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RESEARCH PAPER

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The global biogeography of lizard functional groups

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Abstract

Aim: Understanding the mechanisms determining species richness is a primary goal of biogeography. Richness patterns of sub-groups within a taxon are usually assumed to be driven by similar processes. However, if richness of distinct ecological strategies respond differently to the same processes, inferences made for an entire taxon may be misleading. We deconstruct the global lizard assemblage into functional groups and examine the congruence among richness patterns between them. We further examine the species richness – functional richness relationship to elucidate the way functional diversity contributes to the overall species richness patterns.

Location: Global.

Methods: Using comprehensive biological trait databases we classified the global lizard assemblage into ecological strategies based on body size, diet, activity times and microhabitat preferences, using Archetypal Analysis. We then examined spatial gradients in the richness of each strategy at the one-degree grid cell, biome, and realm scales.

Results: We found that lizards can best be characterized by seven "ecological strategies": *scansorial*, *terrestrial*, *nocturnal*, *herbivorous*, *fossorial*, *large*, and *semi-aquatic*.

There are large differences among the global richness patterns of these strategies. While the major richness hotspot for lizards in general is in Australia, several strategies exhibit highest richness in the Amazon Basin. Importantly, the global maximum in lizard species richness is achieved at intermediate values of functional diversity and increasing functional diversity further result in a slow decline of species richness.

Main conclusions: The deconstruction of the global lizard assemblage along multiple ecological axes offers a new way to conceive lizard diversity patterns. It suggests that local lizard richness mostly increases when species belonging to particular ecological strategies become hyper-diverse there, and not because more ecological types are present in the most species rich localities. Thus maximum richness and maximum ecological diversity do not overlap. These results shed light on the global richness pattern of lizards, and highlight previously unidentified spatial patterns in understudied functional groups.

KEYWORDS

Archetypal Analysis, functional groups, functional richness, lizards, species richness

1 | INTRODUCTION

The marked geographical variation in the number of species stimulates the curiosity of many researchers. Despite the many studies devoted to this issue, the underlying mechanisms remain elusive (Abrahamczyk, Vos, Sedivy, Gottleuber, & Kessler, 2014; Hawkins & DeVries, 2009). One of the underlying causes of this may lie in the fact that such studies usually focus on a particular taxon, disregarding the often strong ecological variability of the species that comprise it.

Much effort has been directed toward studying the spatial richness pattern of particular taxa (e.g., Ceballos, Ehrlich, Soberon, Salazar, & Fay, 2005; Grenyer et al., 2006; Jetz, Thomas, Joy, Hartmann, & Mooers, 2012; Roll et al., 2017). Analysing an assemblage that contains wide variation in traits may mask the processes underlying richness patterns (Proosdij, Raes, Wieringa, & Sosef, 2016). Lumping all species in an assemblage implicitly assumes that species richness of all sub-groups responds to similar underlying drivers. A study of all amphibians, for example, lumps salamanders (Caudata) with frogs (Anura), which have species richness peaks in the temperate zone, and in the tropics, respectively (IUCN, 2017). Thus, in order to understand species richness patterns of a taxon, there is a need to expand the conceptual framework by considering the ecological and physiological traits of its constituent species (Marquet, Fernández, Navarrete, & Valdovinos, 2004).

If richness patterns vary across groups as a function of the ecological traits of constituent species, deconstructing the total assemblage into functional groups may improve our understanding of the causes underlying richness variation (Kissling et al., 2012). For example, the deconstruction of Eurasian lizards by their activity time revealed substantial differences between the richness patterns of nocturnal and diurnal lizards (e.g., diurnal species range further north; Vidan et al., 2017). Species richness patterns may be deconstructed into richness of members of different functional and ecological groups that share similar traits and presumably respond similarly to environmental gradients. It is then possible to evaluate the factors driving the richness of each group and how these groups contribute to the overall richness pattern (Buckley, Hurlbert, & Jetz, 2012; Marquet et al., 2004).

Previous studies on a wide range of taxa have revealed wide differences in richness patterns among functional and ecological groups (e.g., Belmaker, 2009; Lennon, Beale, Reid, Kent, & Pakeman, 2011; Pecuchet et al., 2017). For example, Williams and Hero (2001) found that richness of different frog groups (e.g., generalists and rain forest specialists) show very different patterns, and that combining them may undermine a true understanding of factors driving patterns of species richness. This emphasizes the need for deconstructing groups by functional traits.

Many methods have been used to divide a large clade into ecologically meaningful sub-groups. For example, Kissling et al. (2012) divided the world's avifauna into nine dietary guilds according to species' dietary components. Similarly, Vale and Brito (2015) deconstructed the endemic vertebrates of the Sahara-Sahel into seven functional groups according to their sensitivity and adaptive ability to climate change. Assemblages of vertebrates, plants, and marine taxa have been partitioned according to range size with wide and narrow ranging species analysed separately (e.g., Belmaker & Jetz, 2011; Lennon et al., 2011; Reddin, Bothwell, & Lennon, 2015). In most studies, deconstruction of the entire assemblage was done using a single trait, such as body-size or activity pattern, with the study often conducted at the regional, rather than global level.

We studied the biogeography of functional groups of lizards, the most species rich and ecologically diverse group within the Reptilia, constituting 60% of the entire class (Uetz, 2015). Lizards are a phylogenetically ancient and diverse group, demonstrating wide variation

in morphological, physiological, behavioural and ecological characteristics (e.g., Pianka & Vitt, 2003; Losos, 2009; Mesquita, Faria, Colli, Vitt, & Pianka, 2016). Most importantly, lizards are of great conservation concern because of their small ranges (Meiri et al., 2018; Meiri & Chapple, 2016) and their sensitivity to habitat alterations, climatic changes, direct prosecution and introduced species (e.g., Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009; Sinervo, 2010, Pincheira-Donoso, Tregenza, Witt, & Hodgson, 2013; Slavenko, Tallowin, Itescu, Raia, & Meiri, 2016).

Although several studies have examined regional lizard richness patterns (e.g., Hosseinzadeh, Aliabadian, Rastegar-Pouyani, & Rastegar-Pouyani, 2014; Kissling, Blach-Overgaard, Zwaan, & Wagner, 2016; Lewin et al., 2016, Tallowin, Allison, Algar, Kraus, & Meiri, 2017; Pincheira-Donoso, Tregenza, Butlin, & Hodgson, 2018), the global richness pattern of all known lizard species has only recently been identified (Roll et al., 2017). Only a few studies have examined richness patterns by deconstructing them according to species' traits (by morphological traits: Scheibe, 1987; taxonomy: Powney, Grenyer, Orme, Owens, & Meiri, 2010; range size: Lewin et al., 2016; activity time: Vidan et al., 2017). Recently, multiple traits of 134 lizard species were used to arrange lizards along functional trait combination axes, showing that lizards display diverse and distinct life history strategies (Pianka, Vitt, Pelegrin, Fitzgerald, & Winemiller, 2017). However, to the best of our knowledge, no study has yet combined multiple functional traits with distributional data to examine global lizard (or even reptile) functional diversity gradients.

To explore the similarity and differences among lizard functional groups, we used comprehensive databases of the spatial distribution and ecological traits of lizard species. We divided the global lizard assemblage into distinct 'ecological strategies' using Archetypal Analysis. We then: (a) explored the richness pattern of each strategy; (b) evaluated the contribution of each strategy to the overall lizard richness pattern; and (c) examined the relationship between species richness and functional richness.

2 | MATERIALS AND METHODS

2.1 | Data collection

2.1.1 | Trait information

We selected the following four traits to represent the way in which lizards exploit their habitat: (a) activity time, representing temporal niche, categorized as either diurnal, nocturnal, or cathemeral (active both night and day); (b) diet: categorized as carnivorous (feeding exclusively, or nearly exclusively, on animal material), herbivorous (eating mainly plants), or omnivorous (feeding on both animal and plants, with plants forming <50% of the diet); (c) microhabitat preference, representing local habitat niche. We categorized species as semi-aquatic, fossorial and semi-fossorial, terrestrial, scansorial (tree and/or rock dwelling) or a combination of terrestrial and scansorial (species that are found in various terrestrial habitats); (d) body mass (in grams), a measure of energy and space requirements. Despite mass being a morphological, rather than a purely ecological trait, it has tremendous impact on many ecological aspects (Brown & Maurer, 1986; Peters, 1983; Pianka et al., 2017), and we thus include it as a potentially important ecological axis. Body mass values are based on maximum SVLs per species converted to mass using family-specific equations, adjusted for leg-reduced and legless species (Feldman, Sabath, Pyron, Mayrose, & Meiri, 2016; Meiri, 2010).

All trait information was based on a comprehensive literature-based biological trait database of lizards (e.g., Scharf et al., 2015; Meiri, 2016; Meiri, 2018). We imputed data for species with unknown data when, and only when, trait values for the vast majority of known species in their families (and sometimes in large genera) were the same. Thus, for example, we classified all amphisbaenians as fossorial, all anoles as diurnal, and all *Phymaturus* as herbivorous, even though for some species these data have not been reported. We did not impute size data, because the database (Feldman et al., 2016; Meiri, 2018) contains mass data for all the analysed lizards.

Overall, the imputed data represented less than 1% of all microhabitat preference data, 4% of activity time data and 15% of diet type data. After data imputation we had information on all four traits for 3,538 of the 6,151 known species (~60%; Uetz, 2015). Only these 3,538 species were used in the analyses. While lizards are paraphyletic as snakes evolved from them, we chose to omit snakes from our database because they share many apomorphies that make them ecologically and morphologically very different from all lizards.

2.1.2 | Species distribution

Global geographical distribution data for all 6,151 known lizard species (based on the taxonomy used by Uetz, 2015) were assembled by members of the Global Assessment of Reptile Distributions (GARD; Roll et al., 2017).

We examined the richness of each ecological strategy at three scales: one-degree grid cells, biomes, and realms. We spatially intersected the distribution information from Roll et al. (2017), an equal-area Behrmann projection comprising 9,310 cells (at a resolution of ~ 1°), and calculated richness in each cell. We excluded all grid cells that contained less than 70% land cover. For the biome and realm scales we used the seven biogeographic realms and twelve biomes specified by the World Wildlife Fund (Olson et al., 2001; World Wildlife Fund, 2006). We excluded biomes which poorly represent lizards (including fewer than 500 grid cells with lizards and fewer than 500 species) from the analysis and retained seven main biomes (the tropical biomes considered together, deserts, Mediterranean, temperate (all categories considered together), montane, boreal forest and Taiga, and mangroves). Across grid cells we have, on average, data on all traits for 90% of lizard species because species with missing data have small-ranges and hence occupy very few grid cells and contribute little to species richness (Appendix S1). There was no substantial bias in the representation of the traits of the species used in relation to those with missing traits (Appendix S2).

2.2 | Data analysis

In order to define the optimal number of ecological strategies necessary to characterize the global lizard assemblage, we used Archetypal Analysis (AA) which is increasingly used in economics (Li, Wang, Louviere, & Carson, 2003), human health science (Prabhakaran, 2014), sport (Eugster, 2012) and astronomy (Chan, Mitchell, & Cram, 2003). Recently, Pecuchet et al. (2017) have found it a useful and straightforward tool for characterizing fish life history strategies based on traits. Archetypal Analysis is an unsupervised machine learning technique (Cutler & Breiman, 1994), whereby no a-priori categories are imposed upon the data, and is similar to cluster analysis. It seeks to find the number of archetypes (i.e., clusters) that create the smallest convex hull in a *n*-dimensional space (in this case - trait space) by using the extreme values rather than the centroid of the clusters. Instead of assigning each observation (here, species) to an archetype, AA assigns, for each species, a vector of affinities to each archetype (i.e. a coefficient). Therefore, AA is a probabilistic clustering method (Li et al., 2003). When a species has a coefficient of 1 for a particular archetype and 0 for all others, it is completely assigned to that archetype. Most species are probabilistically assigned to several archetypes, with the partial probabilities summing to one (Hart et al., 2015).

We performed AA using the 'archetype' package in R (Eugster & Leisch, 2009). To find the optimal number of archetypes (k) we calculated, for each predefined k (from 1 to 10), the residuals sum of squares of 100 iterations. We used the "elbow criterion" – an approach to assess the minimum number of archetypes corresponding with a significant decrease in the residual sum of squares (Ketchen & Shook, 1996). We gave each of the four traits the same weight. We initially examined different weight combinations, differentially weighting traits in each combination (e.g., according to the number of categories of each trait), and found that the AA results are robust to different trait weighting schemes. Functional diversity was evaluated using the effective number (Jost, 2006) transformation of the Shannon entropy index. We examined the geographic richness pattern of each strategy by summing the coefficients across all species within each one-degree grid cell.

To check the robustness of our analyses to the types of traits we used – and to examine the effects of shared ancestry on trait clusters, we examined the phylogenetic signal in all traits using Pagel's λ (Pagel, 1999) for continuous traits (i.e. body size). For the categorical traits we use δ-value which calculates the level of uncertainty in ancestral reconstruction. The higher δ-value is the less uncertainty there is in the ancestral reconstruction, i.e. stronger phylogenetic signal (Borges, Machado, Gomes, Rocha, & Antunes, 2019). Body size and activity times were found to be the most phylogenetically conserved traits (δ(activity time)=22.15; δ(diet)=12.18; δ(microhabitat)=6.67; λ(mass)=0.96). We therefore ran sensitivity analyses: one without size data and one without activity time, and examined the number and identity of remaining archetypes, and species mapping onto them, compared to those obtained using the full dataset.

Spatial and statistical analyses were carried out in ArcGIS 10.0 (distributed by ESRI) and R version 3.3.0 (R Development Core Team, 2016). We used the 'vcd' package (Meyer, Zeileis, & Hornik, 2006) to visualize the functional space by mosaic graph; the 'vegan' package (Oksanen et al., 2016) for Shannon entropy; and the 'relaimpo' package (Grömping, 2006) for hierarchical partitioning.

3 | RESULTS

We found that 68% of lizard species are diurnal (2,391 of 3,538 analysed species), 90% are terrestrial and/ or scansorial and 82% are carnivorous.

TABLE 1 The seven ecological strategies resulting from Archetypal Analysis

Category	Trait	Scansorial	Terrestrial	Nocturnal	Herbivorous	Fossorial	Large	Semi-aquatic
Microhabitat	Semi-aquatic	0	0	0	0	0	0	100
	Fossorial	0	0	0	0	100	0	0
	Mixed	39	0	22	22	0	26	0
	Scansorial	61	0	71	52	0	10	0
	Terrestrial	0	100	7	26	0	64	0
Activity	Cathemeral	0	3	16	4	22	5	12
	Diurnal	100	82	0	88	43	91	86
	Nocturnal	0	15	84	8	35	4	2
Diet	Carnivorous	100	100	100	0	92	44	86
	Herbivorous	0	0	0	19	1	45	5
	Omnivorous	0	0	0	81	7	11	10
Mass (log gr.)	Average ± s.d.	1.09 ± 0.55	0.83 ± 0.57	0.95 ± 0.47	1.43 ± 0.75	0.86 ± 0.65	3.31 ± 0.70	2.03 ± 1.15
N (species)		925	851	762	560	258	98	84

The table shows the number of species belonging to each strategy (have a coefficient ≥0.5 for a specific strategy; bottom line), their average body mass, and the percentage of species with different traits within a specific strategy (microhabitat, activity and diet each sums to 100 within each category, e.g., 44% of large species are carnivores, 45% are herbivores and 11% are omnivores). A "Mixed" microhabitat refers to species that are both terrestrial and scansorial.

The three most common functional trait combinations are (a) diurnal, terrestrial, carnivores (20% of the species); (b) diurnal, scansorial, carnivores (16%); and (c) nocturnal, scansorial, carnivores (13%; Appendix S3).

The optimal Archetypal Analysis of the global lizard data revealed seven strategies (Appendix S4). Table 1 depicts the distribution of species among the traits in each strategy. Overall, we define these seven major strategies as:

1. *Scansorial* – small diurnal, carnivorous, scansorial species. *Pristurus rupestris*, for example, a rock-dwelling, small, diurnal gecko represents this strategy (with probability of 92.5%; Figure 1a). *P. rupestris* has a broad distribution in southern Arabia (Arnold, 1993; Garcia-Porta, Simó-Riudalbas, Robinson, & Carranza, 2017)).
2. *Terrestrial* – small diurnal, carnivorous and ground-dwelling species. *Ablepharus kitaibelii*, a small-bodied, carnivorous skink, best represents this strategy (with probability of 99.4%). *A. kitaibelii* is widespread in Eastern Europe, occurring in relatively dry habitats (Herczeg, Kovács, Korsós, & Török, 2007; Valakos et al., 2008; Figure 1b).
3. *Nocturnal* – small terrestrial, scansorial and carnivorous species that are, at least partially, active at night (i.e. they are either nocturnal or cathemeral). More than 400 species have a probability >90% of belonging to the *nocturnal* strategy. *Hemidactylus turcicus*, for example, has a 99.9% probability of belonging to this strategy. This rock-dwelling, nocturnal gecko has an Eastern Mediterranean native distribution range, and is also known as an invasive species e.g., in North and Central America (Rödder & Lötters, 2009; Figure 1c).
4. *Herbivorous* - relatively large, diurnal, terrestrial and scansorial species whose diet includes substantial amounts of plant matter (either as omnivores or herbivores). One of the lizards that represents the *herbivorous* strategy is *Uromastyx ornata* (with probability of 93%). This is a diurnal lizard endemic to the Arabo-Sinai region, which inhabits steep, rocky wadis (SM pers. obs.; Figure 1d).
5. *Fossorial* – living at least partially underground, mainly small, carnivorous, with varied activity times. *Ophiomorus latastii* is one of the lizards that best represent this strategy (with probability of 97%). This is a cathemeral, legless skink that occurs in light soils with high humidity in Israel, Syria and Jordan (Figure 1e).
6. *Large* - very big (all species >200 g), mainly diurnal, terrestrial or scansorial species. The world's largest extant lizard, *Varanus komodoensis*, represents the *large* strategy with a probability of 100%. This terrestrial top-predator occurs on the islands

FIGURE 1 Examples of species that represent the seven strategies: (a) *Pristurus rupestris* represents the *scansorial* strategy (photo: Salvador Carranza); (b) *Ablepharus kitaibelii* – *terrestrial* strategy (photo: David David); (c) *Hemidactylus turcicus* -*nocturnal* strategy (photo: Alex Slavenko); (d) *Uromastyx ornata* – *herbivorous* strategy (photo: Alex Slavenko); (e) *Ophiomorus latastii* – *fossorial* strategy (photo: Simon Jamison); (f) *Varanus komodoensis* – *large* strategy (photo: Claudia M. Hoogmoed); (g) *Uranoscodon superciliosus* – *semi-aquatic* strategy (photo: Marinus S. Hoogmoed) [Colour figure can be viewed at wileyonlinelibrary.com]

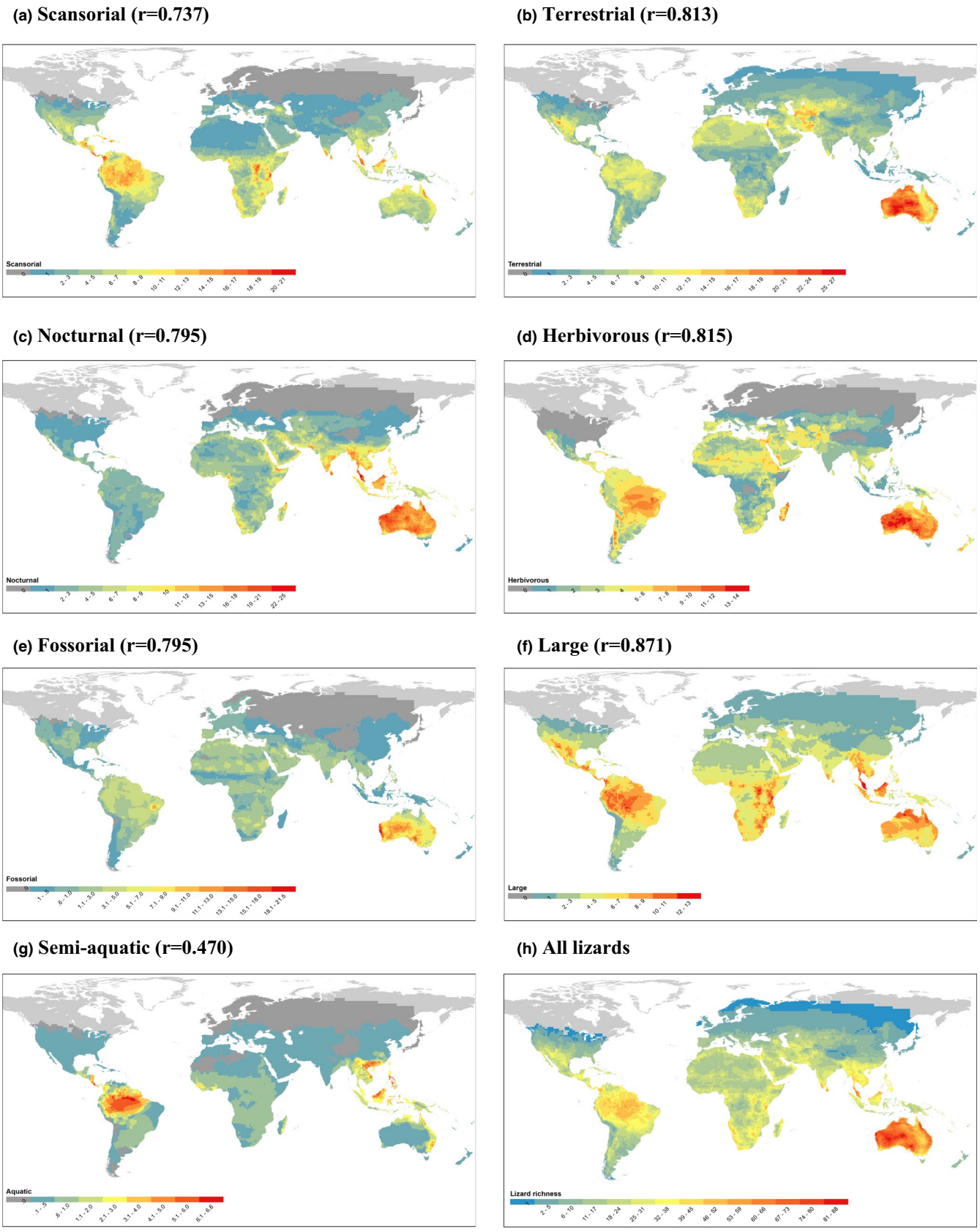

FIGURE 2 Richness map of each strategy in an equal-area Behrmann projection grid (9,310 km^2 cells). Richness was defined as the sum of the strategy coefficient per grid cell. In parentheses is the Pearson correlation coefficient (r) between total lizard richness and the richness of each strategy. Areas in light grey in northern America and Eurasia indicate grid cells with no lizards [Colour figure can be viewed at wileyonlinelibrary.com]

of south-eastern Indonesia (Jessop et al., 2006; Koch, Ziegler, Böhme, Arida, & Auliya, 2013; Figure 1f).

7. *Semi-aquatic* - dwelling in aquatic habitats, relatively large, and generally both carnivorous and diurnal. The *semi-aquatic* strategy is well-characterized by *Uranoscodon superciliosus* (with probability of 99.2%), an iguanian lizard also known as the diving lizard. It is a medium to large lizard from the Amazonian basin, inhabiting vegetated areas near aquatic habitats and feeding on invertebrates (Ávila-Pires, 1995; Bauer & Jackman, 2008; Figure 1g).

The names we chose for the seven archetypes are not inclusive. Thus, while all lizards belonging to the "large" archetype are large-sized, not all large-sized lizards belong to this archetype; and while all "nocturnal" species are active at night, not all species that are active at night were assigned to this archetype, etc. (for example the nocturnal gecko *Stenodactylus sthenodactylus* was classified as terrestrial – not as nocturnal, and the large-bodied iguanas of the genera *Cyclura* and *Iguana* were mostly assigned to the herbivorous and not to the "large" archetype).

Sensitivity analyses without mass or activity times both resulted in six archetypes (Appendix S5). When no mass data were used the resulting archetypes were the same as those in the analysis of all traits, except that the "large" category disappeared. The 98 "large" species were now classified as "herbivorous" (55), "terrestrial" (23), "scansorial" (15) and "nocturnal" (5 species). The vast majority of other species (95.5%) were assigned to the same archetype as before, but 149 species designated "terrestrial" in the full analysis (all either cathemeral or nocturnal) were now classified as nocturnal. When no activity time data were used the resulting archetypes were the same as those in the analysis of all traits, except that the "nocturnal" category disappeared. Most (706) species previously assigned to the "nocturnal" category were assigned to the "scansorial" archetype in this analysis (the other 56 species were assigned to the "terrestrial" archetype). The vast majority (99%) of other species were assigned to the same archetype as in the analysis of the entire dataset (except that 22 "large" species were now classified as "terrestrial", and 5 as "scansorial", and one "terrestrial" species moved to the "large" archetype). Results of these sensitivity analyses are reported in online Appendix S5 in the supplementary material.

We examined the geographic richness pattern of each strategy by summing the coefficients across all species within each one-degree grid cell. The spatial richness patterns of the seven strategies vary widely (Figure 2), with two main global hotspots. Australia is the main hotspot for the *herbivorous*, *nocturnal*, *fossorial*, and *terrestrial* strategies – and for lizards in general. The Amazon basin is the main hotspot for the *semi-aquatic*, and *scansorial* strategies, whereas the *large* strategy has pan-tropical hotspots, especially in both the Amazon Basin and Northern Australia, but also in Africa, SE Asia and

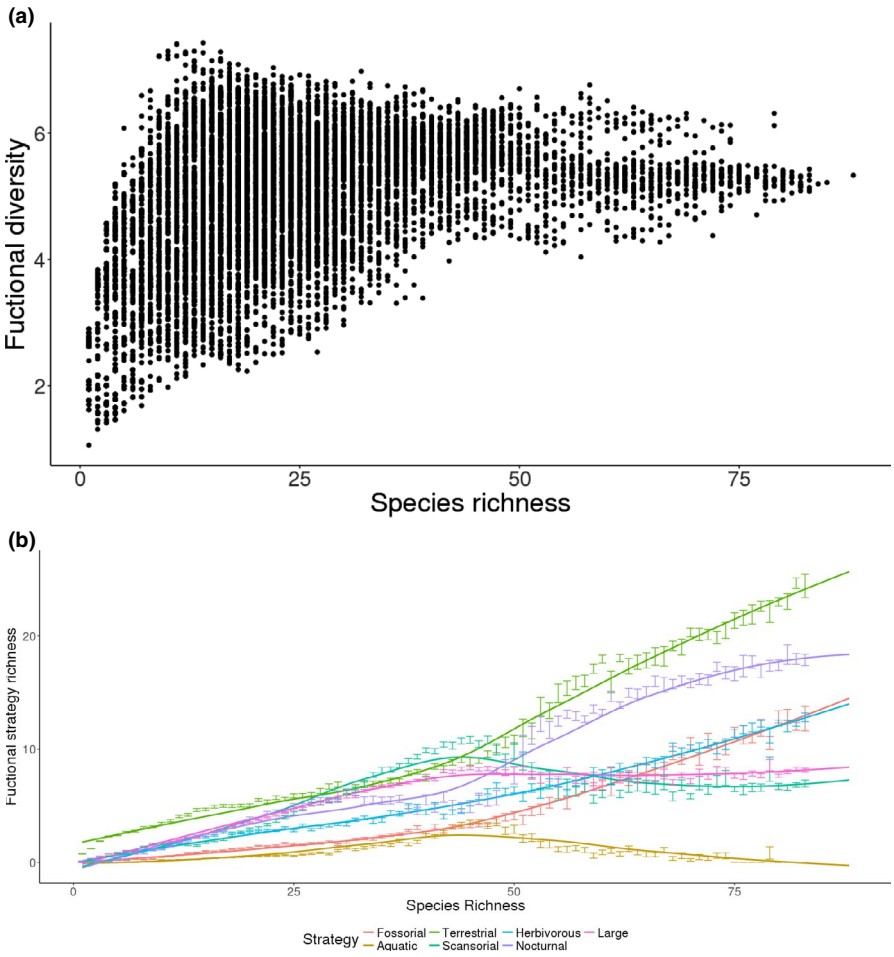

FIGURE 3 The species – functional relationship. (a) The relationship between functional diversity and richness of the global lizard assemblage per grid cell (r = 0.57, *p* value << 0.001). The diversity was evaluated using Shannon entropy i.e., converting the sum of the strategy coefficients to effective numbers (Jost, 2006). (b) The relationship between total species richness within grid cells and richness within each strategy (summed probabilities of all species in a strategy within the cell). The lines represent the mean value of the functional richness per each species richness. The error bars represent the standard errors [Colour figure can be viewed at wileyonlinelibrary.com]

Mexico (Figure 2). The richness pattern of the *semi-aquatic* strategy is similar to that known for amphibians (see map in Buckley & Jetz, 2007). Overall, richness of all strategies is significantly correlated with the richness pattern of all 3,538 lizards in our dataset (Pearson correlation, *p* values <0.001 for all the cases; Figure 2). The pattern of the *large* strategy richness demonstrates the strongest correlation with total lizard richness (r = 0.87; *n* = 2,257 species with coefficient value >0; note that only for 98 species the coefficient was higher than for all other traits) while the *semi-aquatic* strategy demonstrates the weakest correlation (*n* = 1,075 species, r = 0.47; Figure 2).

At the realm scale, we find that the Neotropics has the highest lizard species richness, and the highest functional strategy richness in most strategies (Appendix S6). The exceptions are the *semi-aquatic* strategy, with highest richness in both the Neotropics and Indomalayan realms; the *fossorial* strategy with highest richness in Australia; and the *nocturnal* strategy, which is richest in the Indomalayan realm. The *terrestrial* strategy is the most species-rich functional group in the Nearctic and Palearctic, while the *scansorial* strategy is the most species-rich functional group in the Afrotropics and Oceanian realms. The *terrestrial* and *scansorial* are the most species-rich functional groups in the Neotropics, while the most species-rich functional group in Australasian and Indomalayan realms is the *nocturnal* (Figure 2; Appendix S6A and B). At the biome scale, all strategies have richness peaks in tropical biomes. The *terrestrial* strategy dominates most biomes, except the tropics (where *scansorial* and *nocturnal* strategies are dominant) and mangroves (*scansorial* dominant; Appendix S6C and D).

We expected an overall positive correlation between functional diversity and richness but found that the relationship is not monotonic: functional diversity peaks in areas with medium species richness and slowly decreases toward the most species-rich areas (Figure 3a). This unexpected unimodal association between richness and functional diversity is also revealed in the relationship between richness within strategies and global richness (Figure 3b). The richness patterns of *terrestrial*, *nocturnal*, *herbivorous*, and *fossorial* strategies increase with species richness, whereas the *scansorial*, *large*, and *semi-aquatic* strategies exhibit patterns more similar to the global functional diversity (Figure 4), with highest functional richness in areas with medium species richness (Figure 3b).

4 | DISCUSSION

We deconstructed the global lizard assemblage along multiple ecological axes that offer a novel perspective on lizard diversity patterns. Overall, seven different ecological strategies were defined for lizards, each exhibiting a unique global richness pattern. Importantly, we found that increased species richness is not necessarily associated with increased functional diversity, and that the richest areas are characterized by a high richness in only some of the specific strategies. For example, in Australia, the global lizard hotspot, the *scansorial* and *semi-aquatic* strategies are species-poor. This is probably due to the large expanse of desert habitat, which is devoid of freshwater sources and trees, that *scansorial* and *semi-aquatic* lizards need to thrive.

All else being equal, the probability of an assemblage including species with unique trait compositions increases with the number of species (e.g., Naeem, Bunker, Hector, Loreau, & Perrings, 2009). Indeed, most, if not all, studies that have examined the relationship between functional richness and species richness, found a positive saturating association (e.g., Petchey, Evans, Fishburn, & Gaston, 2007; Farias & Svensson, 2014; González-Maya, Víquez-R, Arias-Alzate, Belant, & Ceballos, 2016). This relationship is not necessarily linear, due to a decrease in the appearance of new traits as the number of species increases (e.g., Farias & Svensson, 2014). Similarly, the relationship between functional and species richness of the global lizard assemblage showed an initial positive and saturating association. At higher richness values a decrease in functional diversity became apparent (Figure 3a). This is also apparent in the relationship between species richness of some functional strategy and overall lizard species richness (Figure 3b). While the number of species in strategies such as *terrestrial* and *nocturnal* monotonically increase with richness, others, such as the *scansorial* and *semi-aquatic*, exhibit a hump-shaped relationship between strategy richness and overall

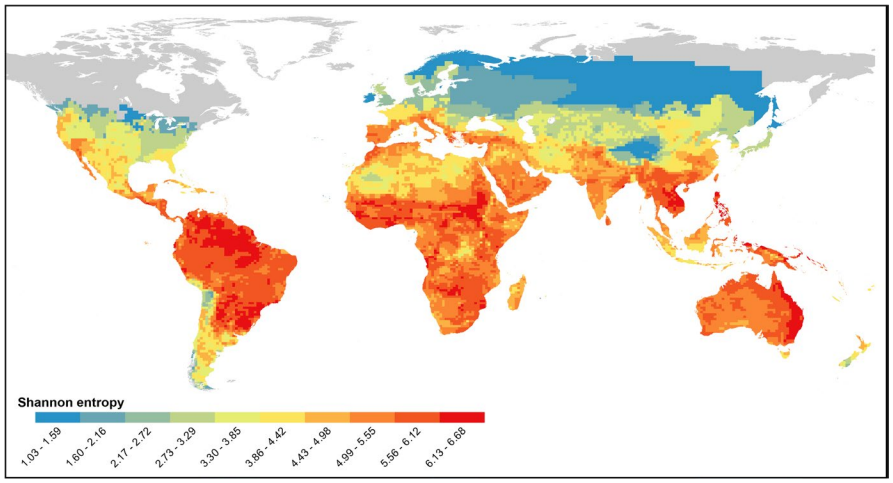

FIGURE 4 Strategy diversity map of the global lizard assemblage in equal-area Behrmann projection grid cells (9,310 km^2). Diversity was evaluated using Shannon entropy. Areas in light grey in northern America and Eurasia indicate grid cells with no lizard species [Colour figure can be viewed at wileyonlinelibrary.com]

species richness. Thus, higher overall richness is not caused by an increase in ecological opportunities leading to diversity of ecological function. Rather, specific strategies seem to become hyper-diverse in the richness hotspots (e.g., *terrestrial* lizards in Australia), and these dominate total richness patterns.

While Australia is the main global hotspot of lizard richness (Roll et al., 2017), an analysis of the seven ecological strategies revealed a more complex picture. The Amazon basin is revealed as another major hotspot. The tropical Amazon basin is a global richness hotspot of all major tetrapod taxa, as well as for numerous invertebrate and plant groups (Buckley & Jetz, 2007; Ceballos et al., 2005; Grenyer et al., 2006; Orme et al., 2005). The Australian hotspot, which is largely comprised of desert, is unique to lizards (Powney et al., 2010; Roll et al., 2017). A comparison of these two regions reveals that there is a spatial partitioning between the two dominant strategies. The *terrestrial* strategy (comprised of diurnal, terrestrial carnivores) is more common in the Old World and, mainly, in Australia, while for the *scansorial* strategy (diurnal, scansorial carnivores) the largest hotspot is in the New World, mainly in the Amazon basin. This pattern probably results from the differences in habitat complexity and microhabitat availability between these two diversity hotspots. While *terrestrial* lizards often prosper in habitats with few trees, such as deserts, *scansorial* species are more restricted to well-wooded habitats such as the Neotropical forests. Interestingly, the *scansorial* strategy is the dominant strategy in the tropical realms (i.e., the Neotropics, Afrotropics, and Oceania; Appendix S6C and D) while its proportion is relatively low in most of the other woody biomes. This strategy may be limited by climatic conditions, such as low temperature, and is therefore less common in colder habitats even if they are rich in woody plants, such as Mediterranean, temperate, and boreal forests – where low night-time temperatures may prevent them from finding suitable thermal retreats.

The *large* strategy, which is characterized by very large-bodied terrestrial and scansorial lizards, has the strongest congruence with the global species-richness pattern and the greatest contribution to the overall functional-strategy pattern (26%; Appendix S7). This is despite the fact that the *large* strategy constitutes fewer than 3% of the lizard species analysed. It has been claimed that species richness patterns are mainly shaped by wide-ranging species (e.g., Belmaker & Jetz, 2011; Reddin et al., 2015), due to their disproportionate contribution to spatial analyses when compared with narrow ranging species (e.g., Lennon, Koleff, Greenwood, & Gaston, 2004). Indeed, despite the small number of *large* lizard species, they have the largest range size among all seven strategies (Appendix S8), and the *large* strategy was present in 99.8% of the grid cells that lizards inhabit.

The richness pattern of the *semi-aquatic* strategy is similar to that found for amphibians (see map in Buckley & Jetz, 2007). The *semi-aquatic* strategy exists in all the realms but is mainly restricted to the tropical biomes and is probably mostly limited by water availability and temperature, as was found for amphibians (Buckley & Jetz, 2007). However, compared with the amphibians, the *semi-aquatic* strategy has discernibly high richness in the Old World, mainly in the Indomalayan realm, where amphibians are relatively not as rich.

The *nocturnal* strategy is almost absent from the New World. *Nocturnal* species occur mainly in the Old World and Australian tropics and, to a lower extent, in the deserts. As opposed to the other strategies, the *nocturnal* strategy is dominated by a specific clade – the Gekkota (Appendix S9), although it contains members of other clades as well (notably Australian *Lerista* skinks). This finding is compatible with previous studies that found that diel activity is highly phylogenetically conserved (Anderson & Wiens, 2017; Roll, Dayan, & Kronfeld-Schor, 2006; Vidan et al., 2017). This raises two interesting questions for future research: (a) Why does nocturnality seldom occur in the New World; and (b) Why does nocturnality remain almost exclusively (94% of species) a gekkotan trait? Answering these questions will require detailed phylogenetic and biogeographic analyses. Excluding data on activity times resulted in most species previously classified to the "nocturnal" archetype being re-assigned to the scansorial archetype (these are, indeed, all scansorial; Appendix S5). As all other archetypes remained the same when we removed this trait (and when removing body size, another strongly phylogenetically conserved trait), we conclude that our classification is robust with respect to phylogenetic non-independence.

Examining the associations between traits, we found that almost no nocturnal-herbivorous lizards exist (fewer than 0.5% of the nocturnal species are herbivores; e.g., the Australian skink, *Liopholis kintorei*). One hypothesis has suggested that herbivore lizards require a high body temperature throughout most of the day in order to facilitate their digestion process (Janzen, 1973; Tracy, Flack, Zimmerman, Espinoza, & Tracy, 2005). As such, it may be hard to achieve this requirement with a nocturnal activity pattern, due to colder night temperatures.

While Australia is the main lizard-richness hotspot on the grid-cell scale, the Neotropics exhibit the highest richness at the realm scale. This difference may be due to the variation in area (the Neotropics is about 2.5 times the size of Australia – 19 vs. 7.6 million km^2). Thus much of the difference at the realm scale can be explained by the species-area relationship (e.g., Rosenzweig, 1995). That said, species in the Neotropics have narrower distributional ranges than in Australia (by a factor of about 5; the median is 97,327 km^2 in Australia and 19,765 km^2 in the Neotropics; $F_{1,2,126} = 225.1$, $p < 0.0001$). As a result, the spatial turnover (β diversity) between lizard species must be higher in the Neotropics. Thus while at the grid scale level richness of most strategies is higher in Australia, high turnover causes the overall high species richness (higher γ diversity) in the Neotropics.

We have analysed a large (>3,500 species) dataset, including all species for which we had data on all the traits we examined. This still misses over 3,000 lizard species for which data were at least partially unavailable. While it is possible that the inclusion of yet more species would have resulted in a somewhat different number or kinds of archetypes, we think this is unlikely. A sensitivity analysis in which we randomly picked just one species per genus resulted in us obtaining the same seven archetypes >90% of the time (about~10% of the randomizations resulted in three archetypes being narrowly preferred over a seven archetype solution, results not shown). For some lizard-rich regions (e.g., the Horn of Africa, Madagascar, New

Guinea) we had relatively few data (Appendix S1). Thus, the inclusion of more species, although most are small ranged, may nonetheless have potentially changed our results somewhat. We emphasize the need to obtain more natural history data for many taxa which are to-date ecologically almost unknown.

This functional-group division reinforces the finding of Pianka et al. (2017) of the marked separation between lizard natural history strategies. Specifically, Pianka et al. (2017) found that body size, along with foraging mode, and clutch size, is a major niche axis differentiating lizard traits. We also find body size to be important in strategy categorization, but it mostly acts to distinguish the *large* strategy, and does not strongly impact the categorization of other species. Additionally, both our analyses and Pianka et al. (2017) find very distinct differences between diurnal and nocturnal lizards within the functional space. We chose not to use traits such as parity mode and clutch size as these fitness-relevant traits are less relevant for understanding lizard function from an ecological, Eltonian perspective. Such traits do not immediately deal with the way a lizard copes with its environment (e.g., Wilman et al., 2014).

5 | CONCLUSION

This study emphasizes the importance of deconstructing global assemblages into unique functional-strategies, in order to better understand overall richness patterns. In doing so for lizards, we have revealed that the Amazon basin is the major hotspot for four of the seven strategies. Categorizing lizards by functional strategy also enabled us to highlight the richness patterns of unique groups with important ecological roles or conservation concern. The *semi-aquatic* lizards predominantly occupying habitats that are under substantial anthropogenic impacts, and analyses such as ours can single them out for conservation purposes. In contrast with previous studies, we find that increases in richness do not necessarily stem from increased functional-strategy diversity. Instead, species diversification within specific strategies can dominate richness patterns. Overall, these findings support the contention that it is important to consider different functional and ecological subgroups when studying richness patterns.

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DATA AVAILABILITY STATEMENT

The lizard distributional data were made available as part of the manuscript by Roll et al. (2017).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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