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The environmental conditions of endemism hotspots shape the functional traits of mammalian assemblages

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Endemic (small-ranged) species are distributed non-randomly across the globe. Regions of high topography and stable climates have higher endemism than flat, climatically unstable regions. However, it is unclear how these environmental conditions interact with and filter mammalian traits. Here, we characterize the functional traits of highly endemic mammalian assemblages in multiple ways, testing the hypothesis that these assemblages are trait-filtered (less functionally diverse) and dominated by species with traits associated with small range sizes. Compiling trait data for more than 5000 mammal species, we calculated assemblage means and multi-dimensional functional metrics to evaluate the distribution of traits across each assemblage. We then related these metrics to the endemism of global World Wildlife Fund ecoregions using linear models and phylogenetic fourth-corner regression. Highly endemic mammalian assemblages had small average body masses, low fecundity, short lifespans and specialized habitats. These traits relate to the stable climate and rough topography of endemism hotspots and to mammals' ability to expand their ranges, suggesting that the environmental conditions of endemism hotspots allowed their survival. Furthermore, species living in endemism hotspots clustered near the edges of their communities' functional spaces, indicating that abiotic trait filtering and biotic interactions act in tandem to shape these communities.

1. Introduction

As extinctions continue to mount in the Anthropocene, understanding the ecological patterns that govern how vulnerable communities assemble and are distributed is vital for the continued preservation of life on Earth [1,2]. Endemic species, or species with small range sizes, are one such vulnerable group. Because of their limited distributions, they are disproportionately affected by anthropogenic effects like habitat fragmentation and climate change [3–5]. The small natural ranges characteristic of endemic species typically represent either remnants of evolutionarily ancient species that were more widespread in the past (e.g. *Ginkgo biloba* [6], or late-stage taxon cycles [7]) or evolutionarily young species that have recently diverged (e.g. the island fox *Urocyon littoralis* [8]) and/or have never proliferated broadly [9,10]. Although patterns of endemism are correlated with richness, endemism hotspots (areas of high endemism) are environmentally distinct from those of high species richness [11,12]. In particular, endemism hotspots have rougher topography and more stable climates over time than expected given the number of species in the hotspot [13].

The abiotic, environmental pattern of vertebrate endemism on continental scales is well studied [13–17]. However, the biological mechanisms underlying the global pattern of endemism is still unclear, and little consensus has been reached on how the biotic, functional traits of vertebrate species within endemism hotspots might covary with this pattern [15,18,19]. Functional traits are

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Table 1. Table describing all traits considered in this analysis, along with their hypothesized relationships to endemism. These hypotheses were developed from prior literature evaluating trait–range size relationships in individual vertebrate species.

trait	calculation	hypothesis	citation
mass	body mass of adult individual	smaller	[24,26,31,34]
body length	total length from tip of nose to anus	smaller	[26]
longevity	maximum age at death	shorter	[32]
female maturity	amount of time needed for a female to reach sexual maturity	older	[35]
gestation length	length of time of fetal growth	longer	[34–36]
litter size	number of offspring born per litter	smaller	[24,32,34,36]
litters per year	number of litters per female per year	lower	[34]
weaning age	age at which independent foraging begins	older	[35]
dispersal rate	distance travelled from place of birth to place of reproduction	lower	[24,33,37]
hibernation	does the species go through hibernation or torpor?	more common	[38]
fossoriality	does the species live below ground?	more common	[29]
diet breadth	number of dietary categories consumed	debated	[19,25,27] (but see [24])
trophic level	herbivore, omnivore, carnivore	debated	[29] (but see [35])
habitat breadth	number of suitable level 1 IUCN habitats occupied	debated	[19,24,39] (but see [40,41])
functional richness	convex hull surrounding trait space	higher	[18]
functional dispersion	mean distance to centre of trait space	debated	[18] (but see [42])
functional evenness	minimum spanning tree in trait space between species	understudied	
functional divergence	mean distance of each species to edge of trait space	understudied	
functional redundancy	average number of species sharing similar traits	higher	[18]

characteristics of an individual or a species that affect its life history and its role within an ecosystem [20]. These traits (e.g. diet, body size and locomotion) can describe a species's life history and behaviour, making explicit the ecological processes that may govern where a species lives [21]. Furthermore, how varied or clustered functional traits are within an assemblage can indicate the strength of species interactions and the degree of trait-filtering and niche partitioning across the assemblage [20,22,23]. Examining the community structure of endemism hotspots and the relationships between functional traits and endemism can therefore provide fundamental insights into the evolutionary, ecological and environmental mechanisms governing vertebrate range sizes and extinction risk.

Because endemic species often maintain unique ecological roles within an ecosystem, endemism hotspots are hypothesized to possess unique functional characteristics [18]. Research on individual species range sizes demonstrated links with environmental niche breadth (the variety of environments a species can tolerate [19,24–26]), trophic level and specialization [25,27], body size [28–30], metabolic rate [31], life-history traits including fecundity and longevity [24,32], and dispersal ability [24,33] (table 1). Many of these functional traits relate to an organism's ability to expand its range. For example, species that are more fecund with broader niches are often able to maintain larger populations and to rebound after disturbances, allowing them to disperse across landscapes more effectively [32,36,43].

The abiotic features characteristic of endemism hotspots (stable climates and rough topography) may additionally act as filters for certain functional traits. Regions with stable climates (for example, tropical areas) are associated with small body sizes and specialized niches [39,44,45]. Along with filtering individual traits, the climate stability inherent to endemism hotspots may also influence the overall spread and clustering of functional traits within an assemblage (table 1). For example, Safi *et al*. [46] observed that strong selection gradients in high latitudes and previously glaciated regions lead to rapid trait evolution and greater variance in functional traits than expected given the number of species. By contrast, mammal species living in stable climates (through time and across seasons) and tropical regions are often 'packed' into trait space, with strong environmental filtering, niche partitioning and slow trait evolution [37,46]. Climate stability and species richness are integral drivers of mammalian endemism [13,15]. Therefore, endemism hotspots may likewise have strong environmental filtering, leading to assemblages that are functionally clustered in trait space when compared to areas of lower endemism.

The observed relationship between climate stability and clustering in trait space suggests that the evolutionary distinctiveness of endemism hotspots may not always manifest itself in particularly diverse ecological or functional communities [47]. However, endemism hotspots are also found in areas of rough topography. In contrast to regions of high stability, areas of complex topography often have stronger selection gradients because of the increasing isolation and novel environments observed along elevational gradients [17,48]. These mountainous regions may therefore lead to higher variation in species traits across an assemblage, as species evolve to colonize new niches created during tectonic uplift [37,49]. Because these areas in general have increased endemism, we might therefore predict greater variance in functional characteristics and higher functional divergence in areas of high endemism [18] (table 1).

It is clear that the same ecological and biogeographic processes can interact at different scales and magnitudes to generate different functional patterns across landscapes. In addition, the relationships between traits of a single species often interact in complex ways, so how the unique environmental and biotic attributes of endemic communities combine to shape community-level functional traits is yet unknown. Because many of these hypothesized relationships are unclear or are currently being debated, it is unknown whether endemism hotspots are dominated by species less able to expand their ranges, by species with the trait-based potential to be more widespread, or by a diversity of functional trait strategies. If biotic interactions and topography influence highly endemic communities more strongly than the environmental stability and high species richness of endemism hotspots, we would expect greater functional dispersion and less functional redundancy in highly endemic assemblages. By contrast, the high species richness and stable environments of endemism hotspots may lead to distinct traitendemism relationships, lower dispersion and higher redundancy. Evaluating the distribution of mammalian functional traits within endemism hotspots allows us to determine which of these mechanisms governs trait evolution in small-ranged species.

In this study, we systematically assess the functional characteristics (i.e. the identity and distribution of functional traits within an assemblage) of terrestrial mammalian assemblages across the Earth. We related both the average trait values and metrics describing the distribution and spread of functional traits within each assemblage (hereafter, 'multidimensional functional metrics') to its endemism. Additionally, we use multiple methods to test whether the trait–range size relationships observed in individual species (table 1) apply to entire assemblages and how the unique conditions of endemism hotspots affect these relationships. If endemism hotspots are dominated by species with traits disadvantageous for expanding their ranges, we hypothesize smaller average body size, lower fecundity, shorter lifespans and smaller niche breadths in highly endemic ecoregion assemblages than in assemblages without many endemic species (table 1). Finally, we test the hypotheses posed by Keppel *et al.* [18] that species living in endemism hotspots will exhibit high diversity and clustering in trait space, as stable climates, rough topography and richness-driven niche partitioning allow small-ranged species to tightly pack the available functional niche space. As a result, we expected that endemic mammals will not fill functionally unique parts of their assemblages' trait spaces, but that highly endemic assemblages as a whole will still show distinct functional characteristics.

2. Methods

(a) Study extent and spatial units

To evaluate how functional traits vary with terrestrial mammalian endemism on an assemblage level across the globe, we first downloaded expert range maps describing the current distributions of 5695 terrestrial mammal species from the International Union for Conservation of Nature (IUCN) [50]. Next, we divided the world into discrete spatial units, using the IUCN range maps to determine which species were found in which assemblages. Following the recommendations of prior literature [12,51] to use biologically relevant spatial units for evaluating endemism, we used World Wildlife Fund (WWF) ecoregions [52] as the units of analysis. These ecoregions partition the terrestrial biosphere into greater than 800 regions of similar predominant vegetation and habitat. Using WWF ecoregions for this study allowed us to divide the global community of mammals into assemblages of species that are likely to interact with each other and be influenced by similar ecological and physiographic processes, in contrast to other, arbitrary study units [12,51,52]. Ecoregions vary widely in size, but ecoregion area has little effect on mammalian endemism patterns not already explained by species richness patterns [13].

(b) Data collection

Following methods described in [13] and electronic supplementary material, appendix S1, we calculated weighted endemism as the sum of the inverse range sizes of all species resident to each ecoregion. To account for the evident influence of species richness on the evolution of traits in vertebrates [30,37,53–56], and disentangle the effects of species richness from those of endemism [12,13], we characterized the endemism of an assemblage using the residuals of the linear relationship between weighted endemism and species richness (henceforth, 'richness-corrected endemism'). Assemblages with greater richness-corrected endemism have more endemism than expected given the number of species within the assemblage. As observed by [13] and shown in figure 1, these assemblages are primarily in areas of high topography that are climatically stable (e.g. coastal mountain ranges) and on islands. We conducted all of our analysis using richness-corrected endemism instead of true weighted endemism; however, the results using weighted endemism itself are found in electronic supplementary material, appendix S5.

The functional traits of each species were collected from the COMBINE dataset [57]. We selected 14 traits relating to each organism's body size, life-history strategies, fecundity and diet (table 1). These traits were selected for their hypothesized relevance for range size or endemism, their usefulness in differentiating among species groups and characterising functional spectra [58], and their completeness within the un-imputed COMBINE dataset (electronic supplementary material, appendix S2). In addition to these traits, we calculated the annual fecundity of each species by multiplying the average litter size by the average number of litters per year [34]. All continuous traits were transformed for normality (body mass, dispersal rate, longevity, gestation length, weaning age and fecundity were log-transformed and body length was Box–Cox transformed) and scaled to unit variance.

(c) Trait–endemism relationships

After collecting individual species traits, we assessed the relationships between these traits and the endemism of each ecoregion. We used two separate frameworks to examine these relationships: a community-level framework (assemblage means) and a combined analysis that incorporates community composition and individual species traits (fourth-corner regression). These two methods have different ecological interpretations and hypotheses. The fourth-corner analysis assesses how species traits influence their preferences along a gradient, whereas the assemblage means discern which traits are more abundant in given environments, regardless of species preference or adaptive potential [59].

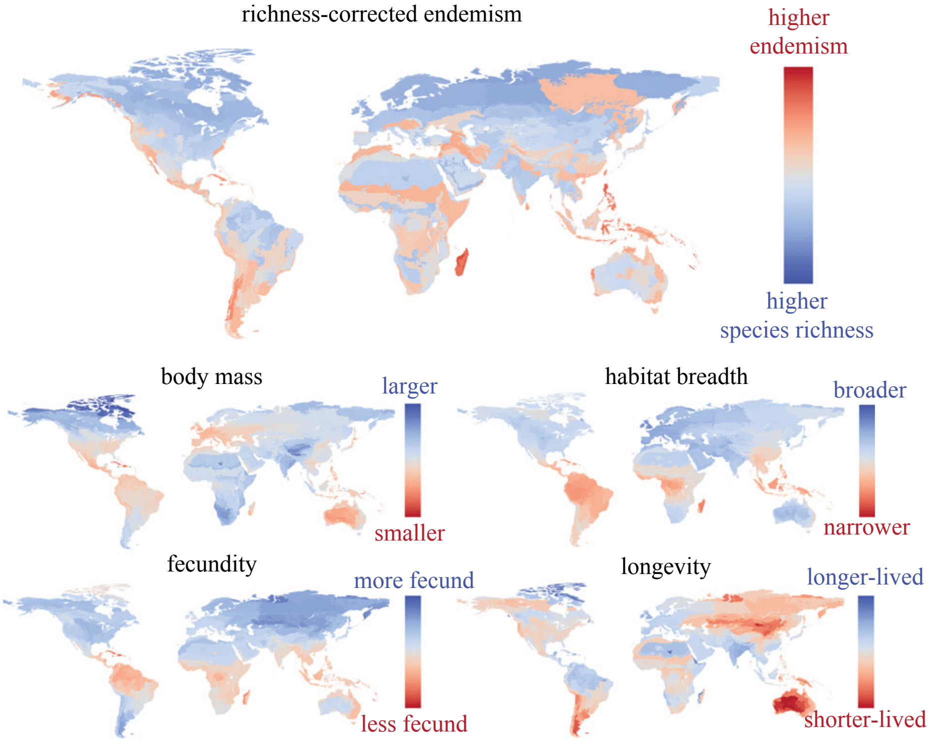

Figure 1. Global maps showing spatial patterns of richness-corrected endemism (top) and the assemblage means of four functional traits (bottom). For endemism, red colours indicate high values (more endemism than expected given the number of species), whereas blue colours indicate low values (less endemism than expected). The four traits were chosen based on their significant relationships to richness-corrected endemism (figure 4). The colour scales of the trait maps are reversed for easier comparisons to richness-corrected endemism.

For the community-level analysis, we first averaged the trait values described in table 1 of every mammal species resident to that ecoregion (henceforth, assemblage means) and calculated the standard deviations. As a measure of trait variation within each assemblage, these standard deviations provide information on the diversity of each trait within the ecoregion assemblages. Next, we developed a generalized linear model (GLM) relating the assemblage means and standard deviations of the trait values to the endemism of the ecoregion. To reduce collinearity, we only used assemblage means and standard deviations that were not highly correlated to any other variable (Spearman's $\rho < 0.7$; electronic supplementary material, appendix S2). Of the assemblage means examined, seven had low enough correlations to use: body mass, maximum longevity, fecundity, hibernation, diet breadth (number of dietary classes consumed; table 1), trophic level and habitat breadth (number of IUCN level 1 habitats occupied; table 1). Because trophic level is categorical (with uninformative mean values), we substituted the percentage of carnivore species within the assemblage for trophic level in our GLM analyses. We also used the standard deviations of fecundity and diet breadth in the model. Overall, 5297 terrestrial mammal species had a full complement of these seven traits and a defined range size. We limited our analysis to ecoregions with more than seven species to reduce the effect of outlier species and to calculate accurate standard deviations (electronic supplementary material, appendix S3), leaving 730 ecoregions. To avoid undue influence of any one assemblage on the model parameters and to provide accurate confidence intervals, we subsampled the data to 500 out of the 730 ecoregions, bootstrapping the GLM 1000 times to evaluate the effect size of the assemblage means on the endemism of each ecoregion.

Mammalian communities on islands have exceptionally high levels of endemism compared to continental communities [60] (figure 1). In addition, insular communities are often phylogenetically and functionally distinct from mainland communities, with greater clustering of functional traits [61], adaptation towards intermediate body sizes (Foster's rule [62]) and slow life histories [63]. Functional characteristics of island assemblages may therefore be driven by different processes and demonstrate different patterns than mainland assemblages. To examine the trait–endemism relationship found on islands, we conducted a separate bootstrapped GLM that excluded the 592 ecoregions located entirely on continents, comparing it to the GLM conducted on the total set of ecoregions.

When relating assemblage means to the environmental characteristics of certain communities, Type I (false positive) errors become more likely because of spatial auto-correlation and shared species between communities [64,65] (but see [59]). Therefore, we augmented the results of the GLM by applying fourth-corner regression [66]. Whereas the GLMs (as community-level analyses) explore the overall trend in species traits across the endemism gradient, fourth-corner regression specifically examines how the occupancy of a species at a set of sites influences the relationship between endemism and a trait [59,67]. This technique outperforms assemblage mean regressions in statistical power and sampling accuracy [65] but unlike GLMs does not take into account the variance of the traits at each site or the trait composition of the overall community [59]. Using the same seven traits as in the GLMs, we conducted 1000 replicates of the fourth-corner regression and adjusted the p-values via the Benjamini and Yekutieli adjustment [68].

The fourth-corner analysis allowed us to examine the direct influences the environmental characteristics of endemism hotspots have on species traits. Adding environmental predictors alongside endemism to the fourth-corner regression can disentangle the specific effects of each predictor on the trait–endemism relationship. Therefore, we included two environmental variables in the fourth-corner regression: the change in temperature since the Last Glacial Maximum (21 000 years ago) and the standard deviation of elevations within the ecoregion [13] (electronic supplementary material, appendix S1). We chose these variables because they are known to strongly correlate with endemism patterns, even compared to other measures of climate stability and topography [13]. By comparing the results of these

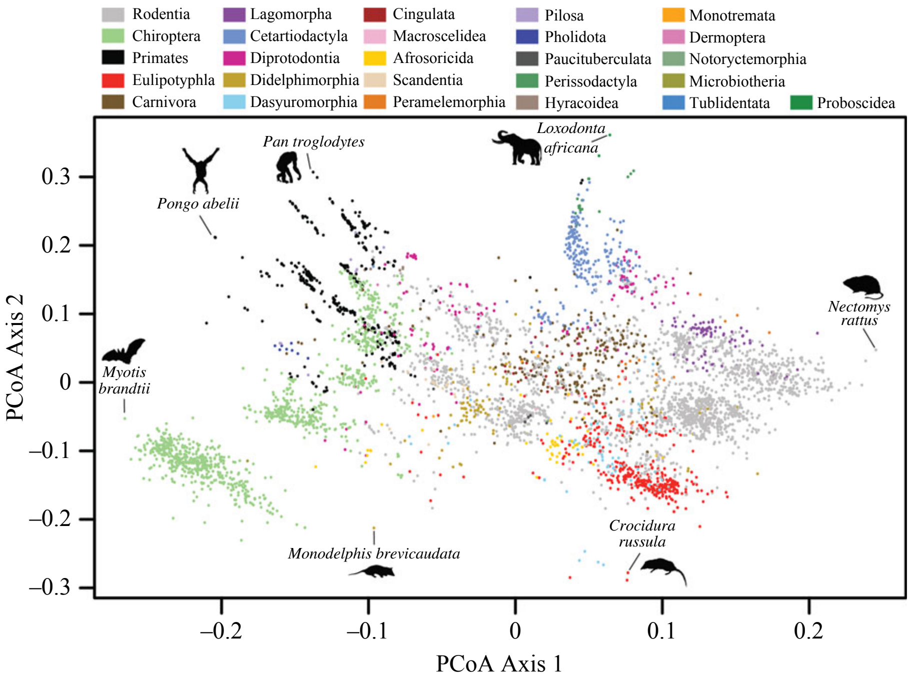

Figure 2. The global functional space used to calculate the multidimensional functional metrics. All species used in the analysis are plotted on the first two PCoA axes generated from the Gower dissimilarity matrix. Species are colour-coded by taxonomic order. PCoA Axis 1 is primarily associated with fecundity, whereas PCoA Axis 2 is associated with body mass. Some example species near the edges of the functional space are identified (species silhouettes from PhyloPic).

environmental predictors to those of the richness-corrected endemism, we can determine which characteristics of endemism hotspots affect which mammalian traits.

Species traits are often phylogenetically conserved, with related species exhibiting similar traits. These traits may serve to limit species ranges, so range size may display a phylogenetic signal [69,70, but see 71,72]. In the fourth-corner regression, which is suited for questions on traits as adaptive forces [59], we adjusted for phylogenetic autocorrelation using Moran's spectral randomization [73]. We used a complete mammalian phylogeny provided by the Phylacine dataset [74]; of the 5297 mammal species used in the GLMs, 5058 were able to be used for the phylogenetic correction. To examine how the phylogenetically imputed records in the COMBINE dataset affected our results, we repeated the fourth-corner regression using only species with reported traits ($n = 670$; electronic supplementary material, appendix S4). For the assemblage means, we did not account for phylogeny. Analyses of community-weighted means are better for testing how species traits vary along a gradient of endemism, irrespective of the adaptive potential of these traits [59]. In addition, correcting for phylogeny while examining shallow-time trait filtering in endemism hotspots may unintentionally remove the very effect we are studying.

Finally, this research links species traits to the current global distribution of mammalian endemism. However, throughout the Holocene humans have significantly altered mammal range sizes by shaping terrestrial habitats [75], reorganizing the composition of vertebrate communities [76], and extirpating species. Currently, both large and small mammal species and those with low reproductive output have elevated extinction risks, although these relationships vary geographically [3,5,77,78]. Furthermore, habitat conversion has pushed large mammals into the margins of their ecological niche [79]. To account for anthropogenic changes in species ranges, we recalculated weighted endemism using a dataset of 'present natural' species ranges from Phylacine [74] and compared it to the weighted endemism derived from the IUCN ranges. We found strong correspondence between endemism calculated from the current IUCN ranges and from the 'present-natural' ranges provided from Phylacine (Spearman's $\rho = 0.877$; electronic supplementary material, appendix S6). Therefore, we used only the current species range data provided by the IUCN for all subsequent analyses.

(d) Functional metrics

We also examined the spread and clustering of functional traits within each ecoregion assemblage and its relationship to endemism using metrics that characterize the distances between species in multidimensional trait space (figures 2 and 3*a*). Multidimensional functional metrics were calculated for each ecoregion (figure 3*a*): functional richness (area of the convex hull surrounding all resident species [80]), functional evenness (branch regularity of the minimum spanning tree between each resident species [80]), functional dispersion (mean distance from each individual species to the centroid of the trait space [82]) and functional divergence (distance of each species to the centre of gravity of the convex hull polygon [80]). Functional richness and dispersion measure the overall variety of functional traits found within an assemblage, indicating the diversity of species' life-history strategies [54,82] (figure 3*a*). In general, a community with high functional richness and dispersion may be better protected against invasions and better able to withstand environmental fluctuations [83]. By contrast, functional evenness and divergence measure the spread and clustering of traits across functional space irrespective of the overall diversity of functional traits [82] (figure 3*a*,*b*). They can describe the degree of niche partitioning and competition within an assemblage [83], although the relationship between competition and trait clustering is often counterintuitive [23]. Finally, we calculated functional redundancy (*sensu* [84]), binning the functional trait values and calculating the average number of species that share unique bin combinations (figure 3*a*). Functional redundancy measures the number of species that share similar functional traits and therefore the amount of niche partitioning within the assemblage. Because it is directly related to species richness, comparing functional redundancy to the other metrics isolates the influence of species richness [84].

To calculate these multi-dimensional functional metrics for each ecoregion assemblage, we computed a Cailliez-corrected Gower dissimilarity matrix, which allows for the inclusion of discrete and continuous trait data, and then conducted a PCoA to generate the

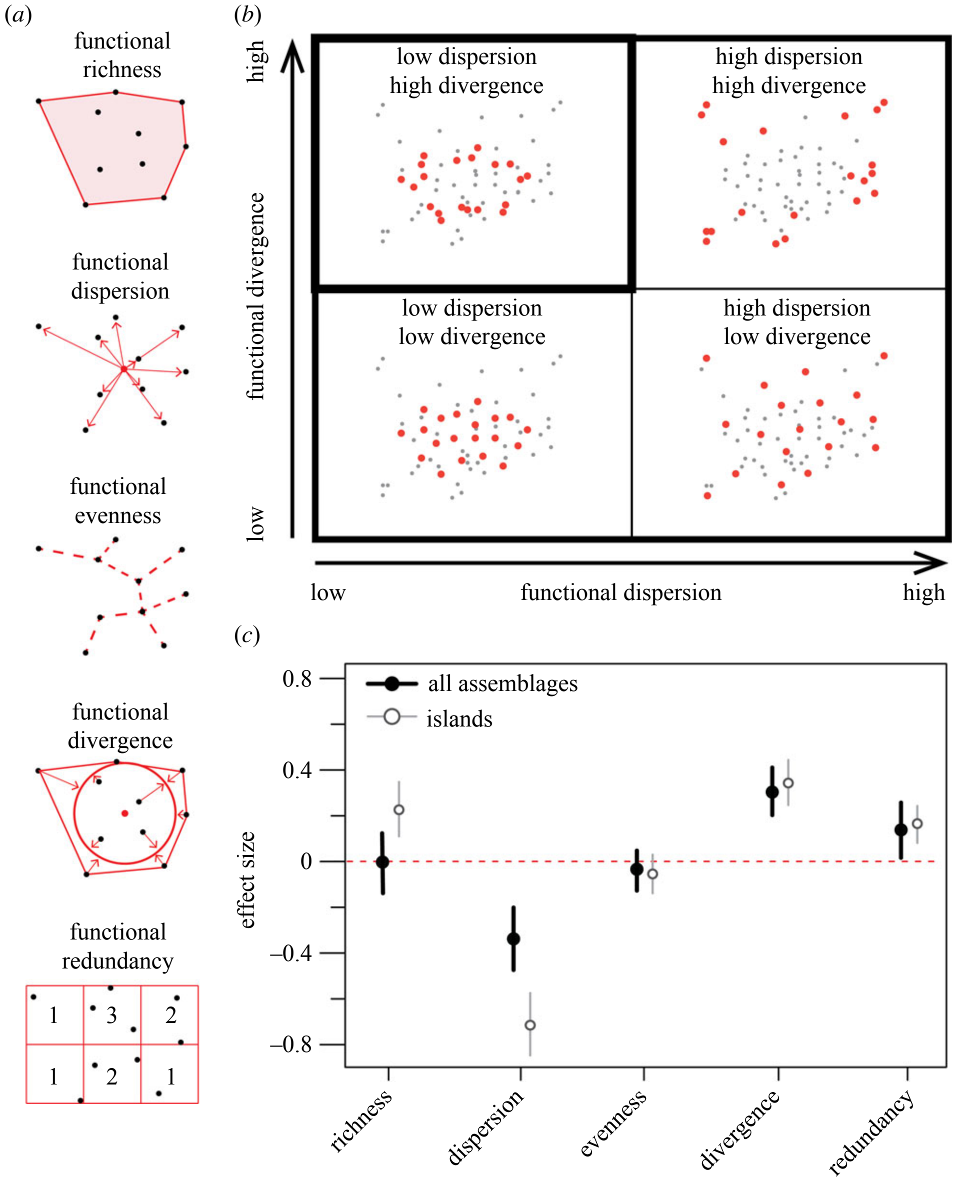

Figure 3. (*a*) Diagrams describing how each multidimensional functional metric is calculated in a 2-dimensional functional space. The figures for functional richness, evenness, and divergence are based on [80] and [81]. (*b*) Conceptual figure demonstrating the differences between functional divergence and functional dispersion. Each quadrant describes an assemblage of 15 species (red dots) within a global community of 60 species (grey dots) in functional space. Assemblages with high divergence (top row) cluster further away from the centre of functional space, whereas those with low divergence (bottom row) are evenly distributed across functional space. Dispersion characterises the overall functional space of each assemblage; assemblages with high dispersion (right column) spread further across functional space than assemblages with low dispersion (left column). Mammalian endemism hotspots follow the top-left pattern. (*c*) Effect sizes of the linear models relating the functional metrics and endemism in global (black points and lines) and island ecoregions (grey points and lines). Mean and 95% confidence intervals for the bootstrapped model coefficients are shown. Points above and below the dashed line indicate positive and negative relationships, respectively. Insignificant effects cross 0.

functional space (figure 2). Because the Gower dissimilarity matrix can be applied to highly correlated and non-continuous data, we used all traits described in table 1 except dispersal rate (which had many fewer records than the other traits; electronic supplementary material, appendix S2), substituting annual fecundity for litter size and number of litters per year. We used the ‘FD’ package in R [85] to calculate all functional metrics except redundancy, which we calculated following [84]. We then constructed GLMs between the functional metrics of each ecoregion assemblage and its richness-corrected endemism. Although functional richness and functional dispersion are moderately correlated ($r = 0.573$), all metrics used describe independent characteristics of assemblages [54,80,82], and the variance inflation factors for the predictors were all lower than 2.5. All analyses were conducted in R (v. 4.1.2, R Core Team, 2021) using various packages (electronic supplementary material, appendix S1).

3. Results

(a) Trait–endemism relationships

GLMs linking richness-corrected endemism and assemblage trait means indicated several consistent trends (figures 1 and 4*a*). Overall, annual fecundity ($\beta = -0.309$, 95% CI: −0.502, −0.102), species longevity ($\beta = -0.242$, 95% CI: −0.358, −0.128), average habitat breadth

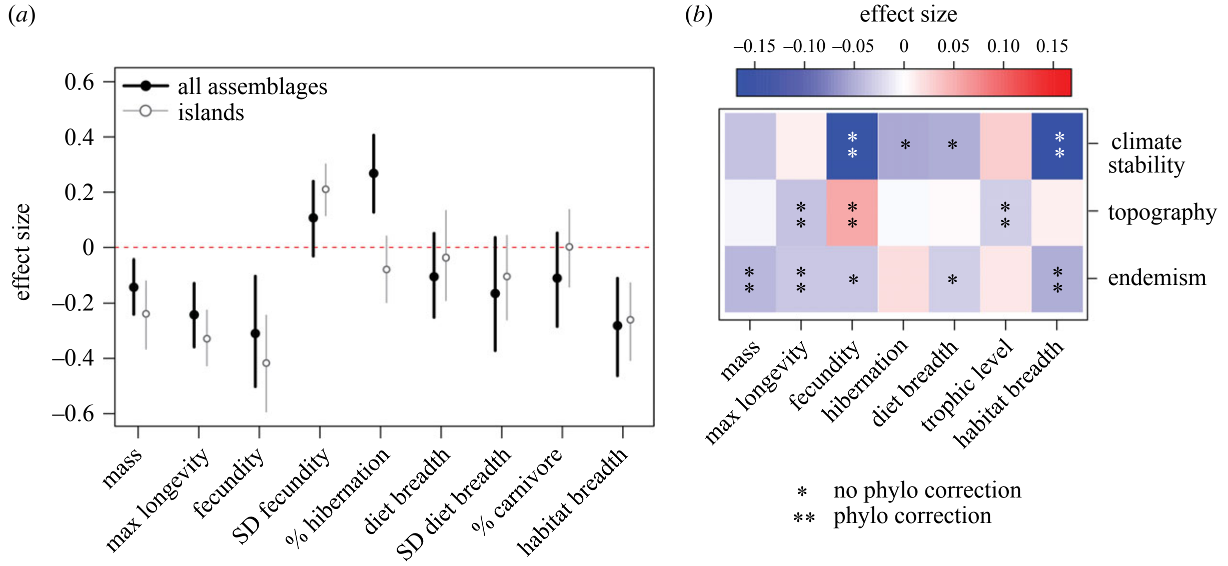

Figure 4. (*a*) Effect sizes of the linear models relating assemblage trait means to richness-corrected endemism across global (black points and lines) and island ecoregions (grey points and lines). The mean and 95% confidence intervals for the bootstrapped model coefficients are shown. Points above and below the dashed line indicate positive and negative relationships between the traits and endemism, respectively. Insignificant effects cross 0. (*b*) Results of the fourth-corner regression between the species traits, the richness-corrected endemism, and environmental variables. The shading of each cell represents the effect-size coefficient; dark blue indicates negative relationships and dark red indicates positive relationships. Asterisks denote statistically significant relationships when phylogeny is (two asterisks) or is not (one asterisk) accounted for.

($\beta = -0.281$, 95% CI: −0.462, −0.110) and body mass ($\beta = -0.142$, 95% CI: −0.240, −0.043) decreased with increasing endemism; whereas the percentage of hibernating species increased ($\beta = 0.268$, 95% CI: 0.127, 0.406). Therefore, mammalian assemblages in endemism hotspots were on average smaller, shorter-lived, less fecund, more likely to hibernate and more specialized in their habitats than species living in areas of low endemism. However, the percentage of carnivores within the assemblage did not vary with endemism ($\beta = -0.109$, 95% CI: −0.284, 0.052), nor did the average diet breadth of the assemblage ($\beta = -0.165$, 95% CI: −0.371, 0.036).

Mammalian assemblages on island ecoregions displayed similar patterns to the global trends (figure 4*a*), with negative relationships between richness-corrected endemism and body mass ($\beta = -0.239$, 95% CI: −0.366, −0.121), longevity ($\beta = -0.329$, 95% CI: −0.426, −0.226), fecundity ($\beta = -0.417$, 95% CI: −0.593, −0.245) and habitat breadth ($\beta = -0.261$, 95% CI: −0.128, −0.407). The magnitude of the effect sizes for mass, longevity and fecundity was greater for island ecoregions than for global ecoregions. Unlike the global patterns, however, variance in fecundity increased with higher island endemism ($\beta = 0.210$, 95% CI: 0.115, 0.301) and likelihood of hibernation did not vary with endemism ($\beta = -0.079$, 95% CI: −0.197, 0.040).

The fourth-corner regression, which examined the relationships between individual species traits, community composition and the environmental characteristics of endemism hotspots, corroborated the results of the GLMs while simultaneously disentangling the effects of environmental characteristics and phylogenetic relatedness. Without phylogenetic correction, body mass, longevity, fecundity and habitat breadth were all negatively associated with richness-corrected endemism, similar to the assemblage mean GLMs (figure 4*b*). However, the percentage of hibernating species was not significantly associated with endemism. In addition, diet breadth, which was insignificant in the GLM, displayed a significant negative association with richness-corrected endemism when phylogeny was not accounted for (figure 4*b*). When the phylogenetic relationships between the species were accounted for, body mass, longevity and habitat breadth retained their significance, but diet breadth and fecundity did not (figure 4*b*).

Including environmental characteristics in the fourth-corner analysis allowed us to identify which aspects of the functional trait patterns are governed by which abiotic characteristics. Topography and climate stability were significantly associated with mammalian functional traits in different ways (figure 4*b*). Many of these patterns echoed the trait–endemism relationships. Areas of rough topography were negatively associated with longevity and trophic level, and fecundity was strongly negatively associated with climate stability and habitat breadth (figure 4*b*). When phylogeny was not accounted for, climate stability was also negatively related to diet breadth and hibernation. However, body mass was related to neither climate stability nor topography, and fecundity was positively associated with areas of rough topography.

(b) Multi-dimensional functional metrics

As with the individual trait means from the ecoregion communities, we found a clear signal between the multi-dimensional functional metrics and richness-corrected endemism of the ecoregion assemblages (figure 3*c*). Functional dispersion was negatively related to richness-corrected endemism ($\beta = -0.340$, 95% CI: −0.476, −0.204) and functional redundancy was positively related (albeit barely; $\beta = 0.125$, 95% CI: 0.003, 0.244). These patterns indicate that mammals living in high-endemism assemblages do not have particularly diverse combinations of functional traits, taking up less functional space than expected by chance. However, functional divergence significantly increased with higher endemism ($\beta = 0.300$, 95% CI: 0.199, 0.407). This positive relationship between functional divergence and endemism suggests that the species within the assemblage tend to cluster near the edges of that assemblage's available functional space (figure 3*b*). Surprisingly, and in contrast to the hypothesis of [18], the functional richness of each assemblage was unrelated to its weighted endemism once species richness was accounted for ($\beta = -0.005$, 95% CI: −0.141, 0.120), although we observed a strong relationship when species richness was not corrected for (electronic supplementary material, appendix S5).

When limiting the analysis to island ecoregions, a similar pattern was observed, with lower functional dispersion ($\beta = -0.714$, 95% CI: −0.846, −0.574) and higher functional divergence ($\beta = 0.343$, 95% CI: 0.247, 0.444) and redundancy ($\beta = 0.166$, 95% CI: 0.082, 0.243) in highly endemic island assemblages, again indicating that species traits on highly endemic islands are not particularly diverse, clustering near the edges of the assemblage's functional space. However, unlike global assemblages, functional richness increased with increasing endemism on islands, even when species richness was accounted for ($\beta = 0.227$, 95% CI: 0.110, 0.348).

4. Discussion

Highly endemic mammalian assemblages have unique functional characteristics, both on the individual species level and as an entire assemblage. The global pattern of mammalian endemism and the environmental conditions of endemism hotspots relate to several mammalian functional traits (figures 1 and 4). On average, mammalian assemblages within regions of high endemism exhibit shorter lifespans, lower fecundity, smaller body sizes and narrower habitat breadths than assemblages without high endemism. The abiotic characteristics of endemism hotspots combine to influence these trait patterns, with areas of rough topography leading to shorter-lived species, and climatically stable regions leading to less fecund and more specialized species (figure 4*b*). In combination, these traits limit the ability of mammalian species to disperse and expand their ranges geographically, with smaller and less fecund species having slower dispersal rates [86,87]. Endemism hotspots therefore seem to be dominated by poor-dispersing mammal species, implying that these species were less likely to have been widespread in the past. In addition, mammalian communities in endemism hotspots are less dispersed across the total functional space of all mammals and more divergent, clustering away from the centre of the functional space (figure 3*c*). These patterns suggest that trait filtering (leading to lower functional dispersion) and competition (leading to higher divergence) may combine to structure endemism hotspots.

(a) Trait–endemism relationships

Small body sizes, narrow habitat breadths, low fecundity and a relatively short lifespans characterize mammalian endemism hotspots (table 1, figures 3 and 4). These traits all relate to the ability of species to rebound and expand their ranges after disturbances. Previous studies have linked body size to range size, indicating that small species are generally more affected by local and landscape-level changes in habitat than are large species [77] and, all else being equal, exhibit poorer dispersal out of climate refugia or into less hospitable environments [32,44]. For example, areas of high endemism in the Neotropics (e.g. Mesoamerica) have had particularly stable climates [88] and harbour mammals with small body masses (figure 1). On islands, the negative relationship between body mass and endemism was particularly strong (figure 4*a*), supporting this hypothesis; however, more research is necessary to fully explore if an advantage like this exists.

In addition to small body size, the disproportionately narrow habitat breadths of the species in highly endemic assemblages further limit the potential for these taxa to expand into areas with different resources (figure 4*a*). Species with wider habitat tolerances can colonize new areas more effectively than can habitat specialists, and they may therefore have been able to expand their distributions more quickly into previously unfavourable habitats [43]. By contrast, habitat specialists may be restricted to localized areas of high environmental stability (figure 4*b*). Researchers have observed similar links between specialization and range size across taxa [19,24,25]. However, the observed habitat specialization of species in a population may change over time, mirroring changes in population density [40], interspecific interactions [56] and anthropogenic land conversion [89]. It is therefore still unclear whether endemic species have narrow habitat niches because of the stability of endemism hotspots or simply because they have small ranges. We found mixed results linking dietary specialization and endemism (electronic supplementary material, appendix S7).

The ability of a species to expand its range through time is not only a function of its size and specialization, but also its ability to reproduce. Low fecundity can result in low abundance [90], which is in turn often correlated with range size [43,91, but see 92]. By contrast, fecund species can rebound quicker and more efficiently after periods of low resource abundance than less fecund species, and are therefore able to outcompete less-fecund species and disperse across landscapes more successfully [32,36]. The combination of high resilience and competitive ability may lead to an overabundance of highly fecund species in areas with variable or marginal intra-annual resource availability [93], where fewer endemic species are found (e.g. the Palaearctic realm; figure 1). Supporting this previous research, we observed strong relationships between average fecundity, endemism and climate stability, in island ecosystems and globally (figure 4).

Species that have fewer offspring per year are hypothesized to live longer, as a correlate to r/K selection theory [94]. Although many mammals display a combination of r-selected and K-selected traits [34], in general K-selected traits are negatively related to r-selected ones [95]. In our study, fecundity and longevity were negatively correlated for individual species ($r = -0.729$), demonstrating markedly different spatial patterns across the globe (figure 1) and in response to environmental factors (figure 4*b*). Surprisingly, however, the assemblage means of both longevity and fecundity substantially decrease with increasing endemism (figure 4*a*). Species with different life-history strategies coexist within an assemblage, and therefore the average trait values of the assemblage do not necessarily exhibit the same species-level tradeoffs [96]. Instead, the breakdown of the fecundity-longevity tradeoff in areas of high endemism suggests that these areas are dominated by species that have either low fecundity or short longevity. The combination of stable climates and rough topography in endemism hotspots appears to drive this pattern; whereas areas of particularly stable climate led to lower fecundity in mammals, areas of high topography led to shorter lifespans (figure 4*b*).

Together these results support a hypothesis posed by Keppel *et al*. [18]: that the environmental conditions of endemism hotspots may allow for species at a reproductive disadvantage to survive that may otherwise have gone extinct, and for mammals those are small average body mass, habitat specialization and low reproductive output.

The strong correlation between the IUCN ranges (which approximate the current range of each species) and the 'present natural' ranges (which estimate the range of each species without anthropogenic disturbances) indicates that our results are robust to anthropogenic effects; however, additional research is necessary to fully illuminate how humans have affected the functional characteristics of endemism hotspots. Given the non-random patterns of anthropogenic effects on species traits [3,5,77], we might hypothesize stronger negative effects of fecundity and stronger positive effects of standard deviation in body mass on endemism.

(b) Functional metrics

Although the patterns of individual traits revealed a reduced capacity for range expansion, they do not confer any information about how functionally diverse the assemblages are. Instead, the multidimensional functional metrics must be used to describe the spread and clustering of species' traits within an assemblage. Keppel *et al.* [18] hypothesized that strengthened biotic interactions and competitive exclusion would cause functional richness to increase with endemism. Although we found this relationship using uncorrected endemism values (electronic supplementary material, appendix S5), it disappeared when species richness was accounted for (figure 3*c*). Instead, the functional dispersion of each ecoregion assemblage (less sensitive to outliers than functional richness; figure 3*a*) significantly decreased with richness-corrected endemism, and functional redundancy increased. Therefore, mammal assemblages in highly endemic ecoregions make up smaller functional spaces and have less trait variation than expected given the number of species living there, and the resident species are more ecologically similar to each other than expected. One potential explanation for these findings is environmental trait filtering, in which abiotic factors limit variation in species traits. The selection pressures inherent to highly variable climates may be stronger drivers of variation in functional traits than the reduced extinction rates found in stable climates [46,54]. However, more research into the relationship between within-species trait variation and functional diversity in areas of high endemism [55] is needed to support this hypothesis.

Despite low functional dispersion suggesting that the abiotic conditions of endemic assemblages are environmentally filtering mammalian traits, the high functional divergence in endemism hotspots indicates elevated rates of niche differentiation and competition [23,83]. As a measure of where the most abundant trait combinations are within the assemblage's trait space, functional divergence is higher when more species have trait combinations that place them at the edges of the assemblage's trait space. Counterintuitively, a clustering signature in trait space often stems from elevated competition between species [23,97]. Although the competitive exclusion principle states that species will differentiate to avoid competition, when there are more species than available niches (as might be the case in highly endemic assemblages under environmental filtering), species tend to cluster near adaptive optima [23]. This pattern is not driven by any single trait, as evidenced by the insignificant relationship between the trait standard deviations and endemism (figure 4*a*). One potential reason for this clustering pattern may stem from the combination of stable climates (leading to stronger biotic interactions and less trait variation [18]) and rough topography (leading to an increase in selection pressure [17,48]) in endemism hotspots, but more research is necessary to fully parse the environmental drivers of trait diversity in endemism hotspots.

The hypothesized combination of environmental filtering and strong biotic interactions in highly endemic mammalian assemblages gives them an unusual functional signature. Although species in endemism hotspots tend to cluster on the edges of the individual assemblage's trait space, these species may not exhibit extreme traits compared to the global trait space of mammals (figures 2 and 3). Sobral *et al.* [98] demonstrated this pattern in island bird species, observing that extinctions did not change the overall functional richness of the island, but that the trait combinations being lost were different than more recent introductions. The difference between the presence of a species and its abundance may help account for these results: abundance-weighted functional dispersion is higher in the tropics (the opposite trend of the dispersion applied here), suggesting that abundant species may have unique functional traits along with their increased range sizes [43,99].

(c) Implications

Highly endemic mammalian assemblages demonstrate trait filtering related to the environmental stability and rough topography of endemism hotspots. The traits corresponding to endemism hotspots are associated with reduced ability for a species to expand its range after a disturbance, suggesting that the environmental conditions of the hotspots allowed such species to survive. The influence of biotic filtering on these assemblages is weaker, with high functional redundancy and an inconsistent link between diet breadth and endemism. However, the combination of abiotic and biotic factors influencing endemism across the globe led to unique assemblage characteristics.

Because of the increasing anthropogenic effects on the environment, understanding how abiotic, biotic and anthropogenic pressures combine to affect the organization of biological communities is crucial for conserving biodiversity. Endemic species provide a useful litmus test to evaluate these questions because their restricted range sizes make them particularly vulnerable to human impacts [3,77], and protecting these species can efficiently conserve biodiversity on regional scales [12]. Some endemism hotspots (especially in remote areas) are currently being prioritized for protection, but hotspots in the tropics may not be adequately protected [100]. We found that the traits are associated with higher endemism are exactly those with the highest current extinction risks. Furthermore, we found that endemism hotspots display an unusual combination of low functional dispersion but high functional divergence, suggesting that the loss of small-ranged, vulnerable species may not change the overall functional diversity of mammals on Earth, but could decrease functional diversity within these hotspots. Finally, this research has demonstrated that relationships between species traits and range size are evident not only for individual species, but also at the assemblage level. Conservation strategies that aim to preserve entire communities and landscapes may therefore be as effective at preventing mammalian extinctions during the Anthropocene as those that focus on a single, threatened species.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The data that support the findings of this study and the R scripts used to conduct the analyses are openly accessible on FigShare at https://doi.org/10.6084/m9.figshare.22344025 [101].

Appendices are provided in the electronic supplementary material [102].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. B.R.S.: conceptualization, data curation, formal analysis, funding acquisition, methodology, software, writing—original draft; J.L.M.: project administration, resources, supervision, validation, visualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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