

# Alternative pathways to diversity across ecologically distinct lizard radiations

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## Abstract

**Aim:** Lizard assemblages vary greatly in taxonomic, ecological and phenotypic diversity, yet the mechanisms that generate and maintain these patterns at a macroecological scale are not well understood. We aimed to characterize the ecological and environmental drivers of species richness patterns in the context of macroecological theory for 10 independent lizard radiations.

**Location:** Global.

**Time period:** Present day.

**Major taxa:** Lizards.

**Methods:** We analysed patterns of species and functional trait diversity in 10 ecologically distinct and widely distributed clades encompassing nearly all known lizard species. Using recently published spatial, phylogenetic, and functional trait datasets, we built spatially explicit structural equation models to ask whether species richness was directly or indirectly related to functional divergence or convergence within communities, and with features of the environment, including measures of productivity, complexity and harshness.

**Results:** Our results show that high species richness is achieved via different pathways in different lizard clades, with both functionally divergent and convergent assemblages harbouring high diversity in different clades. More generally, we also find common, positive effects of temperature, productivity and topography on species richness within lizard clades.

**Main conclusions:** Thermal constraints, topographic complexity and spatial structuring of functional diversity help explain the presence of highly diverse lizard assemblages, suggesting the importance of environmental filters in shaping present-day diversity and assemblage structure. Our results show how different pathways to high richness in different clades have contributed to the overall global pattern of species richness in reptiles.

## KEYWORDS

functional divergence, macroecology, reptiles, species richness, squamates

## 1 | INTRODUCTION

Species richness in lizards is unequally distributed around the world, and in many cases, lizards show discordant diversity patterns compared to other major clades of terrestrial vertebrates. Some of the greatest diversity in lizards is present in the hot and dry deserts of southern Africa, the Arabian Peninsula and western Australia (Pianka, 1973; Roll et al., 2017), biomes relatively low in diversity of other vertebrates. On the contrary, other lizard diversity hotspots, including tropical America and Southeast Asia, are also hotspots for many other groups of vertebrates (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012; Oliveira et al., 2016; Roll et al., 2017). This variation in species richness patterns has made diagnosing the drivers of lizard diversity difficult, and suggests that a range of potential drivers of diversity in lizards exists, some of which may be unique amongst terrestrial vertebrates (Powney, Grenyer, Orme, Owens, & Meiri, 2010; Tallowin, Allison, Algar, Kraus, & Meiri, 2017). Investigating the structure and correlates of diversity of global lizard assemblages across major taxonomic divisions may help to infer the processes that have shaped the range of patterns within lizards, one of the most conspicuous, abundant, and ecologically important groups of terrestrial vertebrates (Pianka & Vitt, 2003).

Species pools from which communities are assembled tend to be comprised of closely related species (Jordan, 1905; Warren, Cardillo, Rosauer, & Bolnick, 2014). Given that allopatric subdivision is the most likely mode of speciation in many vertebrate clades (Mayr, 1963; Skeels & Cardillo, 2019b), sympatry between species is often the result of secondary dispersal after speciation. Therefore, to understand how diversity has arisen, we require an understanding of how closely related species can coexist in the same geographic space. If close relatives are the strongest potential competitors for resources (Darwin, 1859; Elton, 1946), then secondary sympatry must be driven by differences in the ecological niche that limit competition (MacArthur & Levins, 1967). Alternatively, some regions may support ecologically similar species because a shared resource is abundant enough for multiple species to maintain a minimum viable population size (the more-individuals hypothesis; Srivastava & Lawton, 1998; Storch, Bodhalkova, & Okie, 2018). In such cases, sympatry might be unrelated to niche divergence.

These alternative scenarios relate to expectations about the strength of competitive interactions as filters in the formation of assemblages, and we might expect the strength of different assembly mechanisms to vary across environments. For example, the more-individuals hypothesis argues that greater similarity of species' ecological niches in high richness assemblages is possible in ecosystems (such as tropical rainforests) with high environmental productivity and resource availability (Srivastava & Lawton, 1998; Storch et al., 2018). Other hypotheses, however, may make different predictions based on the same variables. For example, biotic interactions, including mutualisms, competition, parasitism and predation, are often considered to be more important in high-productivity ecosystems such as tropical rainforests (Dobzhansky, 1950; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009), which

might lead to species-rich assemblages consisting of ecologically divergent species due to ecological specialization and coevolution.

It is unlikely that a single theoretical model that describes the relationships between species richness, ecological divergence and environmental features can account for the variety of species richness patterns seen in diverse vertebrate radiations such as lizards. This is because different mechanisms may be responsible for generating high richness in different regions, different clades or both. One way to approach testing this idea is by categorizing environmental predictors into broad classes that relate to the key aspects of each hypothesis. For example, several core macroecological hypotheses make predictions related to some measure of either environmental productivity, complexity or harshness (e.g., Fine, 2015; Laliberte, Kiely, et al., 2014) and these three axes of environmental variation can form the basis of a pluralistic explanatory framework for lizard diversity.

Productivity is associated with environmental energy and resource quantities and at large spatial scales is expected to be positively correlated with species richness (Waide et al., 1999). Productivity may promote ecological similarity by increasing the number of individuals that can use similar resources (Srivastava & Lawton, 1998; Hypothesis 1 (H1), Table 1), or drive ecological divergence by promoting biotic interactions (Brown, 2014; H2). Harshness is a measure of environmental extremes such as freezing temperatures or aridity. Harshness may act as an environmental filter, placing constraints on functional or species diversity by restricting the number and kind of species that can tolerate extreme conditions (Kraft et al., 2015; Webb, Ackerly, McPeck, & Donoghue, 2002; H3), or may promote ecological divergence due to increased competition for scarce resources, or selection for novel ecological strategies (Botero, Dor,

**TABLE 1** Six hypotheses that link ecological divergence, species richness, and three major environmental factors, harshness, productivity and complexity, and their predictions for the relationships between variables

Hypothesis		Predictions		
		SR ~ Env	ED ~ Env	SR ~ ED
H1	Productivity: more individuals	+	-/~	-
H2	Productivity: biotic interactions	+	+	+
H3	Harshness: environmental filtering	-	+	+
H4	Harshness: competition	-/~	+	-
H5	Complexity: niche diversity	+	+	+
H6	Complexity: al-lopatric speciation	+	-/~	-

Abbreviations: Env = environment; SR = species richness; ED = ecological divergence. - = negative correlation; + = positive correlation; ~ = no correlation.

McCain, & Safran, 2014; H4). Complexity is a measure of environmental heterogeneity or structure such as topographic ruggedness, which is expected to be positively correlated with species richness. Complexity may promote ecological divergence by increasing the number of environmental niches available in a given area (Badgley et al., 2017; H5), or may increase the opportunity for allopatric speciation without necessarily increasing ecological or phenotypic diversity (Badgley et al., 2017; H6). These six hypotheses are not mutually exclusive and different environmental variables may span different categories (for example, temperature might be a measure of both productivity and harshness). However, this simplified scheme allows us to present a hypothesis testing framework to investigate alternative possible drivers of species richness simultaneously (Table 1).

Recent publication of several large databases (Meiri, 2018; Roll et al., 2017; Tonini, Beard, Ferreira, Jetz, & Pyron, 2016) has now made it possible to begin to explore how the environment and ecological and phenotypic trait diversity interact to shape spatial diversity patterns in lizards on a global scale (e.g., Vidan et al., in press). Different lizard taxa also show varied spatial diversity patterns (e.g., Powney et al., 2010), and this makes them excellent independent case studies to further explore the mechanisms that drive diversity. We therefore predict that different mechanisms may be responsible for the origin of different regional diversity patterns in different taxa. For example, patterns of species and ecological diversity in teiid and gymnophthalmid lizards, which reach their highest levels in high-productivity tropical regions may be best explained by the more-individuals hypothesis (H1) or the productivity/biotic interactions hypothesis (Schemske et al., 2009; H2). Harshness mechanisms (H4) may best explain arid-zone hotspots for groups such as agamid dragons and scincoids, which reach maximum diversity in the western Australian deserts, due to competition-driven niche divergence (Pianka, 1973). Diversity in groups such as liolaemids, with maximum diversity in the Andes, might be best explained by environmental heterogeneity associated with topographic complexity (H5), or allopatric species pumps (Esquerré, Brennan, Catullo, Torres-Pérez, & Keogh, 2019; H6). This study aims to estimate patterns of ecological divergence (hereafter functional divergence as we use functional traits as proxies for species ecological niches) within different taxonomically and ecologically defined lizard taxa, and then to compare the support for the six models described above by testing the relationships between species richness, functional divergence, and major environment features, within each taxon.

## 2 | METHODS

### 2.1 | Clade selection

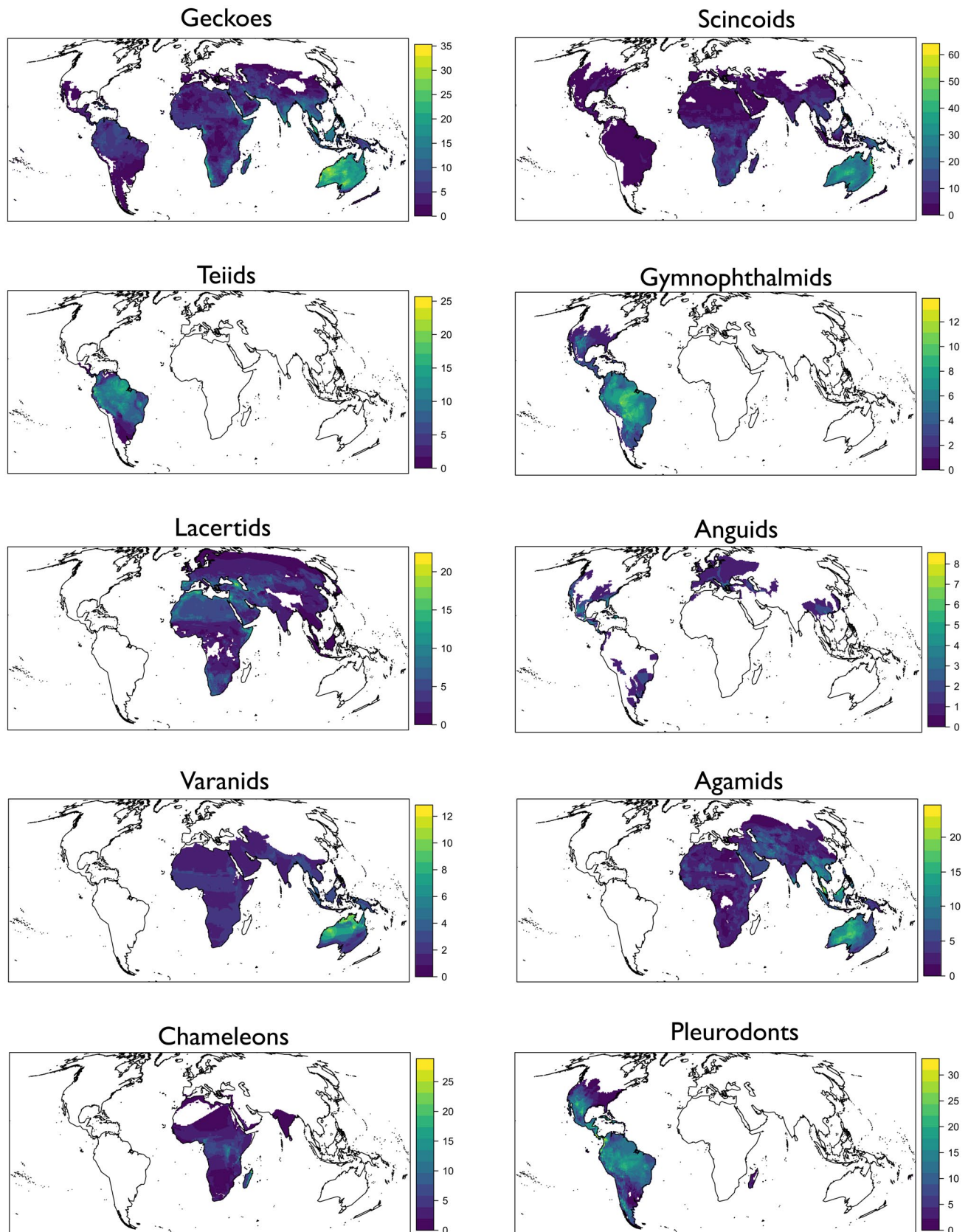
Estimating patterns of functional divergence to understand the drivers of species richness requires comparisons between ecologically similar units that share an evolutionary history. We selected lizards to include all squamate reptiles excluding snakes, amphisbaenians and dibamids, which are vastly different in their ecomorphology. In addition, we divided lizards into ecologically cohesive subclades to

investigate diversity patterns, as the hypotheses we were testing assume that interactions such as competition for shared resources are most likely to take place between closely related species with similar ecologies. While there is value in looking at patterns of diversity at a very broad taxonomic scale (e.g., all lizards), interpretation of functional divergence becomes more difficult. For example, the addition of any very distantly related species to an assemblage might disproportionately and misleadingly influence the measure of functional divergence, such as the presence of one apex-predator monitor lizard (Varanidae) in an assemblage largely consisting of small leaf-litter scincoids (Scincidae). We selected 10 clades: anguids (Anguidae, Anniellidae, and Diploglossidae), varanids (Varanidae), agamids (Agamidae), scincoids and allies (Scincoidea), pleurodons and allies (Pleurodonta), teiids (Teiidae), gymnophthalmids (Gymnophthalmidae), chameleons (Chamaleonidae), lacertids (Lacertidae) and geckoes (Gekkota). These groups not only represent independent monophyletic clades, but vary substantially in their ecology, diversity, and geographic distributions (Figure 1), making them suitable independent case studies to test our hypotheses.

### 2.2 | Spatial, phylogenetic and trait data

We used the most recent estimates of lizard species' geographic distributions and phylogenetic relationships. The phylogeny we used was the consensus super-tree of squamate reptiles from Tonini et al. (2016), a revision of a phylogeny first presented by Pyron, Burbrink, and Wiens (2013). This phylogeny is based on molecular data for roughly 55% of taxa, with the remaining taxa placed using taxonomic inferences (PASTIS; Thomas et al., 2013). Spatial data are from Roll et al. (2017) and contain polygonal maps for almost all squamate reptiles based on expert assessment and occurrence records. Trait data are from Meiri (2018). This comprehensive database contains ecological and phenotypic data for nearly all species of lizards, compiled from the lizard biology literature.

Many of the traits in the database are incompletely sampled across lizard species. To account for this we imputed missing data using random forest machine learning ('missForest' v. 1.4; Stekhoven & Bühlmann, 2012) in R (R Core Team, 2019). We used random forest data imputation because there is a tendency for missing data to be biased with respect to species ecology (particularly species rarity and geographic range location) and multiple imputation has been shown to reduce bias by maintaining the relationships between traits (Penone et al., 2014). Random forest machine learning has been shown to outperform several other imputation methods (e.g., KNN; Troyanskaya et al., 2001) by allowing for complex nonlinear relationships between mixed variable types. Phylogenetic imputation (e.g., PhyloPars; Bruggeman, Heringa, & Brandt, 2009), on the contrary, requires transforming categorical variables into sets of binary variables and as such was not used in this analysis. We used all traits in the Meiri (2018) dataset for data imputation, including taxonomic family included as an additional variable to account for the phylogenetic component of



**FIGURE 1** Geographic patterns of species richness in 10 lizard clades. Species richness was estimated within 50 km × 50 km equal-area grid cells using species range maps from Roll et al. (2017) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

variation in trait values. However, we selected only a subset of traits to use in downstream analysis. First, we selected traits that had > 50% representation across all lizard species. We found nine traits that had > 50% coverage (3,000 + species) and most of these had > 80% coverage (4,800 + species). These traits were maximum snout-vent length (SVL), female SVL, activity time, diet, reproductive mode, smallest and largest clutch size, leg development, and microhabitat. We also obtained body mass data based on a conversion of maximum SVL using family specific equations (Feldman, Sabath, Pyron, Mayrose, & Meiri, 2016; Meiri, 2010, 2018).

We used body mass in place of both maximum and female SVL as it is regarded as one of the most important functional traits in reptiles (Hedges, 1985; Meiri, 2010) and is also highly correlated with maximum and female SVL. We discarded clutch size (largest and smallest) and reproductive mode as these traits were unlikely to be involved in niche partitioning between species. Microhabitat data were originally grouped into seven categories (fossorial, cryptic, saxicolous, arboreal, terrestrial, marine, semi-aquatic); we extended this to eight categories by including a generalist category for species belonging to more than one habitat class. Diet was classified as whether a species consumes mostly plants (herbivorous), mostly animal matter (carnivorous) or mostly animal matter with a significant proportion of plant matter (omnivorous). Leg development was classified as whether a species had four limbs, only forelimbs, only hind limbs or was limbless. Activity time was classified as whether species were nocturnal, diurnal or cathemeral (Meiri, 2018). Body mass data were log transformed to normalize the distribution and make differences between species proportional.

We therefore used five traits for our analyses, body mass (which required imputation in <1% of species), and four categorical variables; activity time, diet, microhabitat (which required imputation in <50% of species) and leg development (no missing data). To ascertain an estimate of imputation error, we subsampled the trait data for all species that had complete observations for the five traits (3,066 species). We then simulated missing data by removing 10% of observations randomly. We imputed these missing data then estimated the imputation error rate as the proportion of falsely classified entries.

Each database had some entries that were not found in the other databases due to taxonomic differences (e.g., synonyms or species descriptions post-dating the publication of the data), or spelling incongruencies. We found 198 species mismatched between the spatial and trait data, all of which were synonyms, so we relabelled databases based on the most up-to-date taxonomy in The Reptile Database (Uetz & Hošek, 2019). There were a further 309 species with trait and spatial data that were not present in the phylogeny. Of these, 201 of those were synonyms and five were misspellings. The remaining 103 species were described after the time of publication of the phylogeny and were excluded from analyses. This resulted in a dataset containing traits, ranges, and phylogenetic relationships for 6,129 species of lizards, or 5,959 after excluding the amphisbaenians, dibamids and species from the ecologically and phenotypically distinct but low diversity Helodermatidae,

Lanthanotidae, Shinisauridae and Xenosauridae. The 10 clades we selected included 1,581 geckoes, 1,704 scincoids, 246 teiids, 144 gymnophthalmids, 318 lacertids, 126 anguids, 78 varanids, 453 agamids, 201 chameleons, 1,108 pleurodonts.

## 2.3 | Geographic sampling

Ecological processes can lead to patterns that emerge at different spatial scales and extents. Macroecological studies typically study ecological processes at broad spatial extents (continental or global) and coarse spatial resolutions (e.g., 100 km × 100 km quadrats; McGill, 2019). However, it is broadly recognized that ecological interactions between species typically occur at finer resolutions (Rahbek, 2005). We sampled 50 km × 50 km equal area grid cells based on a Mollweide projection of the spatial data across the distribution of each clade to provide a reasonable balance of the trade-offs between the extent of our study (global), the resolution of our species-level spatial data (broad spatial polygons), the resolution at which the ecological processes we were interested in may manifest as discernible patterns (local-scale species interactions), and the computational constraints of large spatial datasets.

At broad spatial resolutions (e.g., 50 km × 50 km) a signature of ecological interactions may be difficult to detect because species may occur in allopatry across topographic and environmental gradients within assemblages of this size. We make a distinction here between assemblages (in which species may interact) and communities (in which species do interact), and we attempt to address this in our approach to selecting appropriate predictor variables for modelling species richness and functional divergence (see below). By including a variable to represent topographic complexity, we aimed to distinguish between scenarios where species richness is driven by habitat diversity or allopatry (H5 and H6, Table 1) within assemblages. We also re-analysed the data at a finer spatial scale (25 km × 25 km grid cells), at which ecological interactions may be more likely to structure assemblages (although the same issue is present at this spatial resolution). However, it is noted that at this finer spatial scale we can be less certain of the accuracy of species compositions, because 25 km × 25 km is a finer scale than that at which the spatial data were collected. Results at both spatial scales are qualitatively similar and discussed in Supporting Information Appendix S1. For the remainder of the main text we discuss analyses done at the 50 km × 50 km scale.

We stratified the sampling of sites across ecoregions to make sure we sampled a representative amount of the total ecological and species diversity for each clade. Ecoregions represent ecologically and geographically distinct units that typically share a common fauna (Smith et al., 2018). We converted spatial polygons for each species into a site × species presence absence matrix using the `presab` function in the 'letsR' package in R (Vilela & Villalobos, 2015). We then sampled sites in each ecoregion in proportion to the area occupied by the clade within them, sampling a minimum of one grid cell from each occupied ecoregion. We sampled the number of sites ( $n$ ) for each clade ( $i$ ) according to the function  $n = S^*(A_i/A_{\max})$ ; that is,



the proportion of the area occupied by each clade ( $A_i$ ) compared to the maximum area occupied by any clade ( $A_{\max}$ ) for a maximum of roughly 2,500 sites ( $S$ ). This ensured each clade was sampled at an equal density across their distribution.

## 2.4 | Functional divergence

Different measures of functional diversity capture different aspects of the distribution of traits within an assemblage (Mason, Moullot, Lee, & Wilson, 2005). To determine if lizard species were divergent or convergent within functional trait space across assemblages, we estimated functional divergence (FD) using Rao's quadratic entropy (Rao's  $Q$ ). Rao's  $Q$  is the sum of pairwise distances between species as measured by Gower distances (Podani, 1999) between trait values, scaled between 0 (species are functionally equivalent) and 1 (species are maximally functionally divergent; Botta-Dukát, 2005). We estimated FD based on Gower distance of all five traits together ( $FD_{\text{multi}}$ ), as well as for body mass alone ( $FD_{\text{mass}}$ ), at each site for each clade, using the `rao.diversity` function in the R package 'SYNCSA' (v. 1.3.3; Debastiani & Pillar, 2012). We selected body mass for separate analysis because it is the single trait most likely to reflect broad differences in ecology and life history between species (Hedges, 1985), and we used both  $FD_{\text{multi}}$  and  $FD_{\text{mass}}$  to see if the multivariate and univariate measures of divergence give similar results.

Rao's  $Q$  is not completely independent of species richness. This makes the raw values unsuitable independent predictors of diversity. To understand how the behaviour of FD changes across assemblages and relates to species richness we compared their values to null expectations given a biogeographically constrained null model of community assembly; the dispersal null model (DNM; Miller, Farine, & Trisos, 2017). The DNM simulates assemblages by sampling species from nearby sites with a probability inversely proportional to their distance to the focal site, while approximately maintaining species frequency and site diversity. We calculated site by site distances using great-circle distances with the function `rdist.earth` from the 'fields' package in R (v. 9.6; Nychka, Furrer, Paige, & Sain, 2017). Under the DNM, species from local species pools, which are less likely to be biogeographically constrained from dispersing into a site, will be preferentially sampled. For each clade separately, we estimated FD across each site in each simulated assemblage, for 1,000 simulations of the DNM.

From the distribution of values of FD from each site in the simulated datasets we calculated the standardized effect size (SES) of FD:

$$\frac{FD_{\text{observed}} - \text{mean}(FD_{\text{simulated}})}{SD(FD_{\text{simulated}})} \quad (1)$$

Positive SES values represent assemblages that contain species with more divergent traits than expected under the null model and negative values indicate species are more convergent than expected. Values greater than 1.96 or less than -1.96 are considered

significantly more or less divergent (respectively) than null expectations, given an alpha of .05.

## 2.5 | Modelling species richness

To test our hypotheses about the influence of abiotic factors on species richness directly, or indirectly through their influence on FD, we extracted values for four environmental predictors across sites for each clade. We selected mean temperature of coldest quarter (°C) from the CliMond database (temperature; Kriticos, Jarosik, & Ota, 2014) and Thornwaite's aridity index from the ENVIREM database (aridity; Title & Bemmels, 2018) to represent measures of environmental harshness. 'Harsh' values of these variables are at different ends of their scales, for example harsh conditions of aridity are measured at high values of the aridity index, but harsh values of the temperature variable (for lizards) are expected at low values of temperatures (cold winter temperatures). This means that a positive effect of harshness may be measured as a positive correlation with aridity but a negative correlation with temperature. We selected topographic ruggedness index from the ENVIREM database (topography; Title & Bemmels, 2018) as a measure of environmental complexity, and net primary productivity as a measure of environmental productivity (productivity; Imhoff et al., 2004a, 2004b). All variables were resampled at the same resolution as our sampled sites (50 km × 50 km grid cells) using the 'raster' package in R (Hijmans, 2016) and a single value was extracted for each site.

We were interested in the direct effects of different environmental factors and FD on species richness (species richness ~ FD + environment), as well as the indirect effects of the environment on species richness via direct effects on FD (FD ~ environment). To account for this hierarchy of direct and indirect effects we used piecewise structural equation modeling (pSEM) to investigate the relationships between multiple response and predictor variables. pSEM is a type of pathway analysis that allows users to specify hypothesized causal relationships between multiple response and predictor variables in the same causal network (Lefcheck, 2016). pSEM differs from traditional SEM in that pathways in the model are solved independently, rather than simultaneously finding a global solution (Lefcheck, 2016). This allows for a greater flexibility in the kinds of models that can be fit in the causal network. This is important because spatial data, such as assemblage level estimates of species richness and environmental predictors, can be highly spatially autocorrelated, which will violate the assumptions of standard linear regression (Legendre, 1993). To account for this, we fit spatial autoregressive error models (SARs) along the pathways of our models.

SARs are a modification of standard linear regression with an added error term that accounts for spatial autocorrelation by weighting the influence of neighbouring sites on the contribution of each site, based on a spatial weights matrix. To determine the

appropriate spatial weights matrix, we identified neighbours within seven different distances from each focal site (50, 100, 150, 200, 250, 300, 350 km, and the maximum distance in which all sites have at least one neighbour, which varied between groups), and weighted these neighbours using three different schemes; a row standardized, globally standardized and variance stabilizing (Tiefelsdorf, Griffith, & Boots, 1999). These three coding schemes reflect differences in balancing well-connected sites (globally standardized), weakly connected sites (row standardized) or both (variance stabilizing). We used model selection based on Akaike information criterion and Nagelkerke pseudo- $R^2$  values to determine which spatial weights matrices were used to generate the best fitting models separately for each SAR (e.g., species richness  $\sim$  FD + environment; FD  $\sim$  environment) and for each clade (see Supporting Information Appendix S2). We then used these weights matrices for SAR models in the pSEM framework. Creating spatial weights matrices was done using the `dnearneigh` and `nb2listw` functions in the package 'spdep' (v. 1.1.2; Bivand, Pebesma, & Gomez-Rubio, 2013; Bivand & Wong, 2018).

We fit a pSEM specifying both species richness and FD as a response and FD and environment as predictor variables. We first fit fully specified models where each pathway was specified in the pSEM. We then removed pathways that did not explain a significant amount of variation in the response and heuristically repeated the analysis using tests of d-separation to include or exclude pathways. Tests of d-separation are used to assess the goodness of fit of a pSEM by asking if relationships between pathways that are not specified in the model are independent after considering the pathways that are specified in the model (Shipley, 2000). For each clade we determined the minimum model in which all pathways significantly explained species richness and  $FD_{SES}$ . SARs were fit using the 'spdep' and 'spatialreg' packages in R (v. 1.1.3; Bivand et al., 2013), while pSEM was fit with the 'piecewiseSEM' package in R (v. 2.0.2; Lefcheck, 2016). We repeated analyses using the SES of  $FD_{multi}$  and  $FD_{mass}$ .

## 2.6 | Functional trait diversity

To assess how the 10 different clades varied in trait diversity, we estimated the amount of functional trait space that each clade occupies by estimating the functional richness of each clade, standardized by the total functional trait space occupied by all 10 clades, using the R package 'FD' (v. 1.0.12; Laliberté & Legendre, 2010; Laliberté, Legendre, & Shipley, 2014). The functional richness metric is measured as a proportion of the total convex hull of multidimensional functional trait space of all lizards occupied by the convex hull of each separate clade, and is scaled between 0 and 1. We asked whether functional richness was a linear function of species diversity in each clade using a phylogenetic generalized least squares (PGLS; Freckleton, Harvey, & Pagel, 2002) test on a phylogeny reduced to a single tip for each clade, using the `pgls` function in the 'caper' package (Orme et al., 2018).

## 2.7 | Phylogenetic signal of traits

To understand the distribution of functional diversity across assemblages considering the evolutionary history of each trait, we estimated phylogenetic signal of each of the five traits separately using Pagel's  $\lambda$ . For quantitative traits we estimated  $\lambda$  using the `phylosig` function in 'phytools' (v. 0.6.60; Revell, 2012) and for categorical traits we estimated  $\lambda$  using continuous-time Markov models of character evolution, independently estimating the transition rate between character states (all-rates-different model), with the `fitDiscrete` function in 'Geiger' (v. 2.0.6.1; Harmon, Weir, Brock, Glor, & Challenger, 2008).  $\lambda$  is a branch-length transformation parameter, and its maximum likelihood estimate is widely used as a measure of phylogenetic signal (where a value of 0 indicates no phylogenetic signal and a value of 1 indicates evolution under a Brownian motion model). To assess whether traits showed significant phylogenetic signal we used likelihood ratio tests to compare estimates of  $\lambda$  for each trait along the phylogeny to those estimated when the phylogeny was transformed with  $\lambda = 0$ .

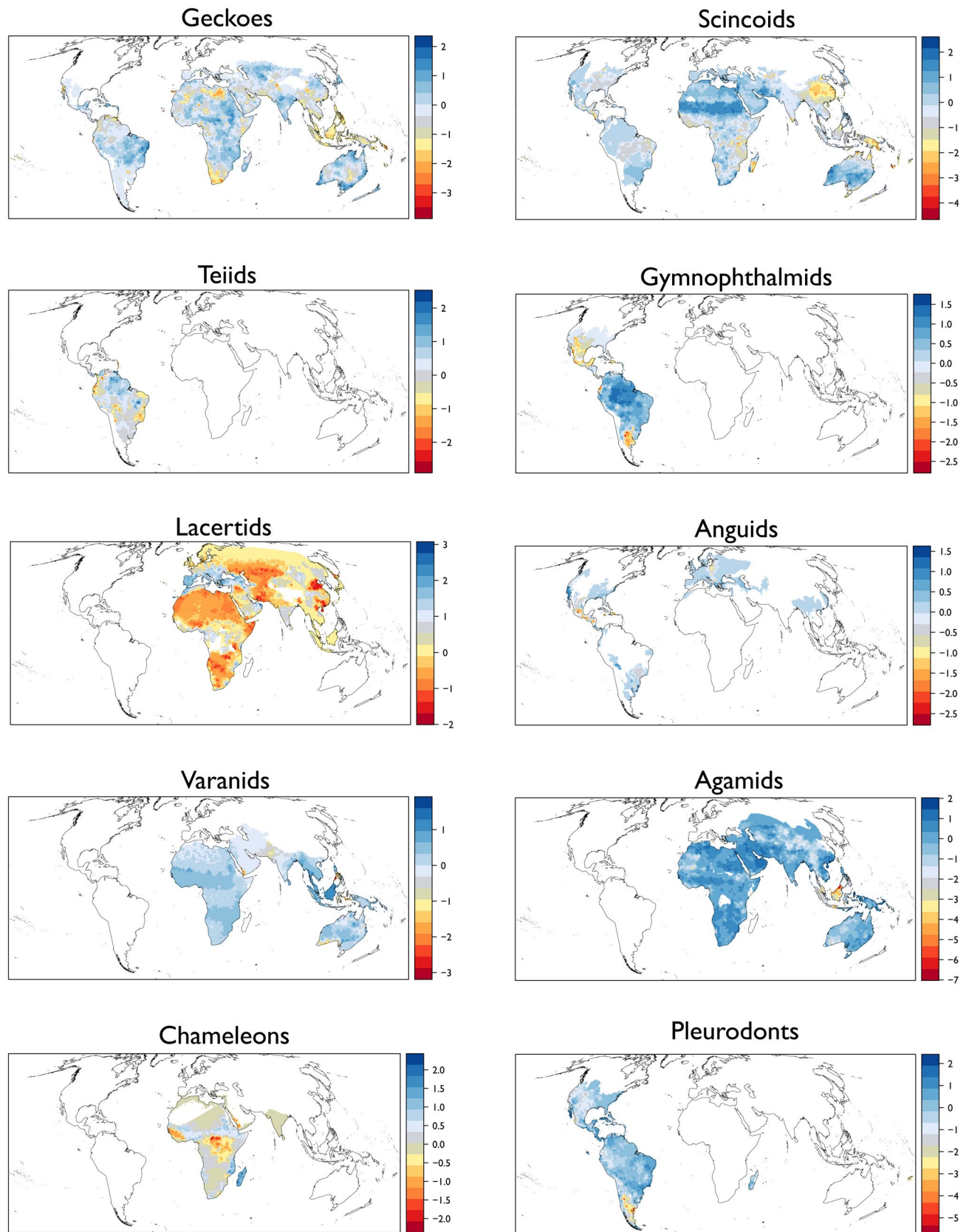
## 3 | RESULTS

### 3.1 | Data imputation

The data imputation error rate, as measured by the proportion of falsely classified traits in the subset of data used for cross-validation, for the three categorical variables was low (7.6%). Missing data were unevenly distributed across the clades used in this study. Varanids had the highest proportion of complete observations for the three categorical traits with missing data (5% for diet, 3% for microhabitat and 6% for activity), while teiids had the highest proportion of missing data (67% missing for diet, 26% for microhabitat and 43% for activity time). Results from piecewise structural equation models (see below) were very similar when using a single trait, body mass (a trait that required imputation for only 23 species, or less than 1% of species) and multiple traits (with imputed data).

### 3.2 | Geographic patterns of functional divergence

Measuring functional divergence (FD) in communities using a multi-trait ( $FD_{multi}$ ) approach as well as for a single trait (body mass;  $FD_{mass}$ ), we found that FD within assemblages was spatially structured and different between lizard taxa (Figure 2). In all clades, for both  $FD_{mass}$  and  $FD_{multi}$ , very few assemblages were significantly divergent, showing values greater than expected based on the dispersal null model ( $FD_{SES} > 1.96$ ), with significantly divergent assemblages accounting for less than 1% of assemblages. On the contrary, for  $FD_{multi}$ , several clades (geckoes, scincoids, anguids, agamids and pleurodonts) showed regions in which assemblages were significantly convergent, with greater than expected functional similarity ( $FD_{SES} < -1.96$ ) compared to the dispersal null model. In these clades,



**FIGURE 2** Geographic patterns of functional divergence ( $FD_{multi}$ ) of five different phenotypic and ecological traits. Values are the standardized effect size (SES) of Rao's Q measured using Gower distances of traits compared to values simulated under a dispersal null model measured in  $50 \text{ km} \times 50 \text{ km}$  grid cells. Positive values (blue) indicate functional divergence and negative values (red) indicate functional convergence compared to the null model. Significant SES values are greater or less than 1.96 and -1.96, respectively [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



convergent assemblages accounted for between 1 and 5% of all assemblages. These were typically concentrated in small areas such as Borneo in agamids or Patagonia in pleurodonts (Figure 2). For  $FD_{mass}$ , convergent assemblages accounted for less than 2% in pleurodonts and scincoids, and less than 1% in all other clades.

### 3.3 | Drivers of species richness and functional divergence

Using spatial autoregressive models (SARs) in a piecewise structural equation model framework, we found that spatial autocorrelation present in the residuals of ordinary least squares models was well accounted for (see Supporting Information Appendix S2). We also found that using a measure of  $FD_{SES}$  based on multiple traits ( $FD_{multi}$ ) or a single trait ( $FD_{mass}$ ) gave largely similar results and we found a positive correlation between standardized coefficients for significant pathways shared between models (Pearson's  $r = .6$ ). Here we will present the results based on  $FD_{multi}$  and describe where  $FD_{mass}$  differs in Supporting Information Appendix S1.

Species richness was significantly related to several different environmental features in each clade, and while no relationships were shared amongst every clade, there were several common relationships, repeatedly appearing in more than five different clades. We found that minimum temperature of the coldest quarter, a measure of environmental harshness, was significantly, positively related to species richness in six different clades (geckoes, scincoids, teiids, varanids, anguids and agamids), meaning richness is lower in cold-climate assemblages (Figure 3). In most cases, temperature was the strongest predictor of richness (Figure 3). Chameleons were the only group to show an opposite pattern where richness was strongly negatively related to temperature.

Topographic ruggedness, a measure of environmental complexity, was positively related to species richness in eight clades (geckoes, teiids, anguids, chameleons, agamids, varanids, pleurodonts and scincoids). Aridity, a measure of environmental harshness, was positively related to richness in four clades (agamids, varanids, pleurodonts and lacertids) and negatively in two clades (scincoids and teiids). Net primary productivity, a measure of environmental energy and resource quantity, was correlated with richness in five clades (teiids, scincoids, agamids, pleurodonts and chameleons).

Species richness was also correlated with functional divergence within assemblages, with  $FD_{SES}$  significantly related to species richness in five of ten lizard clades (Figure 3). In two clades the relationship was positive (varanids and scincoids), while it was negative in three clades (geckoes, pleurodonts and agamids).  $FD_{SES}$  itself was explained by different environmental predictors, suggesting environmental drivers of ecological assemblage structure, and in some cases together with a significant relationship between species richness and  $FD_{SES}$ , suggesting a further, indirect, effect of the environment on species richness. Temperature was positively related to FD in four clades (teiids, lacertids, pleurodonts and chameleons), and in

each case was the strongest relationship in the pathway analysis. Aridity showed a positive effect in three clades (scincoids, chameleons and geckoes) and a negative in two clades (gymnophthalmids and lacertids). Productivity was positively related to FD in two clades (geckoes and teiids), and negatively in three clades (chameleons, agamids and scincoids). Topography was only related to FD in lacertids.

### 3.4 | Functional trait space

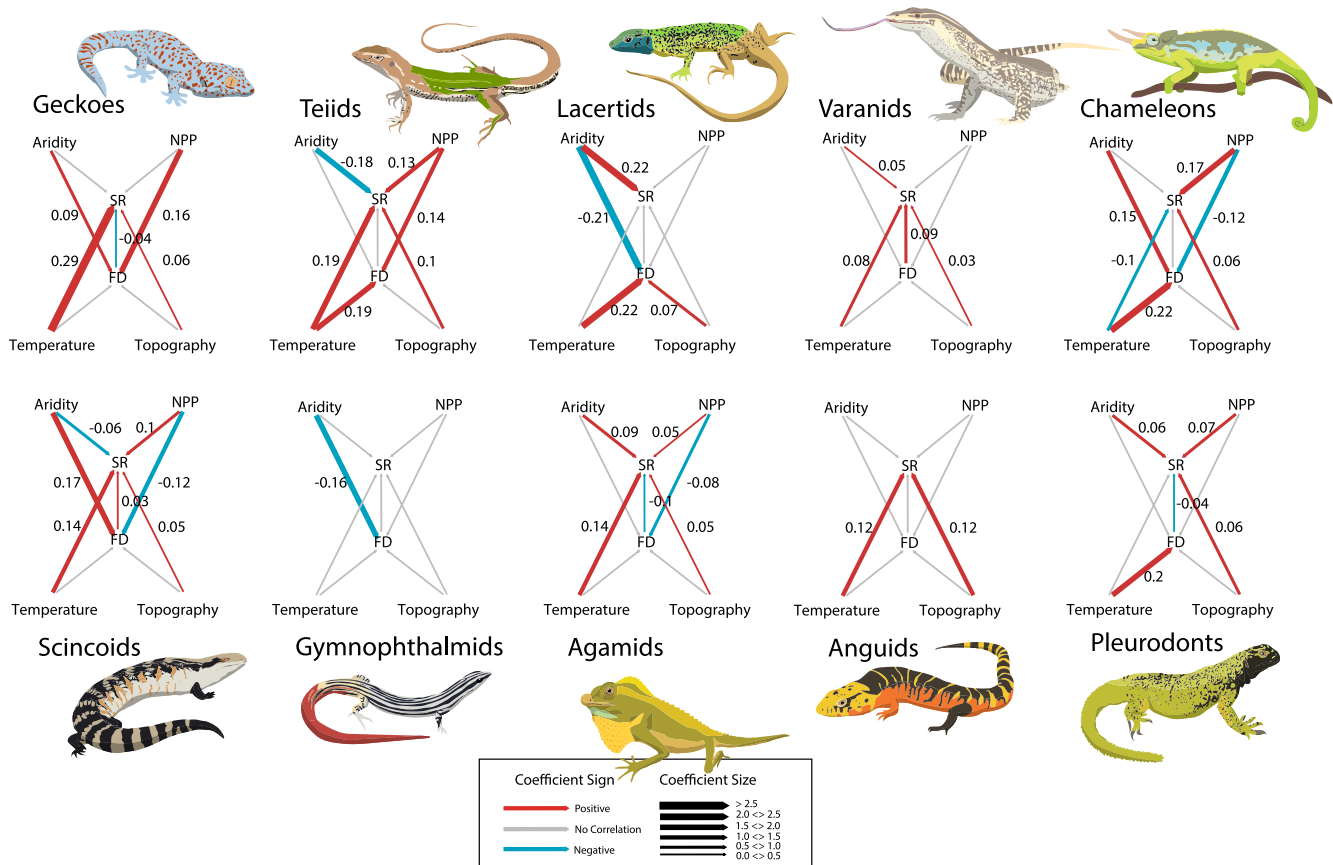
Based on estimates of functional richness of ecological traits within clades, standardized as a proportion of the total functional richness across all clades, we found that clades differed in the total amount of ecological trait space they occupied. This was positively related to clade richness after accounting for phylogeny using PGLS ( $R^2 = .77$ ,  $p < .001$ ). Scincoids and geckoes, the two most species-diverse clades, occupied a large proportion of the overall trait space (functional richness = .91 and .87, respectively). The remaining clades occupied smaller proportions of this space (functional richness = .4 for anguids, .36 for pleurodonts, .29 for chameleons, .28 for teiids, .25 for agamids, .10 for lacertids, .08 for varanids and .05 for gymnophthalmids).

### 3.5 | Phylogenetic signal

We estimated phylogenetic signal as Pagel's  $\lambda$  for five different traits in each of the 10 clades. There were eight instances where a clade showed zero variance for a trait (all species had the same trait value) and 37 of the 42 remaining trait-clade combinations showed significant phylogenetic signal, suggesting that trait distances tend to reflect the divergence times between taxa (see Supporting Information Appendix S3). The exceptions to this, where traits did not show significant phylogenetic signal, were for diet in teiids and anguids, and activity time in varanids, agamids and chameleons. However, values of  $\lambda$  for these traits were still very high ( $> .9$ ), and it is likely that it is because these traits tended to show near zero variation (e.g., are highly conserved), phylogenetic signal was non-significant. For example, activity time is mostly diurnal with only a handful of nocturnal or cathemeral species in varanids, agamids and chameleons. Similarly, diet shows very little variation in teiids and anguids, with only a handful of species that are not carnivorous.

## 4 | DISCUSSION

Lizards are an incredibly diverse group that occupy a wide variety of ecological niches and display an array of phenotypes that is hard to match amongst terrestrial vertebrates, ranging from tiny fossorial skinks with reduced limbs (*Lerista*), to large apex predators like monitor lizards (*Varanus*); from marine foraging iguanas (*Amblyrhynchus*) to gliding canopy dwelling dragons (*Draco*). This ecological diversity has allowed lizards to occupy almost every terrestrial habitat on



**FIGURE 3** Pathways in piecewise structural equations models of species richness and ecological divergence (the standardized effect size of Rao's Q for five different ecological traits). Arrows show all pathways in the full model. Coloured paths indicate significant pathways in the final model, which were chosen using tests of d-separation and comparing goodness of model fit, while grey pathways indicate excluded pathways from the final model. Red pathways indicate positive standardized coefficient estimates for the pathway and blue pathways are negative coefficients. Line width reflects the size of the standardized coefficient, indicated next to each significant path, with strong effect sizes in bolder lines. Illustrations are by Damien Esquerré and show a representative species from each clade: *Gekko gekko* (geckoes), *Ameiva ameiva* (teiids), *Lacerta schreiberi* (lacertids), *Varanus gouldii* (varanids), *Trioceros jacksonii* (chameleons), *Tiliqua scincoids* (scincoids), *Vanzosaura rubricauda* (gymnophthalmids), *Diploglossus monotropis* (anguids), *Lyriocephalus scutatus* (agamids), *Phymaturus maulense* (pleurodonts). FD = functional divergence; NPP = net primary productivity; SR = species richness [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

earth, except for the coldest places at high altitudes and latitudes, owing to one of their most important shared ecological traits: ectothermy, the dependence on environmental temperatures to regulate their own body temperature. Despite these observations, it has long been unclear whether the ecological and phenotypic diversity present in lizards promotes species diversity in lizard assemblages. It has been argued that this is because different lizard lineages in different regions likely respond to different abiotic and biotic factors (Pianka, 1973).

Using a global, macroecological approach, our results support this idea and suggest that there are alternate ecological pathways to diversity amongst lizard clades, with support for three of the six hypotheses for diversity presented in Table 1 (H1, H3 and H6). Given differences in morphology, ecology and biogeography between the major taxonomic divisions of lizards, it is perhaps unsurprising that we do not see a general pattern amongst clades. In some cases (geckoes, agamids and pleurodonts), we see high species richness associated with low functional divergence (FD)

between co-occurring species, while in other cases, high species richness is associated with greater FD (scincoids and varanids), or shows no association (lacertids, chameleons, gymnophthalmids, anguids and teiids). However, despite largely idiosyncratic patterns amongst clades, there are some common trends. One widespread trend, shared by six of ten clades, is a negative association between species richness and environmental harshness, and particularly cold winter temperatures (Figure 3). We also see a positive effect of environmental productivity (net primary productivity) in five clades, and a relatively weaker positive effect of environmental complexity (topographic ruggedness) on species richness in eight of the clades.

#### 4.1 | Functional convergence and divergence

Both functional divergence and convergence have been demonstrated to explain richness in different taxa. For example,

species-rich assemblages have been associated with functional convergence in particular groups of plants (Freschet et al., 2011; Ordoñez & Svenning, 2018), birds (Cooke, Bates, & Eigenbrod, 2019; Pigot et al., 2016), mammals (Cooke et al., 2019) and corals (McWilliam et al., 2018), and functional divergence in carnivorous mammals (Davies, Meiri, Barraclough, & Gittleman, 2007), fish (Mason, Irz, Lanoiselée, Mouillot, & Argillier, 2008), and plants (Kraft, Valencia, & Ackerly, 2008; Skeels & Cardillo, 2019a). Yet, we still do not have a good understanding of why richness is associated with either of these alternative patterns. In lizard assemblages these patterns seem to be independent of fundamental differences between clades, including the geographic distribution of clades (because clades that show similar distribution patterns, for example varanids and agamids, show opposite trends; Figure 1); the number of species in a clade (both small and large clades show similar trends); the functional trait diversity of a clade (clades that are widely and narrowly distributed in functional trait space can show similar trends).

Alternative mechanisms likely underlie functional convergence and divergence in high richness assemblages of different clades (Table 1), and the range of  $FD_{SES}$  values suggests an explanation for the effect of FD on species richness. For most clades, we see very few assemblages that have greater functional divergence than expected under our null model; however, many clades show values of  $FD_{SES}$  skewed towards functional convergence. For clades that show a positive FD–richness relationship, this means that functional traits in high richness assemblages do not tend to be more divergent than null expectations, but low richness assemblages do tend to be more similar than expected. A negative FD–richness relationship means that high richness assemblages tend to be more functionally convergent than expected. Hypotheses that predict that species richness is driven by the evolution of niche diversity, either related to biotic interactions and the limiting similarity principle (H2 and H4, Table 1) or functional divergence in heterogeneous environments (H5), are therefore not well supported, at least along the broad niche axes used in this study (e.g., diet, microhabitat, activity times). This is because we rarely see any assemblages that are structured by strong functional divergence at all. Instead, ecological convergence in both high and low richness assemblages, as well as supporting evidence from a number of significant environmental correlations, suggests a stronger role for environmental filtering effects (H3).

## 4.2 | Environmental filtering

One factor that may drive functional convergence at low species richness across assemblages is environmental filtering (H3, Table 1): when environmental constraints prevent species with (or without) particular traits from persisting. Environmental filtering might reduce phenotypic and functional diversity if more extreme environments select for particular traits and adaptations, as well as reduce species richness if fewer species have evolved adaptations to persist in extreme environments (Currie et al., 2004; Dobzhansky, 1950).

Under this hypothesis we expect environmental features that may place the strongest physiological constraints on lizard clades, such as low water availability in arid regions (Cox & Cox, 2015; Neilson, 2002; Pastro, Dickman, & Letnic, 2013), or cold winter temperatures (Aragón, Lobo, Olalla-Tárraga, & Rodríguez, 2010; Pie, Campos, Meyer, & Duran, 2017), to have the greatest effect in suppressing species richness or FD. Across the 10 lizard clades used in this study, this hypothesis receives the greatest support, with a strong effect of temperature in six clades, and relatively weaker effect of aridity in two clades for species richness, and an effect of temperature on four clades, and aridity on two clades for FD.

Temperature clearly plays an important role in limiting the abundance and distribution of lizard species, since cold temperatures place physiological constraints on metabolic rates of ectotherms (Buckley, Hurlbert, & Jetz, 2012; Buckley, Rodda, & Jetz, 2008). Low diversity of lizard assemblages may follow from this in several ways. (a) Relatively few lizard species have evolved adaptations to these thermal extremes due to evolutionary conservatism of thermal tolerances (Pie et al., 2017). Phylogenetic signal present in many ecological traits suggests that ecological strategies such as reproductive mode, clutch size and body size, which are all related to temperature in lizards (Adolph & Porter, 1993; Pincheira-Donoso, Hodgson, & Tregenza, 2008; Shine, 1985, 2004), are not highly labile. (b) Low diversity of cold regions may be the result of competitive exclusion by endothermic clades that have a greater physiological capacity to maintain activity in cold climates (Buckley et al., 2012). The temperature–diversity correlation may also have a historical basis if, (c) cold regions have more recently been colonized from warmer regions leading to a time-for-speciation effect in warm regions (Wiens & Graham, 2005), or (d) the rate of extinction is greater in colder regions due to greater fluctuations of climate throughout the evolutionary history of lizards (Dynesius & Jansson, 2000; Pyron, 2014).

A measure of harshness on a different environmental axis, aridity, was also associated with species richness in several clades, although the effect was smaller than that of temperature. Two clades showed a negative richness–aridity relationship (scincoids and teiids), and two clades showed a negative FD–aridity relationship (gymnophthalmids and lacertids). Many lizard lineages thrive in arid environments due to adaptations to resist desiccation (Bradshaw, 1988; James & Shine, 2000; Zatssepina et al., 2000). However, the distribution of some clades appears limited by aridity. Teiids, for example, are widespread in the Neotropics but tend to occur at relatively low densities in the drier Cerrado, Chaco and Caatinga biomes, compared with tropical rainforests. Scincoids are exceptionally diverse in the Australian western deserts, but this diversity pattern is not repeated to the same degree in arid biomes on other continents, which may explain a more general negative aridity–diversity relationship in this clade after accounting for spatial autocorrelation.

Although aridity appears to dampen diversity in some clades, others show increased species richness or FD with increased aridity. Lacertids, pleurodonts, agamids and varanids showed a positive richness–aridity relationship and co-occur at high densities in relatively arid regions across their distributions, such as

in southern Africa for lacertids (e.g., *Meroles*, Harris, Arnold, & Thomas, 1998), the south-west deserts of North America in pleurodonts (e.g., Phrynosomatidae, Wiens, Kozak, & Silva, 2013), and the Australian deserts and savannas in agamids and varanids. Scincoids, chameleons and geckoes all show a positive FD–aridity relationship, which seems to be driven by very low FD in less arid regions such as archipelagic Southeast Asia, compared to more arid savannas (e.g., Cerrado geckoes), and deserts (e.g., Saharan scincoids and Madagascan chameleons). The high number of sympatric species in deserts, such as phrynosomatid lizards in North America or *Ctenotus* skinks in Australia, has been attributed to the vast and homogeneous nature of deserts that allows species with a similar climatic niche to have wider distributions and hence tend to overlap (James & Shine, 2000; Vidan et al., in press; Wiens et al., 2013). Therefore, an FD–aridity relationship might also be a product of overlapping widespread species with diverging ecological traits.

### 4.3 | Productivity and topography

One long-standing hypothesis is whether environmental energy may promote species richness by increasing resources to support larger minimum population sizes therefore allowing more species sharing ecological traits to use the same resource base (H1, Table 1). Under the more-individuals hypothesis it is expected that high richness assemblages contain ecologically redundant species and therefore have a negative richness–FD relationship, as well as an effect of productivity directly or indirectly (if productivity is negatively correlated with FD) on diversity. We found that net primary productivity, a measure of environmental energy, was a significant positive predictor of species richness in five clades (teiids, agamids, chameleons, scincoids and pleurodonts), and a negative predictor of FD in three clades (chameleons, agamids and scincoids). This suggests that in some cases high productivity is associated with high species richness and functional convergence of species. However, in only one example, the agamids, do we see high richness associated with functional convergence via this pathway. Previous studies of lizards did not find a relationship between species richness and productivity (Buckley & Jetz, 2010), and overall the support for the more-individuals hypothesis is equivocal (Adler et al., 2011; Currie et al., 2004; Storch et al., 2018). Instead, it has been suggested that the macroecological consequences of ectothermy are that temperature rather than productivity is a better predictor of species distributions and diversity patterns (Buckley et al., 2012). Our results suggest productivity does play an important role in promoting species richness in lizards, but it does not have a widespread effect of promoting greater niche overlap in lizards. More work to understand the mechanism that drives this relationship is needed.

Topographic complexity is a global driver of species diversity in different clades, reflecting the ecological and evolutionary influences of geological processes (Badgley, 2010; Grenyer et al., 2006).

Topographic complexity may increase diversity through two main mechanisms. First climatic and habitat heterogeneity across elevations, aspects and slopes might present ecological opportunity for diversification along different niche axes (H5, Table 1), or by increasing landscape barriers, acting as an allopatric species pump (H6; Badgley et al., 2017). We found that eight clades showed a positive topography richness relationship (geckoes, teiids, agamids, anguids, chameleons, pleurodonts, varanids and scincoids). If complexity increases species richness through niche divergence across habitats, functional divergence is expected to be greater in topographically complex assemblages than in topographically homogenous ones. We observe this pattern only in the lacertids; however, a lack of a richness–topography relationship suggests that this relationship does not act to drive assemblage level diversity in lacertids. Instead, if complexity increases diversity through opportunities for allopatric speciation, we expect functional divergence in topographically complex regions to be less than or equal to topographically homogenous regions, which is the case in the eight clades with a positive richness–topography relationship. The relatively weak but consistent positive effect of topography on diversity supports a role for topographically complex areas acting as ‘species pumps’ to increase diversity in higher taxonomic levels at global scales. This supports a pattern found at lower taxonomic levels in clades such as *Liolaemus* whose radiation is linked to the orogeny of the Andes mountains (Esquerré et al., 2019), but differs from other studies that have found less of a role of topography at regional scales (Buckley & Roughgarden, 2006; Guisan & Hofer, 2003; Tallwin et al., 2017).

### 4.4 | Conclusion

This study investigated the ecological and environmental drivers of species richness in one of the largest and most ecologically diverse vertebrate radiations. Our results show that there can be alternative pathways to high diversity (functional trait convergence and divergence) as well as more general mechanisms resulting from conserved physiological constraints that are common to all lizards (ectothermy), or structural properties of the environment that allow species to partition geographic space (topographic complexity). One assumption that is implicit in the approach we have used in this study is that species richness is at or near ecological equilibrium, that is, that present-day patterns of species richness and trait diversity are reflective of environmental limits on diversity (MacArthur, 1965; Rabosky & Hurlbert, 2015). A historical and evolutionary approach may complement our understanding of the idiosyncratic diversity patterns in lizards if assemblages are not saturated with diversity (non-equilibrium dynamics), and factors such as evolutionary time (e.g., Miller, Hayashi, Song, & Wiens, 2018; Skeels & Cardillo, 2017) or diversification dynamics (e.g., Machac & Graham, 2017) are important in structuring present-day diversity patterns (Fischer, 1960; Rohde, 2006), or trait-diversity patterns (e.g., Oliveira et al., 2016). A promising approach to more



completely understand present-day diversity patterns could be to combine equilibrium and non-equilibrium dynamics into a common model framework (Skeels & Cardillo, 2019a), although this would require more complete knowledge of ecological traits that are important in mediating competitive interactions in lizards. Understanding how the differences between lineages contribute to present-day biodiversity is critical to understanding the origin and maintenance of diversity. This study highlights that within large groups, such as lizards, there are both general and idiosyncratic drivers of diversity.

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## CONFLICT OF INTEREST

The authors declare no known conflicts of interest.

## DATA ACCESSIBILITY

Data used in this study were obtained from Roll et al. (2017), Tonini et al. (2016) and Meiri (2018). The phylogeny, imputed trait data, as well as the site measures of species richness, functional divergence and environmental predictors for each clade, as well as an R script to perform our analyses are available in the Supporting Information (Appendix S4).

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## BIOSKETCHES

**Alexander Skeels, Damien Esquerré and Marcel Cardillo** are researchers from the Research School of Biology at the Australian National University. They are interested in the macroecological and macroevolutionary drivers of biodiversity patterns across a variety of regions, taxa and methodological approaches. Some current projects include understanding how ecological interactions shape diversification and generate biodiversity hotspots, investigating patterns of extinction risk in vertebrates, and the diversification and morphological evolution of different reptile radiations.

## SUPPORTING INFORMATION

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

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