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Global Diversity Patterns are Explained by Diversification Rates and Dispersal at Ancient, Not Shallow, Timescales

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Abstract.—Explaining global species richness patterns is a major goal of evolution, ecology, and biogeography. These richness patterns are often attributed to spatial variation in diversification rates (speciation minus extinction). Surprisingly, prominent studies of birds, fish, and plants have reported higher speciation and/or diversification rates at higher latitudes, where species richness is lower. We hypothesize that these surprising findings are explained by the focus of those studies on relatively recent macroevolutionary rates, within the last ~20 million years. Here, we analyze global richness patterns among 10,213 squamates (lizards and snakes) and explore their underlying causes. We find that when diversification rates were quantified at more recent timescales, we observed mismatched patterns of rates and richness, similar to previous studies in other taxa. Importantly, diversification rates estimated over longer timescales were instead positively related to geographic richness patterns. These observations may help resolve the paradoxical results of previous studies in other taxa. We found that diversification rates were largely unrelated to climate, even though climate and richness were related. Instead, higher tropical richness was related to the ancient occupation of tropical regions, with colonization time the variable that explained the most variation in richness overall. We suggest that large-scale diversity patterns might be best understood by considering climate, deep-time diversification rates, and the time spent in different regions, rather than recent diversification rates alone. [Keywords: Climate; colonization time; diversification rate; latitudinal diversity gradient; lizards; snakes; species richness.]

Among the most striking and consistent biodiversity patterns is the latitudinal species richness gradient, with the number of species increasing from the poles to the equator at both regional and local scales (Hillebrand 2004). Spatial patterns of richness are directly caused by species accumulation and loss through speciation, extinction, and dispersal (Ricklefs 1987), as well as variation in the amount of time in which these processes play out in each region (e.g., Stephens and Wiens 2003). New, large-scale phylogenies and comprehensive databases on species distributions now allow increasingly powerful tests of how these 3 processes drive global richness patterns. These 3 processes do not completely explain patterns of richness. However, since these 3 processes are the only ones that directly change species numbers, all other evolutionary, ecological, and geological variables and mechanisms (e.g., climate, species interactions) must act through these processes in order to influence richness patterns.

A fundamental question is whether global richness patterns are explained by variation in net diversification rates (species accumulation over time, or speciation minus extinction). For example, is high tropical richness explained by clades at low latitudes having higher diversification rates than clades at higher latitudes? While some past studies found the expected pattern of higher diversification rates at low latitudes (Pyron and Wiens 2013; Rolland et al. 2014), others showed no significant pattern, or even faster diversification at higher latitudes (e.g., Weir and Schluter 2007; Wiens et al. 2009; Igea and Tanentzap 2020). However, many previous studies only compared patterns among

a few large regions or binned the earth into 1 temperate region and 1 tropical region (e.g., Rolland et al. 2014; Igea and Tanentzap 2020). Far fewer studies have tested whether diversification rates explain the richness of smaller-scale assemblages.

Several recent studies have now examined covariation in diversification rates and species richness at fine spatial scales across the globe. Among the first, Jetz et al. (2012) examined the relationship between rates and richness for nearly 10,000 bird species across every 110 × 110 km terrestrial grid cell on Earth (n = 12,850). More recent studies have used similar methods to quantify global variation in richness and diversification rates, including studies of marine fish (Rabosky et al. 2018) and terrestrial angiosperms (Dimitrov et al. 2023). These studies (Jetz et al. 2012; Rabosky et al. 2018; Dimitrov et al. 2023) suggested that high-diversity tropical regions had low rates of species proliferation (speciation and/or diversification), whereas the highest average rates were in low-diversity temperate regions. This is a surprising result given previous studies suggesting that diversification rates can influence regional richness (Davies et al. 2004; Pyron and Wiens 2013; Rolland et al. 2014; Schulter 2016). However, these recent studies of smaller-scale assemblages focused on species-level rates, which primarily reflect diversification rates within the last ~20 million years (Jetz et al. 2012; Rabosky et al. 2018; Igea and Tanentzap 2020; Dimitrov et al. 2023). These results provide a snapshot of where diversity has recently accumulated. However, recent diversification hotspots might not match the historical centers of diversification that contributed the most to shaping present-day biodiversity gradients. All else being equal, diversification rates estimated for clades that encompass deeper timescales might influence species richness patterns more strongly than those in the more recent past. Indeed, in a review of smaller-scale studies, only older groups tended to show higher diversification rates in tropical than temperate clades (Schluter 2016). However, no global-scale study has determined the timescales over which diversification rates are correlated with or decoupled from modern richness patterns.

The relationship between species richness and diversification is also part of a broader debate over whether more species-rich regions are those where there has been more time for diversification to occur, or where diversification rates tend to be higher (Jablonski et al. 2006; Mannion et al. 2014; Li and Wiens 2019). A recent study showed that hotspots of marine fossil biodiversity are often regions that were stable for long time periods (Cermeño et al. 2022). However, for most groups, only data from extant species are detailed enough to address this question. For example, in an important study, Meseguer and Condamine (2020) used the fossil record to investigate spatial variation in diversification rates in 4 tetrapod groups. However, for squamates (lizards and snakes) they were unable to determine whether conflicts between rates estimated from phylogenies and from fossils were due to limitations of methods for inferring patterns of extinction from phylogenies, or due to a strong bias in the fossil record towards preservation in temperate regions. Furthermore, they were only able to compare temperate regions to tropical regions in aggregate, due to limitations of the fossil record.

Here we investigate the factors that explain global-scale richness patterns in squamate reptiles (lizards and snakes). Extant squamates presently include ~12,000 extant, described species (Uetz and Hošek 2025), comprising nearly a third of all terrestrial vertebrates (Roll et al. 2017). Squamates are an excellent model system because they occur in most non-polar terrestrial biomes, the geographic ranges of most described species have been mapped (Roll et al. 2017), and large-scale, time-calibrated phylogenies are available (Tonini et al. 2016; Zheng and Wiens 2016). As ectotherms, squamates may also be more representative of other ectothermic terrestrial animals than endothermic birds and mammals (Buckley et al. 2012). Like previous studies, we consider variation in the relationship between diversification rates and species richness globally. However, unlike previous studies, we analyze diversification rates over a broad range of timescales (Supplementary Fig. S1) and determine the timescales over which patterns of diversification are correlated with or decoupled from spatial variation in richness. We also consider alternative explanations for richness patterns, beyond diversification rates, including climate and colonization time. We show how all 3 factors (diversification rates, climate, and colonization times) may combine to explain global-scale diversity patterns.

Materials and Methods

Species Range Data and Estimates of Squamate Diversity

All analyses were conducted in R version 4.1.2 (R Core Team 2017). R code for all analyses is included in Supplementary Dataset S1. We present an overview of our workflow in Fig. 1. Patterns of richness were assessed using Global Assessment of Reptile Distribution (GARD) v1.5 range shapefiles. These are an update to the GARD 1.1 shapefiles of Roll et al. (2017). The new data here include range estimates for 496 additional species. The GARD 1.5 species-ranges were converted to presence-absence matrices on 96 × 96 km raster grids (approximately 1° × 1° at the equator) using the R package *letsR* (Vilela and Villalobos 2015). These 14,800 grid cells were used to summarize global richness patterns on a Behrmann cylindrical equal-area projection, and to test hypotheses about the relationship between environmental variation and diversification rates (Snyder and Voxland 1989). Sampling included all families and genera and 10,213 species (83.8%) out of the 12,194 currently recognized species (Uetz and Hošek 2025). These were all species for which range maps were available.

The grid cells used here were similar in size to those used in earlier studies that related recent diversification

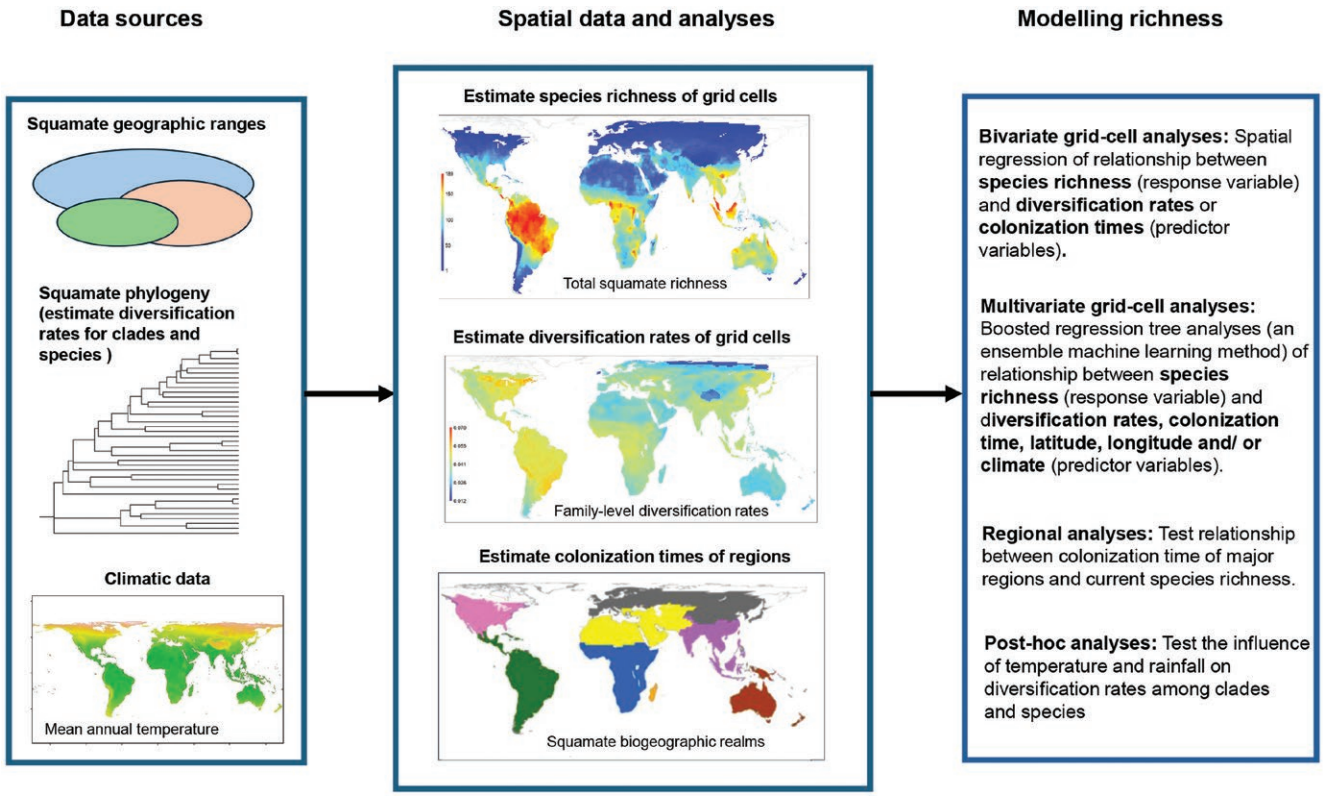

FIGURE 1. Overall project workflow. *Data sources:* Existing data sources were used to: 1) determine which squamate species are present in the 14,800 96 × 96 km global terrestrial grid cells that have at least 1 squamate species, 2) estimate species-level, genus-level and family-level diversification rates (representing different age ranges; Supplementary Fig. S1) based on 2 phylogenetic estimates, and 3) quantify climatic variation (temperature and rainfall) across grid cells and species geographic ranges. *Spatial data and analyses*: Based on these data sources, we estimated 1) species richness and 2) mean diversification rates for each grid cell. We also estimated the time at which clades colonized 8 terrestrial biogeographic realms (Fig. 2), which allowed us to estimate the mean and maximum colonization times of species in each grid cell. *Modelling richness*: These data and analysis results were then used to model the relationship between species richness (response variable) and various combinations of diversification rates, colonization time, temperature, and rainfall (predictor variables). Additional post hoc analyses were conducted to test hypotheses about the relationship between environmental variation and diversification rates.

rates to richness and found no positive relationship (e.g., Jetz et al. 2012; Igea and Tanentzap 2020). In order to compare our results to theirs, it is essential to use a similar spatial scale to isolate the effect of timescale, and not confound differences in spatial and temporal scales. Recent analyses (Caetano et al. 2022) also suggest that the median area of squamate geographic ranges is 17,767 km^2 (n = 10,602 species), with a median size for lizards (the majority of squamates) of 10,140 km^2. This is close to the area of a 96 × 96 km grid cell (9216 km^2), which suggests that our choice of grid cell size was highly appropriate for capturing patterns of squamate spatial distributions. The results of Meiri (2016) and ongoing work by some of the authors (S.M. and U.R.) on squamate range sizes also suggest that many of the ~2000 species not included by Caetano et al. (2022) also have relatively small geographic range sizes.

Macroevolutionary Rate Analyses

Phylogenies used.—We estimated diversification patterns using 2 phylogenies. First, we used a time-calibrated tree of 4162 species based on up to 52 genes (Zheng and Wiens 2016). This tree included 40.8% of the species with range data. To evaluate sensitivity to missing taxa and phylogenetic uncertainty, we also used trees from Tonini et al. (2016) in which missing species were placed (based on their taxonomy) onto a scaffold tree estimated from sequence data (as in Jetz et al. 2012; Rabosky et al. 2018; Igea and Tanentzap 2020). The latter trees included 9754 squamate species, and allowed us to include 90.82% of species with range data in our species-level analyses. We used different sets of these trees in different analyses, as described below. The maximum-likelihood tree from Zheng and Wiens (2016) is available in Supplementary Data set S2 (ZW tree hereafter). The majority-rule consensus tree from the Bayesian posterior distribution of 10,000 trees in Tonini et al. (2016) is available in Supplementary Data set S3 (TEA tree hereafter). By using these 2 trees, we were able to test whether our results were robust to different phylogenetic estimates and missing species. We recognize that other squamate phylogenies are or will become available. However, if our results are robust to these 2 different phylogenies, they should be robust to

other (reasonable) alternative phylogenies as well (e.g., Title et al. 2024).

Species-level rates.—We estimated species-level (i.e., for each species) rates of speciation and/or diversification using 3 different methods. The average diversification rate (DR statistic sensu Jetz et al. (2012) and defined below) or speciation rate (Bayesian Analysis of Macroevolutionary Mixtures [BAMM] and Cladogenetic Diversification rate Shift [ClaDS]) of species in each grid cell was calculated to map geographic variation in these rates.

Species-level diversification rates were first estimated using the DR statistic (Jetz et al. 2012). This estimator was also used in the analyses of Jetz et al. (2012) and Rabosky et al. (2018). The DR statistic is defined as 1 divided by the evolutionary distinctiveness of each species, where distinctiveness is calculated using the equal proportions measure (Isaac et al. 2007). We implemented this measure using the R package *Picante* (Kembel et al. 2010) and code included in Supplementary Data set S1. These analyses were performed on the ZW tree and the TEA tree. We repeated analyses of the DR statistic using values calculated from 100 trees chosen randomly from the Bayesian posterior distribution of 10,000 trees of Tonini et al. (2016). We provide these 100 trees, distinct from the TEA consensus tree, in Supplementary Data set S4. We only used trees with the maximum number of species for these latter analyses (i.e., not the ZW tree of 4162 species), since the DR statistic is calculated for each species and does not correct for incomplete taxon sampling.

We repeated analyses of species-level rates using speciation rates estimated with BAMM (Rabosky 2014), as used in previous studies (Rabosky et al. 2018; Igea and Tanentzap 2020). We also used the R package *ClaDS* (Maliet et al. 2019; Maliet and Morlon 2022). We applied BAMM and ClaDS to the consensus tree obtained from the distribution of phylogenies from TEA, which had more tips than ZW. To infer the consensus tree, we included only the species with DNA sequence data, summarized variation in molecular rates, and estimated divergence times from 10,000 phylogenies using the function "sumt" in MrBayes v3.2 (Ronquist et al. 2012), following Tonini et al. (2016). The final tree included 5320 species representing all 73 squamate families. This consensus tree is provided in Supplementary Data set S5. We used this smaller tree because it should more accurately reflect the true branch lengths (i.e., all species are included based on actual sequence data), and because BAMM and ClaDS incorporate corrections for incomplete species sampling. We provide additional details of the BAMM and ClaDS analyses in Supplementary Appendix S1. Speciation rates (species level) estimated using BAMM are reported in Supplementary Data set S6. Rate estimates from ClaDS are given in Supplementary Data set S7, and the code for estimating the DR statistic is in Supplementary Data set S1. All supplementary datasets are available on Dryad (https://doi.org/10.5061/dryad.0zpc8671s).

Genus-level rates.—In addition to species-level rates, we also estimated genus-level diversification rates. We first used the method-of-moments (MoM) estimator (Magallón and Sanderson 2001) utilizing stem-group ages and richness of genera (additional details in Supplementary Appendix S1, including discussion of identifiability issues sensu Louca and Pennel 2020). We focused on this method for estimating rates deeper in the tree because simulation studies (Kozak and Wiens 2016; Meyer and Wiens 2018; Meyer et al. 2018) show that it is generally accurate (given both constant and variable rates within clades) and allows for extensive variation in diversification rates across the tree (Supplementary Appendix S2). Empirical analyses show that rate estimates from this method are strongly correlated with those from others (e.g., ClaDS; Yu and Wiens 2024; this study). All genus-level MoM diversification rates and stem ages for each species are provided in Supplementary Data set S8, with additional information for genera (stem ages, species richness, and rates from different ε values) given in Supplementary Data sets S9 and S10. We did not repeat the analyses using genus-level rates across a wider range of methods because our initial bivariate analyses showed that these genus-level rates were uncorrelated with spatial richness patterns, as found in our species-level analyses and those in previous studies (e.g., Jetz et al. 2012; Rabosky et al. 2018; Igea and Tanentzap 2020).

Family-level rates.—To investigate rates at deeper timescales, we used 2 methods to estimate diversification and speciation rates for families. First, we used the MoM estimator utilizing stem-group ages and richness of families, as described above for genera (see also Supplementary Appendix S3). We performed these analyses using both trees. All family-level MoM diversification rates are given for each species in Supplementary Data set S8, with additional information for families (stem ages, species richness, and rates from different ε values) in Supplementary Data sets S11 and S12.

Second, we estimated family-level speciation rates using ClaDS (Maliet et al. 2019; Maliet and Morlon 2022). In contrast to MoM, which estimates diversification rates for specified nodes, ClaDS models continuous rate variation throughout a tree. We summarized mean branch-specific speciation rates for all branches (i.e., both tips and internal nodes) within each family. To do this, we used the function "findMRCA" from the R package *phytools* (Revell 2012) and the function "getEdges" from the R package *evomap* (Smaers and Mongle 2019). Family-level rates were based on the average across all branch-specific speciation rates within a family (i.e., both internal and terminal branches). Family-level rates from ClaDS are given in Supplementary Data set S8. All analyses of family-level rates gave qualitatively identical results, regardless of whether we used

MoM or ClaDS estimates (see Results), and regardless of which tree was used to generate MoM estimates.

Since family-level rates were crucial to our conclusions, we also tested whether rates estimated using MoM and ClaDS were correlated with family-level rates (for snakes) estimated from 2 additional methods, BAMM (Rabosky 2014) and Phylogenetic ANalyses of DiversificAtion (RPANDA, Morlon et al. 2011, 2016), using estimates from previous studies (Bars-Closel et al. 2017; Meyer and Wiens 2018). We found that rates estimated using all 4 methods were generally correlated (Supplementary Appendix S4), but estimates from BAMM and RPANDA seemed problematic in some cases. Simulations show that BAMM tends to strongly underestimate rate heterogeneity across trees (Meyer and Wiens 2018; Meyer et al. 2018). Rate estimates from RPANDA (Morlon et al. 2011, 2016) have also been found to be problematic in empirical (Bars-Closel et al. 2017) and theoretical studies (Burin et al. 2019; Louca and Pennell 2020). Our results were consistent with these findings (Supplementary Appendix S4). Family-level rate estimates for snakes are listed in Supplementary Data set S13.

Spatial Analyses of Macroevolutionary Rates

We calculated species richness and average speciation and diversification rates in all terrestrial 96 × 96 km grid cells globally, using the 10,213 squamate species for which range data were available. For species-level rates, we simply used the average rate across all sampled species in that grid cell (for a given estimator). For genus and family-level rates, we assigned species in each grid cell to a clade (genus or family), estimated rates for that clade, assigned each species a rate based on its clade, and then calculated the mean rate among species in each cell. The final product was a weighted average rate per cell, with genera and families represented by more species in a given cell contributing more to that cell's mean rate. R scripts to reproduce global species richness and diversification-rate rasters used in our study, and the analyses based on them, are included in Supplementary Data set S1.

Estimates of family and genus-level diversification rates are global, estimated from all species regardless of where they occur, whereas the estimates of species richness that we compare them to are from local grid cells. Therefore, the species richness used to estimate diversification rates is different from the spatial richness patterns that we are trying to explain since any given grid cell contains only a subset of the species in that clade. High-richness cells can have low mean diversification rates, and low-richness cells can have high mean rates. Simulation and empirical studies also show that diversification rates and richness can be uncoupled, even when that richness is used to calculate the diversification rates (Kozak and Wiens 2016; Scholl and Wiens 2016; Yu and Wiens 2024). Our analyses should not be taken to indicate that the environmental conditions where species occur now are necessarily related to their diversification rates in deep time (indeed, our results show evidence to the contrary). Instead, we test whether species assemblages with presently high or low richness are composed of species from clades with high or low diversification rates, and the impact of estimating those rates over different timescales. Thus, our analyses can help identify the time ranges and processes that were most important in generating modern patterns of spatial richness.

The spatial relationships between diversification rates and species richness among grid cells were analyzed using a modified *t*-test that assesses whether the correlation between 2 spatial patterns is stronger than would be expected by chance given spatial autocorrelation (Clifford et al. 1989; Dutilleul et al. 1993). We implemented this test in the R package *SpatialPack* (Osorio et al. 2012). We used the default setting for the number of cells for Moran's I, which quantifies the strength of observed spatial autocorrelation. When the number of cells to calculate Moran's I was chosen using Sturge's formula (Osorio et al. 2012), the results were qualitatively identical to those reported here.

We compared mean speciation and mean net diversification rates among species in each grid cell to the total richness of all species in each grid cell. We also explored correlations between mean diversification rates and the richness of the subset of species for which a given rate measure could be calculated. For example, we conducted 1 analysis using richness for 3999 species that were both in the tree of Zheng and Wiens (2016) and had range data, not for all 10,213 species with range data. These analyses yielded similar results (Supplementary Table S1) to analyses including all species (see Results). We did not focus on these results because we wanted to explain richness patterns among all species, but they demonstrated that our main results should not be an artifact of mismatched sampling of species for estimating diversification rates versus richness patterns.

We also analyzed correlations between richness and diversification rates for clades of selected age ranges. These analyses used rates based on sets of named clades (genera and families) with different stem-group ages, differing by 5 or 10 myr (million year) intervals (e.g., all clades 50 myr or older vs all clades 60 myr or older). For age bins younger than 40 myr ago, 5 myr intervals were used to more densely sample time intervals most similar to those captured by the DR statistic. There were relatively few genera < 25 myr old, and so we used this as a cutoff. Rates for grid cells were estimated as described above. In a given grid cell, species were sometimes excluded from mean rate estimates because they did not belong to clades with stem ages in that time interval. In contrast, richness was based on all species in each grid cell (but see Supplementary Table S1). Correlations included all grid cells with at least 1 species for which diversification rates could be estimated (i.e., grid cells that contained no species from clades in a given time interval were excluded). *P*-values

were based on a Dutilleul-modified t-test (Dutilleul et al. 1993) for assessing correlations with spatial data. All genus-level and family-level stem ages used to assign species to bins are given for each species in Supplementary Data set S8.

Climate, Species Richness, and Diversification Rates

A frequently discussed hypothesis to explain global richness patterns is that temperature drives variation in diversification rates and diversification rates drive variation in richness (e.g., Rohde 1992; Allen and Gillooly 2006; Sibley et al. 2012). Squamates tend to exhibit higher richness in warmer regions (Raz et al. 2024), and this could underlie the relationships observed between diversification rates and richness across space. What follows is an outline of the analyses that included climate. Many additional details are given in Supplementary Appendix S5.

To test whether diversification rates and richness were related to climate, we first identified the 3 climate variables that were most strongly correlated with richness (Supplementary Table S2): Bio 1 (mean annual temperature), Bio 3 (temperature isothermality: amplitude of day-to-night temperatures oscillations relative to the summer-to-winter (annual) oscillations), and Bio 6 (minimum temperature of the coldest month). From among all precipitation variables, we also identified the variable, Bio 13 (wettest month precipitation), that was most tightly correlated with richness (Supplementary Table S2). We then obtained climatic values for each species for each of these variables (Supplementary Data set S14). We next tested for a relationship between species' family-level diversification rates (rates of families to which species belong) and the within-species minimum, maximum, and mean values of these 4 climatic variables. We also directly tested for a spatial relationship between temperature and mean diversification rates of grid cells.

We then examined whether models that included diversification rates as predictors explained more spatial variation in richness than models based on environmental variation alone, using boosted regression trees (BRT). BRT is an ensemble machine-learning method that is robust to the use of correlated predictor variables with complex interaction effects and/or patterns of covariation, and with virtually any distribution (Elith et al. 2008). BRT is also commonly used with spatial data. We implemented BRT in the R package *gbm* (Ridgeway 2007). We compared the pseudo r^2 of models that included versus excluded diversification rates. We built models using Bio1, Bio3, and Bio13 as predictors (see further details in Supplementary Appendix S5). In some models, we also include spatial predictors: either latitude alone or both latitude and longitude as covariates (additional predictor variables). We refer to these 5 variables as the "spatial variables."

Models reported here were generally built using 30,000 trees and a maximum interaction depth of 3 (see Supplementary Data set S1). Preliminary analyses that used different interaction depths (1, 2, or 3) and more trees (up to 500,000) yielded similar results. We performed one set of analyses that included diversification rates and 1 set that excluded them. We repeated analyses using rates estimated from the ZW tree and the TEA tree. We used the northernmost half of grid cells for model training and the southernmost half for computing out-of-sample estimates of the loss function. Results were qualitatively identical (with respect to the hypotheses tested) when training and out-of-sample cells were selected randomly from among all grid cells. We tested whether the pseudo r^2 of models that included diversification rates were higher than models that excluded them. BRT analyses of family-level rates were also repeated using both MoM and ClaDS estimates of diversification and speciation rates (respectively) for families.

Throughout the paper, we frequently describe how much variation in species richness is "explained" by a given factor. In this context, we mean "explain" in a statistical sense, rather than in a narrative sense.

Climate, Richness, and Colonization Times

We also examined whether spatial correlations between temperature and richness were related to colonization times, given that they were not strongly related to variation in diversification rates (see Results). Here, we tested for a correlation between the richness of different climatic zones and the relative time when they were first occupied by extant lineages (following Kozak and Wiens 2012; Hutter et al. 2013; Wiens et al. 2013). In brief, we assigned each species to 1 of 10 bins, based on mean values of Bio1 (mean annual temperature) across their geographic ranges. We then reconstructed ancestral values of Bio1 across the tree, determined the oldest reconstructed node with values in each bin, and then tested for a correlation between the richness of each bin and its oldest occupation time (among lineages that have persisted to the present day). Details and caveats of these analyses are given in Supplementary Appendix S6.

To more directly quantify the relationship between colonization time and richness, we reconstructed dispersal events among biogeographic realms. These realms followed Falaschi et al. (2023), and are depicted in Fig. 2. Each species used in the spatial analyses was assigned to 1 of 8 terrestrial biogeographic realms, or to the marine realm (9 realms in total). Most species occurred in only 1 realm. But for species that occurred in > 1, they were assigned (by Falaschi et al. 2023) to the realm where the majority of their geographic range area occurred. Note that there were only 894 species (out of 9949) that occurred in > 1 realm and among these 479 species had > 90% of their range in just 1 realm and 374 species had > 95%. We reconstructed past dispersal among regions (realms) using maximum-likelihood estimation in BioGeoBEARS v 1.1.3 (Matzke 2013). We implemented BioGeoBEARS using a maximum ancestral range size of 3 regions, the default

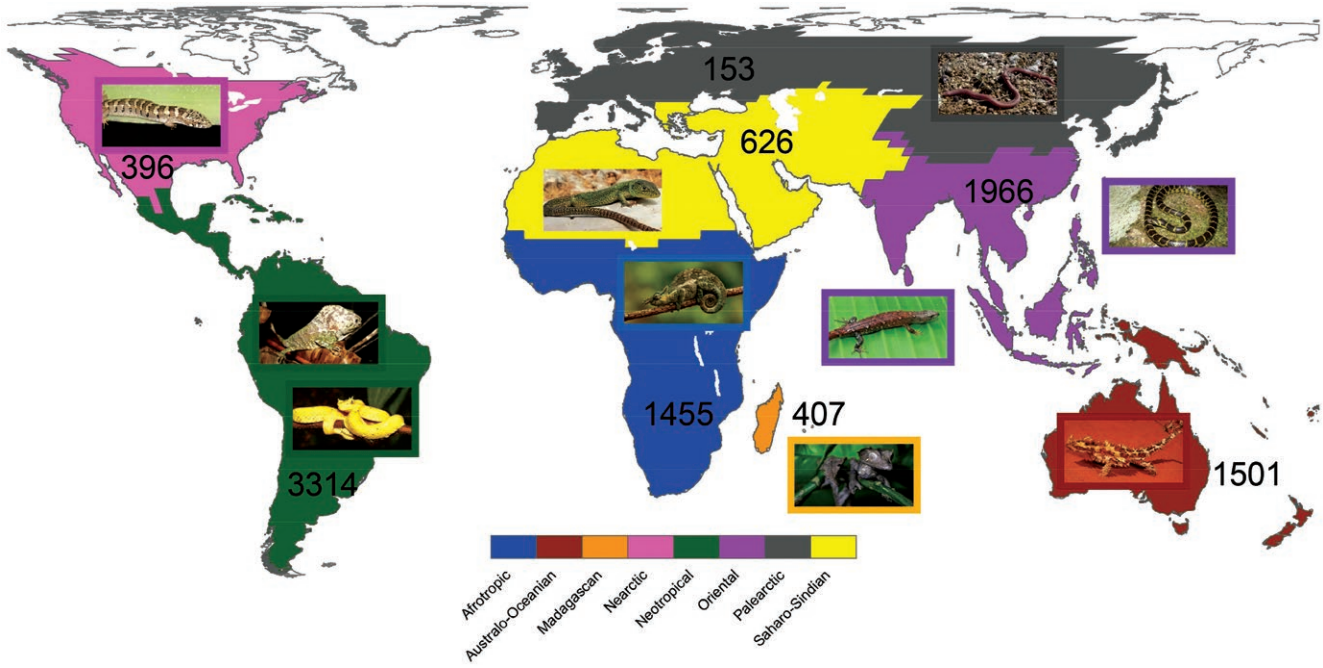

FIGURE 2. Biogeographic realms used for analyses of colonization times. The realms are based on biogeographic analyses by Falaschi et al. (2023). For each realm we show the number of species from our global presence-absence matrix that are endemic to that realm. In addition to the 8 realms shown here, the realm-level analyses included an additional realm (Marine) with 8 species included in our reconstruction of past dispersal events. We also show representative species from each region and representing major squamate clades, including Nearctic (Anguimorpha: *Elgaria kingii*), Neotropical (top: Iguania: Pleurodonta: *Corytophanes cristatus*; bottom: Serpentes: *Bothriechis nigroadspersus*), Palearctic (Amphisbaenia: *Blanus cinereus*), Saharo-Sindian (Lacertoidea: *Lacerta media*), Afrotropic (Iguania: Acrodonta: *Kinyongia tavetana*), Madagascan (Gekkota: *Uroplatus phantasticus*), Oriental (left: Scincoidea: *Tropidophorus hainanus*: right: Serpentes: *Lycodon flavozonatus*), Australo-Oceanian (Iguania: Acrodonta: *Moloch horridus*). Images are from J.J. Wiens except for *Lacerta* (Simon Jamison), *Kinyongia* (Javier Lobon-Rovira), *Moloch* (Jules Farquhar), and *Uroplatus* (Jonathan Ben Simon).

setting of no dispersal constraints, both dispersal-extinction-cladogenesis (DEC) and DEC + J (DEC + jump dispersal) models (Matzke 2014), and multiple estimates from each (i.e., conditional likelihoods, down-pass, and up-pass estimates). Both models and all estimates from each model were qualitatively identical with respect to all hypotheses tested. We only report results using the simpler DEC model (and conditional likelihood estimates) due to concerns with the DEC + J model (Ree and Sanmartín 2018). We acknowledge that the maximum range-size setting was somewhat arbitrary, but very few squamate species occurred in > 2 of these regions. We also acknowledge that placing constraints on recent dispersal between many pairs of realms would be reasonable, but our main focus was on ancient dispersal. Reconstructions used the ZW tree, which included more genes than the TEA tree. See Supplementary Data set S15 for a list of the species in each realm and the R code and input data for BioGeoBEARS.

We analyzed the output of BioGeoBEARS using the "nodepath" function in the R package *ape* v 5.7-1 (Paradis et al. 2004). We traced the path of each species from the tip to the root of the tree, recording the age (in millions of years before the present) and region with the highest conditional likelihood at each node. We then noted the age of the youngest node in which the region or combination of regions with the highest conditional likelihood differed from the region that the species occurred in. This corresponds to the maximum age for which there is evidence that a lineage was endemic to the same realm as the tip species being considered. For brevity, we refer to this age as the estimated colonization time for each species, even though it refers to the colonization time of a lineage that a species belongs to and not the species itself. We also conducted preliminary analyses using the minimum colonization time of species in each region (i.e., the oldest node in which the character state with the highest likelihood is the same as the tip and not separated from the tip by nodes with different states). These analyses yielded qualitatively identical results to those we present here (with respect to all hypotheses tested) and therefore we do not report them. The colonization times of realms and estimates of the number of species in each are given in Supplementary Data set S16, and all estimated colonization times for species are given in Supplementary Data set S17.

We first determined whether there was a correlation between the oldest colonization time of any species in each of the 8 realms and the number of species in that realm. This approach was similar to past analyses of colonization times and species richness

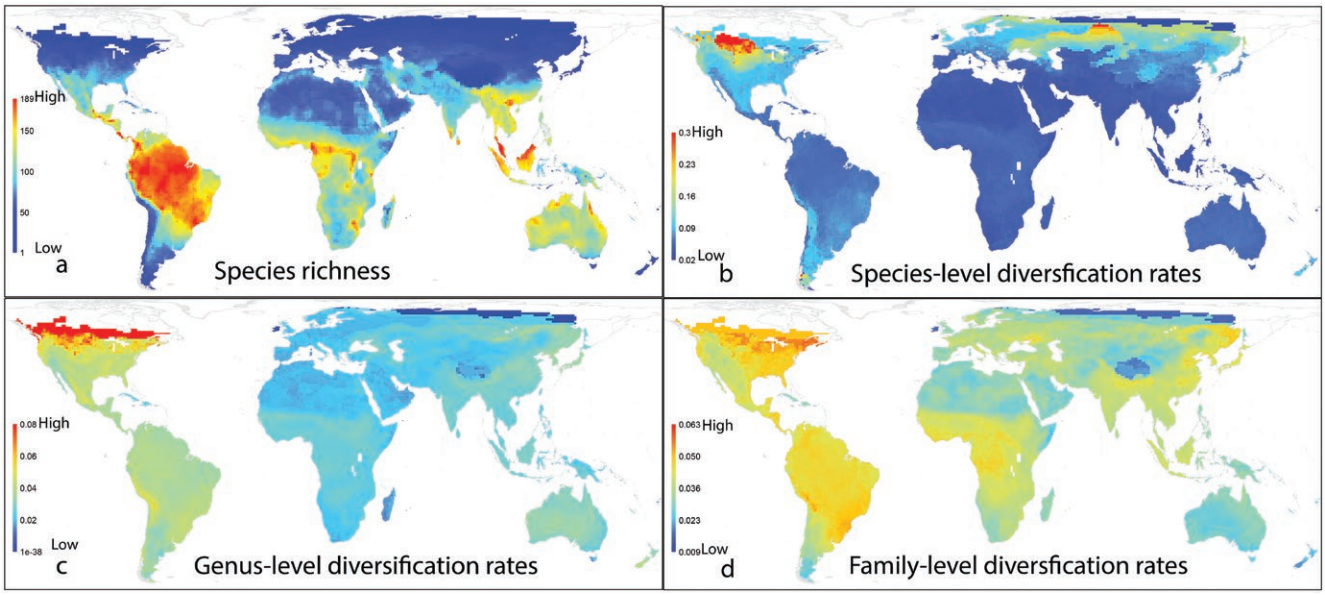

FIGURE 3. Global patterns of richness and diversification rates in squamate reptiles. For each 96 × 96 km terrestrial grid cell, we show: (a) species richness, and (b) average diversification rates of species in each grid cell, based on species-level diversification-rate estimates using the DR statistic. We also show average diversification rates of species in each cell based on rates estimated from the genera (c) and families (d) to which those species belong, based on the MoM estimators. Diversification rates are in units of species per million years. The tree used to estimate diversification rates is from Zheng and Wiens (2016). Note that the scale has been adjusted between plots to maximize the visibility of patterns of variation between regions.

(e.g., Stephens and Wiens 2003; Wiens et al. 2009). We found that the regional richness of each realm was significantly, positively correlated with the age of first colonization (see Results). We next investigated the relationships between colonization time and the richness of the same smaller-scale assemblages used for global analyses of diversification rates. Previous studies of the relationship between lineage age and species richness across species assemblages have sometimes focused on the ages of named taxa, for example tabulating the average family age of species in these assemblages (e.g., Dimitrov et al. 2023). However, there is no clear mechanistic relationship between the age of a named taxon that occurs in multiple regions and its richness in a given region. Even if a named higher taxon is endemic to a single region, the timing of colonization of the region by that clade may or may not correspond to the age of that taxon. For example, a lineage could colonize a region and then diversify into multiple clades that are each named as higher taxa.

Instead of measuring the colonization times of species in assemblages indirectly, we calculated 2 measures of colonization time for species within each grid cell: 1) average colonization time of all species present in the grid cell; and 2) maximum colonization time of any species present in the grid cell. The former metric might underestimate the time available for lineage accumulation, whereas the latter might overestimate this time. Therefore, we used both metrics to bracket the likely range of possibilities. We then regressed the mean and maximum colonization time against the total richness of species in each grid cell using a Dutilleul-modified *t*-test. Analyses of species richness with BRT were also repeated including either mean or maximum colonization time as additional predictor variables.

We acknowledge that we did not include rates of dispersal as a variable in these analyses. Previous analyses suggest that this is not a generally important variable relative to the timing of dispersal for explaining regional richness (Li and Wiens 2019), but there are cases where it may be important (e.g., elevational diversity gradients in birds; van Els et al. 2019). Interestingly, previous analyses among squamate families suggest that variation in their diversification rates is explained most strongly by variation in their family-level dispersal rates, more so than other ecological and morphological variables (Li and Wiens 2022). Thus, dispersal rates may be important for clade-level richness patterns in squamates rather than regional richness patterns.

RESULTS

Squamate Richness and Diversification Rates at Different Timescales

Squamate richness patterns (Fig. 3a) were broadly similar to those in other terrestrial vertebrate groups (Buckley et al. 2010; Jetz et al. 2012; González-del-Pliego et al. 2019; Raz et al. 2024). Specifically, richness peaks in wet tropical regions of Africa, South America, and

Table 1. Correlations between species richness and diversification rates for sets of clades of different ages

Age range (myr)	*n*	Correlation	*P*-value
0 to 25	1766	–0.279	0.100
0 to 30	2728	–0.193	0.278
0 to 35	3646	–0.225	0.261
0 to 40	4163	-0.008	0.968
40 or older	10159	**0.378**	**0.005**
50 or older	7578	0.034	0.754
60 or older	7523	0.034	0.755
70 or older	6885	**0.612**	**0.001**
80 or older	6102	**0.591**	**0.001**
90 or older	4871	**0.660**	**<0.001**

Note: *P*-values are based on Dutilleul-modified *t*-tests to account for spatial autocorrelation. Diversification rates were based on sets of named clades (genera and families) with different stem-group ages, in 5- and 10-million-year (myr) intervals. "*n*" indicates the number of species for which diversification rates could be calculated in each age range. Here, diversification rates were compared to the total richness of all species with distributional data (for analyses including only species with rate estimates, see Supplementary Table S1). Intervals of 5 myr were used for bins younger than 40 myr to more densely sample time intervals most similar to those of past studies of species-level diversification rates. Note that there were relatively few species ($n = 745$) in genera less than 20 myr old and so we did not include a 0 to 20 myr time interval. Significant correlations ($P < 0.05$) are boldfaced. All diversification rates in these specific analyses were estimated using MoM estimators.

Asia, and is lowest at high latitudes and in some arid regions (Fig. 3a). However, squamates are unusual compared to most other tetrapod groups, in showing relatively high richness in some desert regions (particularly in Australia).

We found no significant positive correlations between species richness and diversification rates at the species level using the DR statistic (Fig. 3b,c and Supplementary Table S3), consistent with recent global-scale studies in other organisms. Using the ZW tree, there was a significant, negative correlation between rates and richness ($r = -0.31$, $P = 0.0225$, $n = 14{,}800$ grid cells), whereas with the TEA tree, the correlation was non-significant ($r = -0.04$; $P = 0.7853$). Results were similar (Supplementary Table S4) using species-level rates calculated using BAMM (TEA: $r = 0.02$; $P = 0.9266$) and ClaDS (TEA: $r = 0.13$; $P = 0.4904$). Using 100 trees randomly sampled from a Bayesian posterior distribution of possible fully resolved trees from TEA, only 3/100 trees showed significant positive correlations at α=0.05 between species-level rates calculated using the DR statistic and species richness (correlations and *P*-values for all 100 trees in Supplementary Dataset S18).

Counterintuitively, but consistent with previous studies, assemblages with high species-level diversification rates occurred in low-richness regions at high latitudes (Fig. 3b and Supplementary Fig S2a). Genus-level rates showed similar patterns to species-level rates, with high rates in low-diversity northern temperate areas (Fig. 3c and Supplementary Fig. S2b) and no significant correlations between diversification rates and richness overall (Supplementary Table S3).

In contrast to results for genus and species-level diversification rates, family-level diversification rates were strongly and positively correlated with richness patterns globally using estimates from both MoM (Supplementary Table S3; ZW tree: $r = 0.37$; $P = 0.0225$; TEA: $r = 0.44$; $P = 0.0086$) and ClaDS (TEA: $r = 0.38$; $P = 0.0236$; Supplementary Table S4). Specifically, high-richness areas of Asia, Africa, and South America had relatively low genus-level and species-level diversification rates, but high family-level rates (Fig. 3d and Supplementary Fig. S2c). Some high-latitude areas in the Northern Hemisphere also had high family-level rates, which may help explain why previous clade-based studies found mixed evidence for an effect of tropical distribution on squamate diversification rates (Pyron 2014; Bars-Closel et al. 2017). These high family-level rates at high latitudes may be explained by the dominance of rapidly diversifying clades of colubrid snakes (e.g., Colubrinae, Natricinae, Viperidae). Conversely, low diversification rates in Australia (relative to richness) may be explained by the low numbers of species from these young and rapidly diversifying clades (e.g., Australia has few colubrids and no vipers) relative to the high richness of various lizard families with lower diversification rates. In summary, we found dramatic differences in correlations between richness patterns and diversification rates for families, genera, and species (Supplementary Tables S3 and S4). This pattern is likely explained by differences in clade ages (Supplementary Table S3 and Supplementary Fig. S1), with families representing longer and older timescales (median age: ZW tree = 85.4 myr; TEA = 75.4) than genera (ZW = 40.3; TEA = 34.5) or species (ZW = 12.9; TEA = 10.3).

To further explore the timescale over which diversification rates may help explain current richness patterns, we conducted analyses across different time windows. We compared rate-richness correlations among species in non-overlapping named clades (families and genera) of different age ranges, using MoM estimates (Table 1). For clades 40 myr old or younger, correlations between diversification rates and richness were negative, and never statistically significant (Table 1). This age bracket includes the ~1–20 myr old time range that was the focus of previous studies (Jetz et al. 2012; Rabosky et al. 2018; Igea and Tanentzap 2020). By contrast, all statistically significant correlations were positive and only occurred among clades older than 40 myr (Table 1). We note that there is considerable variation in the strength of the correlation among older time periods (e.g., the

correlation is significant at 40 myr but not at 50 or 60 myr). Nevertheless, there is clearly an overall pattern in which the strongest negative correlation is at the youngest time period, the strongest positive correlation is at the oldest time period, and all correlations before 40 myr are negative and all those after 40 myr are positive.

For groups in which estimates from all 3 methods were available, rates estimated using BAMM for individual clades tended to be correlated with those from the MoM estimators and ClaDS (Supplementary Table S5). In contrast, rates estimated using BAMM for the whole tree (rather than individual clades) and from RPANDA were not correlated either with each other or any other rate estimates (Supplementary Table S5). See Supplementary Appendix S2 for additional details. We found no evidence that rate estimates from the MoM estimators were problematic.

Diversification Rates, Environmental Variation, and the Ultimate Causes of Squamate Diversity Patterns

Our results (Table 1 and Supplementary Tables S3 and S4) suggest that variation in diversification rates drives some of the variation in richness among assemblages. However, these results do not explain why diversification rates vary. We address that question here. More generally, we address how climate might drive richness patterns. Richness gradients may arise from environmental conditions affecting diversification rates. However, it is unclear whether peaks in squamate richness in warm regions are driven by diversification rates, since family-level rates (Fig. 3d) show peaks both in tropical areas and (some) temperate areas (e.g., North America).

To investigate relationships between climate, diversification, and richness, we first identified the climatic variables most strongly correlated with richness (Supplementary Table S2). Two temperature variables (mean annual temperature [Bio1] and isothermality [Bio3]) and 1 rainfall variable (wettest month precipitation, Bio13) showed strong relationships with richness (Supplementary Table S2). We found only a single barely significant ($r^2 = 0.054$; $P = 0.046$) relationship among 24 comparisons of these climatic variables and diversification rates among families using phylogenetic regression analyses (Supplementary Appendix S5 and Supplementary Table S6). Furthermore, using Dutilleul-modified *t*-tests, we found either no significant correlations or only negative correlations between average species-level diversification rates and temperature across space (Supplementary Table S7). Thus, both

Table 2. Pseudo r^2 of boosted regression-tree models excluding and including diversification rates as predictors

	Zheng and Wiens (2016) tree				Tonini et al. (2016) consensus tree			
Rate measure	*n*	Correlation with richness	Pseudo r^2 spatial only	Pseudo r^2 with div. rate	*n*	Correlation with richness	Pseudo r^2 spatial only	Pseudo r^2 with div rate
Species level	14,737	–	0.333	0.367	14,793	–	0.316	0.413
Genus level	14,799	–	0.324	0.658	14,799	–	0.314	0.584
Family level	14,800	+	0.302	0.704	14,800	+	0.304	0.663

Note: All models of terrestrial squamate species richness included 5 spatial variables: mean annual temperature (Bio1), temperature isothermality (Bio3), wettest month precipitation (Bio13), latitude, and longitude. Models differed in whether they included or excluded diversification (div. rate) rates as predictors. Sample size (*n*) indicates the number of grid cells for which a given diversification rate could be quantified (out of 14,800 grid cells total). Note that family-level rates were positively correlated with species richness, whereas species and genus-level rates were negatively correlated with richness (based on plots of marginal effects; Supplementary Fig. S3). Here species-level rates were estimated using the DR statistic, and genus and family-level rates were estimated using the MoM estimator.

Table 3. Influence of predictor variables in boosted regression-tree models of squamate species richness, excluding and including family-level diversification rates (from the MoM estimator)

	All spatial variables		Longitude excluded		Latitude and longitude excluded	
Predictors	Relative influence		Relative influence		Relative influence	
	With div. rates	No div. rates	With div. rates	No div. rates	With div. rates	No div. rates
Latitude	47.12	50.77	48.62	53.26	NA	NA
Bio1	20.19	28.10	19.29	29.00	57.55	69.65
Div. rate	22.75	NA	25.10	NA	27.31	NA
Longitude	6.17	13.37	NA	NA	NA	NA
Bio3	1.62	4.43	2.81	8.38	7.73	15.65
Bio13	1.98	3.32	4.17	9.34	7.39	14.70
Pseudo r^2	*0.704*	*0.302*	*0. 805*	*0.618*	*0.783*	*0.612*

Note: Rates were estimated using the MoM estimator and the tree of Zheng and Wiens (2016). Relative influence is based on the number of times a variable is selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees summarized. These values always sum to 100 for a given model. Results are shown for models including diversification rates (with div. rates) and without (no div. rates). Bio1: mean annual temperature, Bio3: temperature isothermality, amplitude of day-to-night temperatures oscillate relative to the summer-to-winter (annual) oscillations, BIO13: rainfall of the wettest month.

diversification rates and climatic variables were related to species richness, but diversification rates and climate were not related to each other either across species or space.

We then tested whether models that included diversification rates explained more variation in richness than models based on environmental variation alone using BRT. Temperature (Bio1, Bio3) and rainfall (Bio13) variables were used as predictors in models with ln-transformed richness. Latitude and longitude were used as additional predictors to account for spatial autocorrelation (Tables 2–4 and Supplementary Table S8), but results excluding these variables were similar (Tables 3 and 4 and Supplementary Tables S9 and S10) likely because BRT is generally robust to spatial effects (Elith et al. 2008). Multivariate analyses showed that models based on temperature and rainfall predict up to ~67% of the variation in richness (Supplementary Table S9), with mean annual temperature being the most influential environmental variable (Tables 3 and 4 and Supplementary Supplementary Table S8). Models that included species-level diversification rates explained 10% (or less) additional variation in richness compared to models that excluded them (Table 2 and Supplementary Tables S9 and S10). Some models including genus-level rates predicted more variation in richness (Table 2) but yielded negative relationships between richness and rates (Supplementary Fig. S3b). By contrast, models that included family-level diversification rates explained an additional 17.2–39.7% of the spatial variation in richness (Tables 2–4 and Supplementary Tables S8–S10) and had overall positive relationships with richness (Supplementary Fig. S3c).

Results from family-level rates estimated using ClaDS were qualitatively similar to those using MoM rates, with models that included family-level rates always better at predicting richness than models based on spatial variables alone (Table 4). Overall, deep-time diversification rates explained considerable variation in richness that was not correlated with climate.

Given the non-significant relationships between diversification rates and temperature across families (Supplementary Tables S6) and space (Supplementary Table S7), what then explains the strong positive relationship between temperature and squamate richness (Supplementary Table S2)? One potential explanation is that major squamate clades might have originated in warm environments, and colonized cooler climates more recently, leaving less time to build up richness in these regions. This hypothesis is supported by ancestral reconstructions of climate across squamate phylogeny (Supplementary Fig. S4), which inferred that squamates occurred ancestrally in warm areas (see also Pie et al. 2017) with mean annual temperatures > 20 °C. Colonization of cooler climates (< 4 °C), occurred only recently, in several independent clades (Supplementary Fig. S4). We also tested this hypothesis by assigning

Table 4. Influence of predictor variables in boosted regression-tree models of squamate species richness, excluding and including family-level diversification rates (from ClaDS)

Predictors	All spatial variables		Longitude excluded		Latitude and longitude excluded	
	Relative influence		Relative influence		Relative influence	
	With div. rates	No div. rates	With div. rates	No div. rates	With div. rates	No div. rates
Latitude	47.00	50.56	48.36	53.41	NA	NA
Bio1	22.45	28.38	21.22	28.92	58.41	69.64
Div. rate	16.46	NA	22.94	NA	25.72	NA
Longitude	10.19	13.46	NA	NA	NA	NA
Bio3	2.14	4.30	3.57	8.40	7.63	14.71
Bio13	1.75	3.31	3.91	9.27	8.23	15.65
Pseudo r^2	*0.559*	*0.311*	*0.773*	*0.616*	*0.735*	*0.608*

Note: Rates were estimated with ClaDS and the consensus tree of Tonini et al. (2016) with 5,320 species. Relative influence is based on the number of times a variable is selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees summarized. These values always sum to 100 for a given model. Results are shown for models including diversification rates (with div. rates) and without (no div. rates). Bio1: mean annual temperature, Bio3: temperature isothermality, amplitude of day-to-night temperatures oscillate relative to the summer-to-winter (annual) oscillations, BIO13: rainfall of the wettest month.

Table 5. Analysis of colonization times of biogeographic realms and species richness

Rate estimate	*n*	Correlation	*P*-value
Colonization time of realms	9	0.717	0.037
Average colonization time of grid cells	14,735	0.627	<0.001
Maximum colonization time of grid cells	14,735	0.790	<0.001

Note: We reconstructed past dispersal events among 8 terrestrial biogeographic realms (and 9 in total) regions using a DEC (Matzke 2014) model implemented in BioGeoBEARS (Matzke 2013), based on the tree of Zheng and Wiens (2016). For a given species, we define "colonization time" as the depth of the youngest node in the tree in which the region with the highest likelihood differs from the region in which the species occurs. *n* indicates the number of spatial units included in each analysis. For analyses of the richness of realms, we compared the number of species in each realm to the oldest colonization time of any species endemic to the realm. We also focused on the same grid cells used in analyses of diversification rates and richness, comparing the richness of species in grid cells to either the oldest colonization time of any species or the average colonization time of all species in each cell. *P*-values for grid cells are based on a Dutilleul-modified *t*-test for assessing bivariate correlations with spatial data. Significant correlations ($P < 0.05$) are boldfaced.

all squamate species to 1 of 10 bins, based on values of Bio1 across their ranges (Supplementary Table S11). We found a tight positive correlation (Spearman's ρ = 0.900, $P = 0.002$) between the number of squamate species in each bin and the estimated age at which each bin was first colonized. Thus, colonization time seems to better explain the relationship between climate and species richness in squamates than diversification rates.

Finally, we directly investigated the relationship between colonization time and species richness across the globe, using both realms and grid cells (Table 5). These analyses showed that there was a strong correlation between the number of species in the 8 biogeographic realms and the inferred age of first colonization of squamates in each realm (Spearman's ρ = 0.717; $P = 0.037$; Supplementary Fig. S5 and Table 5). Analyses of richness in grid cells also showed that both the mean and maximum colonization times of species in grid cells were strongly correlated with the number of species in each cell ($r = 0.627$ and 0.790; Supplementary Fig. S6 and Table 5). These conclusions were supported regardless of whether DEC or DEC + J models were used to reconstruct past dispersal events among realms, though we only report results using DEC models (see Methods).

When we incorporated colonization time as an additional predictor variable into BRT models of global variation in richness, we found that both temperature and colonization time were positively related to richness (Table 6 and Supplementary Table S12). But the amount of variation explained by temperature (i.e., the relative influence score of temperature) was much lower when colonization time is directly represented in models. In BRT analyses that excluded colonization time, temperature (Bio1) was the most influential predictor variable (apart from latitude when present as a covariate), with a relative influence score between 22% and 70% (Table 4). However, when we included the maximum colonization time of species in each grid cell as an additional predictor, colonization time showed a similar or stronger relative influence score compared to temperature, and the relative influence score of temperature dropped to 18–44%. BRT analyses also confirmed that even when models directly incorporated variation in colonization time, including family-level diversification rates as a predictor improves the pseudo r^2 of models by roughly 20%. Models that included maximum colonization time, temperature, and family-level diversification rates were able to predict global variation in species richness with up to 86% accuracy (Supplementary Table S12).

Discussion

In this study, we identify the factors that shape global species richness patterns in the largest clade of terrestrial vertebrates: squamate reptiles. Our results shed light on the general processes that drive large-scale diversity patterns. We suggest a resolution to the apparent conflicts in the relationship between species richness and diversification rates reported in previous studies by considering diversification rates at different timescales. We also show how diversification rates, climate, and colonization times can contribute to richness patterns in counterintuitive ways. In squamates, current richness patterns are related to diversification rates at ancient timescales and to current climate, but these ancient diversification patterns are not related to current climate. Instead, the climate-richness relationship is strongly related to the more ancient colonization of warmer (e.g., tropical) climates relative to cooler (e.g., temperate) ones. Importantly, many recent analyses of the latitudinal diversity gradient have considered only recent diversification rates, with no consideration of colonization time at all.

The number of species in biogeographic realms was strongly correlated with their colonization times (Table 5). The richness of species in smaller-scale assemblages (grid cells) was also correlated with both the maximum and average colonization times of species (Tables 5 and 6 and Supplementary Table S12). Analyses among clades

Table 6. Influence of predictor variables (including colonization time of biogeographic realms) in boosted regression-tree models of squamate species richness, excluding and including family-level diversification rates

Predictors	Mean colonization time		Max. colonization time	
	Relative influence		Relative influence	
	With div. rates	No div. rates	With div. rates	No div. rates
Colonization time	10.34	15.57	43.82	49.67
Latitude	46.11	45.27	21.93	22.34
Bio1	19.18	26.15	14.41	17.23
Div. rate	17.46	NA	13.92	NA
Longitude	3.97	7.69	3.16	5.92
Bio3	1.74	2.79	1.49	2.45
Bio13	1.19	2.53	1.27	2.39
Pseudo r^2	*0.781*	*0.483*	*0.829*	*0.543*

Note: Rates were estimated using MoM and the tree of Zheng and Wiens (2016). Colonization times for species in 8 biogeographic realms were estimated using the same tree and the DEC model implemented in BioGeoBEARS. Relative influence is based on the number of times a variable is selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees summarized. These values always sum to 100 for a given model. Results are shown for models including diversification rates (with div. rates) and without (no div. rates), Bio1: mean annual temperature, Bio3: temperature isothermality, BIO13: rainfall of the wettest month, and either the mean or maximum colonization time of species in each grid cell.

showed no relationship between temperature and the diversification rates of families (Supplementary Table S6), nor any direct correlation between temperature and the diversification rates of squamate assemblages (Supplementary Table S7). In contrast, ancestral character reconstructions showed that there was a strong tendency for older clades to occur in warmer regions (Supplementary Fig. S4 and Supplementary Table S11). Much of the influence of temperature on richness appeared to be related to colonization time, with the relative influence score of temperature in models that included colonization time (Table 6) lower than in models that excluded it (Table 3). We acknowledge that temperature still influenced richness patterns in addition to colonization time (Table 6), but the underlying mechanisms are unclear. One potential explanation is that there are temperature-related patterns of colonization within each biogeographic realm that are not captured by our coarse-scale analyses of 8 terrestrial realms. Regardless, our results show that climate and diversification rates can both contribute to richness patterns independently. They also show that phylogenetic history (e.g., colonization time) is a powerful driver of richness patterns (Table 5 and Supplementary Figs. S5 and S6), even at ancient timescales and when richness patterns are strongly related to current climate (Supplementary Table S2). We acknowledge that our results are based on statistical correlations and do not "prove" what causes these richness patterns. However, this limitation is shared with most other empirical studies of this topic (i.e., experiments are not an option).

Our results support previous studies that emphasized the importance of colonization time (e.g., evolutionary time, time for speciation, tropical conservatism hypotheses) in explaining the latitudinal diversity gradient and richness patterns in general (e.g., Jansson et al. 2013; Economo et al. 2018; Li and Wiens 2019), despite recent opinions to the contrary (Saupe 2023). Previous studies have also shown that colonization time often seems to underlie relationships between climate and species richness (e.g., Kozak and Wiens 2012; Wiens et al. 2013). While the analyses of colonization time can often help explain current richness patterns, they do not necessarily address why a given group originated where it did. In the case of the latitudinal diversity gradient, 1 potential explanation for why many groups originated in the tropics is that the tropics were more extensive until recently (~30–40 myr ago; Wiens and Donoghue 2004; Fine and Ree 2006). This could potentially help explain a tropical origin for squamates, and also why ancient diversification rates, but not recent ones, underlie current squamate richness patterns.

Our findings may help resolve the seemingly contradictory results of past studies on global richness patterns and diversification rates. Our results agree with a number of previous studies in birds, mammals, fish, and angiosperms (Weir and Schluter 2004, 2007; Jetz et al. 2012; Rabosky et al. 2018; Igea and Tanentzap 2020; Dimitrov et al. 2023) in showing that speciation rates in the recent past (the last ~20 myr or less) are only weakly, or even negatively, correlated with present-day richness (Supplementary Tables S3 and S4). For the first time, we also consider variation in diversification rates across a wide range of timescales in the same group of organisms (Table 1). The only other empirical analysis that we are aware of to consider patterns in clades of different age ranges in same group is one that appears in the supplementary materials of Rabosky et al. (2018). They considered variation in "node density" among clades up to 50 myr old (see their Supplementary Fig. S6), which closely corresponds to the age-range of species-level analyses in this study (Fig. 3a). Both our results (Table 1, first 4 rows), and those of Rabosky et al (2018; their Supplementary Fig. S6), show a negative correlation between diversification rates and richness that is strongest in the youngest clades.

Our analyses showed that only when older clades are considered (especially > 70 myr) are there significant, positive correlations between diversification rates and richness (Fig. 3c; Table 1; and Supplementary Tables S3 and S4). Our results are consistent with the review by Schluter (2016), who found that differences in diversification rates between temperate and tropical clades were larger at older timescales, suggesting that the latitudinal diversity gradient was shaped by ancient diversification. These findings are also supported by simulations (Pontarp and Wiens 2017) showing that differences in diversification rates among regions tend to dominate patterns of richness over long timescales but have little effect on richness at shorter timescales, where colonization times dominate instead. These 2 studies and our results together support the idea that diversification rates measured over longer timescales (i.e., from older clades) can have a greater impact on present-day richness patterns than diversification rates in the more recent past (i.e., from species and genera).

The mismatch between recent diversification rates and present-day richness patterns is surprising, and has several possible explanations. One possibility is that high-richness regions where squamates experienced high diversification rates in the past are approaching a dynamic balance between speciation and extinction rates, and remaining ecological opportunities are in more depauperate areas (see Vidan et al. 2019). Another possibility is that recent diversification rates reflect glacial history. Many areas where recent diversification rates are high (Fig. 3b,c) have only become habitable for squamates in the relatively recent past (< 15,000 years in most cases; Clark et al. 2009). The few clades that occupy these regions contain species with large geographic ranges (Roll et al. 2017), which can be associated with high diversification rates in some groups (e.g., Jablonski and Roy 2003). Glacial cycles appear to have accelerated diversification rates in North American and Eurasian taxa in other groups (beetles: Ribera and Vogler 2004; birds and mammals: Weir and Schluter 2007). One obvious scenario is that glacial cycles promoted diversification in temperate squamate clades, and then these clades colonized northern areas following glacial retreats. However, speciation events

in squamates generally predate the Quaternary glaciations, and few squamate species that arose during this time period occur in the area with the highest diversification rates (northern North America). For example, in a study of 242 squamate sister-species pairs (using the ZW tree), only 23 were < 2.6 million years old (9.5%), and only 2 of these pairs ranged into northern North America (Jezkova and Wiens 2018). Instead, high diversification rates in cooler regions may reflect assemblages with a higher proportion of rapidly dispersing, rapidly diversifying, and cold-tolerant snake clades (e.g., Colubrinae, Natricinae, Viperidae) and a lower proportion of more cold-intolerant lizard clades with slower diversification and dispersal rates. Although we have not resolved why cooler regions had high diversification rates in the recent past, our results demonstrate that this is a separate issue from explaining why tropical regions are so diverse.

In summary, results from squamates suggest that the degree to which diversification rates influence spatial richness patterns varies with the timescale over which diversification rates are measured. Recent diversification rates were poorly matched to modern richness patterns. This is consistent with the conclusion that in relatively young groups the dominant factor explaining spatial variation in richness is colonization time rather than diversification rates. Nevertheless, we show that diversification rates over deeper time are crucial to understand global richness patterns. Multivariate models that include diversification rates estimated over deep timescales explained an additional 17.2–39.7% of the variation in squamate richness (Tables 2–4 and Supplementary Tables S8–S10) compared to models that included only climatic variables. We also show that squamates have likely inhabited warm regions for longer than they have inhabited colder regions (Supplementary Fig. S4). This earlier diversification in warmer environments seems to contribute the most to their present-day diversity gradients. Our results also resolve the paradox that many clades are diversifying most rapidly in areas where they are species poor (Jetz et al. 2012; Rabosky et al. 2018; Igea and Tanentzap 2020). Patterns of rate variation in the last ~1 to 20 million years have been insufficient to overturn global patterns of diversity that developed over much longer and deeper timescales.

We also show that a strong relationship between current climate and richness does not mean that phylogenetic history is unimportant for explaining these richness patterns, even when diversification rates and climate are uncorrelated. To the contrary, we show that colonization time statistically explains much of the variation in the richness of biogeographic realms, and has more of an influence on the richness of species assemblages than diversification rates. Overall, our results show that explaining large-scale patterns of species richness requires considering deep-time diversification rates, climate, and the timing of colonization of different regions, and not simply diversification rates at shallow timescales.

Supplementary Material

Data available from the Dryad Digital Repository: https://dx.doi.org/10.5061/dryad.0zpc8671s

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Data Availability

All the original data and scripts necessary to reproduce the analyses reported in this study can be accessed through the Dryad link: https://doi.org/10.5061/dryad.0zpc8671s. These include Supplementary Datasets S1–S19. Supplementary Datasets S1–S18 are described above. Supplementary Data set S19 contains the global presence-absence matrix as well as additional GIS files needed to reproduce global maps and analyses that include environmental data (see Supplementary Dataset S1 for more information). The GARD 1.5 species-range shapefiles, from which the global presence-absence matrix was derived, can be accessed at https://datadryad.org/stash/dataset/doi:10.5061/dryad.9s4mw6mh3.

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