and Vrba 2005c). Consequently, species with faunivorous diets may persist across diverse environments by adjusting prey identity rather than foraging mode. This suggests that broad geographic distribution does not always imply trophic plasticity, supporting the notion that generalism is a multidimensional trait (Devictor et al. 2010), and that spatial and dietary flexibility can evolve independently. In contrast, biome specialists exhibited sharp dietary contrasts across environments, with those in cold, unproductive biomes relying primarily on vegetative material, while tropical specialists consumed more fruits, nectar, and invertebrates (Fig. 5).

By integrating classical metrics (e.g. FDis, redundancy, uniqueness) with spatial overlap measures (nestedness and turnover), our framework offers a more mechanistic understanding of functional structure. It reveals not just how much of the trophic space is filled, but also who fills it and how uniquely. This framework informs conservation by revealing when species loss could result in either minimal functional impact or substantial functional erosion. Specialist species – particularly in productive tropical biomes – emerge as irreplaceable providers of ecological functions, while generalists ensure continuity and buffer ecosystems against environmental change. Conservation strategies must therefore aim to preserve both dimensions of functionality: the breadth provided by generalists and the depth afforded by specialists. This integrated view is key for conservation strategies that protect ecosystem function and evolutionary potential.

Looking ahead, future research would benefit from finer-grained dietary data at the species level. Our categorization, though comprehensive, simplifies complex trophic behaviours, particularly in species-rich biomes. For example, frugivorous species may differ in the specific types of fruit they consume or in their seasonal specialization. Such micro-dietary partitioning, especially among tropical specialists, may drive niche differentiation not captured by broad dietary classes (Eby 1998, Cromsigt and Olff 2006, Schleuning et al. 2011). Expanding datasets with detailed foraging observations, stable isotopes, or DNA metabarcoding could illuminate hidden layers of trophic specialization and sharpen our understanding of functional roles.

More broadly, our findings underscore the importance of combining species-level trait analyses with community-level summaries in macroecological studies. Relying solely on aggregate metrics risks masking underlying ecological vulnerabilities, particularly those associated with specialist loss or functional homogenization under environmental change.

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Sara Gamboa: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Sofía Galván**: Writing – review and editing (equal). **Mar Sobral**: Conceptualization (equal). **Manuel Hernández Fernández**: Writing – review and editing (equal). **Sara Varela**: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

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Supporting information

The Supporting information associated with this article is available with the online version.

References

Adams, C. S., Saenz, D., Kidd, K. R. and Schalk, C. M. 2022. Disparate patterns of taxonomic and functional predator diversity under different forest management regimes. – Ecol. Indic. 136: 108591.

Adkins, J., Hammill, E., Abdulwahab, U. A., Draper, J. P., Wolf, J. M., McClure, C. M., González Ortiz, A. A., Chavez, E. A. and Atwood, T. B. 2023. Environmental variables drive spatial patterns of trophic diversity in mammals. – Ecol. Lett. 26: 1940–1950.

Aquilué, N., Filotas, É., Craven, D., Fortin, M. J., Brotons, L. and Messier, C. 2020. Evaluating forest resilience to global threats using functional response traits and network properties. – Ecol. Appl. 30: e02095.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. – Global Ecol. Biogeogr. 19: 134–143.

Bates, D., Maechler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Bliss, L. C. 1962. Adaptations of arctic and alpine plants to environmental conditions. – Arctic 15: 117–144.

Blonder, B., Lamanna, C., Violle, C. and Enquist, B. J. 2014. The n-dimensional hypervolume. – Global Ecol. Biogeogr. 23: 595–609.

Bonan, G. B. and Shugart, H. H. 1989. Environmental factors and ecological processes in boreal forests. – Annu. Rev. Ecol. Syst. 20: 1–28.

Boyle, J. 2017. GeoRange: calculating geographic range from occurrence data. – R package ver. 0.1.0, https://CRAN.R-project.org/package=GeoRange.

Brodie III, E. D. and Brodie Jr, E. D. 1999. Predator–prey arms races: asymmetrical selection on predators and prey may be reduced when prey are dangerous. – J. Bio Sci. 49: 557–568.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. – Am. Nat. 124: 255–279.

Brown, J. H. and Lomolino, M. V. 1998. Biogeography. – Sinuer Associates Publishers.

Brown, J. H. and Maurer, B. A. 1989. Macroecology: the division of food and space among species on continents. – Science 243: 1145–1150.

Cantalapiedra, J. L., Hernández Fernández, M. and Morales, J. 2011. Biomic specialization and speciation rates in ruminants (Cetartiodactyla, Mammalia): a test of the resource-use hypothesis at the global scale. – PLoS One 6: e28749.

Carlson, C. J., Albery, G. F., Merow, C., Trisos, C. H., Zipfel, C. M., Eskew, E. A., Olival, K. J., Ross, N. and Bansal, S. 2022. Climate change increases cross-species viral transmission risk. – Nature 607: 555–562.

Carmona, C. P., De Bello, F., Mason, N. W. H. and Lepš, J. 2016. Traits without borders: integrating functional diversity across scales. – Trends Ecol. Evol. 31: 382–394.

Clavel, J., Julliard, R. and Devictor, V. 2011. Worldwide decline of specialist species: toward a global functional homogenization? – Front. Ecol. Environ. 9: 222–228.

Cloyed, C. S., Balmer, B. C., Schwacke, L. H., Wells, R. S., Berens McCabe, E. J., Barleycorn, A. A., Allen, J. B., Rowles, T. K., Smith, C. R., Takeshita, R., Townsend, F. I., Tumlin, M. C., Zolman, E. S., and Carmichael, R. H. 2021. Interaction between dietary and habitat niche breadth influences cetacean vulnerability to environmental disturbance. – Ecosphere 12: e03759.

Cours, J., Elo, M., Pithon, J., Triviño, M., Mönkkönen, M., Hagge, J., Lehikoinen, A. and Duflot, R. 2025. Changes in abundance and distribution of European forest bird populations depend on biome, ecological specialisation and traits. – Ecography: e07582.

Cromsigt, J. P. G. M. and Olff, H. 2006. Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach. – Ecology 87: 1532–1541.

Cruz, L. R., Muylaert, R. L., Galetti, M. and Pires, M. M. 2022. The geography of diet variation in Neotropical Carnivora. – Mamm. Rev. 52: 112–128.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S. and Mouquet, N. 2010. Defining and measuring ecological specialization. – J. Appl. Ecol. 47: 15–25.

Díaz, S. et al. 2016. The global spectrum of plant form and function. – Nature 529: 167–171.

Dray, S. and Dufour, A. B. 2007. The ade4 package: implementing the duality diagram for ecologists. – J. Stat. Softw. 22: 1–20.

Duffy, J. E., Cardinale, B. J., France, K. E., McIntyre, P. B., Thébault, E. and Loreau, M. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. – Ecol. Lett. 10: 522–538.

Dunnington, D. and Pebesma, E. 2023. wk: lightweight well-known geometry parsing. – R package ver. 0.9.1, https://CRAN.R-project.org/package=wk.

Eby, P. 1998. An analysis of diet specialization in frugivorous *Pteropus poliocephalus* (Megachiroptera) in Australian subtropical rainforest. – Aust. J. Ecol. 23: 443–456.

Fargallo, J. A., Navarro-López, J., Cantalapiedra, J. L., Pelegrin, J. S. and Hernández Fernández, M. 2022. Trophic niche breadth of Falconidae species predicts biomic specialisation but not range size. – Biology 11: 522.

Field, C. B., Behrenfeld, M. J., Randerson, J. T. and Falkowski, P. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. – Science 281: 237–240.

Fischer, F. M. and de Bello, F. 2023. On the uniqueness of functional redundancy. – npj Biodiversity 2: 23.

Fontaneto, D., Panisi, M., Mandrioli, M., Montardi, D., Pavesi, M. and Cardini, A. 2017. Estimating the magnitude of morphoscapes: how to measure the morphological component of biodiversity in relation to habitats using geometric morphometrics. – Sci. Nat. 104: 55.

Futuyma, D. J. and Moreno, G. 1988. The evolution of ecological specialization. – Annu. Rev. Ecol. Syst. 19: 207–233.

Galván, S., Varela, S. and Gamboa, S. 2025. Classic hypotheses of area, time, and climatic stability fall short in explaining high tropical species richness. – J. Biogeogr. 52: e15126.

Gamboa, S., Condamine, F. L., Cantalapiedra, J. L., Varela, S., Pelegrín, J. S., Menéndez, I., Blanco, F. and Hernández Fernández, M. 2022. A phylogenetic study to assess the link between biome specialization and diversification in swallowtail butterflies. – Global Change Biol. 28: 5901–5913.

Gamboa, S., Galván, S. and Varela, S. 2024. Vrba was right: historical climate fragmentation, and not current climate, explains mammal biogeography. – Global Change Biol. 30: e17339.

Gamboa, S., Castro Insua, A., Galván, S., Sotelo, G., Matamala-Pagès, M., Oliver, A., Rey-Rodríguez, I., Méndez-Quintas, E. and Varela, S. 2025a. Lepidochroma: colour palettes inspired by butterflies. – R package ver. 0.1.0, https://CRAN.R-project.org/package=lepidochroma.

Gamboa, S., Galván, S., Sobral, M., Hernández Fernández, M. and Varela, S. 2025b. Data from: The division of food space among mammalian species on biomes. – Dryad Digital Repository, https://doi.org/10.5061/dryad.mcvdnckc7.

Gonzalez, P., Neilson, R. P., Lenihan, J. M. and Drapek, R. J. 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. – Global Change Biol. 19: 755–768.

Hawkins, B. A., Thomson, J. R. and Mac Nally, R. 2018. Regional patterns of nectar availability in subtropical eastern Australia. – Landsc. Ecol. 33: 999–1012.

Hernández Fernández, M. and Vrba, E. S. 2005a. Rapoport effect and biomic specialization in African mammals: revisiting the climatic variability hypothesis. – J. Biogeogr. 32: 903–918.

Hernández Fernández, M. and Vrba, E. S. 2005b. Macroevolutionary processes and biomic specialization: testing the resource-use hypothesis. – Evol. Ecol. 19: 199–219.

Hernández Fernández, M. and Vrba, E. S. 2005c. Body size, biomic specialization and range size of African large mammals. – J. Biogeogr. 32: 1243–1256.

Hernández Fernández, M. et al. 2022. Macroevolution and climate changes: a global multi-family test supports the resource-use hypothesis in terrestrial mammals. – Hist. Biol. 34: 1471–1479.

Herrera, C. M. 1984. A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. – Ecol. Monogr. 54: 1–23.

Hope, A. G. 2020. Arctic tundra mammals. – In: DellaSala, D. A. and Goldstein, M. I. (eds), Encyclopedia of the world's biomes. – Elsevier, pp. 356–373.

Jetz, W. and Rahbek, C. 2002. Geographic range size and determinants of avian species richness. – Science 297: 1548–1551.

Keyel, A. C. and Wiegand, K. 2016. Validating the use of unique trait combinations for measuring multivariate functional richness. – Methods Ecol. Evol. 7: 929–936.

Kissling, W. D., Böhning–Gaese, K. and Jetz, W. 2009. The global distribution of frugivory in birds. – Global Ecol. Biogeogr. 18: 150–162.

Kruse, S., Shevtsova, I., Heim, B., Pestryakova, L. A., Zakharov, E. S. and Herzschuh, U. 2023. Tundra conservation challenged by forest expansion in a complex mountainous treeline ecotone as revealed by spatially explicit tree aboveground biomass modeling. – Arct. Antarct. Alp. Res. 55: 2220208.

Laliberté, E. and Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. – Ecology 91: 299–305.

Laliberté, E., Legendre, P., Shipley, B. and Laliberté, M. E. 2014. Package 'fd'. Measuring functional diversity from multiple traits, and other tools for functional ecology. – R package, https://CRAN.R-project.org/package=FD.

Laurie, A. and Seidensticker, J. 1977. Behavioural ecology of the sloth bear (*Melursus ursinus*). – J. Zool. 182: 187–204.

Lawton, J. H. 1999. Are there general laws in ecology? – Oikos 84: 177–192.

Levis, N. A. and Pfennig, D. W. 2019(1897). Plasticity-led evolution: evaluating the key prediction of frequency-dependent adaptation. – Proc. R. Soc. B 286: 20182754.

Li, D., Wu, S., Liu, L., Zhang, Y. and Li, S. 2018. Vulnerability of the global terrestrial ecosystems to climate change. – Global Change Biol. 24: 4095–4106.

Lintulaakso, K. and Kovarovic, K. 2016. Diet and locomotion, but not body size, differentiate mammal communities in worldwide tropical ecosystems. – Palaeogeogr. Palaeoclimatol. Palaeoecol. 454: 20–29.

Losada, M., Suárez-Couselo, M. and Sobral, M. 2024. Geographic distribution of mammal diets. – Web Ecol. 24: 71–79.

Loxdale, H. D. and Balog, A. 2025. Preface: the paradox of generalism, a philosophical perspective. – Front. Ecol. Evol. 13: 1562456.

Lüdecke, D. 2018. ggeffects: tidy data frames of marginal effects from regression models. – J. Open Source Softw. 3: 772.

MacDougall, A. S., McCann, K. S., Gellner, G. and Turkington, R. 2013. Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. – Nature 494: 86–89.

Marchand, P. J. 2014. Life in the cold: an introduction to winter ecology. – Univ. Press New England.

Menéndez, I., Gómez Cano, A. R., Cantalapiedra, J. L., Peláez-Campomanes, P., Álvarez-Sierra, M. Á. and Hernández Fernández, M. 2021. A multi-layered approach to the diversification of squirrels. – Mamm. Rev. 51: 66–81.

Metz, L., Monteiro-Filho, E. L. A., Fusco-Costa, R., D'Bastiani, E. and Padial, A. A. 2024. Unravelling the trophic guild structure of Neotropical Carnivora: diet specialisations, spatial variation and phylogenetic drivers. – Mamm. Rev. 54: 13–29.

Moen, J. 1990. Summer grazing by voles and lemmings upon subarctic snow-bed and tall herb meadow vegetation – an enclosure experiment. – Ecography 13: 316–324.

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H. and Bellwood, D. R. 2013a. A functional approach reveals community responses to disturbances. – Trends Ecol. Evol. 28: 167–177.

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, T., Renaud, J. and Thuiller, W. 2013b. Rare species support vulnerable functions in high-diversity ecosystems. – PLoS Biol. 11: e1001569.

Naeem, S. 1998. Species redundancy and ecosystem reliability. – Conserv. Biol. 12: 39–45.

Oksanen, J. et al. 2022. vegan: community ecology package. – R package ver. 2.5-7. 2020, https://CRAN.R-project.org/package=vegan.

Paradis, E. and Schliep, K. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. – Bioinformatics 35: 526–528.

Pebesma, E. 2018. Simple features for R: standardized support for spatial vector data. – R J. 10: 439–446.

Peck, L. S., Convey, P. and Barnes, D. K. A. 2006. Environmental constraints on life histories in Antarctic ecosystems: tempos, timings and predictability. – Biol. Rev. 81: 75–109.

Petchey, O. L. and Gaston, K. J. 2002. Functional diversity (FD), species richness and community composition. – Ecol. Lett. 5: 402–411.

Pinheiro, J., Bates, D. and R Core Team 2023. nlme: linear and nonlinear mixed effects models. – R package ver. 3.1-162, https://CRAN.R-project.org/package=nlme.

Poglayen-Neuwall, I. and Toweill, D. E. 1988. *Bassariscus astutus*. – Mamm. Species. 327: 1–8.

QGIS Development Team 2022. QGIS geographic information system. – QGIS Association, www.qgis.org/.

Ratcliffe, F. 1932. Notes on the fruit bats (*Pteropus* spp.) of Australia. – J. Anim. Ecol. 1: 32–57.

Richardson, A. D., Carbone, M. S., Keenan, T. F., Czimczik, C. I., Hollinger, D. Y., Murakami, P., Schaberg, P. G. and Xu, X. 2013. Seasonal dynamics and age of stemwood nonstructural carbohydrates in temperate forest trees. – New Phytol. 197: 850–861.

Rodríguez, M. Á., Olalla-Tárraga, M. Á. and Hawkins, B. A. 2008. Bergmann's rule and the geography of mammal body size in the Western Hemisphere. – Global Ecol. Biogeogr. 17: 274–283.

Schleuning, M., Blüthgen, N., Flörchinger, M., Braun, J., Schaefer, H. M. and Böhning-Gaese, K. 2011. Specialization and interaction strength in a tropical plant–frugivore network differ among forest strata. – Ecology 92: 26–36.

Shepherd, U. 1998. A comparison of species diversity and morphological diversity across the North American latitudinal gradient. – J. Biogeogr. 25: 19–29.

Song, S. J. et al. 2020. Comparative analyses of vertebrate gut microbiomes reveal convergence between birds and bats. – mBio 11: e02901-19.

Stone, A. I. 2007. Responses of squirrel monkeys to seasonal changes in food availability in an eastern Amazonian forest. – Am. J. Primatol. 69: 142–157.

Thomas, J. S., Gamboa, S., Hernández Fernández, M., Murillo, O. and Pelegrin, J. S. 2024. Macroevolutionary processes in turtles (Testudines): a view from biomic specialization and historical climatic changes. – Front. Ecol. Evol. 12: 1474500.

Villéger, S., Mason, N. W. H. and Mouillot, D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. – Ecology 89: 2290–2301.

Vrba, E. S. 1987. Ecology in relation to speciation rates: some case histories of Miocene – recent mammal clades. – Evol. Ecol. 1: 283–300.

Vrba, E. S. 1992. Mammals as a key to evolutionary theory. – J. Mammal. 73: 1–28.

Walter, H. 1970. Vegetationszonen und Klima. – Verlag Eugen Ulmer.

Whittaker, R. H. 1975. Communities and ecosystems. – Macmillan.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. – Springer.

Williams, C. M., Henry, H. A. L. and Sinclair, B. J. 2015. Cold truths: how winter drives responses of terrestrial organisms to climate change. – Biol. Rev. 90: 214–235.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M. and Jetz, W. 2014. EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals: ecological archives E095-178. – Ecology 95: 2027.

Wilson, D. E. and Reeder, D. M. (eds) 2005. Mammal species of the world: a taxonomic and geographic reference. – Johns Hopkins Univ. Press.

Yan, H., Schmid, B., Xu, W., Bongers, F. J., Chen, G., Tang, T., Wang, Z., Svenning, J. C., Ma, K. and Liu, X., 2024. The functional diversity–productivity relationship of woody plants is climatically sensitive. – Ecol. Evol. 14: e11364.

Young, R. A. 1976. Fat, energy and mammalian survival. – Am. Zool. 16: 699–710.