# Time Explains Regional Richness Patterns within Clades More Often than Diversification Rates or Area

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ABSTRACT: Most groups of organisms occur in multiple regions and have different numbers of species in different regions. These richness patterns are directly explained by speciation, extinction, and dispersal. Thus, regional richness patterns may be explained by differences in when regions were colonized (more time for speciation in regions colonized earlier), differences in how often they were colonized, or differences in diversification rates (speciation minus extinction) among regions (with diversification rates potentially influenced by area, climate, and/or many other variables). Few studies have tested all three factors, and most that did examined them only in individual clades. Here, we analyze a diverse set of 15 clades of plants and animals to test the causes of regional species richness patterns within clades. We find that time was the sole variable significantly explaining richness patterns in the best-fitting models for most clades (10/15), whereas time combined with other factors explained richness in all others. Time was the most important factor explaining richness in 13 of 15 clades, and it explained 72% of the variance in species richness among regions across all 15 clades (on average). Surprisingly, time was increasingly important in older and larger clades. In contrast, the area of the regions was relatively unimportant for explaining these regional richness patterns. A systematic review yielded 15 other relevant studies, which also overwhelmingly supported time over diversification rates (13 to 1, with one study supporting both diversification rates and time). Overall, our results suggest that colonization time is a major factor explaining regional-scale richness patterns within clades (e.g., families).

*Keywords:* area, biogeography, diversification, species richness, time for speciation.

## Introduction

Explaining patterns of species richness is a major goal of ecology, biogeography, and evolutionary biology. Much literature on species richness has emphasized the latitudinal diversity gradient (e.g., Willig et al. 2003; Mittelbach et al. 2007). But richness patterns are far more varied and widespread. For example, almost every group of organisms occurs in multiple regions and typically has different numbers of species in each region. What general factors might explain these patterns?

Within a given region, species richness depends directly on three main processes: speciation, extinction, and dispersal (e.g., Ricklefs 1987). Speciation and dispersal add species to a region, whereas extinction subtracts species. Therefore, richness patterns among regions will reflect the balance of these three processes. Given this perspective, three main hypotheses can directly explain richness patterns. First, richness may be higher in those regions that the clade occupied earlier. This will allow more time to build up richness in those regions, particularly through in situ speciation (often called the time-for-speciation effect; Stephens and Wiens 2003). The effect of time can be examined by looking for relationships between the oldest colonization of a region and its current richness (assuming that subsequent colonization events are relatively unimportant) or between the summed ages of all colonization events and current richness (assuming that all colonization events contribute to richness, with older events being more important). Second, richness may be higher in regions colonized more frequently from other regions (e.g., MacArthur and Wilson 1967), regardless of the age of these colonizations. Although dispersal may tend to homogenize richness among regions overall, more limited dispersal to some regions could lower their richness relative to others. Third, richness may be higher in regions where one or more ecological variables increase net diversification rates of lineages there (where diversification is speciation minus extinction over time). These ecological variables might include climate, area, carrying capacity, or other abiotic or biotic differences among regions (e.g., Mittelbach et al. 2007; Wiens 2011). For example, regions with more favorable climates, larger areas, or higher carrying capacities might promote diversification by allowing more species to co-occur without competitive exclusion (i.e., extinction), and larger regions might promote allopatric speciation (e.g., Rosenzweig 1995). These three factors (coloniza-

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tion time, number of colonization events, and diversification rates) are not mutually exclusive and might act together to explain richness patterns. Note that carrying capacity (i.e., a measure of finite resources that allow species to co-occur locally and/or regionally) is sometimes considered a separate explanation relative to time and diversification rates (e.g., Mittelbach et al. 2007). However, based on first principles, carrying capacity cannot influence richness without acting through the processes of speciation, extinction, and dispersal. Furthermore, simulations explicitly show that carrying capacity impacts richness through its effects on diversification and colonization success and that diversification rates can predict richness patterns of habitats better than carrying capacity even when habitats vary primarily in carrying capacity (Pontarp and Wiens 2017). Therefore, carrying capacity is not here considered an alternative explanation relative to colonization time, colonization frequency, and diversification rates.

The relative importance of these three hypotheses (time, colonization frequency, and diversification rate) for explaining regional richness patterns within clades remains poorly understood for several reasons. First, many studies failed to test all three hypotheses. For example, some studies of the latitudinal diversity gradient tested for higher diversification rates in tropical clades without testing the effects of colonization time using biogeographic reconstructions (e.g., Rolland et al. 2014). Second, many studies have tested two or more competing explanations (e.g., time, diversification) but focused on individual clades in isolation (e.g., families; Kozak and Wiens 2012). Third, some studies have tested these hypotheses in multiple clades but focused on particular richness patterns (e.g., latitudinal diversity gradient [Jansson et al. 2013], high Andean richness [Hutter et al. 2017]). However, these studies may not represent an unbiased estimate of the causes of regional richness patterns within clades. For example, studies of latitudinal diversity might be more likely to find a significant impact of diversification rates than an unbiased selection of clades. Thus, we lack an overall picture of what explains species richness patterns among regions within clades.

Here, we test which of these three hypotheses most frequently explains species richness patterns among regions within clades. Rather than focusing on a single clade or richness pattern, we conduct a systematic search for any studies that examined phylogeny and biogeography in well-sampled clades. We then test three competing hypotheses to explain richness patterns among regions within each clade (using the regions defined in the original studies). These hypotheses relate to the time-for-speciation effect (using the age of the oldest colonization of each region or summed ages of all colonization events), the number of colonization events, and overall diversification rates in each region. We also conduct a systematic review of previous studies testing these hypotheses.

## Material and Methods

### *Selection of Studies*

We conducted a systematic search of the literature to find studies that included (*a*) likelihood-based reconstructions of biogeographic history, (*b*) five or more biogeographic regions, and (*c*) a time-calibrated, species-level phylogeny including ≥80% of described species in the clade. Five regions were necessary because regions were the units of analysis and it would be difficult to obtain significant results with fewer regions. However, we placed no restrictions on the size of regions (e.g., spanning different continents vs. small areas within a continent). Note that the regions used here were those delimited and analyzed in the original studies (which were not focused on richness patterns). The exact value of 80% completeness is arbitrary, as is any cutoff. We estimated the richness of each region based on species included in the tree. Otherwise, we could not estimate diversification rates for individual colonization events. Therefore, we sought phylogenies with relatively complete sampling. If sampling of clades and regions was generally proportional to their true richness, we predicted that 80% sampling should be sufficient to detect significant patterns. Our generally significant results suggest that our analyses were not swamped by random errors associated with incomplete sampling. Furthermore, failing to sample a minority of species in a clade or region seems unlikely to generate statistically significant, misleading results. Conversely, we might have obtained similar results with less complete sampling, and we also include results from two clades with >60% sampling (these yielded significant results that were concordant with those from more well-sampled trees). We also tested whether completeness impacted our main results and found no significant effect (see "Results").

We also excluded biogeographic studies in which the main focus of the original study was explaining richness patterns. Instead, we conducted a systematic review of these previous studies on species richness patterns and avoided counting these studies twice.

Two systematic searches were conducted to find potentially usable studies. First, the Web of Science was searched on September 26, 2016, using the search terms Topic = (time-calibrated phylogeny) AND Topic = (biogeography). The search included only studies from 2008–2016 (inclusive). We did not search for earlier studies because they would predate the most widespread model used in likelihood-based biogeographic analyses (Ree and Smith 2008). This search yielded 108 studies.

Second, a Google Scholar search on September 28, 2016, used the same search criteria, yielding 903 studies. These studies were sorted by relevance and examined in sets of 20, stopping when a set included no relevant studies. Only the first 400 yielded relevant studies.

These two searches collectively identified >100 potentially relevant studies. However, most were eliminated by the criteria listed above, especially incomplete species sampling and too few regions. Thirteen studies met all our criteria (table 1), spanning many different regions, habitats, and clades. We also present results from two studies that had only 63% and 69% of described species included in the tree. Trees used are given in appendix A (apps. A–D are available online) and are available in the Dryad Digital Repository: https://dx.doi.org/10.5061/dryad.72b792p (Li and Wiens 2019). Note that throughout the article, we also refer to each study as a clade, but we recognize that each clade is itself composed of clades (or "subclades").

### *Definition of Regions*

As mentioned above, we used the regions defined in the original biogeographic studies. Thus, the regions used were presumably those most relevant to the organisms in question for each study (e.g., based on their patterns of species endemism). Regions differed in size between studies, based largely on the spatial scale of the study (table 1; app. B). Thus, some studies were effectively global in scale ($n = 6$), with regions often corresponding to different continents or oceans. Other studies were confined to the New World ($n = 3$) or to a single continent or part of a continent (e.g., South Africa; $n = 5$) or single archipelago ($n = 1$). Importantly, our main analyses are based on comparing regions within a study, not regions across studies. Therefore, differences in the size of regions across studies should not be problematic. We also explicitly tested whether mean size of regions impacted our main results across studies and found that it did not.

### *Quantifying Richness Patterns*

We estimated richness for each region based on the assignment of each species to those biogeographic regions that were delimited in the 15 original studies. Some species occurred in multiple regions and were simply added to the richness of each region in which they occurred.

### *Estimating Colonization Times and Frequencies*

We used two standard approaches to estimate the impact of colonization time on richness patterns, utilizing the biogeographic reconstructions from the original studies. First, we estimated the oldest inferred dispersal event into that region (age of first colonization [AFC]). We then tested for a relationship between the AFC and current richness of each region. This approach assumes that the oldest colonization event primarily drives richness patterns. Second, we estimated the age of each colonization of each region and summed these colonization times (summed ages of colonizations [SAC]). We also used the biogeographic reconstructions to quantify the total number of times that each region was colonized (number of colonization events [NCE]). We tested the relationships between each of these three variables and species richness for each study.

**Table 1:** Summary of the studies included in this analysis

| Study | Clade (larger group of organisms) | Species in tree (% of total) | No. regions, geographic scope(s) | Age of clade (Ma) |
|---|---|---|---|---|
| Bengtson et al. 2015 | *Metalasia* (plants) | 58 (100) | 6, South Africa | 6.9 |
| Sun et al. 2014 | Schistochilaceae (plants) | 53 (~85.5) | 7, global | 98.9 |
| Vitales et al. 2014 | *Cheirolophus* (plants) | 21 (100) | 5, Macaronesia | 1.0 |
| Toussaint and Condamine 2016 | *Nicrophorus* (beetles) | 54 (~80.0) | 6, global | 108.5 |
| Frey and Vermeij 2008 | *Nerita* (gastropods) | 61 (~87.0) | 5, marine, global | 56.0 |
| Ludt et al. 2015 | *Prionurus* (fishes) | 7 (100) | 5, marine, global | 12.1 |
| Ma et al. 2016 | Epinephelidae (fishes) | 143 (~87.0) | 6, marine, global | 36.1 |
| Mariguela et al. 2016 | Triportheidae (fishes) | 19 (~86.4) | 8, South America | 20.7 |
| Metallinou et al. 2015 | *Ptyodactylus* (lizards) | 7 (~87.5) | 5, Africa, Arabia | 26.5 |
| Tolley et al. 2013 | Chamaeleonidae (lizards) | 174 (90) | 6, terrestrial, global | 64.9 |
| Iverson et al. 2013 | Kinosternidae (turtles) | 25 (100) | 11, New World | 75.8 |
| Beckman and Witt 2015 | *Astragalinus*, *Spinus* (birds) | 20 (~95.2) | 9, New World | 4.1 |
| Buckner et al. 2015 | *Saguinus* (monkeys) | 38 (~80.9) | 10, Africa | 9.1 |
| Martins and Melo 2016 | *Centris*, *Epicharis* (bees) | 167 (69.0) | 5, New World | 93.3 |
| Day et al. 2013 | *Synodontis* (fishes) | 81 (62.8) | 6, Africa | 34.7 |

Note: The two studies at the bottom are those with <80% completeness. Note that our brief summaries of the geographic distribution of each clade are oversimplifications (e.g., clades listed as "global" occur on multiple continents but not necessarily every continent). Clade ages are crown group ages.

We used the biogeographic reconstructions (from the original studies) to infer the number and timing of colonization events for each region. In general, a colonization event was inferred for a branch when the ancestral node was inferred to be in one region and the terminal node was inferred to be in another. The exact timing of a colonization event on a branch is not generally inferred. Therefore, we simply assumed that each colonization event occurred in the middle of the branch (i.e., mean of the ancestral and terminal node ages for that branch, or the crown and stem ages). Of course, it is unlikely that each colonization event occurred in each branch's exact middle. However, this seemed more realistic than assuming that all events occurred at the ancestral or terminal node of each branch. Furthermore, our primary interest was in relative ages of colonization events (and their relationship to richness patterns), not the precise, absolute ages. To obtain node ages, we obtained the original treefiles from each study and used FigTree version 1.4.0 (associated with BEAST; Rambaut and Drummond 2007) to estimate clade ages.

A region was inferred to be the ancestral state for a given node when that region had the highest proportional likelihood (relative to other regions). When the most strongly supported region was ambiguous for a given node (i.e., different regions equally likely), we generally inferred the colonization based on the next (most recent) node on the tree. However, in some cases, two regions (or more) were inferred for a given node (i.e., assuming that the ancestral species occurred in multiple regions). Allowing for this scenario avoided nonsensical inferences, such as treating every species in a subclade as a separate colonization of the same region. A widespread ancestral species was inferred for a node when all descendants of the next four adjacent nodes immediately above that node were uniformly present in both regions. Four is an arbitrary cutoff. Given a partly symmetrical subclade, there are different ways of counting four adjacent nodes. In cases where different ways of counting led to different inferences for a node, we considered both regions present for that node.

Some species are present in a region due to very recent colonization events, which were inferred based on changes between ancestral nodes and current species distributions. These colonization events were also included. Again, we used the age of the middle of these (terminal) branches as the age of the colonization event.

### *Estimating Diversification Rates*

To investigate impacts of diversification rates on regional richness patterns, we estimated a mean net diversification rate (NDR) for each region, based on diversification rates estimated for each colonization event and weighted by the number of species derived from each colonization event. To estimate the diversification rate associated with each colonization event (i.e., each representing a separate subclade), we used the method-of-moments estimator for stem group ages (Magallón and Sanderson 2001; MS). This MS estimator requires the age of each clade, the number of species, and a relative extinction fraction (epsilon). Epsilon corrects for clades that are unsampled due to extinction (Magallón and Sanderson 2001). Therefore, epsilon is usually assumed across an entire tree rather than estimated separately for individual clades. The age and number of descendant species associated with each colonization event were obtained from the tree, after identifying colonization events from the biogeographic analyses described above. We assumed an intermediate epsilon (0.5). Previous studies show that different epsilon values change estimated rates but have generally little impact on relationships between diversification rates and other variables (e.g., Scholl and Wiens 2016) and between true and estimated stem group rates (Meyer and Wiens 2018). The stem group age for a colonization was the ancestral node of the branch on which the dispersal event was inferred to have occurred. We used stem group ages because it is not possible to estimate crown group ages for clades (i.e., colonization events) represented by a single species and because stem group estimators are generally more accurate (Meyer and Wiens 2018). Overall, the MS estimators are demonstrably accurate (Kozak and Wiens 2016; Meyer and Wiens 2018; Meyer et al. 2018) and have been widely used, including studies that found significant relationships between diversification rates and richness patterns among clades (e.g., Scholl and Wiens 2016) and regions (e.g., Hutter et al. 2017).

To convert diversification rates estimated for each colonization event to an overall rate for each region, we first assigned each species to a colonization event (using the biogeographic reconstructions described above) and a diversification rate to each species. Then we estimated a weighted diversification rate for each region by adding the rates for all species in the region and dividing by the number of species in that region. Thus, a colonization event that generated many species in the region has a stronger influence on the weighted rate than a colonization yielding two species. For example, imagine a region that has been colonized by two subclades: one (subclade A) has a very high diversification rate but is represented by only two species, and another (subclade B) is represented by 99 species but with a very low diversification rate. Failing to weight the diversification rates by the number of species in each subclade could lead to the obviously incorrect inference that the relatively high species richness of the region (101 species) was explained by the high diversification rate in the two species of subclade A. Therefore, the approach we used is preferable to simply averaging rates across all colonization events within a region without weighting on the basis of the number of spe-

cies descended from each colonization. Nevertheless, we did perform a set of analyses using average diversification rates, which generally yielded results similar to those based on the weighted rates (i.e., few significant relationships between regional richness and diversification rates). Estimates of species richness, ages, and diversification rates from each colonization of each region are given in appendix B.

Some authors have claimed that the net diversification rate estimator used here requires a positive relationship between ages and richness of clades (e.g., Rabosky et al. 2012). However, simulations show that the accuracy of MS estimators can be high regardless of whether the relationship between age and richness is positive or negative (Kozak and Wiens 2016). Furthermore, simulations show that the MS estimators can be robust to heterogeneous rates within clades, both among subclades (Meyer and Wiens 2018) and over time (Meyer et al. 2018).

We did not use Bayesian analysis of macroevolutionary mixtures (BAMM; Rabosky 2014) to estimate diversification rates. Simulations show that it strongly underestimates the true variation in diversification rates among clades across trees, assigns incorrect rates to most clades, and yields much weaker relationships between true and estimated diversification rates than stem group MS estimators (Meyer and Wiens 2018; Meyer et al. 2018). Moreover, BAMM can yield problematic results in empirical analyses of species richness patterns (Hutter et al. 2017), like the present study.

We did not use methods that explicitly estimate diversification rates for regions because current implementations (i.e., GeoSSE; Goldberg et al. 2011) allow analysis of only two regions. Furthermore, this approach could not be applied to many of the clades included here because they contain relatively few species. We note that GeoSSE can potentially avoid incorrect inferences of ancestral regions caused by strong effects of regions on diversification rates. However, our results show little evidence for such effects (and only in clades with <50 species, most likely too few for GeoSSE).

### *Statistical Analyses*

We took a three-part approach to the statistical analyses (in R ver. 3.3.1; R Core Team 2016) for each of the 15 studies. First, we performed ordinary least squares regression between species richness (dependent variable) of each region and each of the independent variables calculated above for each region (AFC, SAC, NCE, and NDR). These analyses were performed using both raw richness and ln-transformed richness. Summaries of overall AFC, SAC, NCE, and NDR for each region are given in appendix C. Note that we initially performed Shapiro-Wilk tests to evaluate whether species richness (or ln richness) was normally distributed among regions and found results consistent with normality for most clades (11/15; table D1; tables D1–D14 are available online). We also performed nonparametric Spearman rank correlation tests on the four clades that deviated significantly from normality, but we generally emphasize the regression results from all 15 clades so that all results can be compared directly.

Second, we performed multiple regression analyses, specifically, when two or more independent variables each showed significant (or nearly significant, $P < .10$) relationships with richness in pairwise analyses. In these cases, all significant or nearly significant independent variables were included in the multiple regression analyses. However, since AFC and SAC both measure the time-for-speciation effect, we did not include these as separate variables in the same analysis. Instead, we included whichever had the better fit to richness in that clade (based on $r^2$ values). We performed separate multiple regression analyses using raw and ln-transformed richness. We also tested to what extent the different predictor variables were related to each other (for all clades).

We also performed multiple regression analyses when no independent variables showed a significant relationship with richness separately, in case a combination of variables significantly explained richness patterns. In these cases, we analyzed all combinations of independent variables but did not include both AFC and SAC in the same model.

Third, based on the preceding analyses, we identified the best-fitting model for a given study. The best-fitting model was based on comparison of Akaike information criterion (AIC; Burnham and Anderson 2002) values across single and multiple regression analyses. However, AIC values from analyses of raw and ln-transformed richness may not be directly comparable. Therefore, for a given study, we only compared AICs of models using the same richness transformation. When two models gave similar AIC values (within 2 AIC units), we chose the model with fewer variables. Last, we chose between the best models for each richness type (raw vs. ln transformed), based on their $r^2$. We also calculated standardized partial regression coefficients to determine the relative contribution of each variable to multiple regression models.

Following standard practice, we did not use phylogenetically corrected statistics because regions were analyzed (not clades). There is no phylogeny among regions.

By testing both ln richness and raw richness, we allow richness to increase either exponentially or linearly over time (respectively). The claim that time explains little variation in regional richness (based on reanalysis of four studies; Rabosky 2012) seems to be rooted in the unnecessary assumption that richness increases only exponentially over time (see reanalyses in Wiens et al. 2013, their app. S6).

We also performed a series of analyses to test for possible sources of bias in our main results. Given that time-related variables were generally supported as the most important, we tested how the amount of variance explained by time (i.e., the best-fitting time-related variable in each study)

was related to (i) clade age, (ii) total richness of the clade, (iii) completeness of taxon sampling, (iv) mean size of the regions in a study, and (v) the number of regions per study. We also tested whether studies in which time was supported as the most important variable tended to be older, richer, or more completely sampled, using unpaired *t*-tests.

### *Analyses of Area*

We also performed analyses testing whether the area of these regions explained their variation in species richness within clades. However, we caution that even if there were a perfect relationship between area and richness in every clade, these relationships would still need to be explained by speciation, extinction, and/or dispersal and the variables that address their effects (AFC, SAC, NCE, and NDR). Unfortunately, none of the 15 studies provided data on the area of the regions they used. Nevertheless, for some studies, the authors used standard biogeographic regions for which area estimates were already available (e.g., Pyron and Wiens 2013). For others, the size of areas could be estimated from the political units they encompassed (and publicly available data on the size of these units). For another set of studies, the authors provided maps of the regions they used, and we estimated their areas using the image analysis program ImageJ (http://rsb.info.nih.gov/ij/) and then scaled these to areas of known size. Data on the area of regions are provided in appendix C. We tested for relationships between richness and area using both raw and $\log_{10}$-transformed area and richness data.

We acknowledge that some readers might conclude that we should have included climate or related variables (e.g., productivity) as well. However, obtaining these data for the hundreds of species in all of these studies would not be straightforward (especially for the marine species). Moreover, it is not clear which climatic variables would be most relevant for each clade. Finally, even a perfect climate-richness relationship for each clade would still have to be explained by the factors that directly impact richness (speciation, extinction, dispersal) and the related variables that we include here. Nevertheless, climate-richness relationships were addressed in some studies in our literature review.

### *Literature Review*

We performed a systematic review to find previous studies that compared the impact of time and diversification rates on richness patterns. In our experience, relatively few studies have analyzed the effect of time on richness patterns, whereas many have analyzed diversification rates (but not necessarily focusing on regional richness patterns). Therefore, we focused our search on studies that tested the time-for-speciation effect (noting that this should still include studies that rejected this hypothesis). A Google Scholar search was conducted on August 28, 2017, using the search terms "time-for-speciation" and "richness." The 501 studies found were sorted by relevance and examined in sets of 20, stopping when no sets included relevant papers (at 360). Second, the Web of Science was searched on September 3, 2017, using the same search criteria, yielding 21 studies. We then summarized studies that tested both the time-for-speciation effect and diversification rates. We only considered studies that statistically tested for relationships between time and richness among multiple regions or habitats (most did not explicitly test NCE). We did not consider studies that merely analyzed patterns of phylogenetic diversity, although these might also reflect time. Our survey also included studies of local richness and richness among habitats.

## Results

### *New Analyses*

Thirteen studies met all our criteria (table 1) and included plants ($n = 3$), insects ($n = 1$), gastropods ($n = 1$), and vertebrates ($n = 8$). They also spanned many different regions and habitats (terrestrial, freshwater, marine) and overall clade ages ranging from 1.0 to 108.5 myr old. We also included two studies that met most criteria but had less complete phylogenies (for insects and fish). These were within the same age range.

Time was a major factor explaining richness patterns among regions in all 15 clades (figs. 1, 2). For example, in analyses of pairwise relationships between raw richness and the four predictor variables (fig. 1), time (AFC, SAC) was the single most important variable (highest $r^2$) for explaining richness patterns in most clades (13/15). NCE and NDR were the most important in only one clade each.

When considering both pairwise and multiple regression analyses and raw and ln-transformed richness (tables 2, D2–D6), the best-fitting model included time as the sole predictor variable for richness for most clades (10/15), either with other variables showing insignificant effects or with multiple regression models showing poorer fit. Time alone explained >90% of the variation in species richness among regions in most of these clades (7/10; table 2).

For five clades, multiple regression models had the best fit, and time (AFC or SAC) was included in all five models, along with diversification rates (tables 2, D4, D5). NCE was included in three. Time had the strongest contribution to richness in three of these five clades, and diversification rates had the strongest contribution in the other two (tables 3, D7, D8).

Overall, all 15 clades supported time as a significant factor explaining richness patterns (table 2). Only five showed

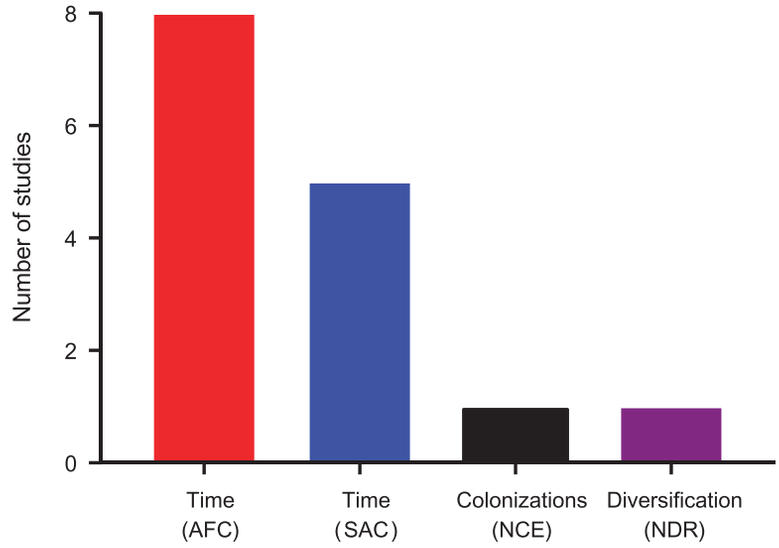


**Figure 1:** Summary of the single variable with the strongest influence on species richness patterns among regions within each clade, based on $r^2$ values from 15 clades (studies). The variables are age of first colonization event (AFC), summed ages of colonization events (SAC), number of colonization events (NCE), and net diversification rates (NDR). The results show that the two variables based on the time-for-speciation effect (AFC, SAC) generally have the strongest impact on richness patterns. The full results for each clade are given in table D2, available online (based on raw richness values; results for ln-transformed richness are in table D3, available online).

a significant effect of diversification rates also, and only two showed a stronger contribution of diversification rates than time (table 3).

These results were largely consistent regardless of the geographic scope of the study, the number or size of regions used, the age of the clade, or the clade's overall species richness or how complete the taxon sampling was (details in tables D9, D10). Nevertheless, there were some surprising patterns. The variance in regional richness explained by time was not significantly related to the completeness of taxon sampling ($r^2 = 0.168$, $P = .1290$), mean size of regions ($r^2 = 0.162$, $P = .1367$), or the number of regions per study ($r^2 = 0.151$, $P = .1520$). However, this variance was strongly and positively related to clade age ($r^2 = 0.399$, $P = .0115$) and total clade richness ($r^2 = 0.536$, $P = .0019$). Similarly, those clades in which richness was explained only by time tended to be older (unpaired *t*-test: mean difference = 50.76 myr; $P = .0065$; table D10) and more species rich (mean difference = 61.3 species; $P = .0404$) but not more completely sampled ($P = .2571$). Thus, it was only in younger clades that diversification rates helped explain richness patterns. Clades that were globally distributed (tables 1, D10) tended to be older ($P = .0967$) but not significantly richer ($P = .2711$), less completely sampled ($P = .7846$), or with more variance explained by time ($P = .1110$). There was also a tendency for SAC to be more important than AFC in younger clades than older clades (mean SAC = 27.97 Ma; mean AFC = 58.59 Ma), but this was not significant ($P = .1346$).

We also confirmed that the different predictor variables were generally uncorrelated with each other (table D11). Further, we confirmed that four clades in which normality was rejected gave generally similar results using nonparametric correlation tests (table D12). We also confirmed that using mean diversification rates among colonization events for each region yielded generally similar results to those using rates weighted by the richness of each clade in the region (table D13). We refer readers to these tables for details and exceptions.

Finally, we tested whether the richness of regions was related to their area (table D14). We found a significant positive relationship between richness and area in only two clades. The nonsignificant relationships were typically weak (all $r^2 < 0.500$) and were even negative in three clades.

### *Literature Review*

Our systematic search found a total of 15 studies that explicitly tested whether richness patterns were explained by time or diversification rates (table 4). Among these 15 studies, 14 supported time. Among these 14, only one also supported the diversification rate hypothesis. Only one study among the 15 supported diversification rates and rejected time. Importantly, this was a study of all amphibians over deep timescales (270 myr). Many other studies (8/15) were of younger amphibian clades that strongly supported the time effect. We also list five other studies that tested time

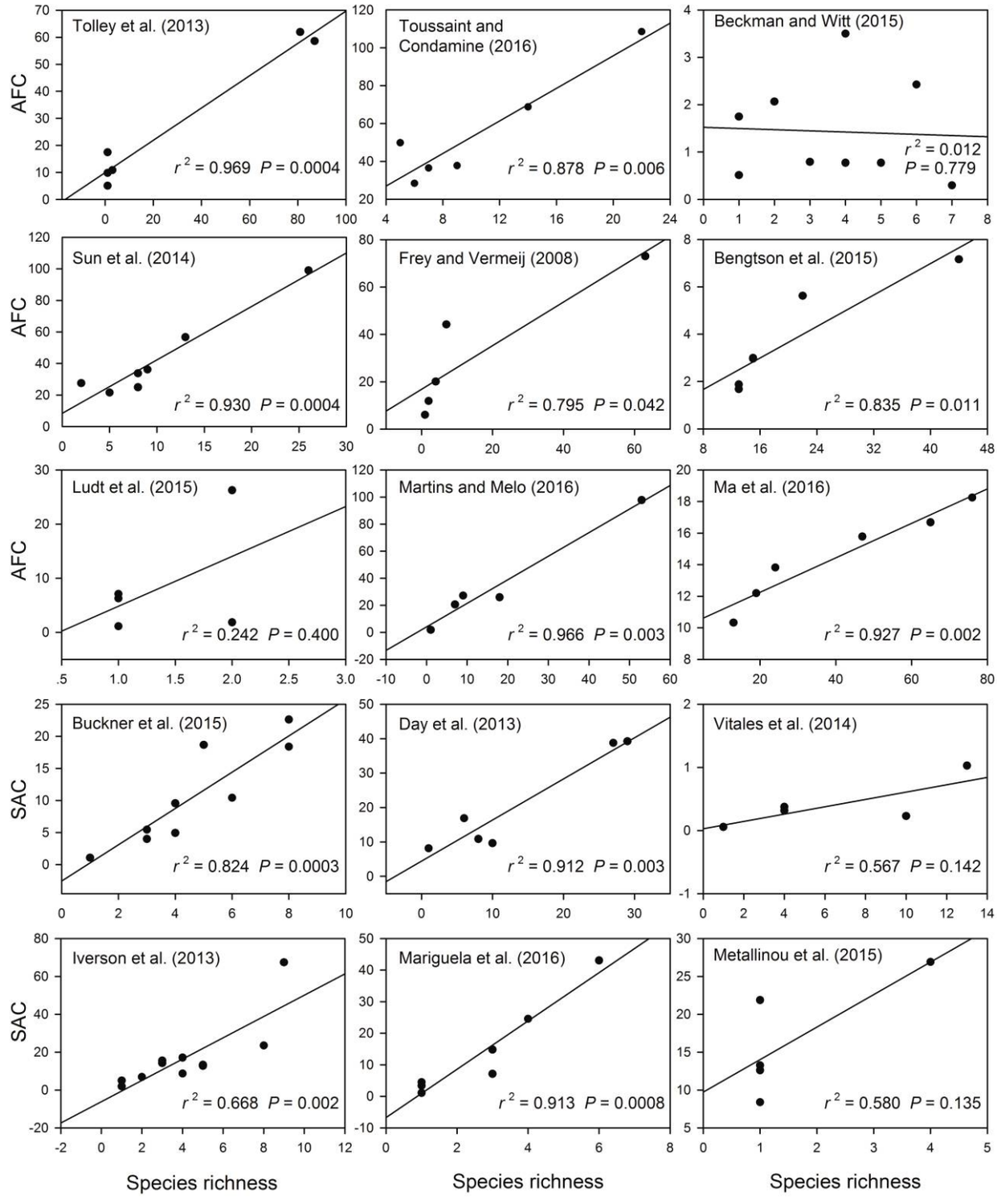


**Figure 2:** Relationships between species richness and colonization time among regions for each clade. Results are shown for raw richness and time (age of first colonization event [AFC], summed ages of colonization events [SAC]) for all data sets for illustrative purposes, even though ln-transformed richness sometimes has a better fit and even though time is not the most important variable for explaining regional richness in every data set (although it is in most; fig. 1). The time-related variable shown for each clade (either AFC or SAC) is the one with the strongest relationship with raw species richness patterns among regions (based on $r^2$). The best-fitting model for each clade is summarized in table 2.

**Table 2:** Summary of the best-fitting model for each study

| Study, organism(s) | Independent variables in best-fitting model | Best-fitting model | |
|---|---|---|---|
| | | $r^2$ | $P$ |
| Bengtson et al. 2015, *Metalasia* (plants) | AFC with ln richness | .926 | .002 |
| Sun et al. 2014, Schistochilaceae (plants) | AFC with raw richness | .930 | .0004 |
| Vitales et al. 2014, *Cheirolophus* (plants) | SAC + NDR with ln richness | .988 | .012 |
| Toussaint and Condamine 2016, *Nicrophorus* (beetles) | AFC with raw richness | .878 | .006 |
| Frey and Vermeij 2008, *Nerita* (gastropods) | AFC with ln richness | .959 | .004 |
| Ludt et al. 2015, *Prionurus* (fishes) | AFC + NDR or SAC + NDR with raw or ln richness | .970 | .031 |
| Ma et al. 2016, Epinephelidae (fishes) | AFC with ln richness | .977 | .0002 |
| Mariguela et al. 2016, Triportheidae (fishes) | SAC + NCE + NDR with raw richness | .997 | .0002 |
| Metallinou et al. 2015, *Ptyodactylus* (lizards) | SAC with raw richness or ln richness | .580 | .135 |
| Tolley et al. 2013, Chamaeleonidae (lizards) | AFC with raw richness | .969 | .0004 |
| Iverson et al. 2013, Kinosternidae (turtles) | SAC with raw richness | .668 | .002 |
| Beckman and Witt 2015, *Astragalinus*, *Spinus* (birds) | AFC + NCE + NDR with ln richness | .971 | .0003 |
| Buckner et al. 2015, *Saguinus* (monkeys) | SAC + NCE + NDR with raw richness | .941 | .0004 |
| Martins and Melo 2016, *Centris*, *Epicharis* (bees) | AFC with raw richness | .966 | .003 |
| Day et al. 2013, *Synodontis* (fishes) | SAC with raw richness | .912 | .003 |

Note: For each clade (study), we performed analyses using both raw species richness of regions and ln-transformed richness. The results presented here used whichever measure of richness yielded the highest $r^2$. AFC = age of first colonization; NCE = number of colonization events; NDR = net diversification rates; SAC = summed ages of colonization. Full results for raw richness are given in tables D1 (pairwise) and D5 (multiple regression) and for ln-transformed richness in tables D3 (pairwise) and D6 (multiple regression); full results for the two less complete clades (at bottom) are given in table D4 (tables D1–D14 are available online).

but not the diversification rate hypothesis and generally found strong support for time.

## Discussion

In this study, we analyze 15 clades of plants and animals to test the causes of species richness patterns among regions within clades. Our results show that in most clades (87%), richness patterns were determined primarily by time (fig. 1; table 2). Thus, groups generally have more species in regions where they have been present (and speciating) the longest. Diversification rates and the number of colonization events helped explain richness patterns in some cases, but neither explained richness to the exclusion of the time-related variables in our results. In clades in which multiple factors contributed to richness patterns, time was still generally the most important factor (table 3). Importantly, the fact that diversification rates were not generally supported suggests that factors that might impact richness through their influence on diversification rates (e.g., area, productivity) were not the main factors underlying richness patterns in most of these clades or that their effects were not generally through diversification. Furthermore, we explicitly included area and found that it generally had no effect on these regional richness patterns. In addition to our new analyses, we also conducted a systematic review of previous studies comparing the time and diversification rate hypotheses, which focused on individual clades. These results also strongly supported the time hypothesis over the diversification rate hypothesis (13 studies to 1, with another supporting both; table 4). Importantly, these previous studies included analyses of richness patterns among local sites and among habitats, and some revealed that time can actually explain climate-richness relationships (e.g., Wiens et al. 2011, 2013; Kozak and Wiens 2012), rather than time and climate being competing explanations. For example, three studies (Wiens et al. 2011, 2013; Kozak and Wiens 2012) showed strong relationships between species richness and climate and between the timing of colonization of different climatic zones and their current richness but not between climate and diversification rates. Overall, it would be nonsensical to suggest that including data on climate or productivity would overturn our conclusions here, even if there were strong relationships between richness and productivity or climate (instead this pattern would imply that time underlies these richness-productivity or richness-climate relationships).

We recognize that some readers may ask: who cares about richness patterns within clades? After all, the causes of the latitudinal diversity gradient have been a central topic in ecology for centuries (Willig et al. 2003). In contrast, the richness patterns analyzed here were generally not even the focus of the studies we used (table 1). Although the richness patterns in any particular clade are not necessarily of widespread interest, these lower-scale richness patterns are far more ubiquitous. That is, not every genus shows a latitudinal diversity gradient, but almost every genus has more

**Table 3:** Contribution of individual variables to the best-fitting multiple regression models

| Study, organism(s) | Multiple regression model | Contribution of each independent variable in best-fitting model | | |
|---|---|---|---|---|
| Vitales et al. 2014, *Cheirolophus* (plants) | ln(richness) vs. (SAC + NDR): $r^2 = .988$, adj. $r^2 = .975$, $P = .012$ | ln(richness) vs. SAC: SPRC = .511, $P = .010$ | ln(richness) vs. NDR: SPRC = .464, $P = .013$ | ... |
| Ludt et al. 2015, *Prionurus* (fishes) | Richness vs. (AFC + NDR): $r^2 = .970$, adj. $r^2 = .939$, $P = .031$ | Richness vs. AFC: SPRC = .432, $P = .028$ | Richness vs. NDR: SPRC = .507, $P = .020$ | ... |
| Mariguela et al. 2016, Triportheidae (fishes) | Richness vs. (SAC + NDR + NCE): $r^2 = .997$, adj. $r^2 = .995$, $P = .0002$ | Richness vs. SAC: SPRC = .487, $P = .002$ | Richness vs. NDR: SPRC = .249, $P = .005$ | Richness vs. NCE: SPRC = .259, $P = .008$ |
| Beckman and Witt 2015, *Astragalinus*, *Spinus* (birds) | ln(richness) vs. (AFC + NDR + NCE): $r^2 = .971$, adj. $r^2 = .938$, $P = .0003$ | ln(richness) vs. AFC: SPRC = .242, $P = .048$ | ln(richness) vs. NDR: SPRC = .290, $P = .009$ | ln(richness) vs. NCE: SPRC = .406, $P = .004$ |
| Buckner et al. 2015, *Saguinus* (monkeys) | Richness vs. (SAC + NDR + NCE): $r^2 = .941$, adj. $r^2 = .912$, $P = .0004$ | Richness vs. SAC: SPRC = .548, $P = .002$ | Richness vs. NDR: SPRC = .095, $P = .026$ | Richness vs. NCE: SPRC = .270, $P = .040$ |

Note: For five clades, the best-fitting model was a multiple regression model (table 2). Here, we summarize the contribution of each variable to the best-fitting model, including standardized partial regression coefficients (SPRC) and *P* values for each variable. The SPRC indicates how much of the adjusted $r^2$ is explained by each independent variable (with the other variables held constant). Full results for raw richness are given in table D5 and for ln-transformed richness in table D6 (tables D1–D14 are available online). Contributions of each variable to the multiple regression models are given in tables D7 and D8.

**Table 4:** Summary of studies that tested the effect of time on spatial richness patterns and whether they supported time (time for speciation) or diversification rates

| Study | Time for speciation | Diversification rates | Organism | Units | Geographic scope | Time frame (myr) |
|---|---|---|---|---|---|---|
| Wiens et al. 2006 | Yes | No | Hylid frogs | Regions | Global | ~65 |
| Wiens et al. 2007 | Yes | No | Plethodontid salamanders | Elevational bands | Middle America | ~42 |
| Smith et al. 2007 | Yes | Yes | Hylid frogs | Elevational bands | Middle America | ~45 |
| Li et al. 2009 | Yes | No | Cyprinid fish | Elevational bands | Asia | ~12 |
| Wiens et al. 2009 | Yes | No | Ranoid frogs | Regions | Global | ~100 |
| Kozak and Wiens 2010 | Yes | No | Plethodontid salamanders | Elevational bands | Eastern North America | ~65 |
| Wiens et al. 2011 | Yes | No | Hylid frogs | Local sites | Global | ~80 |
| Kozak and Wiens 2012 | Yes | No | Plethodontid salamanders | Local sites | Global | ~60 |
| Hutter et al. 2013 | Yes | No | Centrolenid frogs | Elevational bands | South America | ~35 |
| Pyron and Wiens 2013 | No | Yes | Amphibians | Regions | Global | ~270 |
| Wiens et al. 2013 | Yes | No | Phrynosomatid lizards | Precipitation zones | North and Middle America | ~55 |
| Wu et al. 2014 | Yes | No | Babblers (birds) | Elevational zones | China | ~10 |
| Lv et al. 2016 | Yes | No | Arvicoline rodents | Climatic zones | Global | ~12 |
| Mota-Rodrigues et al. 2017 | Yes | No | Turtles | Regions | Global | ~158 |
| Miller and Wiens 2017 | Yes | Generally no | Amniote animals | Habitat (marine-terrestrial) | Global | ~310 |
| Tested time for speciation only: | | | | | | |
| Stephens and Wiens 2003 | Yes | Not tested | Emydid turtles | Regions | Global | ~50 |
| Roncal et al. 2011 | Yes | Not tested | *Geonoma* (palms) | Regions | South America | ~18 |
| Chejanovski and Wiens 2014 | Yes | Not tested | Hylid frogs | Climatic zones | Eastern North America | ~55 |
| Pinto-Sanchez et al. 2014 | Yes/no | Not tested | Terraranan frogs | Regions/local sites | Neotropics | ~70 |
| Skeels and Cardillo 2017 | Yes | Not tested | Four plant genera | Habitat | Africa, Australia | Various |

Note: Studies are divided between those that tested both time-for-speciation and diversification rates and those testing only time. Studies are listed chronologically (by publication date) within categories. The time frame is based on the overall (crown group) age of the clade. Several studies were included that tested for relationships between diversification rates and factors related to richness (e.g., latitude, elevation, climate) but did not directly test diversification rates versus richness patterns. Note that several studies were included that test richness patterns among habitats and among local sites, whereas the main analyses of our study only tested richness patterns among regions. For Pinto-Sanchez et al. (2014) there is a positive relationship between time and regional richness but not local richness.

species in some regions than others. Our results show that these lower-scale richness patterns tend to be explained by time. Furthermore, this same complaint (i.e., who cares about "other" richness patterns?) could also be raised about the effects of area on species richness (e.g., MacArthur and Wilson 1967), a fundamental ecological principle. We argue that a major goal of ecology is to understand what drives richness patterns in general, not just a few well-known diversity gradients.

The importance of time for explaining richness patterns appears to be widespread, but an important issue is whether our selection of clades was biased to favor this hypothesis. Here, we selected groups based on an unbiased, systematic search of biogeographic studies, but we focused on groups with relatively complete species-level sampling. This was necessary to infer colonization events (and the associated richness patterns and diversification rates) directly

from the phylogeny. This focus on completeness likely biased our selection of studies toward younger and smaller clades. Indeed, our analyses do not include clades with >200 species or that are >110 myr old (table 1). Phylogenetically sampling most species in a clade presumably becomes more logistically challenging as the clade's richness increases. Therefore, our study is biased toward the younger side of the spectrum of all possible clade ages. However, across the Tree of Life, there are far more younger clades than older clades (e.g., Aves is a single older clade, containing >2,000 bird genera, all younger clades).

These findings are potentially consistent with simulations showing that time of colonization is the dominant factor explaining regional richness patterns over shorter timescales whereas diversification rates dominate over longer timescales (Pontarp and Wiens 2017). This temporal dichotomy is also supported by recent analyses of South American amphibians (Hutter et al. 2017), which showed that time dominated elevational richness patterns in clades within the Andes, whereas diversification rates explained differences in richness across clades among major regions (e.g., Andes vs. Amazon). Similarly, analyses across amphibians and mammals suggest that diversification rates underlie the latitudinal diversity gradient (e.g., Pyron and Wiens 2013; Rolland et al. 2014), whereas analyses at smaller phylogenetic scales do not support diversification rates (e.g., Soria-Carrasco and Castresana 2012) and often support time instead (e.g., Wiens et al. 2006, 2009; table 4). Along these lines, Schluter and Pennell (2017) concluded that speciation rates at recent timescales do not explain richness gradients. However, their conclusion was not based on new analyses nor a systematic literature review.

What might explain this temporal dichotomy, with time seemingly being more important over shorter timescales and diversification rates over long timescales? Hutter et al. (2017) noted that differences in richness among regions caused by diversification rate differences might take tens of millions of years to develop and be detectable (e.g., requiring multiple successive in situ speciation events). In contrast, a richness gradient related to time could develop very rapidly, for example, if a single species from a high-richness area rapidly colonized several previously uninhabited regions, such that these new regions had low richness and colonization ages. This would generate a strong relationship between richness and colonization times among regions. Thus, gradients related to colonization time might be more rapid if they depend more on dispersal (which could take only years) than extensive speciation (which often takes millions of years).

Importantly, our results here suggest that this temporal dichotomy may not be so simple. Specifically, we found that time alone tended to explain richness patterns among regions in clades that were older and more species rich (tables 1, 2), and that there were strong relationships between clade age, richness, and the amount of variance in regional richness explained by time (tables D9, D10). In contrast, diversification rates were generally included in the best-fitting models (along with time) only in younger and smaller clades. Our results show that time can remain important for richness patterns for at least 100 million years (myr), and that diversification rates can be important for explaining richness patterns over relatively short timescales (1.0–12.1 myr; tables 1, 2). Some previously published studies also showed that colonization time can be more important for explaining richness patterns than diversification rates over very long timescales (table 4), including a study of regional richness across all turtles (~158 myr) and richness among habitats across all amniotes (~310 myr).

We acknowledge that our literature survey (table 4) might have biases also. For example, we searched for (and only included) studies that explicitly tested the time hypothesis (given that such studies appear to be far less common than those analyzing diversification rates). Researchers that strongly supported the diversification-rate hypothesis may not have bothered to test the time-for-speciation hypothesis, and so did not list it among their keywords (although support for the diversification-rate hypothesis does not rule out the time hypothesis, as our results demonstrate; tables 2, 3). However, our results do not support this idea. Among the 14 studies that tested both the time and diversification hypotheses (and listed keywords), only 3 included "time-for-speciation" as a keyword, and only 7 included "diversification." Therefore, our search found the relevant studies, regardless of the keywords used, and authors listed keywords independently of which hypothesis was supported. Furthermore, our new analyses reported in this study should not have this particular bias, and support the literature survey. Regardless of whether our literature survey is completely unbiased, it nevertheless revealed numerous case studies in which the time hypothesis was supported over the diversification-rate hypothesis. We also note that there are many studies that we excluded from this survey because their methods did not fully meet our criteria (i.e., not directly testing time and diversification rates vs. richness among regions or habitats). The most extensive study in this category is that of Jansson et al. (2013). These authors tested the time and diversification-rate hypotheses among 57 clades of plants, insects, birds, and mammals and found that time generally explained latitudinal richness patterns whereas diversification rates did not, strongly supporting the conclusions of our study.

We focused here on explaining richness patterns among regions but the causes of these patterns may differ from those driving richness patterns among clades. One explanation for such differences is that named clades of the same rank may tend to be of similar age, whereas biogeographic dispersal can occur at any time point during a clade's history (Wiens 2011). Our results here suggest that time is the major

variable explaining richness patterns among regions within clades. In contrast, analyses across the Tree of Life strongly suggest that richness patterns among named clades of the same rank are generally explained by diversification rates and not clade ages (Scholl and Wiens 2016). However, that study focused on older clades (families to kingdoms). An analysis of predominantly younger clades (McPeek and Brown 2007) suggested that time, and not diversification rates, explains richness patterns among clades at shallower timescales (e.g., <10 myr old). We did not attempt to address this question here because many studies were of smaller groups with few named clades to compare. In summary, our results here suggest that richness patterns among regions (not among named, ranked clades) are explained more often by time than diversification rates. However, it is possible that time explains richness patterns among younger named clades also.

Our results suggest that richness patterns among regions within clades are often explained by the time spent in each region but do not address why different groups originated where they did. A group's region of origin might be explained by factors not examined here. For example, if the latitudinal diversity gradient is often explained by groups originating in the tropics (e.g., Jansson et al. 2013), this raises the question: why did so many groups originate in the tropics? This latter pattern might simply be explained by an even deeper origin of tropical clades or by higher rates of tropical diversification (e.g., higher speciation rates and/or lower extinction rates in the tropics). Along these lines, other factors might contribute to the time-for-speciation effect in ways that are not apparent from our analyses. For example, time seems to explain the marine-terrestrial diversity gradient in amniotes, but extinction of older marine clades also seems to contribute to this pattern, even though this is not detectable from analyses of extant taxa alone (Miller and Wiens 2017). Overall, we have tried to eliminate these types of biases by including a diversity of groups that are not associated with any particular richness pattern.

Changing biogeographic connections between regions over time might also influence richness patterns, but they presumably would do so by influencing the timing and/or frequency of colonization of each region. Therefore, their potential effects on richness should be determined by the variables that were directly analyzed here. Moreover, patterns of regional connectivity seem likely to be specific to particular locations, times, and organisms. Here, we have tried to focus on more general explanations for species richness patterns among regions within clades.

We recognize that some readers might assume that biogeographic reconstructions will be biased toward reconstructing the area with the most species as ancestral for the clade, making support for the time hypothesis inevitable. We think that there is little basis for this assumption. Importantly, biogeographic regions were treated as discrete states, and so the ancestral state for a clade should depend on which states are closest to the base of the tree, regardless of how many species have each state. This issue may be more problematic for continuous variables (e.g., climate, elevation), but previous studies explicitly tested for this potential bias with continuous data and found little evidence for it (e.g., Kozak and Wiens 2010; Hutter et al. 2013; Wiens et al. 2013). On the other hand, it might be difficult for a region (state) occupied by only one species to be reconstructed as ancestral for a clade. But in this scenario (a rare state at the tree's base), the reconstruction for the clade's root should be ambiguous, rather than supporting the common state. Further, this scenario does not explain why the other hypotheses (diversification rate, colonization events) were not supported instead. Overall, this potential bias seems unlikely to explain the strong support for the time hypothesis over other hypotheses in our results (table 2) and in the results of other studies (table 4).

We also recognize that some readers may consider it obvious that time explains richness patterns among regions, whereas others may be unconvinced by the number of clades included here. Although our results might be considered obvious by some, others have specifically claimed that time explains little variation in regional richness among regions (Rabosky 2012). We find here that time explains 73% of the variance in regional richness among regions (mean of 15 studies; table D9). Furthermore, regardless of whether the dominance of the spatial time-richness relationship could have been predicted without our study, the fact remains that relatively few researchers have actually tested this hypothesis. For example, our systematic literature review (table 4) included 20 studies, but 75% of these studies were effectively from one research group. Examining table 4 will also show that most previous studies on this topic each focused on a single clade (e.g., family), and almost all were vertebrates. In contrast, our new analyses here were based on a diverse set of 15 clades, including multiple plant and invertebrate clades. The results among these clades were relatively consistent (fig. 1; table 2) and consistent with those of 15 previously published studies (table 4). Thus, we see no evidence to suggest that our results will be overturned by simply including more clades. Overall, the best resolution for both concerns may be for future studies to also test the time hypothesis for explaining richness patterns.

Finally, our results show that area was not generally important for explaining these richness patterns. Moreover, the fact that we found strong relationships between area and richness in two clades might overestimate the overall importance of area (especially given that time significantly impacts richness in every clade). Specifically, if the identity of the oldest region (first colonized) was completely random with respect to area, then we should expect the oldest-colonized region to be the largest one in a proportion of studies equal to $1/n$, where $n$

is the number of regions per study. Here, the mean number of regions across the 15 studies is 6.67. Therefore, by chance alone, we would expect a strong relationship between area and richness in ~2.24 studies. Indeed, we found a significant relationship between area and richness in only two studies. In one (Frey and Vermeij 2008), time (AFC) is the only variable in the best-fitting model, whereas in the other (Mariguela et al. 2016), three variables contribute to explaining richness, with time (SAC) being the most important. Overall, these results are consistent with the idea that time consistently explains richness and area does not, and the few strong relationships between area and richness might be explained by a chance alignment between time and area among regions. Also consistent with this hypothesis, we found no evidence that area increases richness through impacts on diversification rates in these two cases. Our point here is not that area never impacts species richness. Instead, we suggest that time is generally more important than area for explaining richness patterns among regions within clades, because it can take substantial time for richness to build up within a region through in situ speciation, regardless of the region's area.

## Conclusion

In this study, we analyzed data from 15 clades of plants and animals to estimate the major factors explaining richness patterns among regions. These clades ranged from being globally distributed to those confined to a single continent and spanned from 1 to >100 myr in age. Our results show that the time of colonization was the major factor explaining these regional richness patterns within clades and was generally more important than diversification rates, the number of dispersal events, or area. We conducted a systematic review of previous studies that also strongly supported this conclusion. We suggest that the time hypothesis should be included in future studies that address the origins of spatial richness patterns.

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Four species of chameleons, one from Asia and three from Madagascar. In Madagascar, chameleons have been present and speciating for 62 million years and have dozens of species (>80 described species). In Asia, chameleons have been present for only 11 million years, and there are only three species present. Yet Asia has a much larger area than Madagascar, and both contain extensive tropical regions. Overall, time explains species richness patterns in chameleons more than area. Photos (clockwise from top left): Indian chameleon (*Chamaeleo zeylanicus*) photographed in the Biligiriranga Hills, India; brown leaf chameleon (*Brookesia superciliaris*); short-horned chameleon (*Calumma brevicorne*); and Parson's chameleon (*Calumma parsonii*), photographed in Andasibe, Madagascar. All photos by John J. Wiens.