

Patterns of Local Community Composition Are Linked to Large-Scale Diversification and Dispersal of Clades

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Submitted February 19, 2017; Accepted September 12, 2017; Electronically published December 20, 2017

Dryad data: <http://dx.doi.org/10.5061/dryad.9bs8n>.

ABSTRACT: At any location, a group of organisms may be represented by several clades. What determines which clades will dominate local communities in terms of their species richness? Here, this relatively neglected question is addressed by analyzing 166 local assemblages of snakes distributed globally. For most regions, local assemblages are dominated by clades with higher global-scale diversification rates and more frequent dispersal into each region, and not by clades that have been present in that region longer. This result contrasts with many other studies of local richness (in other organisms), which show strong impacts of regional colonization time on overall local species richness of clades. Furthermore, even though local assemblages are assembled independently on different continents, most regions have converged on similar patterns of proportional richness. Specifically, a few rapidly diversifying clades dominate most communities around the world. The high diversification rates of these clades are then linked to their high dispersal rates. Similar patterns may occur in many groups, such as plants, frogs, salamanders, birds, and mammals.

Keywords: biogeography, community, diversification, phylogeny, snakes, species richness.

Introduction

One of the most basic descriptors of a community is how many species it contains of each taxonomic group. For example, a community may have 10 species of one genus and only two of another. Such a pattern becomes particularly interesting when it is repeated across communities within a region and across regions globally. What might explain why some clades often dominate local communities (in terms of species richness) while others do not? Surprisingly, this fundamental question about the basic structure of communities has not been a major focus of recent ecological research. Nevertheless, much research has focused on important related topics, such as patterns of overall community

richness (e.g., Ricklefs and Schluter 1993; Harrison and Cornell 2008), phylogenetic structure of communities (e.g., Cavender-Bares et al. 2009), and the relative abundance of species rather than the relative richness of clades (e.g., Hubbell 2001; ter Steege et al. 2013). There is also an extensive literature on the ratio of species to genera in communities and regions (e.g., Elton 1946; Strong 1980; Enquist et al. 2002; Krug et al. 2008).

A prominent study by Ricklefs and Renner (2012) addressed another related question: is richness of clades correlated across sites? These authors examined trees from seven tropical forest sites in South America, Asia, and Africa. They found that species richness per family was positively correlated in pairwise comparisons between sites across regions. They concluded that this pattern was explained by traits of families that are conserved across regions. However, they did not directly address the relative richness of different clades across communities, nor did they test explanations for these patterns.

The relative richness of clades in local communities has several potential (nonexclusive) explanations (table 1). In general, richness patterns will be directly determined by the processes that change species numbers: dispersal, extinction, and speciation (e.g., Ricklefs 1987). These processes should also directly determine the relative richness of clades in local communities. Different ecological mechanisms (e.g., competition, niche divergence) may then drive the processes of speciation, extinction, and dispersal to ultimately explain relative richness. However, the relative importance of these ecological mechanisms will depend on how these three processes (speciation, extinction, dispersal) directly determine species richness patterns.

Perhaps the simplest explanation for relative richness patterns is that clades that are present in a region longer will have more time to build up higher regional richness (e.g., through speciation within the region), leading to higher proportional richness of these clades locally, relative to clades arriving in the region more recently (table 1). This time-for-speciation effect is demonstrably important for explaining local richness

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Table 1: Summary of hypotheses to explain why some clades have higher species richness in local sites (i.e., communities or assemblages) and the patterns that they predict

Hypothesis	Explanation	Prediction
Colonization time	Local sites in a given region will be dominated by clades that arrived in the region earlier and have had more time for speciation within the region, increasing the clade's regional and local species richness relative to other clades	Strong relationship between the time that each clade has been present in a region (i.e., based on the earliest colonization estimated by biogeographic reconstructions) and its mean proportional local richness across sites in the region
Dispersal frequency	Local sites will be dominated by clades that dispersed into the region more frequently, increasing the clade's regional and local species richness relative to other clades	Strong relationship between the number of times that each clade has independently colonized the region (i.e., from biogeographic reconstructions) and its mean local proportional richness across sites in the region
Diversification rate	Local sites will be dominated by clades that have higher diversification rates, increasing their regional and local species richness relative to other clades; numerous factors may explain the differences in diversification rates, potentially including local-scale species interactions	Strong relationship between the diversification rate of each clade and its mean proportional richness across local sites in the region

patterns within clades, both among regions and among habitats within regions. The time hypothesis has been directly supported in groups including treefrogs, salamanders, and glassfrogs (Wiens et al. 2011; Kozak and Wiens 2012; Hutter et al. 2013) and indirectly supported in others, such as damselflies (Brown et al. 2000), turtles (Stephens and Wiens 2003), and bats (Stevens 2006). However, it is unclear whether this time-for-speciation effect (i.e., differences in when clades arrived) explains the relative richness of different clades at the local scale within regions.

A second explanation is that clades dominate local assemblages because of the frequency of their dispersal rather than the timing of dispersal (table 1). For example, a clade might build up high richness in a region and local communities through multiple colonization events by different species in the same clade. However, the frequency of dispersal alone seems unlikely to be the sole explanation for proportional richness patterns. For example, a clade cannot colonize a region multiple times unless many species are present in adjacent regions, a pattern that must also be explained. Thus, this factor seems more likely to work in conjunction with others (e.g., within-region speciation).

A third explanation is that clades diversify at different rates, which then translates into differences in relative richness locally (table 1). The estimated net diversification rate of a clade (speciation – extinction) is related to its richness and age (e.g., Magallón and Sanderson 2001): older clades with few species have lower rates, and younger clades with many species have higher rates. Clearly, a clade with a very low diversification rate will have few species globally and in local communities. However, a clade with many species and a high global diversification rate need not dominate com-

munities across its geographic range. For example, it might have high local richness where it originated but lower richness in regions colonized more recently. Furthermore, diversification rates might vary strongly among geographic regions, such that global-scale rates are uninformative for predicting local-scale richness patterns. Few studies (if any) have tested whether diversification rates explain the relative richness of clades in local communities. In a similar vein, Heard and Cox (2007) analyzed the “diversity skewness” of primate communities (i.e., tree imbalance, potentially reflecting higher diversification rates in some clades) but did not relate diversification rates to the proportional richness of clades in local communities.

A closely related explanation is that local-scale species interactions determine global-scale diversification patterns, instead of the other way around (e.g., as discussed by Harrison and Cornell 2008). For example, one clade might consistently have more species than another because it outcompetes species from other clades at the local scale (e.g., a clade that monopolizes more diverse resources locally might prevent other clades from diversifying in association with use of different resources). This dominance might then translate into a higher diversification rate globally. There is evidence that sympatry between clades can lower their diversification rates (e.g., Kozak and Wiens 2010; Silvestro et al. 2015). However, these past studies did not relate these patterns of diversification to patterns of dominance of particular clades in local communities. These latter two explanations (diversification vs. interactions) are potentially difficult to distinguish. Nevertheless, establishing a link between diversification rates and proportional richness patterns in local communities is necessary to determine whether either ex-

planation is relevant at all. For example, if the proportional richness of clades at local sites in a region are determined by when each clade arrived in that region (not diversification rates), then neither of these hypotheses is relevant (i.e., impact of global diversification on local richness vs. impact of local interactions on global diversification). Therefore, I consider this latter explanation part of the diversification rate hypothesis.

These three hypotheses (table 1) need not be mutually exclusive, and different explanations might apply to different clades or to the same clade in different regions. For example, local richness patterns in clades with poor dispersal ability and/or in geographically isolated regions (e.g., Australia, Madagascar) might tend to be dominated by colonization times and/or high diversification rates of endemic clades, whereas patterns in clades with high dispersal rates or in less isolated regions (e.g., Asia, Middle America) might show a stronger influence of dispersal frequency or global-scale diversification rates of widespread clades.

Here, I test the causes of proportional richness patterns in local assemblages in snakes. Snakes are a diverse and globally distributed group, consisting of ~24 families and ~3,600 described species (Uetz and Hosek 2015). Snakes offer a useful model system because (a) data on local species composition is available for many sites (see below), (b) broad-scale geographic ranges of species are relatively well documented (Uetz and Hosek 2015), and (c) a time-calibrated phylogeny is available that includes 1,262 species (Zheng and Wiens 2016). These ingredients are particularly useful for assessing the roles of dispersal and diversification in local richness patterns.

In this study, I compile and analyze data on local richness of snakes from 166 sites distributed among 12 global biogeographic regions. I first determine the relative proportion of species from each family-level clade at each site. For each region, I estimate the mean proportional richness of clades across sites. I also perform biogeographic reconstructions across the phylogeny to determine when and how often each clade colonized each region. I then use phylogenetic regression to test whether clades that colonized a region earlier (or more frequently) dominate local communities (or “assemblages”) in that region (colonization time and dispersal frequency hypotheses; table 1). I then use data on global richness and ages of clades to estimate their diversification rates. For each region, I then use phylogenetic regression to test whether the mean proportional local richness of clades is related to their global-scale diversification rates (diversification rate hypothesis; table 1). I also test some of the factors that might influence global-scale diversification rates of clades, including their geographic extent (number of regions a clade occurs in) and inferred number of dispersal events (number of shifts between regions for a clade).

Material and Methods

Local Assemblages

The literature was searched (repeatedly over several years) for studies including snake faunas of local sites (e.g., Duellman 2005) and for species lists from national parks, nature reserves, and similar sites (e.g., using Google searches). Sites and references are given in appendix A; appendixes A–N are available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.9bs8n> (Wiens 2017a). Usable lists of species were generated for 166 local assemblages (app. B). Marine sites were not considered. Sites were excluded if they had low richness relative to other sites in the same region and similar habitat (potentially due to incomplete sampling) but quantifying sampling effort was not generally possible. Sites were preferred that were relatively small and contained a single habitat type (e.g., desert, tropical rain forest) but multiple microhabitats (e.g., forests, ponds, streams). Sites were also targeted to encompass as many different subregions and habitat types as possible within each region. In a few regions (e.g., Australian Wet Tropics, Eastern Palearctic), few studies of local sites were found, but detailed species-level range maps were available instead. In these cases, one or more arbitrary locations within the region were selected, and local species composition was inferred based on these range maps.

Two potential concerns might be raised regarding the sizes of sites. First, many sites contained multiple microhabitats and (in some cases) habitats. Thus, these may not be local sites or communities in the same sense as for sessile organisms (e.g., plants). However, a given individual snake can utilize multiple microhabitats (e.g., tree, ground, pond), and many species can occur in multiple habitats (e.g., both grassland and forest). Thus, the larger scale for local community used here should be appropriate for snakes (alternatively, one could simply replace the word “community” with “assemblage” or another less standard term). Similarly, local sites differed in area, and larger sites might have more species due to greater area. However, the focus here was on proportional richness of clades at each site, not overall richness (overall richness was not compared between sites). Nevertheless, data on area (ha) were obtained for many sites (app. A), and area showed no relationship with richness ($n = 111$, $r^2 = 0.007$, $P = .39$). Therefore, results should not be biased by site area. Furthermore, the units of analysis here were clades and their mean proportional species richness among all the sites within a region. Therefore, any potential issues with any particular site should have limited impact on the analysis of clades in a region. Clearly, it would be preferable to have standardized sampling of multiple sites in all regions, but such data are unavailable for snakes (and most other organisms) at the global scale. It is also unclear how heterogeneity in site size or sampling effort would actually bias the results

to favor one hypothesis over another (again, the units of analysis here are clades and not individual sites). Finally, the spatial scale used here is similar to that used in previous studies that showed a strong impact of time on overall local richness (e.g., Wiens et al. 2011; Kozak and Wiens 2012; Hutter et al. 2013), in contrast to the results here.

A total of 24 clades were used to quantify proportional richness of clades (fig. 1; apps. C, D; table D1). Some families were not present in any sampled communities (e.g., Acrochordidae, Bolyeriidae, Calabariidae, Xenophidiidae) and were therefore not included. Other families were included and treated as separate clades (17 total), except for the hyperdiverse Colubridae. For colubrids, species were assigned to seven subfamilies, which some authors treat as separate families (e.g., Uetz and Hosek 2015). Among these 24 higher taxa, two were nonmonophyletic in the tree used (Zheng and Wiens 2016). First, two genera usually placed in Lamprophiidae (*Oxyrhabdium*, *Micrelaps*) were closer to Elapidae than other Lamprophiidae. Second, three genera usually placed in Colubrinae (*Ahaetulla*, *Chrysopelea*, *Dendrelaphis*) grouped with Grayiinae instead. Because of uncertainty about their placement, these five genera were excluded from subsequent analyses.

Species numbers for each clade at each site were used to estimate each clade's local proportional richness (i.e., the number of species in that clade divided by overall local snake richness; values for each assemblage are in app. C). The mean proportional richness for each clade across all assemblages in a region was then estimated (app. D; table D1). Proportional richness values in each local assemblage were generally similar to these mean values for the region (see below and table 2). Furthermore, excluding a few sites that differed from the mean values should have little impact on the mean values. Clades present in a region, but absent at a given site, were given a value of zero when estimating mean proportions across sites. Estimating a clade's mean local richness among sites based only on sites in which it was present in a region would overestimate its mean local richness among sites across the region (e.g., imagine a clade present at a frequency of 25% but occurring at only one site in the region). However, clades absent entirely from a region were excluded. It would make little sense to include, for example, clades present only in the Old World in an analysis of South American communities: their diversification rates would be irrelevant to local richness and the overall importance of dispersal would be inflated (e.g., numerous Old World clades would have zero dispersal events to New World regions and zero local richness in every region and community). A few species of uncertain clade assignment (e.g., the colubrine and lamprophiid genera mentioned above) were also excluded.

A total of 12 standard ecoregions (exact definitions follow Pyron and Wiens 2013) were used: Tropical South Amer-

ica ($n = 24$ sites), Temperate South America ($n = 5$), Middle America ($n = 19$), West Indies ($n = 6$), Nearctic ($n = 21$), Afrotropical ($n = 23$), Madagascar ($n = 6$), Western Palearctic ($n = 23$), Eastern Palearctic ($n = 5$), South Asia ($n = 10$), Southeast Asia ($n = 11$), and Australasia ($n = 13$). Because separate analyses were conducted for each region, unequal numbers of sites between regions (or other differences) should have no impact. Similarly, the fact that fewer or different ecoregions could be recognized (e.g., 11, but excluding reptiles, in Holt et al. 2013) should also have little effect, since results were generally similar among regions. In fact, some of the few regions with more unusual richness patterns (e.g., West Indies, Temperate South America) were not recognized as distinct by Holt et al. (2013), which suggests that following their classification strictly would ignore relevant variation.

A set of analyses was performed to explicitly test whether the mean proportional richness calculated across the sites for each region reflected the patterns of richness for most sites within that region. Specifically, a nonparametric Spearman's rank correlation was done between the mean proportional richness of clades for the region and the proportional richness of clades for each site in that region. The results (table 2; app. C) show that richness patterns in most sites in most regions are significantly correlated with the mean richness pattern for the region. The major exception was those regions with very few clades ($n = 4$). These regions showed similar mean correlations to other regions but higher P values. There were also some cases in which sites were not significantly correlated with the mean regional pattern because of variation within a region. For example, in the Australasian region, elapids dominate most communities in Australia but not in New Guinea. Again, eliminating outlier sites that differed from the mean regional pattern should have very little impact. Furthermore, subdividing regions would be difficult and should not overturn the main results.

The estimates of mean proportional richness of clades within a region might potentially be biased by sites that are geographically close to one another. However, multiple sites within the same country were generally in different geographic subdivisions (e.g., different states) or different parts of these subdivisions (e.g., different parts of states). In those cases in which sites were relatively close to each other (e.g., same national park), it was clear that these sites did not dominate the mean proportional richness patterns for the region, because their ρ values (indicating similarity to the regional mean values; see above) were not unusually high (app. C), typically with one or more sites below the average ρ value for the region (table 2).

Additional analyses were performed to address how results were influenced by the choice of clades, either treating all Colubridae as one clade (18 clades overall) or all

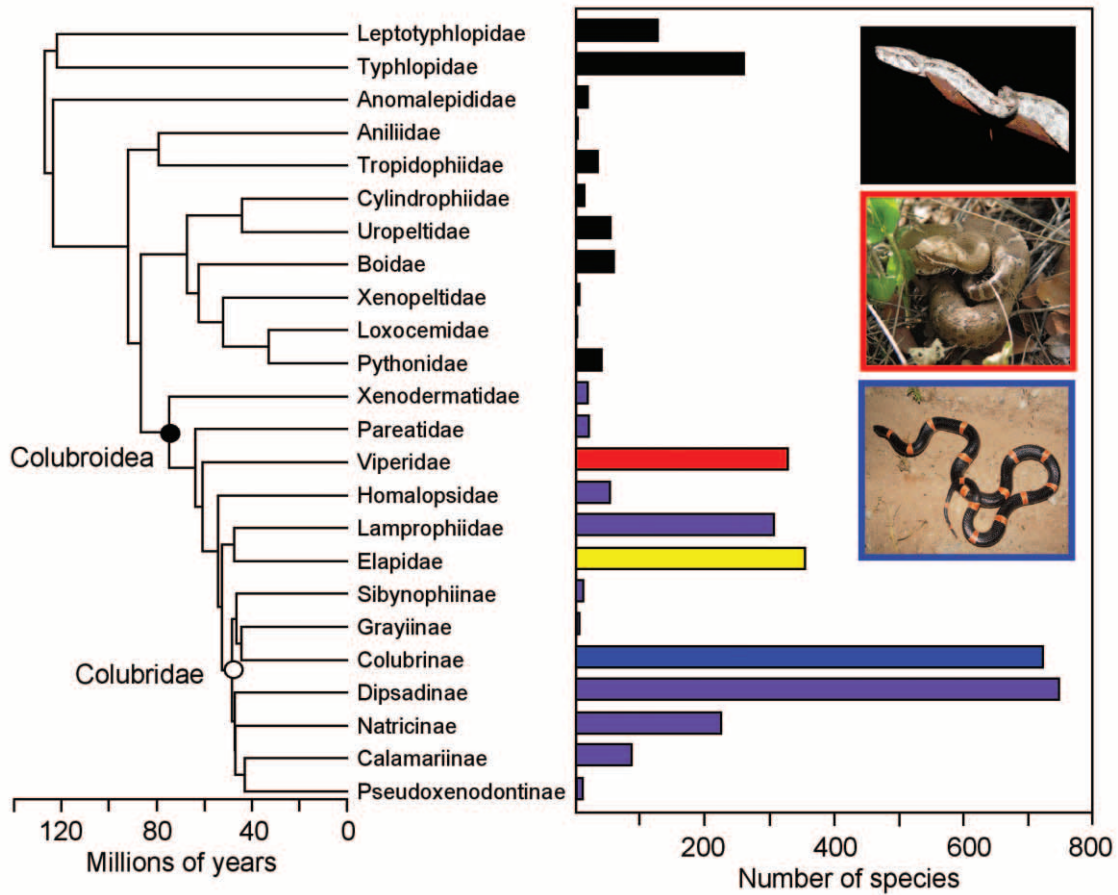
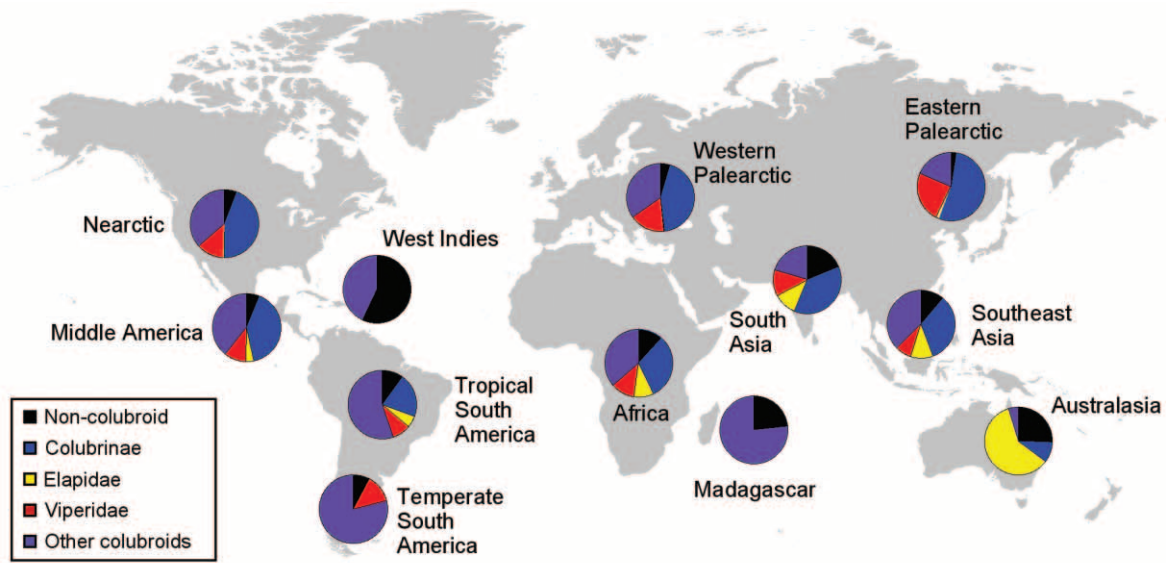


Figure 1: Summary of mean proportional richness of different snake groups in local communities in each of 12 regions (above), phylogeny of snake clades included here (lower left), and global richness of each clade (lower right). To simplify visualization, some clades are grouped into nonmonophyletic categories (noncolubroids, noncolubrine colubroids), since many clades in these categories have low proportional richness. However, dipsadines dominate among noncolubrine colubroids in the West Indies and Middle and South America, whereas lamprophiids dominate in Africa and Madagascar. Snake images from the author (top, *Boa constrictor*; middle, *Crotalus willardi*; bottom, *Rhinocheilus lecontei*). Map from freevectormaps.com.

Table 2: Summary of results for Spearman's rank correlation between each clade's proportional richness at each site and the mean proportional richness across sites in a region

Regions	No. clades	Sites with significant correlation with regional pattern/total sites in region	Mean correlations across all sites in region	
			ρ	P
Tropical South America	10	23/24	.882	.0114
Temperate South America	4	0/5	.910	.1197
Middle America	11	19/19	.822	.0120
West Indies	4	0/6	.800	.1898
Nearctic	7	15/21	.817	.0655
Afrotropical	10	22/23	.840	.0176
Western Palearctic	8	16/23	.778	.0634
Eastern Palearctic	8	4/5	.829	.0343
South Asia	13	8/10	.764	.0198
Southeast Asia	15	11/11	.797	.0038
Australasia	7	7/13	.728	.1458

Notes: Full results for each site are given in appendix C, available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.9bs8n> (Wiens 2017a). The number of sites with a significant correlation ($P < .05$) is shown, along with mean ρ and P value across all sites in the region. Note that P values depend on the number of clades in a region and not the number of sites. Thus, there are no significant correlations in regions with only four clades. Madagascar is not listed here because it has only three clades.

colubroids as one clade (12 clades). Results were broadly similar to the main analyses using 24 clades (app. D), but relationships were often nonsignificant given the reduced sample sizes of clades (apps. E, F). Therefore, the main analyses used 24 clades.

Two other factors might seem relevant but are actually somewhat tangential to the main focus of the study. First, species abundances were not analyzed, because the focus here is on proportional richness of clades and not relative abundance of species. Furthermore, quantitative data on species abundance were not generally available, and most snake species tend to be similarly uncommon (e.g., relative to lizards; Duellman 2005). Second, the relationship between local and regional richness (e.g., Harrison and Cornell 2008) was not examined because the focus here is on the relative richness of different clades locally, not the overall richness of communities. Overall richness of communities is the focus of studies of local versus regional richness.

Biogeographic Analyses

In order to reconstruct the timing and number of colonization events for each region for each clade, dispersal events among the 12 regions were estimated across the tree of 1,262 species (app. G). Each species was first assigned to one or more of the regions listed above (app. H), using distributional information from Uetz and Hosek (2015). The C++ version of LaGrange (Ree and Smith 2008) was then implemented with the software RASP (Reconstruct Ancestral State in Phylogenies; Yu et al. 2015). The oldest colonization time for each region was estimated based on the

oldest branch that was unambiguously reconstructed as occurring in that region, following standard practice in similar studies (e.g., Wiens et al. 2011; Kozak and Wiens 2012; Hutter et al. 2013). Following the standard threshold, a branch was unambiguously assigned to a region when that region's proportional likelihood was ≥ 0.87 . When likelihoods were lower, the branch was assigned to the region with the higher proportional likelihood. If proportional likelihoods were 1 for two regions for the same branch (e.g., given widespread species), then the colonization date was assigned based on the next (more recent) unambiguous branch. The colonization time was considered the midpoint age of the earliest branch on which the clade occurred in that region. When a clade's ancestor was inferred to be present in a region prior to splitting within the clade, the clade's crown group age was used (a conservative estimate of its time in the region). The stem group age was used for monotypic groups (which lack a crown age). From these biogeographic reconstructions, the following values were also estimated: (a) the number of times a clade was inferred to have colonized a given region (apps. D–F), (b) the total number of dispersal events among the 12 regions for each clade (app. I; table I1), and (c) the total number of regions in which a clade occurs (app. I; table I2).

Given that the species-level sampling in the phylogeny is incomplete, some colonization events may be missed. Thus, in a few cases, a clade was recorded in a community, but a colonization event for that region for that clade was lacking in the tree. In these cases, one colonization event (of unknown age) was considered to have occurred. However, this should have little impact on the analyses overall, since these

cases involved colonization events that yielded relatively few species in the region overall.

Diversification Analyses

The net diversification rate for each clade was estimated using the standard method-of-moments estimator (r) for stem group ages (Magallón and Sanderson 2001, eq. [6]). The stem group estimator was utilized because it (a) incorporates the entire history of the clade (i.e., from when a clade first splits from its sister taxon), avoiding potential artifacts associated with ancient clades with very recent crown groups; (b) is fully robust to incomplete taxon sampling within clades; (c) allows monotypic and species-poor clades to be included; and (d) should be more accurate than crown group estimators, given that the accuracy of these estimators increases with clade age (Kozak and Wiens 2016) and that crown ages are younger than stem ages. Net diversification (r) was estimated based on the clade age (t), the total number of described species (n ; from Uetz and Hosek 2015), and an assumed relative extinction fraction (ε), such that $r = \ln(n(1 - \varepsilon) + \varepsilon)/t$. Here, ε corrects for the biased inclusion of clades (extant only) across the entire tree. Following standard practice, three values for ε (0.0, 0.5, 0.9) were used. However, different values had limited impact on the overall results, and only results from the intermediate value (0.5) are presented in the main text.

Some authors have stated that this rate estimator assumes constant diversification rates and will therefore be inaccurate without a strong positive relationship between clade age and richness (e.g., Rabosky et al. 2012). However, these authors did not actually show that these methods gave inaccurate estimates under these conditions. Recent simulations show that these estimators can be accurate (i.e., strong correlations between true and estimated rates) regardless of relationships between clade age and richness (Kozak and Wiens 2016; Meyer and Wiens, forthcoming). Furthermore, the stem group estimator will correctly assign high rates to young clades with many species (and lower rates to older clades with fewer species), regardless of variation in instantaneous rates within clades.

Some readers might be tempted to suggest that it is circular to use diversification rates to address richness patterns, given that diversification rates are estimated (in part) from species richness. However, this study is analyzing patterns of proportional local richness of clades within regions, which is clearly not the same thing as the global richness of the clade used to estimate its net diversification rate. Furthermore, even if this study were focused on the global richness of clades, it is not inevitable that species richness and diversification rates will be correlated among clades, as shown by simulations (Kozak and Wiens 2016) and empirical analyses (Scholl and Wiens 2016). For example, fast

rates in young, species-poor clades can potentially uncouple diversification rates and richness.

Diversification rates for families were also estimated using BMM 2.3.0 (Rabosky 2014), as described in appendix J. However, this gave problematic results overall. Specifically, diversification rate estimates from BMM and the net rate estimators were significantly correlated, but different rate estimates from BMM for the same clade were not (i.e., rates estimated for a clade from the whole tree or from that clade in isolation often gave different rate estimates, even though these rate estimates should be identical; for details, see app. K; tables K1–K4). Similar results were obtained for snake clades by Meyer and Wiens (forthcoming). Simulation results (Moore et al. 2016; Meyer and Wiens, forthcoming) also suggest that BMM can give inaccurate diversification rate estimates. Therefore, the results are based on the net rate estimator described above, not BMM. A criticism (Rabosky et al. 2017) of the simulation study by Moore et al. (2016) does not justify using BMM here, because the empirical results here show that BMM gives misleading estimates in the real world for these data.

In theory, one could estimate the diversification rate associated with each colonization of each region by each clade. However, this would require assigning each species in each region to a colonization event, and taxon sampling in the tree was inadequate for this purpose. Thus, the analyses implicitly assume that variation in diversification rates among regions within a single clade do not obscure the impact of global-scale rates. The overall results of this study generally support this assumption, showing a strong impact of global-scale diversification rates on patterns of proportional richness of clades within regions (table 3).

Many factors may potentially influence diversification rates of clades, including local-scale ecology (e.g., diet, microhabitat), large-scale patterns of climatic and geographic distribution, and rates of change in ecological, morphological, and genomic traits (recent review in Wiens 2017b). Two potentially important and interrelated factors are the geographic extent of a clade and its rate of dispersal to new regions. Species richness and area are often related, potentially through the effects of area on diversification (e.g., Rosenzweig 1995). Dispersal to new areas may open up new opportunities for diversification that might otherwise be constrained by competition in the ancestral region (e.g., Schluter 2000). Therefore, analyses were performed to test whether these two factors (geographic extent, dispersal rate) were related to global-scale diversification rates of clades (see below).

Statistical Analyses

Phylogenetic generalized least squares regression (PGLS) in the R package *caper* (Orme 2013) was used to test whether the mean proportional species richness of clades in each re-

Table 3: Results for the phylogenetic generalized least squares regression between each clade’s proportional richness at local sites (mean across sites in a region; dependent variable) and three independent variables: the timing of the first colonization of that clade in the region, the clade’s net diversification rate (for $\epsilon = 0.5$), and the number of colonization events by that clade into the region (log transformed)

Regions	No. clades	Time of first colonization		Diversification rate		No. colonization events	
		r^2	P	r^2	P	r^2	P
Tropical South America	10	.076	.545	.461	.018	.552	.007
Temperate South America	4	.023	.954	.814	.103	.902	.051
Middle America	11	.407	.032	.524	.005	.503	.012
West Indies	4	.139	.756	.879	.064	.764	.134
Nearctic	7	.112	.570	.322	.189	.642	.022
Afrotropical	10	.000	1.000	.480	.015	.011	.917
Western Palearctic	8	.154	.395	.452	.054	.272	.188
Eastern Palearctic	8	.020	.887	.311	.145	.556	.023
South Asia	13	.096	.347	.493	.003	.464	.004
Southeast Asia	15	.008	.907	.487	.001	.368	.007
Australasia	7	.114	.632	.293	.299	.000	.998

Note: All three variables were tested across all clades occurring in each region. Significant results are in boldface. The sample size is the number of clades in each region. Multiple regression results are in appendix D, table D2, available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.9bs8n> (Wiens 2017a).

gion were explained by (a) their oldest colonization time in the region, (b) the number of times the clade colonized the region, and/or (c) the net diversification rate of the clade globally. Each of these three independent variables was tested separately in each region, using the proportional richness of clades as the dependent variable. However, Madagascar was excluded because too few clades occur there ($n = 3$). A reduced tree was used for each analysis in each region (including only clades occurring there). For PGLS analyses, branch lengths were transformed based on the likelihood-estimated value of phylogenetic signal (λ ; Pagel 1999), and the κ and δ transformations were each set to 1 (following standard practice). In addition to pairwise analyses, multiple regression analyses were performed when two or more variables showed significant (or nearly significant) relationships with proportional richness. An analysis including all three variables was also performed for each region, and the relative contribution of each variable to this model was evaluated using standardized partial regression coefficients (following Moen and Wiens 2017). However, the three-variable model often had poorer fit than those with fewer variables. Model fit was compared using the Akaike information criterion (AIC). Relationships among the three predictor variables were also tested for each region using PGLS. Data for each region for each analysis are provided in appendixes D–F; trees including all clades are provided in appendixes L–N.

Some of the factors that might help explain variation in diversification rates among clades were also tested. PGLS analyses were used to test whether diversification rates (dependent variables) were higher in clades that occurred in more regions and had more dispersal events (independent

variables) and whether these two values (number of regions, dispersal events) were positively related (with number of regions as the dependent variable and dispersal events as independent). These analyses were conducted on the tree of 24 clades (app. L), with $\epsilon = 0.5$. The total number of dispersal events and the total number of regions in which clades occur were log transformed (i.e., $\log_{10}(\text{variable} + 0.5)$) to improve linearity and normality. Data for these variables are given in appendix I.

The absolute number of dispersal events is potentially influenced by the number of species in a clade. After all, a clade with only one species might have only a limited number of dispersal events. Therefore, analyses were conducted using two simple estimates of dispersal rate: the number of dispersal events divided by the stem age of the clade (events per unit of time) and the number of dispersal events divided by the number of species in the clade (events per species). These variables were also tested for their relationships with diversification rates.

Results

Overall Patterns

Patterns of mean proportional local richness, phylogeny, and global richness of clades are summarized in figure 1. The proportional richness of clades at local sites was the main focus of this study, and for each region, the patterns of richness at individual sites were generally strongly correlated with the mean values for the region (table 2). Overall, the mean proportional local richness of clades was most strongly related to the global diversification rates of clades

in 7 of the 11 included regions, and diversification rates explained >45% of the variation in proportional richness in 8 regions (table 3). The number of colonization events by each clade into the region explained the most variation in proportional richness in the other four regions and >45% of this variation in seven regions (table 3). The timing of colonization did not explain the most variation in proportional richness (or >45%) in any region and had a significant effect on proportional local richness in only one region (Middle America; table 3). Diversification rates and proportional richness of clades were significantly related in 5 of 11 regions (table 3), including the most species-rich regions globally (Tropical South America, Middle America, Afrotropical, South Asia, Southeast Asia). Two additional regions showed strong relationships ($r^2 > 0.80$) that were nonsignificant given the few clades present ($n = 4$; Temperate South America, West Indies). Four other regions (also with fewer clades) did not show significant relationships (Australasia, Nearctic, Eastern Palearctic, Western Palearctic). Colonization events per clade were significantly related to their proportional richness in seven regions (table 3; all but Afrotropical, Australasian, Western Palearctic, and West Indian regions).

Comparison of the AIC of single and multiple regression models for each region showed that models with one predictor variable often had the best fit (app. D; table D2), with some regions showing colonization events as the most important variable (Tropical and Temperate South America, Nearctic, Eastern Palearctic) and others supporting diversification rates instead (e.g., Australia, Southeast Asia, West Indies). In Middle America, a model including diversification rates and time had the best fit, although the improvement in fit was negligible (1.061 AIC units) relative to the next best model (including diversification rates alone). Similarly, for the Afrotropical and Western Palearctic regions, a model including all three variables had the best fit, but again the improvement in fit was very small (<1.2 AIC units) relative to the next best model (diversification rates alone). In South Asia, a model including all three variables had the best fit by a more substantial margin (3.808 AIC units). Across all regions, models that included both diversification rates and number of colonization events generally explained similar amounts of variation in proportional richness relative to models including one (or both) of these variables separately. Thus, for example, diversification rates and number of colonization events might each separately explain ~50% of the variation in proportional richness, but a model including both often explained <60%. These two variables were strongly related among clades both globally (see below) and within many regions (app. D; table D3). Multiple regression analyses including all three variables simultaneously showed that diversification rates and number of colonization events combined always explained the

majority of variation in proportional richness of clades for each region, but with diversification rates having a consistently stronger effect than the number of colonization events (app. D; table D2).

These overall patterns were generally similar using alternative estimates of diversification rates (app. D; tables D4, D5) and alternative ways of subdividing clades (apps. E, F). Specifically, mean proportional local richness of clades was most strongly linked to diversification rates and the number of colonization events, whereas the timing of colonization of each region had generally little impact. When considering only 12 clades, the number of colonization events was the dominant factor.

Clade diversification rates (24 clades, $\varepsilon = 0.5$) were significantly related to their total number of dispersal events among regions ($r^2 = 0.546$, $P < .001$) and the total number of regions where they occurred ($r^2 = 0.469$, $P < .001$). The number of regions and the number of dispersal events were strongly related ($r^2 = 0.872$, $P < .001$). There was also a strong relationship between the dispersal rate (events/time) and diversification rate of clades ($r^2 = 0.560$, $P < .001$), but not between diversification rate and the per-species dispersal rate ($r^2 = 0.045$, $P = .319$). These latter results suggest that accelerated diversification is coupled with accelerated dispersal but that the ratio of species (and, possibly, speciation) to dispersal is similar across clades. Thus, it appears that many clades have similar numbers of species per dispersal event but that some clades may have exceptional diversification rates because they disperse rapidly and repeatedly among regions (although more diversification may also facilitate more dispersal).

Patterns among Clades

These overall results can be explained in terms of the dynamics of specific clades. All regions contain communities with both “primitive” snake lineages (including blind snakes, boas, pythons, and relatives) and “advanced” snakes (Colubroidea, including the highly venomous elapids, viperids, and the hyperdiverse Colubridae). Primitive snake lineages failed to dominate communities in almost all regions (fig. 1), even though they have been present in many regions longer than any colubroid clades. These noncolubroid clades generally have lower diversification rates (0–0.090, $\varepsilon = 0.5$; app. K).

In contrast, colubroids dominate communities in almost every region (fig. 1). Mean proportional local richness of Colubroidea was >72% in almost every region and >90% in many (Nearctic, Eastern and Western Palearctic, Middle America, Tropical and Temperate South America; app. F). The sole exception was the West Indies (43%). These shared patterns across continents arose largely through independent evolution of species on different continents, rather than dispersal of a set of widespread species shared across

communities in different regions. For example, among the 1,262 species included in the biogeographic analyses (app. H), most species (76.1%) are confined to a single region, 21.2% occur in only two regions, 1.8% occur in three regions, and less than 1% occur in four or more regions.

Remarkably, one rapidly diversifying clade within Colubroidea (Colubrinae; $r = 0.131$, where r is the diversification rate) was the most species rich in local communities in most regions across the globe, regardless of when they arrived, including the Palearctic, Asia, Nearctic, and Middle America (but absent in Temperate South America, Madagascar, and the West Indies). Yet, even among colubroid lineages, colubrines were frequently not the first lineages to colonize these regions. Colubrines also showed numerous colonization events into almost all regions where they occur (mean = 14.9, range = 2 – 26; app. D). They also show the most rapid dispersal rate (per unit time) of any snake clade (4.43 events per million years, more than twice that of the next fastest clade). In contrast, their per-species dispersal rate (0.273 events per species) is almost identical to the average value across all 24 clades (mean = 0.272). Colubrines show extensive dispersal along with within-region speciation.

Three important exceptions to the pattern of colubrine dominance were in Tropical South America (dominated by the rapidly diversifying dipsadines, $r = 0.124$, with colubrines a distant second), Africa (dominated by lamprophiids, $r = 0.105$, with colubrines a close second), and Australasia (dominated by elapids, with a moderately fast diversification rate, $r = 0.117$). In all three cases, colubrines arrived after the currently dominant colubroid clade in the region (and by substantial margins in the Australasian and Afrotropical regions).

Intriguingly, two other colubroid lineages (elapids, viperids) have dispersed almost as widely as colubrines but were generally less diverse locally (fig. 1). Viperids occur on all continents with snakes, except Australasia. Viperids frequently co-occur with colubrines but are generally less diverse locally. Nevertheless, they colonized several regions before colubrines (e.g., Afrotropical, Eastern Palearctic, Western Palearctic, South Asia), often with numerous colonization events. Similarly, elapids occur on all continents with snakes and often co-occur with colubrines. Elapids colonized before colubrines in the Eastern Palearctic and Southeast Asia but are less diverse locally in both. Colubrines colonized before elapids in Afrotropical, Western Palearctic, South Asia, Nearctic, Middle America, and Tropical South America.

Discussion

This study addresses a fundamental but underexplored topic in ecology: the relative species richness of different clades in

local communities. The results from snakes showed that local communities within each region were generally dominated by clades with higher diversification rates globally and that colonized the region more frequently, not by clades that colonized the region earlier. Moreover, there were strong relationships between diversification rates and how frequently (and how rapidly) clades dispersed, as well as between diversification rates and the geographic extents of clades.

These results are surprising on two main levels. First, the results here on relative local richness between clades differ strikingly from studies of local richness patterns within clades, which showed that the relative timing of colonization of each region strongly impacted local richness, whereas diversification rates did not (e.g., Wiens et al. 2011; Kozak and Wiens 2012; Hutter et al. 2013). Second, these results show that global-scale diversification rates strongly impact local-scale richness patterns. Within a region, it is intuitive that a rapidly diversifying clade can generate many species, which can then outnumber species of other clades regionally and at local sites. Remarkably, the results here show that a rapidly diversifying clade can spread globally and dominate almost everywhere it occurs, regardless of how long other clades have been there. This is the case with colubroid snakes overall, and especially with the Colubrinae. Colubrines have spread repeatedly to almost every continent (typically colonizing each region >10 times) and are the richest clade in many regions, including some regions where they arrived later than many other snake clades. However, there were also a few cases in which colubrines arrived later than other colubroid clades, and these other colubroid clades dominated those regions instead (elapids in Australasia, dipsadines in Tropical South America, lamprophiids in Africa).

How general are these patterns? This is difficult to say without similar analyses in other groups. Nevertheless, many well-known groups of organisms are also numerically dominated by relatively young clades with high richness, rapid diversification rates, and near-global geographic extent (e.g., angiosperm plants [Magallón et al. 2015], placental mammals [Meredith et al. 2011], passerine birds [Ericson et al. 2014], neobatrachian frogs [Roelants et al. 2007; Wiens 2007]). This numerical dominance is almost certainly reflected in local richness patterns in most global regions. Therefore, it seems likely that the patterns found here in snakes may apply to many other organisms.

Intriguingly, in salamanders and frogs, it appears that the proportional local richness of clades is also explained by differences in their diversification rates, even though differences in local richness among regions are explained primarily by colonization time. For example, plethodontids dominate salamander communities in those regions with the highest salamander richness (Appalachia, Central America;

Petranka 1998; Kozak and Wiens 2012), and plethodontids have the highest diversification rate in salamanders (Gómez-Rodríguez et al. 2015). Yet, patterns of local plethodontid richness among regions are explained by time rather than diversification rates (Kozak and Wiens 2012). Similarly, in frogs, local richness patterns are dominated by the clade Neobatrachia (based on sites from Moen et al. 2016), a clade with very high diversification rates relative to other frogs (e.g., Roelants et al. 2007; Wiens 2007). Nevertheless, analyses within frog families show strong impacts of time on local richness patterns but not of diversification rates (e.g., Wiens et al. 2011; Hutter et al. 2013).

Many patterns in biology depend on the scale at which they are examined. Thus, examining relative richness of clades at different phylogenetic or geographic scales might reveal somewhat different patterns. Importantly, the spatial scale for local sites used here is similar to that in studies showing time of colonization (rather than diversification rates) as the main driver of overall local richness (e.g., Wiens et al. 2011; Kozak and Wiens 2012; Hutter et al. 2013). Different patterns might emerge at a smaller spatial scale. Similarly, the timing of colonization might be more important than diversification rates over shorter temporal and phylogenetic scales (e.g., Hutter et al. 2017; Pontarp and Wiens 2017), especially in groups that have not yet become globally widespread. Conversely, biogeographic timing might be less important at deeper timescales (although the number of colonization events might remain important).

An important question arising from this research is: what explains the differences in diversification rates and colonization frequency among these snake clades? At least two (non-exclusive) explanations seem likely. First, intrinsic factors in some clades might explain their rapid radiation. Second, local-scale species interactions might determine the global-scale patterns of diversification. There may also be some combination of these first two explanations. The results here do not resolve this question but offer some relevant observations. The rapid radiation of colubroid snakes is well known (e.g., Stanley 1979), but the causes have remained unclear. The results here show that colubroid snakes have not simply diversified rapidly overall. Instead, only certain colubroid clades have high diversification rates, and those clades now dominate most communities worldwide (colubrids, dipsadines, lamprophiids). Many other colubroid clades of similar age have failed to radiate as successfully and rapidly (e.g., pareatids, xenodermatids, calamariines, grayiines, pseudoxenodontines, sibynophiines).

The ecological and evolutionary lability of these three colubroid clades might explain their success. First, the results here show a strong relationship between diversification rates of snake clades and how often they have dispersed and to how many regions (and their dispersal rate per unit time). Thus, many colubroid lineages that failed to diversify

rapidly are largely confined to single continents (e.g., Asia for xenodermatids, pareatids, homalopsids, and calamariines). Furthermore, many of these clades are confined largely to mesic habitats in tropical and subtropical regions (Pough et al. 2016). Climatic niche conservatism may limit their ability to spread across regions and continents. This explanation may also apply to many noncolubroid lineages, most of which are confined to mesic tropical and subtropical regions (e.g., aniliids, anomalepidids, cylindrophiiids, uropeltids, xenopeltids). The rapidly diversifying lineages occur in both tropical and temperate habitats and both mesic and arid conditions (app. D). Second, the rapidly radiating clades are ecologically diverse on niche axes that might be important for local-scale niche differentiation and resource partitioning. Thus, colubrids, dipsadines, and lamprophiids each collectively include sets of species spanning diverse microhabitats (e.g., aquatic, arboreal, terrestrial, burrowing), having diverse diets (e.g., invertebrates, vertebrates), and with a wide range of body sizes (data in, e.g., Ashe et al. 2002; Duellman 2005; Pough et al. 2016; Bars-Closel et al. 2017). In contrast, many clades that failed to diversify rapidly in terms of species richness also failed to diversify ecologically. For example, many slowly diversifying snake clades are primarily burrowers (e.g., aniliids, cylindrophiiids, leptotyphlopids, loxocemids, xenopeltids, uropeltids) or aquatic (grayiines, homalopsids; Bars-Closel et al. 2017). Future studies should test whether ecological diversification drove species diversification of these hyperdiverse colubroid clades. It will be especially important to disentangle whether these clades are more species rich because they are ecologically diverse or are ecologically diverse because they are more species rich (i.e., by using estimates of rates of change in ecological variables).

The results here show other intriguing patterns that should be explored in future studies. One particularly interesting pattern involves the viperids and elapids, two families that possess remarkable venom systems and include most of the snake species that are dangerous to humans (Pough et al. 2016). The results show that elapids and viperids are often depauperate in local communities (fig. 1), even though they are as widespread as colubrids (and sometimes arrived in particular regions earlier). Yet, elapids dominate Australia, where colubrids arrived much later. These patterns suggest that competition might limit the diversification and local richness of these venomous snake clades. The results also show that some of the most rapidly diversifying clades repeatedly diversified in sympatry with each other (e.g., dipsadines and colubrids in Middle and Tropical South America; lamprophiids and colubrids in Africa), in contrast to the general idea that sympatry between clades constrains diversification (e.g., Schluter 2000).

In summary, this study provides an initial exploration of a fundamental but neglected aspect of communities: the rel-

ative richness of co-occurring clades. The results show that proportional richness of clades locally is explained primarily by global-scale diversification rates of clades and their frequent dispersal into each region, rather than the timing of colonization. Further testing the generality and causes of these patterns will be an important area for future research.

Acknowledgments

I am very grateful to Verônica Thiemi-Tsutae de Sousa for all her extensive work on this project. I thank Tania Hernández-Hernández for assistance calculating standardized partial regression coefficients. I thank Yannis Michalakis, David Coliar, and two anonymous reviewers for helpful comments on the manuscript. I thank the National Science Foundation (DEB 1655690) for support.

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Associate Editor: David C. Collar
Editor: Yannis Michalakis



Snakes belonging to the family Colubridae from the Jinggang Mountains of China. *Left*, a Sichuan mountain keelback snake (*Opisthotropis latouchii*). *Right*, a yellow-banded big-tooth snake (*Lycodon flavozonatus*). Photo credit: John J. Wiens.