Occurrence data uncover patterns of allopatric divergence and interspecies interactions in the evolutionary history of Sceloporus lizards

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Abstract
As shown from several long-term and time-intensive studies, closely related, sympatric species can impose strong selection on one another, leading to dramatic examples of phenotypic evolution. Here, we use occurrence data to identify clusters of sympatric Sceloporus lizard species and to test whether Sceloporus species tend to coexist with other species that differ in body size, as we would expect when there is competition between sympatric congeners. We found that Sceloporus species can be grouped into 16 unique bioregions. Bioregions that are located at higher latitudes tend to be larger and have fewer species, following Rapoport’s rule and the latitudinal diversity gradient. Species richness was positively correlated with the number of biomes and elevation heterogeneity of each bioregion. Additionally, most bioregions show signs of phylogenetic underdispersion, meaning closely related species tend to occur in close geographic proximity. Finally, we found that although Sceloporus species that are similar in body size tend to cluster geographically, small-bodied Sceloporus species are more often in sympathy with larger-bodied Sceloporus species than expected by chance alone, whereas large-bodied species cluster with each other geographically and phylogenetically. These results suggest that community composition in extant Sceloporus species is the result of allopatric evolution, as closely related species move into different biomes, and interspecies interactions, with sympathy between species of different body sizes. Our phyloinformatic approach offers unique and detailed insights into how a clade composed of ecologically and morphologically disparate species are distributed over large geographic space and evolutionary time.

Keywords
bioregions, infomaps, phenotypic evolution, sceloporus, sympathy, trait divergence
1 INTRODUCTION

The current availability of geographically informed, organismal data offers opportunities for new insights into evolutionary processes such as trait divergence and sympatric diversification that have been traditionally studied through time-intensive fieldwork. Often, selective forces lead to phenotypes that allow species to occupy distinct ecological niches while living in sympathy with other closely related species (Lack, 1947; López Juri et al., 2015; Pacala & Roughgarden, 1982). This is particularly apparent in adaptive radiations in which species evolve specialized morphologies that allow them to exploit distinct microhabitats. For example, the Caribbean anoles have evolved disparate limb morphologies that allow them to occupy different ecological niches, thereby reducing competition (Losos, 1992; Losos et al., 1998). Similar examples of adaptive radiation and convergent evolution (ecomorphs) have been found in other island species (Darwin’s finches: Grant & Grant, 2006, Hawaiian silverswords: Blonder et al., 2016, Hawaiian spiders: Gillespie, 2004) and on larger scales, for example, in Europe and North America fishes (Lamouroux et al., 2002). Coexistence with closely related species and niche-partitioning are clearly also important drivers for mainland communities (Kartzinel et al., 2015; Mujic et al., 2016), but their effects can be difficult to detect, for example, as in the composition of plants in the Amazon rain forest (Kraft & Ackerly, 2010) and the assemblage of bat species on a latitudinal gradient across the Americas (Stevens et al., 2003). In part, these mainland community patterns are obscured by power limitations of the existing methods (Kraft & Ackerly, 2010) and the relatively small sample sizes imposed by the time-intensive nature of collecting the necessary data. Here, we use the power of massive data available in online databases and recent advances in data manipulation and statistical modeling to study patterns of sympathy and body size across a diverse genus of lizards.

Gause’s competitive exclusion principle dictates that two species occupying the same niche should not be able to coexist (Gause, 1934; Mayfield & Levine, 2010). However, it has been long known that closely related taxa occur together more often than expected by chance alone (Elton, 1946; Moreau, 1948; Williams, 1947) and may also expand the range of physical conditions in which other species can live (e.g., by providing refuges: Bulleri et al., 2016) or shape phenotypes through character displacement (Dayan & Simberloff, 2005; Losos, 2000; Moritz et al., 2018; Schluter & McPhail, 1993). For example, the plethodontid salamanders, *Plethodon hoffmani* and *P. cinereus*, are identical when living in allopatry (Adams & Rohlf, 2000). However, when the two species are in sympathy, they exhibit differences in jaw morphology that allow them to partition their prey resources so that *P. hoffmani* eats larger, faster prey while *P. cinereus* eats smaller, slower prey (Adams, 2004). Sympatric European lacertid lizards similarly exhibit small changes in head morphology that allow the partitioning of food resources by species, sexes, and age category (Herrel et al., 2001). Other studies have emphasized evolution via selective migration (Gillespie, 2004; Li et al., 2015), phenotypic convergence in older lineages (Tobias et al., 2014), and interactions with phylogenetically unrelated competitors (Wilcox et al., 2018). Theoretical discussions of these forces (e.g., Edwards et al., 2018; Mittelbach and Schemske 2015) suggest that there is still much to learn about the selective impact of phenotypically similar sympatric taxa.

Body size is a convenient and effective trait for analyzing the relationship between abiotic factors, like climate, and morphology (Bergmann, 1847), and often serves as a starting point to understand trait divergence in sympatric species (Echeverría-Londoño et al., 2018; Thomas et al., 2009). The relationship between body size and sympathy has been studied in many groups of amphibians and reptiles (Dunham et al., 1978; Kozak et al., 2009; Moen & Wiens, 2009; Okuzaki et al., 2010; Soule, 1966). For example, in the Australian Gehyra lizards, differences in body size are greater in sympatric lineages than in allopatric lineages (Moritz et al., 2018) suggesting that body size divergence is a key element of the process by which species coexist.

The genus *Sceloporus* serves as an ideal system to study the forces involved in the evolution of species in sympathy and how body size is distributed over geographic space and evolutionary time. *Sceloporus* lizards, also known as spiny or fence lizards, have been well studied in terms of behavior (Carpenter et al., 1977; Hews et al., 2013), physiology (Anigilletta et al., 2004; Beal et al., 2014), and phylogenetic relationships (Leaché et al., 2016; Sites et al., 1992; Wiens et al., 2010). Moreover, the genus *Sceloporus* has a large geographic distribution that encompasses much of North America and Central America (Sites et al., 1992), is speciose with nearly 100 species (Leaché et al., 2016), and possesses a tremendous amount of ecological diversity inhabiting lowland deserts, high-elevation alpine forests, and grasslands (IUCN, 2018). *Sceloporus* species also can be found in sympathy with other congeners at varying degrees, but this has only been studied at a small, local scale (Grummer et al., 2015; Serrano-Cardozo et al., 2008). Although the genus *Sceloporus* does not possess a tremendous amount of morphological disparity, it offers an intriguing opportunity for discovery analyses using publicly available data over a large geographic area.

Here, we use information from large, open-source databases to study the biogeographic and phenotypic patterns of congenic sympatry among *Sceloporus* species. First, we use spatial distribution data and phylogenies to ask how species are spatially grouped, and how sympathy relates to phylogenetic divergence. Specifically, do closely related species cluster geographically or are they evenly spread across the landscape? In particular, we apply a bioregions approach (Vilhena & Antonelli, 2015). Bioregions are a powerful way to describe species distributions and can be used in evolutionary biology to infer historical processes that led to current day distributional patterns (Matzke, 2014; Ree & Smith, 2008). We also test whether characteristics of each geographic area correlate with species richness to determine if particular factors are contributing to the biogeographic patterns of the clade. Then, we infer how body size is distributed over different spatial regions and has evolved through time. Finally, we combine occurrence data, phylogenies, and body size to ask whether species of different
body sizes co-occur more often than by chance to understand how phenotypic diversity varies across space.

2 | MATERIAL AND METHODS

2.1 | The biogeography of congeneric sympatry

We obtained point-occurrence data for 69 species of Sceloporus lizards from the Global Biodiversity Information Facility (Tgbif, 2018), using the "rgbif" v0.9.9 package (Chamberlain,) in R (R Core Team, 2017). The most recent phylogenetic analysis of the genus by Leaché, Banbury (Leaché et al., 2016) identifies 97 Sceloporus species and sampled 86 species to construct the phylogeny. Our study includes 69 of these species that are also represented in GBIF. The remaining species are known from very few records. The 13 species that are identified by the Leaché, Banbury (Leaché et al., 2016) phylogeny but not in our current study are roughly evenly distributed geographically, phylogenetically, and by size, such that excluding them from our analyses is unlikely to bias our results. For each species in our study, we removed all points that were likely errors, clearly falling outside of the geographic ranges provided by International Union for Conservation of Nature (IUCN, 2018). Our final data set consisted of 133,665 occurrence points for the 69 species (Table 1).

We used the Infomap Bioregions application to determine how species are spatially grouped (Edler et al., 2017). We used this approach because the program uses a novel adaptive resolution method that is less sensitive to biases from incomplete species distribution data (Edler et al., 2017). Infomap Bioregions is a network approach (Vilhena & Antonelli, 2015) that uses adaptive spatial resolution to cluster point-occurrence data from multiple species into geographic grid cells. The software creates a bipartite network of species and grid cells, connecting each species to geographic cells in which it occurs. The program then aggregates geographic cells for which there are occurrence points into larger geographic regions, creating larger regions in areas with similar species composition. The result is a detailed map with designated bioregions that are composed of unique species assemblages.

The Infomap Bioregions application has several input parameters including minimum and maximum cell size and maximum and minimum number of occurrence points per cell. We tested various combinations of parameters and found that a minimum cell size below 2° produced patchy, discontinuous bioregions. Setting the maximum cell size above 4° led to large, uninformative regions that are identified by the Leaché, Banbury (Leaché et al., 2016) phylogeny but not in our current study are roughly evenly distributed geographically, phylogenetically, and by size, such that excluding them from our analyses is unlikely to bias our results. For each species in our study, we removed all points that were likely errors, clearly falling outside of the geographic ranges provided by International Union for Conservation of Nature (IUCN, 2018). Our final data set consisted of 133,665 occurrence points for the 69 species (Table 1).

We gathered Snout-to-Vent Length (SVL) measurements for adult males from each of the Sceloporus and outgroup species from the literature (Table 1) to test how body sizes have evolved through evolutionary time and are distributed across the phylogeny. First, we generated a histogram with the mean SVLs of each Sceloporus species and used the natural breaks in the data to visually generate three body size categories: large, medium, and small. We then used "phytools" v0.6–99 (Revell, 2012) in R (R Core Team, 2017) to reconstruct ancestral body sizes of the continuous SVL values using three models of evolution: Brownian motion (BM), Ornstein-Uhlenbeck (OU), and Early-burst (EB). We used log-likelihoods to compare the model fit and checked for convergence. We then estimated the degree of phylogenetic signal (Pagel’s λ) for the SVL size data to determine the degree to which phylogenetic history constrains body size evolution. We performed this analysis using phylogenies from both Leaché, Banbury (Leaché et al., 2016) and Wiens, Kuczynski (Wiens et al., 2010), but since our results were similar both in terms of phylogenetic signal and ancestral state reconstruction, we present only the results using the Leaché, Banbury (Leaché et al., 2016) phylogeny here.

2.3 | Sympatry and body size evolution

For each species, we estimated the degree to which the focal taxon occurs with species of the same or different body size. To do this,
Table 1  Number of occurrence points used to characterize the range of each species, the mean Snout-to-Vent Length (SVL, with number of individuals used to obtain that estimate in parentheses), and the published reference from which we obtained body size data. Also included are size data for the outgroup used in the ancestral reconstruction analysis

| Species            | N occurrence points | Average SVL (mm) (N) | Source                                      |
|--------------------|---------------------|----------------------|---------------------------------------------|
| Sceloporus adleri  | 426                 | 65.3 (14)            | Fitch (Fitch, 1978)                         |
| Sceloporus aeneus  | 2035                | 53.0 (148)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus arenicolus | 141               | 54.5 (507)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus bicanthalis | 326               | 43.6 (56)            | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus bulleri  | 140                 | 100.7 (10)           | Fitch (Fitch, 1978)                         |
| Sceloporus carinatus | 397               | 52.9 (2)             | Rivera et al., unpublished                  |
| Sceloporus caudus   | 341                 | 67.9 (11)            | Smith (Smith, 1939)                         |
| Sceloporus chrysostictus | 2089             | 54.0 (163)           | Fitch (Fitch, 1978)                         |
| Sceloporus clarkii  | 653                 | 103.0 (56)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus consobrinus | 1888              | 60.3 (45)            | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus couchii  | 827                 | 58.0 (32)            | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus cowliesi | 1,043               | 62.5 (2)             | Rivera et al., unpublished                  |
| Sceloporus cryptus  | 58                  | 61.6 (6)             | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus cyanogenys | 1,066             | 96.0 (8)             | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus dugesii  | 393                 | 65.9 (7)             | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus edwardtaylori | 143              | 107.0 (7)            | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus formosus | 1,106               | 68.0 (111)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus gadoviae | 606                 | 64.9 (6)             | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus graciosus | 10,982             | 55.2 (182)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus grammicus | 15,050             | 60.1 (412)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus grandaevus | 835               | 72.1 (5)             | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus heterolepis | 55                | 59.7 (37)            | Smith (Smith, 1939)                         |
| Sceloporus horridus | 2,825               | 85.5 (82)            | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus hunsakeri | 641                | 73.9 (20)            | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus insignis | 63                  | 89.5 (10)            | Fitch (Fitch, 1978)                         |
| Sceloporus internasalis | 174              | 80.1 (2)             | Rivera et al., unpublished                  |
| Sceloporus jalapae  | 582                 | 49.3 (17)            | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus jarrovii | 3,825               | 69.7 (668)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus lcki | 432                 | 71.4 (24)            | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus maculosus | 133               | 48.4 (7)             | Smith (Smith, 1939)                         |
| Sceloporus magister | 4,807               | 111.5 (53)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus malachiticus | 667              | 79.1 (146)           | Fitch (Fitch, 1978)                         |
| Sceloporus megalepidurus | 593              | 47.3 (76)            | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus melanorhinus | 580               | 84.6 (32)            | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus merriami | 3,071               | 52.2 (355)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus microlepidotus | 2,514             | -                    | NA                                          |
| Sceloporus minor | 540                 | 70.3 (169)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus mucronatus | 2085              | 87.0 (146)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus nelsoni | 1,146               | 60.16 (26)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus occidentalis | 30,367             | 68.4 (46)            | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |
| Sceloporus ochoterenae | 348               | 48.2 (143)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017) |

(Continues)
we used a custom-built Python program (Python Core Team, 2018) to assemble lists of all pairwise distances between the 133,665 geographic occurrence points. Then, for each Sceloporus species, we compiled a list of sympatric congeners, characterizing each species as being sympatric with a second species if at least 10 occurrence points for the target species were 5 km or closer to an occurrence point for the second species. We then added in the body size data, categorizing each species as small, medium, or large, and counting the total number of Sceloporus species from each body size category occurring in sympathy with each target species. Finally, we calculated a measure of “Divergent Sympatry” for each species: a chi-squared value comparing the number of small, medium, and large sympatic congeners with the expected number of each size class given the distribution of sizes across the genus. We multiplied this measure by −1 if the difference between observed and expected counts was due to the target species being found more commonly with similarly sized congeners for clarity in the visualization of these results. We considered the distribution of body sizes at the level of bioregions, asking whether the observed number of small, medium, and large Sceloporus species in each bioregion differed from that expected given the frequency of species of each size class in the genus as a whole. Lastly, we used a phylogenetic generalized least square (PGLS) on SVL using a model of Brownian motion. We extracted the residuals of the PGLS and regressed these against the chi-squared

| Species            | N occurrence points | Average SVL (mm) (N) | Source                                                                 |
|--------------------|---------------------|----------------------|------------------------------------------------------------------------|
| Sceloporus olivaceus  | 2,991               | 82.9 (34)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017)             |
| Sceloporus orcutti   | 2,313               | 102 (17)            | Fitch (Fitch, 1978)                                                   |
| Sceloporus ornatus   | 244                 | -                    | NA                                                                     |
| Sceloporus parvus    | 782                 | 50.0 (?)            | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017)             |
| Sceloporus pictus    | 110                 | 48.9 (8)            | Fitch (Fitch, 1978)                                                   |
| Sceloporus poinsettii | 3,847               | 96.8 (79)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017)             |
| Sceloporus pyrocephalus | 462                 | 62.0 (84)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017)             |
| Sceloporus scalaris  | 811                 | 45.5 (45)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017)             |
| Sceloporus scitulus  | 328                 | 70.2 (2)            | Rivera et al., unpublished                                             |
| Sceloporus serrifer  | 1,153               | 76.9 (7)            | Smith (Smith, 1939)                                                   |
| Sceloporus siniferus | 3,222               | 52.5 (235)          | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017)             |
| Sceloporus slevini   | 483                 | 47.5 (2)            | Smith (Smith, 1939)                                                   |
| Sceloporus smaragdinus | 539                | 67.2 (14)           | Fitch (Fitch, 1978)                                                   |
| Sceloporus smithi    | 26                  | 82.4 (57)           | Smith (Smith, 1939)                                                   |
| Sceloporus spinosus  | 1960                | 92.7 (164)          | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017)             |
| Sceloporus squamosus | 733                 | 51.6 (2)            | Rivera et al., unpublished                                             |
| Sceloporus subpictus | 29                  | 63.5 (1)            | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017)             |
| Sceloporus taeniocnemis | 899            | 77.2 (2)            | Rivera et al., unpublished                                             |
| Sceloporus teapensis | 458                 | 55.9 (24)           | Fitch (Fitch, 1978)                                                   |
| Sceloporus torquatus | 3,318               | 101.5 (37)          | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017)             |
| Sceloporus tristichus| 405                 | 58.6 (24)           | Fitch (Fitch, 1978)                                                   |
| Sceloporus undulatus | 178                 | 55.8 (177)          | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017)             |
| Sceloporus vandenburgianus | 663             | 60.2 (34)           | Fitch (Fitch, 1978)                                                   |
| Sceloporus variabilis| 9,255               | 62.0 (457)          | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017)             |
| Sceloporus virgatus  | 1,299               | 50.4 (22)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017)             |
| Sceloporus woodi     | 287                 | 51.9 (78)           | Jiménez-Arcos, Sanabria-Urbán (Jiménez-Arcos et al., 2017)             |
| Sceloporus zosteromus| 1,262               | 103.7 (1)           | Rivera et al., unpublished                                             |
| Petrosaurus thalassiusinus | –               | 110.0 (?)           | Goldberg and Beaman (Goldberg & Beaman, 2004)                         |
| Phrynosoma solare    | –                   | 115.0 (?)           | Brennan and Holycross (Brennan & Holycross, 2006)                      |
| Urosaurus ornatus    | –                   | 59.0 (?)            | Brennan and Holycross (Brennan & Holycross, 2006)                      |
| Uta stansburiana    | –                   | 50.0 (?)            | Stebbins (Stebbins, 1985)                                             |
values from the divergent sympathy analysis to correlate body size with our measure of divergent sympathy and taking phylogenetic history into account.

3 | RESULTS

3.1 | Patterns of sympathy across bioregions

Using the Infomap Bioregions application and the GBIF occurrence data from 69 species of Sceloporus, we identified 16 distinct regions (Figure 1; Table 2). Nearly, all regions contained multiple Sceloporus species, with the exception of Region 5 that had a single species (S. grandaeus). Conversely, some species (e.g., S. grammicus and S. variabilis) occurred in more than one bioregion because of their large distributions (Figure 2).

We found a positive relationship between the number of biomes and number of species across bioregions (Figure 1b: LM: F$_{1,14}$ = 11.17, R$^2$ = 0.44, p = .005). For example, Region 2, with only temperate biomes, and Region 3, with only a single subtropical biome, have only 2 Sceloporus species each (Figure 1; S. consobrinus and S. areniculus in Region 2; S. ndulates and S. woodi in Region 3). In contrast, Region 11 which contains a wide range of biomes (e.g., arid deserts, savannas, dry forests, and rainforests) has 27 Sceloporus species.

We found a latitudinal gradient where the regions with the fewest species tended to be near the northern part of the genus range, while the regions with the largest numbers of species were located centrally and to the south (Figure 1). For example, Region 11 and Region 14 harbored a large number of species and were closer to the equator than Regions 2 and 3.

Overlaying the Leaché, Banbury (Leaché et al., 2016) phylogeny on the map (Figures 3 and Figure 4), we found that sister species often co-occurred closely in geographic space. This was also supported by our community structure analysis across bioregions (Table 3). We found that the majority of bioregions show a pattern of phylogenetic clustering indicated by negative standardized effect sizes and small p-value quantiles. For example, the centers of the ranges for sister species S. cryptus and S. subpictus are close to each other in geographic space, as are the range centers of sister species S. adleri and S. scitulus (lower part of Figure 3). Thus, most bioregions contained species from only one or a few clades (Figure 4). We found that only five bioregions showed a moderate pattern of phylogenetic overdispersion, Regions 1, 2, 5, 9, and 15 indicating that these bioregion harbor species that are not closely related. One notable exception was the speciose Region 11 in central Mexico, which contained species from almost every clade (N = 27; Figure 4).

We found no relationship between the number of species present and land area (Pearson’s correlation: p = 0.18, df = 14, p > .05) or latitude (Pearson’s correlation: p = -0.34, df = 14, p > .05) of each bioregion. However, the number of species within a bioregion was positively related to our measure of elevation heterogeneity (standard deviation of elevation) (Pearson’s correlation: p = 0.51, df = 14, p = .04).

3.2 | Body size evolution

We found three discrete size categories for the Sceloporus clade (Figure 5). Additionally, we found that a Brownian motion (BM) model of continuous character evolution (log Likelihood: -445.9, σ$^2$ = 8.07) best explained the evolution of body size. The OU model (log Likelihood: -445.9, σ$^2$ = 8.07, α = 0.0) was identical to the BM model because the alpha parameter in the OU model is 0 indicating only Brownian motion is driving body size evolution. The Early-Burst (EB) model did not converge, and therefore, we
omitted these results. The ancestor to all Sceloporus lizards was likely medium in body size, ~76 mm SVL, with larger bodies evolving only recently in evolutionary time (Figure 6). In addition, body size categories tended to cluster phylogenetically (Figure 6). An estimate of phylogenetic signal confirmed that body size is evolving with high phylogenetic constraint (Pagel’s $\lambda = 0.99$; Log likelihood = 270.34). Thus, closely related species tend to be similar in body size. Increases in body size occurred abruptly in a few lineages and were then retained over long periods of evolutionary time (Figure 6).

### 3.3 | Sympatry and body size evolution

Our chi-squared analysis found evidence that small Sceloporus species are spatially distributed so that they often co-occur with different sized species (Appendix S2). Conversely, large species were most often found to co-occur with other large species than by chance alone. More than % of small-bodied Sceloporus species (14 of 22 species) exhibited positive divergent sympatry, occurring more often with medium- or large-bodied congeners than expected given the numbers of species in each size class (Figure 7a). Five of the 22 small-bodied species exhibited some degree of divergent sympatry, and only 3 species showed convergent sympatry (occurring primarily with other small-bodied species), and a goodness-of-fit test suggested a strong difference between the observed counts (14:5:3) and a uniform expectation (Figure 7a; $\chi^2 = 8.4$, $df = 1$, $p < 0.01$). In contrast, medium-sized Sceloporus species showed only weak evidence of assortment by size, instead occurring with small-, medium-, and large-bodied congeners in proportions roughly comparable to the number of species of each size class available in the genus as a whole (Figure 7b; $\chi^2 = 0.9$, $df = 1$, $p = .63$). More surprisingly, we found that large-bodied Sceloporus species often co-occur with other large Sceloporus species, leading to a significant pattern of negative divergent sympatry (Figure 7c; $\chi^2 = 6.2$, $df = 1$, $p = .02$). Our correlation analysis between the PGLS residuals of body size and our measure of divergent sympatry confirmed that larger species show a pattern of negative divergent sympathy while smaller species show a pattern of positive divergent sympathy (Pearson’s correlation: $\rho = -0.41$, $df = 64$, $p = .0008$).

At the level of bioregions, we also found evidence of divergent sympathy by small-bodied Sceloporus species and convergent sympathy of large-bodied Sceloporus species. Only Region 3 contained multiple species and was solely comprised of a single size class, while 9 of the 15 regions with multiple species contained all three size categories. We found a disproportionately large number of large- and medium-bodied species and fewer small-bodied species in Regions 10, 12, and 14. There were no regions with a disproportionately large number of small-bodied species.

| Bioregion | Number of species | Biome description |
|-----------|-------------------|-------------------|
| Bioregion 1 | 6 (1S, 2M, 3L) | Montane forest, arid desert, temperate steppe, and Mediterranean vegetation |
| Bioregion 2 | 2 (1S, 1M, 0L) | Temperate broadleaf forest and temperate steppe |
| Bioregion 3 | 2 (2S, 0M, 0L) | Subtropical rainforest |
| Bioregion 4 | 4 (0S, 1M, 3L) | Arid desert and subtropical dry forest |
| Bioregion 5 | 1 (1S, 0M, 0L) | Subtropical dry forest |
| Bioregion 6 | 3 (0S, 2M, 1L) | Montane forests |
| Bioregion 7 | 3 (1S, 1M, 1L) | Arid desert |
| Bioregion 8 | 5 (1S, 2M, 2L) | Temperate broadleaf forest, semiarid desert, subtropical dry forest, temperate steppe and arid desert |
| Bioregion 9 | 12 (4S, 3M, 5L) | Montane forest, arid desert, and semiarid desert |
| Bioregion 10 | 12 (1S, 6M, 5L) | Montane forest, arid desert |
| Bioregion 11 | 27 (10S, 10M, 7L) | Subtropical dry forest, montane forest, grass savanna, arid desert, and tropical rainforest |
| Bioregion 12 | 7 (0S, 4M, 3L) | Subtropical dry forest |
| Bioregion 13 | 8 (2S, 3M, 3L) | Subtropical dry forest |
| Bioregion 14 | 16 (3S, 5M, 8L) | Montane forest and tropical rainforest |
| Bioregion 15 | 4 (2S, 0M, 3L) | Subtropical dry forest |
| Bioregion 16 | 3 (1S, 1M, 1L) | Montane forest and tropical rainforest |

Note: In the number of species column, values in parentheses indicate how many species of each size category are found within each region where S = small, M = medium, and L = large. See Figure 1 for locations of each Bioregion. See Appendix S1 for more detailed descriptions using the ecoregion classifications of Olson, Dinerstein (Olson et al., 2001).
FIGURE 2 A map showing the recovered bioregions from the clustering analysis. Also shown is the phylogeny used in the analyses modified from Leaché, Banbury (Leaché et al., 2016). Next to the species is a pie chart indicating which bioregion each species belongs to and colors of the pie slices correspond to colors of the bioregions in the map.

4 | DISCUSSION

Using public information from large open-source databases and phylogenetic information, we found several important insights into the geography of congeneric sympatry and phenotypic divergence in Sceloporus lizards. First, closely related species tend to be in close geographic proximity (phylogenetic underdispersion) and share similar body sizes, suggesting that they have been evolving gradually. The large number of closely related, sympatric species in ecologically diverse regions, and the positive relationship between habitat heterogeneity and the number of species present in a bioregion suggest that most speciation occurred over short time frames and in near allopatry. One notable exception was the undulatus group, which is geographically widespread across the United States despite only minimal speciation. The undulatus clade seems to exemplify Rapoport’s rule (Stevens, 1989) as the group is found at higher latitudes and species have exceptionally large ranges with only two widespread undulatio species occurring in the Southeast United States and two widespread undulatues species occurring in the Midwest United States. The group seems to have migrated over large distances in a relatively short period of time (Rivera et al., 2020) with few speciation events occurring. Additionally, the group shows little phenotypic diversification (Leaché, 2009) with most species being medium in body size while only two species, S. woodi and S. virgatus, were small.

Second, we found that the ancestor of all Sceloporus was likely a medium-bodied species with small-bodied species evolving soon after. The fossil record indicates that the second oldest Sceloporus fossil had unicuspid teeth (Holman, 1987) and may have been the ancestor to S. merriami, a small species. Furthermore, large body sizes evolved more recently in the clade’s history in a few lineages, where it was then retained over long periods of evolutionary time. Putting biogeography and morphological evolution together, we found evidence for high functional diversity and geographic sorting across bioregions. The majority of bioregions had a nearly equal representation of body size categories with the exception of Regions 10 and 12 where medium and large species were overrepresented. Species also seem to sort geographically so that small-bodied species co-occur...
more often with larger-bodied species, perhaps to reduce ecological competition or interference like in other lizard species (Losos, 1990; Moritz et al., 2018). In contrast, large-bodied Sceloporus species most often co-occur with other large-bodied species, perhaps reflecting phylogenetic constraints on body size evolution and limited dispersal. Future studies may want to investigate the relationship between species distributions, body size, and habitat at smaller spatial scales and to explore functional diversity through more detailed analysis of phenotypes.

### 4.1 Bioregions and sympatry

Sceloporus species are unevenly distributed across North America, with some geographically large regions, like the southern and western United States, having few species, whereas geographically smaller regions, like central Mexico and south Central America, have many species. This pattern seems to follow the latitudinal diversity gradient where biodiversity increases from poles to the tropics (Hillebrand, 2004) and Rapoport’s rule where species at higher latitudes have lower rates of spatial turnover and larger ranges (Stevens, 1989). The undulatus clade exemplifies this as these nine northern species span the entire United States. Conversely, species assemblages at lower latitudes tend to have higher richness and turnover rates (Stevens, 1989). This also seems to be the case in Sceloporus as the small area from central Mexico to Panama harbors 65 species, over half of the total diversity of the genus. Other factors may also contribute to the high species richness in relatively small bioregions. For example, the Trans-Mexican volcanic belt (Region 11), which formed during the Eocene and Miocene periods (Ferrari et al., 2012), is a relatively small geographic region that includes several volcanic peaks that rise above 3,000 m, and the region is a biodiversity hotspot with a string of sky islands (Hafner & Morrone, 2017; Mastretta-Yanes et al., 2015). Likewise, Region 14 harbors 16 species, is close to the equator, and has a large mountain range named Cordillera de Talamanca that traverses Costa Rica and Panama. This high habitat heterogeneity likely contributes to increased allopatry and speciation within these two regions. This was also supported by our correlation analysis showing that regions with more elevation heterogeneity have a higher species richness compared to regions with low elevation heterogeneity. This pattern may also be explained by the elevation diversity gradient where biodiversity is highest at middle elevation (McCain, 2005), but this has yet to be explicitly tested. Additionally, the lower turnover rates in areas close to the equator may because Central American is vastly smaller in area compared to North America so species tend have smaller ranges.

Early research suggested that the genus Sceloporus originated in Mexico given the diversity seen today (Hall, 1973). More recent studies, however, found that Sceloporus most likely originated much further north in what is now the northern United States and...
Based on fossil evidence and paleoclimatic reconstructions, Mexico was too hot and dry and, therefore, unsuitable for the genus until about 6 million years ago (Lawing et al., 2016). We note that Lawing, Polly (Lawing et al., 2016) estimated the limits of the realized niche using the abiotic BIOCLIM variables and did not include other abiotic or biotic factors that are also driving the evolution of ranges in the lineage. When the global climate cooled later in the Miocene, speciation rates within the genus *Sceloporus* increased (Leaché et al., 2016), which coincides with *Sceloporus* entering central Mexico. Rapid diversification may have been mediated by topographical complexity as land uplift in the volcanic belt began some 20 MYA and continues today (Dimmitt et al., 2015). The complex topography of the Trans-Mexican volcanic belt would have allowed novel and disparate niches to emerge which *Sceloporus* could have exploited. This would have led to a rapid diversification and build-up of endemic species assemblages seen today.

In addition to Rapoport’s rule, the lack of diversity at higher latitudes may reflect historical events like glacial maxima and shifts in climate regime. If taxa were unable to find refuges from increasing glacier event, species would fail to recolonize and be extirpated (Grubb et al., 1987) leaving only lineages farther south. Second, the emergence of new unsuitable habitat may also contribute to this pattern. *Sceloporus* lizards may have been extirpated in Canada and parts of the United States due to the rise of the Rocky Mountains, which blocked moisture from the midcontinent (Dimmitt et al., 2015). This allowed the Great Plains of North America to emerge but also created more xeric conditions (Dimmitt et al., 2015) that may have excluded *Sceloporus* from this newly formed habitat. The *undulatus* clade may be a secondary rerecolonization of *Sceloporus* to more northern regions that were previously uninhabitable due to shifts in climate regime or glaciers. Speciation in this group would have occurred more gradually as the clade spread across the United States. Whether glacial events, shifts in climate regime, or geological activity contribute to the biogeographic pattern of *Sceloporus* is unknown; however, these would explain the lack of richness in northern North America. Additionally, lizards are generally poor dispersers (Escobedo-Galván et al., 2011) and take long periods of evolutionary time to occupy new geographic ranges. Thus, large-bodied *Sceloporus* species may cluster geographically in present time because they are recently evolved and have had less time to disperse. It may also be the case that because larger species have larger home ranges and are therefore more likely to overlap, however this has yet to be studied. Alternatively, large-bodied *Sceloporus* species may differ in niche breadth compared to their smaller congeners reducing the potential habitats they can use and restricting large-bodied lizards to particular areas. We have some evidence for this pattern as large-bodied lizards can be found in montane, subtropical and tropical forests or arid deserts, but this has yet to be studied.

**Figure 5** Distribution of body sizes (adult male Snout-to-Vent Length) for 69 *Sceloporus* species. We used the natural breakpoints, vertical red lines, in the histogram to bin species into three size classes.
Body size and trait divergence

In general, *Sceloporus* do not show the same pattern of morphological and ecological specialization as other closely related clades (Warheit et al., 1999). By taking our approach, we can begin to identify large-scale patterns of diversification that are normally difficult to obtain. For example, resource availability may drive small species to be geographically spread to reduce competition. Conversely, large species are often found with other large species and alternative reproductive and foraging strategies may facilitate co-occurrence. This seems to be the case for two large species, *S. torquatus* and *S. spinosus*, which are often found in sympatry. Interestingly, their peak mating seasons are separated by several months (Feria-Ortiz et al., 2001; Valdés-González & Ramírez-Bautista, 2002). *S. spinosus* is oviparous, has peak mating activity in April and May, and eats insects and other invertebrates (Valdés-González & Ramírez-Bautista, 2002). *S. torquatus*, on the other hand, is viviparous, mates in the fall (Feria-Ortiz et al., 2001) and is omnivorous, increases intake of plant material during the summer,
but mainly feeds on insects and other arthropods in early and late season (Búrquez et al., 1986). Sceloporus species tend to increase their activity, including foraging, during the peak mating season, and, at least in males, reducing activity during nonbreeding seasons (Rose, 1981). By employing strategies like offsetting breeding seasons or modification of diet and activity through the year, species may be able to live in sympatry with reduced antagonistic interactions.

A limitation in our study was the lack of intraspecific variation in the body size data. Phenotypic variation has long been known to be an important measure that can affect the response to selective pressures, how species interacts with abiotic and biotic factors, and even community dynamics (Bolnick et al., 2003). Thus, ignoring intraspecific variation may overlook fundamental processes that dictate species assemblages and the ecological breadth of a species (Violle et al., 2012). The lack of intraspecific size data can become an issue for species with large distributions, like S. grammicus and S. variabilis, because populations are bound to differ in body size and sampling effort may not be even across the range. This may have led to incorrect classification of the size, small versus medium, for example, which would affect our chi-squared analysis, ancestral reconstruction, and understanding of how species’ phenotypes are distributed. This can be overcome by measuring a large number of individuals and equal sampling efforts across the range of the species. In our case, S. grammicus and S. variabilis both had large sample sizes, 412 and 457 individuals, respectively, but some species, like S. zosteromus may be more vulnerable to bias.

4.3 A different approach to studying diversification

As large data sets become more accessible through open-source databases, we can begin to address questions at a larger scale. For example, GBIF is thought to be a good estimate for species richness.
completeness in both the United States (~75%–80%) and Mexico (~60%) (Meyer et al., 2015) allowing researchers to address questions about all of North America, rather than a small area. Additionally, much of the data that populates large databases come from reputable sources like museums. For example, between 70% and 80% of occurrence data for the clade Lampropeltis comes from museums volunteers and are accurate in terms of species identification and locality.

Although little work has been done describing bioregions in terms of ectotherms in North America, a study by Burbank and Gehara (Burbrink & Gehara, 2018) found that the clade Lampropeltis, New World kingsnakes, showed a similar composition of bioregions as found in our study. For example, we found distinct bioregions in the west coast, east coast, central, and southwest United States and this same pattern was found by Burbank and Gehara (Burbrink & Gehara, 2018); however, the size of the bioregions slightly differed. Bioregions differed dramatically in Mexico and across Central America. We found ~10 bioregions across southern North America and Central America, while Burbank and Gehara (Burbrink & Gehara, 2018) only found two. This difference in the number of bioregions is likely explained by the disparity in diversity between Sceloporus and Lampropeltis. There are ~25 species of Lampropeltis across the Americas, while Sceloporus has ~100 species with a majority of the diversity centered in Mexico. The great diversity of Sceloporus coupled with high endemism may also explain the fine partitioning of bioregions found in Mexico compared to the two large regions found by Burbank and Gehara (Burbrink & Gehara, 2018).

Many insular examples exist of closely related species occupying a single geographic region and exhibiting the phenotypic consequences that arise from such sympatry (Lack, 1947; Losos et al., 1998; Seehausen, 2006). These examples have led to groundbreaking work in evolutionary biology and pushed the field forward, yet they may represent the exception rather than the rule. Here, we emphasize and promote the use of open-source databases to perform macroscale analyses across large geographic areas that were previously difficult to achieve. Additionally, large-scale analyses provide a novel view into continental systems to gain new insights on macroevolutionary processes that create large-scale patterns of diversity.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

Julio Rivera: Formal analysis (equal); Writing-original draft (equal); Writing-review & editing (lead). Heather N. Rich: Conceptualization (lead); Formal analysis (equal); Writing-original draft (lead). Michelle Lawling: Conceptualization (equal); Formal analysis (supporting); Writing-review & editing (supporting). Michael S. Rosenberg: Conceptualization (supporting); Formal analysis (supporting); Writing-review & editing (supporting). Emilia P Martins: Conceptualization (lead); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

All data in this study were downloaded from open-source material online. See Methods section of the manuscript for details. Generally, occurrences were downloaded from GBIF, and size data were collected from published and unpublished literature.

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REFERENCES

Adams, D. C. (2004). Character displacement via aggressive interference in Appalachian salamanders. Ecology, 85(10), 2664–2670. https://doi.org/10.1890/04-0648
Adams, D. C., & Rohlf, F. J. (2000). Ecological character displacement in Plethodon: Biomechanical differences found from a geometric morphometric study. Proceedings of the National Academy of Sciences, 97(8), 4106–4111. https://doi.org/10.1073/pnas.97.8.4106
Angilletta, M. J. Jr, Steury, T. D., & Sears, M. W. (2004). Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. Integrative and Comparative Biology, 44(6), 498–509. https://doi.org/10.1093/icb/44.6.498
Beal, M. S., Lattanzio, M. S., & Miles, D. B. (2014). Differences in the thermal physiology of adult Yarrow’s spiny lizards (Sceloporus jarrovii) in relation to sex and body size. Ecology and Evolution, 4(22), 4220–4229.
Bergmann, K. (1847). On the relation of the heat economy of animals to their size. Göttinger Studien, 3(1), 595–708.
Blonder, B., Baldwin, B. G., Enquist, B. J., & Robichaux, R. H. (2016). Variation and macroevolution in leaf functional traits in the Hawaiian silversword alliance (Asteraceae). Journal of Ecology, 104(1), 219–228. https://doi.org/10.1111/1365-2745.12497
Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. American Naturalist, 161(1), 1–28. https://doi.org/10.1086/343878
Brennan, T. C., & Holycross, A. T. (2006). A Field guide to amphibians and reptiles in Arizona. Arizona Game and Fish Department.
Bulleri, F., Bruno, J. F., Silliman, B. R., & Stachowicz, J. J. (2016). Facilitation and the niche: Implications for coexistence, range shifts and ecosystem functioning. Functional Ecology, 30(1), 70–78. https://doi.org/10.1111/1365-2435.12528
Burbrink, F. T., & Gehara, M. (2018). The biogeography of deep time phylogenetic reticulation. Systematic Biology, 67(5), 743–755. https://doi.org/10.1093/sysbio/syv019
Burbiecez, A., Flores-Villela, O., & Hernandez, A. (1986). Herbivory in a small iguanid lizard, Sceloporus torquatus torquatus. Journal of Herpetology, 20(2), 262–264. https://doi.org/10.2307/1563955
Carpenter, C. C., & Ferguson, G. W. (1977). Ecology and Behaviour. In C. Ganz, & D. W. Tinkle (Eds.), Ecology and Evolution. 4(22), 743–755. New York Academic Press.
Chamberlain, S., & Bgbif: Interface to the Global ‘Biodiversity’ Information Facility API, version R package. 0.9.9 ed2017.
Dayan, T., & Simberloff, D. (2005). Ecological and community-wide character displacement: The next generation. Ecology Letters, 8(8), 875–894. https://doi.org/10.1111/j.1461-0248.2005.00791.x

Bürquez, A., Flores-Villela, O., & Hernandez, A. (1986). Herbivory in a small iguanid lizard, Sceloporus torquatus torquatus. Journal of Herpetology, 20(2), 262–264. https://doi.org/10.2307/1563955
Carpenter, C. C., & Ferguson, G. W. (1977). Ecology and Behaviour. In C. Ganz, & D. W. Tinkle (Eds.), Variation and evolution of stereotyped behaviour in reptiles (pp. 335–554). New York Academic Press.
Dimmitt, M. A., Comus, P. W., & Brewer, L. M. (2015). A natural history of the sonoran desert, 2nd edition. University of California Press.

Dunham, A. E., Tinkle, D. W., & Gibbons, J. W. (1978). Body size in island lizards: A cautionary tale. Ecology, 59(6), 1230–1238. https://doi.org/10.2307/1938236

Echeverría-Londoño, S., Enquist, B. J., Neves, D. M., Violle, C., Boyle, B., Kraft, N. J. B., Maitner, B. S., McGill, B., Peet, R. K., Sandel, B., Smith, S. A., Svenning, J.-C., Wiser, S. K., & Kerkhoff, A. J. (2018). Plant functional diversity and the biogeography of biomes in North and South America. Frontiers in Ecology and Evolution., 6(219), 1–12. https://doi.org/10.3389/fevo.2018.00219

Edler, D., Guedes, T., Zizka, A., Rosvall, M., & Antonelli, A. (2017). Infomap Bioregions: Interactive mapping of biogeographical regions from species distributions. Systematic Biology., 66(2), 197–204.

Edwards, K. F., Kremer, C. T., Miller, E. T., Osmond, M. M., Litchman, E., Echeverría- Londoño, S., Enquist, B. J., Neves, D. M., Violle, C., Boyle, B., Elton, C. (1946). Competition and the structure of ecological communities. Ecology, 79(12), 1853–1868. https://doi.org/10.1111/ele.13142

Elton, C. (1946). Competition and the structure of ecological communities. Journal of Animal Ecology., 15(1), 54–68. https://doi.org/10.2307/1625

Escobedo-Galván, J. A., González-Salazar, C., López-Alcaide, S., Arroyo- Peña, V. B., & Martínez-Meyer, E. (2011). Will all species with temperature-dependent sex determination respond the same way to climate change? A reply to Kallimanis (2010). Oikos, 120(5), 795–799.

Feria- Ortiz, M., Nieto- Montes de Oca, A., & Salgado- Ugarte, I. H. (2001). Diet and reproductive biology of the viviparous lizard Sceloporus torquatus torquatus (Squamata: Phrynosomatidae). Journal of Herpetology., 35(1), 104–112. https://doi.org/10.2307/1566029

Ferrari, L., Orozco- Esquivel, T., Manea, V., & Manea, M. (2012). Evolutionarily stable communities: A framework for understanding the role of trait evolution in the maintenance of diversity. Ecology Letters, 21(12), 1853–1868. https://doi.org/10.1111/j.1461-0248.2012.02364.x

Elton, C., Dimmitt, M. A., Comus, P. W., & Brewer, L. M. (2015). Reptiles in Research: Investigations of Ecology, systematics, and behavior in the evolution of the crevice-using species of Sceloporus (Sauria, Iguanidae). Harvard University.

Hall, W. P. (1973). Comparative population cytogenetics, speciation, and evolution of the crevice-using species of Sceloporus (Sauria, Iguanidae). Harvard University.

Hall, W. P. (1973). Comparative population cytogenetics, speciation, and evolution of the crevice-using species of Sceloporus (Sauria, Iguanidae). Harvard University.

Herrel, A., De Grauw, E., & Lemos-Espina, J. A. (2001). Head shape and bite performance in xenosaurid lizards. Journal of Experimental Zoology., 290(2), 101–107. https://doi.org/10.1002/jez.1039

Hew, D. K., & Martins, E. P. (2013). Visual and chemical signals of social communication: Providing the link to habitat and environment. In W. Lutterscheidt (Ed.), Reptiles in Research: Investigations of Ecology, Physiology and Behavior from Desert to Sea (pp. 111–141). Nova Publishers.

Hillebrand, H. (2004). On the Generality of the Littoral Diversity Gradient. The American Naturalist., 163(2), 192–211. https://doi.org/10.1086/381004

Holman, J. A. (1987). Herpetofauna of the Egelhoff site (Miocene: Barstovian) of north-central Nebraska. Journal of Vertebrate Paleontology., 7(2), 109–120. https://doi.org/10.1080/0272463.1987.10011646

IUCN. (2018). The IUCN Red List of Threatened Species 2018 [Version 2018–1].

Jiménez-Arcos, V. H., Sanabria-urbán, Ñ., & Cueva del Castillo, R. (2017). The interplay between natural and sexual selection in the evolution of sexual size dimorphism in Sceloporus lizards (Squamata: Phrynosomatidae). Ecology and Evolution., 7(3), 905–917.

Kartzinel, T. R., Chen, P. A., Coverdale, T. C., Erickson, D. L., Kress, W. J., Kuzmina, M. L., Rubenstein, D. I., Wang, W., & Pringle, R. M. (2015). DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. Proceedings of the National Academy of Sciences., 112(26), 8019–8024. https://doi.org/10.1073/pnas.1503283112

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. Bioinformatics, 26, 1463–1464. https://doi.org/10.1093/bioinformatics/btp166

Kozak, K. H., Mendryk, R. W., & Wiens, J. J. (2009). Can parallel diversification occur in sympatry? Repeated patterns of body-size evolution in coexistence clades of North America salamanders. Evolution, 63(7), 1769–1794.

Kraft, N. J. B., & Ackerly, D. D. (2010). Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. Ecological Monographs., 80(3), 401–422. https://doi.org/10.1890/09-1672.1

Lack, D. (1947). Darwin’s Finches. Cambridge University Press.

Lamouroux, N., Poff, N. L., & Angermeier, P. L. (2002). Interglacial convergence of stream fish community traits along ecomorphic and hydraulic gradients. Ecology, 83(7), 1792–1807.

Lawing, A. M., Polly, P. D., Hewes, D. N., & Martins, E. P. (2016). Including fossils in phylogenetic climate reconstructions: A deep time perspective on the climatic niche evolution and diversification of spiny lizards (Sceloporus). The American Naturalist., 188(2), 133–148.

Leaché, A. D. (2009). Species tree discordance traces to phylogeographic clade boundaries in north american fence lizards (Sceloporus). Systematic Biology., 58(6), 547–559. https://doi.org/10.1093/sysbio/syp057

Leaché, A. D., Banbury, B. L., Linkern, C. W., & Nieto-Montes de Oca, A. (2016). Phylogenomics of a rapid radiation: Is chromosomal evolution linked to increased diversification in north american spiny lizards (Genus Sceloporus)? BMC Evolutionary Biology., 16(1), 63. https://doi.org/10.1186/s12862-016-0628-x

Li, S.-P., Cadotte, M. W., Meiners, S. J., Hua, Z.-S., Jiang, L., & Shu, W.-S. (2015). Estimating the temporal and spatial extent of gene flow among sympatric lizard populations (genus Sceloporus) in the southern Mexican highlands. Molecular Ecology., 24(7), 1523–1542.

Halfn, G., & Morrone, J. J. (2017). An analytical review of Halfn’s Mexican transition zone, and its relevance for evolutionary biogeography, ecology and biogeographical regionalization. Zootaxa, 4226(1), zootaxa.4226.1.1. https://doi.org/10.11646/zootaxa.4226.1.1
Warheit, K. I., Forman, J. D., Losos, J. B., & Miles, D. B. (1999). Morphological diversification and adaptive radiation: A comparison of two diverse lizard clades. *Evolution*, 53(4), 1226–1234. https://doi.org/10.1111/j.1558-5646.1999.tb04535.x

Wiens, J. J., Kuczynski, C. A., Arif, S., & Reeder, T. W. (2010). Phylogenetic relationships of phrynosomatid lizards based on nuclear and mitochondrial data, and a revised phylogeny for *Sceloporus*. *Molecular Phylogenetics and Evolution*, 54(1), 150–161. https://doi.org/10.1016/j.ympev.2009.09.008

Wilcox, T. M., Schwartz, M. K., & Lowe, W. H. (2018). Evolutionary community ecology: Time to think outside the (taxonomic) box. *Trends in Ecology & Evolution*, 33(4), 240–250. https://doi.org/10.1016/j.tree.2018.01.014

Williams, C. B. (1947). The generic relations of species in small ecological communities. *Journal of Animal Ecology*, 16(1), 11–18. https://doi.org/10.2307/1502

**SUPPORTING INFORMATION**

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

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