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Cite this article: Westeen EP, Yuan ML, Wang IJ. 2025 Ecomorphology is associated with speciation and co-occurrence in *Sceloporus* lizards. *Proc. R. Soc. B* **292**: 20251305.
https://doi.org/10.1098/rspb.2025.1305

Received: 19 May 2025
Accepted: 30 October 2025

Subject Category:
Evolution

Subject Areas:
evolution, ecology

Keywords:
phenotypic evolution, morphometrics, species coexistence, sympatry, trait divergence

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8172460.

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Ecomorphology is associated with speciation and co-occurrence in *Sceloporus* lizards

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Closely related species can impose strong forces of selection on one another through competition, leading to dramatic examples of phenotypic evolution. Niche partitioning can promote the use of novel resources between co-occurring species to reduce competitive overlap and thereby drive phenotypic divergence. Quantifying this potential relationship between ecology and morphology among species can reveal how opportunity and constraint interact to shape patterns of phenotypic evolution and how phenotypic diversity can facilitate co-occurrence. We explored the dynamics of ecomorphological evolution in relation to speciation and co-occurrence in *Sceloporus* lizards, a speciose group spanning North and Central America, where species often occur in sympatry. We collected data for 80 species and demonstrated strong relationships between multivariate morphology and ecology, finding that *Sceloporus* species occur in six ecological modes with associated morphologies (ecomorphs). The evolution of arboreality was a major transition that expanded morphospace, allowed for the evolution of further ecological novelty, and is associated with increased speciation rates. Across their range, *Sceloporus* ecomorphs are spatially overdispersed, suggesting that interspecific competition may limit the ability of similar species to coexist. By quantifying ecomorphological diversity across a diverse radiation, our results shed new light on how phenotypic variation accumulates and its implications for coexistence between closely related species.

1. Introduction

What drives the evolution of phenotypic diversity, and what are its consequences? Habitat partitioning that leads to phenotypic differentiation is often a key first stage in vertebrate radiations [1]. Notable examples are *Anolis* lizards in which specialized limb, digit and toe morphologies are associated with vertical habitat partitioning [2], stickleback fishes that have repeatedly evolved benthic and limnetic forms [3] and Darwin's finches for which divergence between ground and tree clades gave way to further phenotypic novelty [4]. Dissecting this relationship between organismal ecology and morphology, or ecomorphology, can provide insights into the interplay of adaptive phenotypic evolution, speciation, and community dynamics [5]. Divergent ecomorphology can facilitate the use of different resources, thereby reducing competitive overlap in sympatry [6–8]. Ecomorphological divergence may be particularly important for facilitating coexistence between closely related species, which tend to be ecologically and morphologically similar [9].

Ecological opportunity, which comes in many forms [10], creates the potential for diversifying selection to generate phenotypic diversity. For example, arrival to new areas such as islands or lakes can allow lineages to exploit novel resources [11–13], which is often aided by competitor or predator release [14]. Ecological opportunity need not result from geographic shifts or expansion, though—for example, accessing novel microhabitats within a lineage's existing range can also provide sufficient opportunity to promote phenotypic novelty [15]. In fact, phenotypic evolution itself may generate ecological opportunity (e.g. bats evolving powered flight) [10]. Furthermore, many radiations reveal a suite of divergent traits that interact to improve whole-organism performance and allow access to novel niche space [2,16–18]. Examinations of both multivariate morphology and ecology can therefore help us better understand how ecological opportunity and phenotypic evolution interact to shape biodiversity.

Comprehensively understanding ecomorphological evolution requires characterizing the spatial and phylogenetic context in which it occurs. Examining these together can uncover the roles that factors such as interspecific competition have played in the diversification history of different groups. For example, whether phenotypic traits are shared or divergent between sister taxa can suggest whether neutral or deterministic forces, respectively, have played a role in shaping their evolution [19]. Similarly, quantifying the distribution of phenotypic diversity across space can provide insights into community sorting mechanisms and the selective pressures acting on niche evolution. Ecomorphologically diverse communities are often formed when similar species are limited in their ability to co-occur (e.g. limiting similarity resulting in a pattern of overdispersion), whereas communities of ecomorphologically similar species can reveal that species with certain traits are more successful in a given environment (e.g. habitat filtering resulting in a pattern of underdispersion [20]).

Sceloporus lizards are an ecologically diverse, species-rich clade with a geographic distribution throughout North and Central America in which species often occur in sympatry [21,22]. With over 100 described species, they are the most speciose genus in the family Phrynosomatidae. *Sceloporus* lizards exhibit a great deal of ecological variation, inhabiting a broad range of habitats such as lowland deserts, cloud forests, high alpine forests, grasslands, and sand dunes [23]. The diversification history of this group has received extensive study, and there is known rate heterogeneity with a period of rapid diversification in one clade (hereafter, the 'rapid radiation') beginning 20–25 Myr [24]. If phenotypic evolution is associated with speciation in this group, we might expect species in the rapid radiation to exhibit greater ecomorphological divergence. While previous work found that *Sceloporus* are comparatively less phenotypically disparate than another iguanian lizard radiation of similar age—the genus *Anolis* [25]—there may yet be interesting ecomorphological dynamics to uncover. For example, recent work has suggested that ecomorphological diversity reduces competitive overlap between *Sceloporus* species [26] and that communities tend to be phylogenetically clustered but exhibit body size diversity [22]. Hence, *Sceloporus* lizards provide an excellent opportunity to study phenotypic evolution in relation to ecology, phylogenetic history, and interspecific interactions.

Here, we examine the relationship between ecology and morphology across *Sceloporus* and how ecomorphology is related to speciation and co-occurrence in this diverse radiation. We collected data on the morphology, ecology and geographic distribution of 80 taxa to answer three key questions on the evolution of phenotypic diversity: (1) What is the relationship between ecology and morphology across this group? (2) What is the tempo and mode of ecomorphological evolution? and (3) Are ecomorphs spatially overdispersed, as we would expect under limiting similarity? Examining how ecomorphological diversity arises and its role in structuring co-occurrence patterns can provide a more complete understanding of the causes and consequences of phenotypic evolution.

2. Methods

(a) Data

We collected morphological data from 330 individual *Sceloporus* lizards (adult males) including museum specimens and field-caught animals. Individuals spanned 79 species plus the ecologically unique White Sands form of *S. cowlesi* which we manually added to the phylogeny of Leaché *et al.* [24] using divergence times from Laurent *et al.* [27]. After pruning a time-calibrated phylogeny for *Sceloporus* [24], our dataset included 80 taxa for which we had morphological, ecological and phylogenetic data (out of 85 unique *Sceloporus* species in the Leaché *et al.* tree) and 77 for which we conducted geographic analyses (excluding three island endemic species which are the sole inhabitants of their respective islands).

We measured a suite of morphological traits from all individuals: body size as given by snout-to-vent length (SVL), head length, head width, body width, humerus length, radioulna length, forefoot length, forelimb length, femur length, tibiofibular length, hindfoot fourth toe length, hindfoot length, hindlimb length and dorsal scale count following [28]. Body size is associated with locomotion and jumping [29], thermal physiology [30,31], climate and microhabitat [29,32] and prey size [33]. Limb lengths, and especially hindlimbs, are associated with perch height and diameter [34,35], as is foot morphology [29]. Longer limbs are also associated with increased sprint speed [5,36–38]. Head width is associated with bite force and dietary breadth [39]. Scale counts are associated with climate and are thought to reduce evaporative water loss [28,40].

We measured an average of 3.7 specimens per species, ranging from 1 to 16. Ethanol-preserved individuals came from the Museum of Vertebrate Zoology (MVZ) and the Museum of Natural History at the University of Colorado, Boulder (UCM; electronic supplementary material, table S1). We obtained digital photographs of additional specimens via VertNet from the Museum of Comparative Zoology (MCZ) at Harvard University and from UCM as part of the oMeso project (NSF Award No. 2001474).

We took standardized digital photographs of all specimens and measured morphology from these images. E.P.W. photographed specimens on a white background with a ruler in the frame for scaling, using a Nikon D3500 digital camera coupled with a Nikkor AF-P 18–55 mm lens. To reduce measurement errors due to changes in perspective, we took photographs at multiple angles with the features of interest in the same plane as the ruler. We used a polarizing filter coupled with two Neewer CN-160 LED lights with linear polarization sheets attached to them to remove any glare on wet (e.g. ethanol-preserved) specimens.

We collected measurements in Adobe Photoshop by setting a custom scalebar based on the ruler in each photo. Measurements were replicated by at least two independent reviewers or by the same reviewer at separate timepoints. We averaged measurements per specimen, and any measurements that differed by more than 10% of the average measurement value were discarded for inconsistency. Once we had the mean measurement for each trait per specimen, we then calculated species averages for each trait, resulting in a single set of measurements for each species. Finally, we regressed all morphological traits against body size (SVL) using phylogenetic regressions with lambda optimization to account for the observed degree of phylogenetic signal and used the residuals in downstream analyses as body size-corrected measures [41].

We used ecological data from the literature to define habitat categories for each species [42–44]: arboreal, saxicolous, generalist, terrestrial, bunchgrass-dwelling and sand-dwelling, following [43]. Arboreal species are defined as those that predominantly perch in trees. Saxicolous, or rock-dwelling, include species that primarily use rocks, including boulders, rocky outcroppings and canyon walls. Generalists are defined as species with evidence for three or more habitat preferences (e.g. arboreal, saxicolous and terrestrial). Terrestrial species may use a variety of objects as perches but predominantly perch low to the ground. The bunchgrass class refers to the *scalaris* clade of lizards that are strongly associated with bunchgrass clusters in which they take refuge [45]. Finally, the sand category represents two species, *S. arenicolus* and *S. woodi*, as well as the White Sands form of *S. cowlesi* that exclusively inhabit sand dunes or sand 'islands' in the case of *S. woodi*.

For some analyses, we reduced this categorization scheme into two categories representing the major variation in habitat ecology: predominantly scansorial (arboreal and saxicolous), and predominantly terrestrial (terrestrial, bunchgrass and sand), with generalist species classified on a case-by-case basis [46]. Hereafter, we refer to these ecological groupings as 'full scheme' and 'reduced scheme' for the six and two category classifications, respectively. Both the full and reduced ecological categorizations with associated citations may be found in electronic supplementary material, table S1. Ecological groupings are not intended to explain the totality of species' habitat use but rather to represent general trends. We complemented our ecological categorizations with geographic range data downloaded from the Global Assessment of Reptile Distributions (GARD) dataset, which provides range polygons based on occurrence records and expert opinion [23].

(b) What is the relationship between ecology and morphology?

To assess the relationship between ecology and morphology, we performed a phylogenetic principal components analysis (pPCA) [41] on our phenotypic data, which included SVL alongside residuals for all other traits. A strong relationship between these variables will manifest as putative ecomorphs—groups of species that exhibit similar morphology and occupy similar niches but are not necessarily close phylogenetically [47]—occupying different parts of morphospace. We then examined PC loadings to evaluate which morphological traits captured different axes of the variance between species. We then used phylogenetic analysis of variance (ANOVA) to test whether univariate morphological traits differ between ecological groups [41].

Then, we examined whether we can predict ecology based on multivariate morphology using linear discriminant analysis [48]). We performed all analyses on the entire tree and on only the rapid radiation to test the hypothesis that species in the rapid radiation are more morphologically differentiated than those in the more basal groups. We also performed all analyses using the full and reduced ecology classification schemes.

Next, we examined evidence for ecomorphological convergence across the *Sceloporus* tree. We computed the Wheatsheaf index (w), which examines phenotypic distance in relation to phylogenetic distance and where stronger convergence is represented by a larger value [49]. Convergence requires multiple origins as well as low divergence relative to time and is thus a special case of the 'w' metric. We computed w for all ecological groupings, using PC1 and PC2 as our phenotypic data, and conducted 1000 bootstrap replicates to estimate a p-value using the 'windex' package [50].

(c) What are the dynamics of ecomorphological evolution?

To quantify the degree to which phylogenetic history influences ecological mode, we calculated phylogenetic signal using the $\boldsymbol{\delta}$ approach of Borges *et al.* [51]. We calculated phylogenetic signal for phenotype, given by PC1 and PC2, as Blomberg's K, the ratio of observed to expected phenotypic variance under Brownian motion (BM), and Pagel's λ, a scaling factor for correlations between species respective to a BM expectation [41,52,53].

We then fit a series of models of evolution to our trait data as PC1 and PC2 using functions in the R package 'OUwie' [54]. The models included: BM, a random walk [53]; BM with different rate parameters for each regime (BMS); Ornstein-Uhlenbeck (OU), a random walk where characters are attracted to a single optimum [55]; an OU model with different means for each character state and a single α (strength of selection towards the optimum) and σ^2 (drift parameter) (OUM); an OU model that assumes different state means and different rate values (OUMV); an OU model with different means and different α values (OUMA); and an OU model that assumes different state means, different rate values and different α values (OUMVA). We used the reduced ecological scheme as our selective regimes and PC1 and PC2 as our character traits. If the ecological categories have different trait optima, this will reveal that habitats are associated with unique ecomorphological traits.

To evaluate the evolutionary dynamics of ecological states, we then conducted maximum-likelihood ancestral state reconstruction and transition rates (q) estimation using the 'ace' function in the R package 'ape' [56]. We performed ancestral state reconstructions using the 'equal rates', 'symmetrical' and 'all rates different' models and compared models using AIC scores and pairwise-likelihood tests. In addition, we performed stochastic character mapping implemented in 'SIMMAP' to estimate the number of transitions between ecological states [41,57]. We performed 999 simulations and averaged the number of transitions across all simulations. To compare with our maximum-likelihood ancestral state reconstruction, we also calculated the posterior probability of each ancestral state by summarizing across simulations.

To assess whether ecology is associated with speciation across *Sceloporus*, we tested for trait-dependent speciation in the hidden state speciation and extinction (HiSSE) framework [58]. This framework is advantageous because it allows both observed characters and concealed (hidden) states, which reduce the prevalence of type I errors common to other SSE family models [58,59]. SSE methods in general are sensitive to states that have evolved only once or few times and can lead to spurious results when these traits are modelled [60]. Therefore, we used the reduced scheme for ecology that classified species as either predominantly terrestrial or scansorial. We built four models: the null model included equal rates for speciation (λ), extinction (μ) and transitions (q), and did not include hidden states. Second, the 'hidden state' model included two hidden states and allowed λ and μ to vary as functions of the unobserved states only. Third, our 'ecology' model allowed all three parameters to vary with ecological state. Fourth, our 'ecology + hidden' model allowed all three parameters to vary with ecology state as well as two hidden states. All models were fit using the 'hisse' package in R.

(d) What is the spatial distribution of ecomorphological diversity?

To visualize the spatial distribution of *Sceloporus* diversity, we constructed maps of *Sceloporus* species richness and ecomorph richness at 5 arc-minute resolution. We used the GARD dataset, which provides range polygons based on occurrence records and expert opinion [23], and functions developed by Davis Rabosky *et al.* [61] to create our maps.

Next, we investigated whether the distribution of ecomorphology is: (1) spatially overdispersed (a tendency for different ecomorphs to co-occur), which is consistent with limiting similarity in which similar species cannot coexist due to competitive overlap; (2) underdispersed (a tendency for same ecomorphs to co-occur), which is consistent with habitat filtering in which the environment selects for species with certain traits; or (3) neutral with respect to species richness. To do so, we used spatial autoregressive (SAR) models implemented in the package 'spdep' to map the distribution of residuals of a linear regression of ecomorph richness on species richness while accounting for spatial autocorrelation [62]. We excluded island endemics (*S. angustus*, *S. becki* and *S. grandaevus*) from co-occurrence analyses as they are the sole *Sceloporus* inhabitants of their respective islands. We then mapped the residuals of our resulting model; ecomorphological overdispersion with respect to species richness will result in positive residuals, underdispersion will result in negative residuals, and a neutral relationship will result in a residual of 0.

To further assess whether ecomorphs are more spatially overdispersed than expected by chance, we conducted a permutation test by shuffling ecomorph assignments among species (while keeping the distribution of range polygons fixed) and re-running SAR models 1000 times to generate a null distribution. We compared the slopes of the ecomorph richness to species richness relationship from the shuffled distributions to the observed slope and calculated a one-tailed p-value as the number of instances that a simulated slope was greater than the observed slope, indicating a stronger relationship, divided by the number of simulations.

To investigate whether ecomorphs had different constraints on sympatry, we calculated range overlap for every pair of species in our dataset. We used a 20% range overlap threshold as a proportion of the focal species range size to determine whether the species are considered sympatric, following previous studies [63–65]. We then calculated for each species how many times it overlapped with species of the same ecomorph class and the proportion of the total number of species with which it overlaps to account for differences in overall range size between species. Ecomorphs with more constraints on limiting similarity should overlap with species of their own ecomorph class less than with those of other ecomorph classes. We then computed the overlap between all pairs of ecomorphs and visualized these relationships using a heatmap [66]. We compared this with a heatmap of overlap in morphospace between ecological groups to evaluate how ecomorphological similarity may influence co-occurrence.

3. Results

(a) What is the relationship between ecology and morphology?

We found that all morphological traits were significantly correlated with body size (all $p < 0.05$). So, for all traits besides body size (SVL), we used residuals of a phylogenetic regression against body size in downstream analyses. We found that ecological groups classified by habitat usage (arboreal, $n = 19$; saxicolous, $n = 20$; generalist, $n = 15$; terrestrial, $n = 14$; bunchgrass, $n = 9$; sand, $n = 3$) occupy different regions of morphospace, with some more distinct than others (figure 1). Our first PC axis, PC1, explained 86% of the variance in morphology, and body size loaded highly onto this axis. Hindlimb length, hindfoot length and forelimb length all loaded highly onto PC2, which explained 9.3% of the variance. In our phylomorphospace plot (figure 1C), bunchgrass morphs cluster tightly in a position with the smallest body size and reduced limbs and digits. The sand morphs all cluster with their sister species but, in general, occupy the space adjacent to bunchgrass and terrestrial morphs. Terrestrial morphs cluster tightly and overlap with some generalists and some scansorial species outside the rapid radiation. Generalists occupy the centre of morphospace and exhibit the greatest variance along PC2. Arboreal and saxicolous morphs achieve the largest body sizes and overlap the most of any groups; however, the saxicolous species occupy two separate portions of morphospace, with the more basal saxicolous species (which are primarily crevice dwellers) clustering with terrestrial and generalist species, while species in the rapid radiation, which largely use rock walls, boulders and rocky outcrops, cluster with arboreal species (figure 1C). The more basal groups, overall, are restricted in morphospace, occupying only 25% of morphospace based on convex hulls computed for each set of species, clustering with low scores on PC1 and intermediate to high scores on PC2, representing small body size and average to elongated limbs.

Species in the rapid radiation occupy novel morphospace (89% of total morphospace) compared to the more basal groups; for instance, arboreal morphs reveal high scores along PC1 representing the evolution of larger body size compared to basal group species. Bunchgrass morphs, on the other hand, occupy unique morphospace with low scores on both PC axes, representing small bodies and reduced limbs (figure 1C). When species are grouped into a reduced scheme with only two ecological categories, scansoriality (arboreal and saxicolous) and terrestriality (terrestrial, sand and bunchgrass), we see even greater separation in morphospace, particularly within the rapid radiation (electronic supplementary material, figure S1).

Several univariate measures of morphology were significantly predicted by ecological classification. Arboreal morphs are significantly larger than generalist, terrestrial, sand and bunchgrass morphs ($t < -3.38$ and $p < 0.05$ in all comparisons). Hindlimb length also differed significantly, with bunchgrass morphs having shorter hindlimbs for their body size compared to generalist and terrestrial morphs (all $t < -3.23$, $p < 0.05$), as did hindfoot length, with bunchgrass morphs again having smaller feet compared to arboreal, generalist and terrestrial morphs (all $t < -3.34$, $p < 0.05$). Bunchgrass morphs also had significantly shorter fourth toes than arboreal, generalist and sand morphs (all $t < -3.77$, all $p < 0.05$). Results from all comparisons may be found in electronic supplementary material, table S3.

Linear discriminant analysis predicted ecology from multivariate morphology (using our full scheme) with an accuracy of 68% for all species, which increased to 78% when only the rapid radiation was examined. The most miscategorized groups were arboreal and saxicolous. Using the reduced ecology scheme, accuracy jumped to 91% for the full tree and 96% for the rapid radiation. We found terrestrial ($w = 2.769$, $p = 0$), sand ($w = 6.61$, $p = 0.047$) and bunchgrass ($w = 1.825$, $p = 0.03$) ecomorphs to have significantly low phenotypic divergence according to the Wheatsheaf index, suggesting that these ecological modes may select for particular morphological traits, whereas other ecologies may be more flexible.

(b) What are the dynamics of ecomorphological evolution?

Our analysis did not detect a significant phylogenetic signal for ecological class (full scheme, $\Delta A = 7.13$, $p = 0.19$, reduced scheme, $\Delta A = 2.99$, $p = 0.4$). For our SIMMAP analysis, the symmetrical model was identified as the best fit for the full ecology dataset (ΔAIC = 9). We estimated an ancestral state for the crown group *Sceloporus* using the full ecological scheme as terrestrial (0.504), generalist (0.182) or saxicolous (0.178), based on the scaled likelihood at the root (other probabilities <0.05; figure 2A). We recovered 51.78 transitions between ecological states across the tree, with the most frequent transitions occurring as terrestrial to generalist states (10.86 transitions) and back (9.57 transitions; figure 2B). We found that arboreality evolved a single time at the base of the rapid radiation (posterior probability = 0.90).

Under the reduced ecology scheme, our best fit model was an equal rates model (ΔAIC = 22). We found more support for a terrestrial ancestor (scaled likelihood at the root = 0.611) than a scansorial ancestor (scaled likelihood = 0.389). We recovered 21.29 transitions over the tree, with slightly more (12.4 transitions) being from scansoriality to terrestriality than vice versa.

From our analyses of phylogenetic signal in morphology given by PC1 and PC2, we obtained values of $\lambda_{\mathrm{PC1}} = 0.793$ and $K_{\mathrm{PC1}} = 0.676$, and $\lambda_{\mathrm{PC2}} = 0.348$ and $K_{\mathrm{PC2}} = 0.176$. We found that an OUMV model—OU with multiple optima and varying rates—best fit the evolution of PC1 (ΔAICc = −8.19; $\alpha_{\mathrm{scansorial}} = \alpha_{\mathrm{terrestrial}} = 6.70$; $\sigma^2_{\mathrm{scansorial}} = 1.05$, $\sigma^2_{\mathrm{terrestrial}} = 0.26$; $\theta_{\mathrm{scansorial}} = 0.128$, $\theta_{\mathrm{terrestrial}} = -0.007$), while an OUM model— OU with multiple optima and shared rates—best fit PC2 (ΔAICc = 2.85; $\alpha_{\mathrm{scansorial}} = \alpha_{\mathrm{terrestrial}} = 1.468$; $\sigma^2_{\mathrm{scansorial}} = \sigma^2_{\mathrm{terrestrial}} = 0.513$; $\theta_{\mathrm{scansorial}} = 0.006$, $\theta_{\mathrm{terrestrial}} = 0.303$). The best fit model for our HiSSE analysis was the ecology + hidden model (table 1), suggesting that ecological mode is associated with increased speciation rates, but that effect is secondary to an unmeasured state. Our parameter estimates support heterogeneous transition rates (figure 2B).

(c) What is the spatial distribution of ecomorphological diversity?

We found that the spatial distribution of ecomorphological diversity is correlated with species diversity ($R^2 = 0.812$, $p < 0.001$), and both ecomorph and species richness peak in Mexico (figure 3A,B). Our SAR model revealed a slope of $\beta = 0.520$, suggesting that for every two species in a given grid cell roughly one additional ecomorph is found. The distribution of residuals reveals that, across much of the range of *Sceloporus*, there are more ecomorphs than expected based on species richness. Areas of high species richness show positive residuals, while large temperate areas where only a handful of species occur (e.g. the USA, excluding the desert southwest) are effectively neutral with respect to comparisons based on species richness. Our permutation test also revealed that ecomorphs are significantly spatially overdispersed compared to null expectations ($p = 0.023$; figure 3D).

Our comparisons of co-occurring congeners by ecomorph category revealed that bunchgrass, sand and terrestrial ecomorphs are less likely to co-occur with species of their same ecomorph type than arboreal and saxicolous ecomorphs (all $p < 0.001$). Bunchgrass, sand and terrestrial ecomorphs overlap in morphospace but are unlikely to co-occur in geographic space, whereas arboreal and saxicolous ecomorphs overlap in morphospace and often co-occur geographically (figure 3E,F).

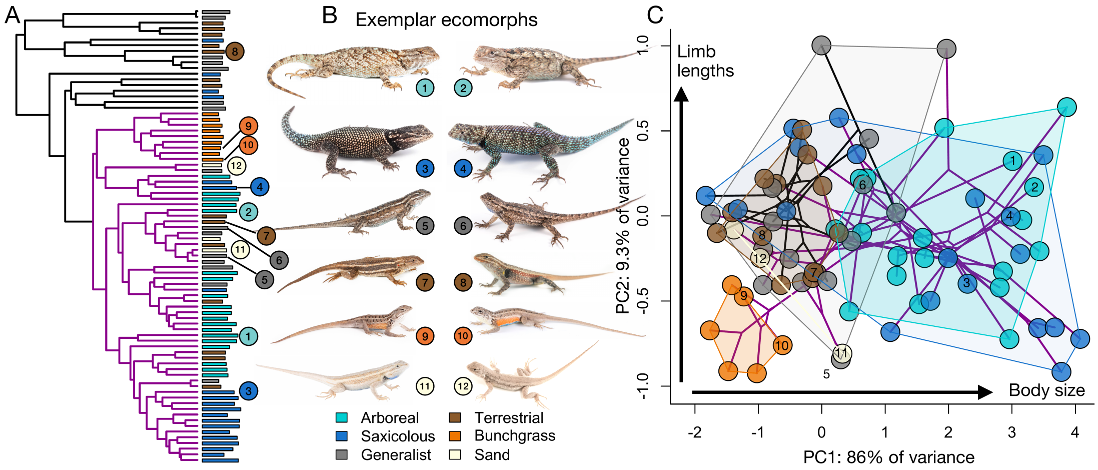

Figure 1. (A) Phylogeny of *Sceloporus* lizards from Leaché *et al.* [24]; bar length at tips represents relative body size, given by SVL, and colorized by ecology. The rapid radiation is denoted by purple branches. (B) Exemplar ecomorphs reveal phenotypic convergence and/or conservatism. (C) Phylomorphospace for species in this study, visualized using the first two principal components of a phylogentic PCA. Convex hulls group species by ecology. Photos 1–11 by Erin P. Westeen and José G. Martínez-Fonseca, photo 12 © Joel Sartore/Photo Ark.

4. Discussion

To understand how phenotypic diversity evolves in closely related species and how it can enable co-occurrence that allows for the evolution of greater biodiversity, we examined ecomorphology in a diverse and widespread group of lizards. As a critical first step, our results demonstrate a strong relationship between ecological mode and multivariate morphology. We found that a shift to arboreality at the base of the rapid radiation in *Sceloporus* is associated with increased speciation and the evolution of both phenotypic and ecological novelty. Consequently, we found that ecomorphology plays a role in species co-occurrence across the range of the genus, with a predominant pattern of spatial overdispersion of ecomorphs, suggesting that limiting similarity may structure *Sceloporus* communities. This study provides new insights into the evolution of ecomorphological diversity and its consequences for speciation and coexistence in closely related species.

(a) What is the relationship between ecology and morphology?

We found a strong relationship between ecology and morphology, with both our univariate and multivariate analyses underscoring that body size and limb lengths are key traits that differ between *Sceloporus* ecomorphs (electronic supplementary materials, tables S2 and S3; figure 1C). Across lizard diversity, the relationship between body size and limb lengths is associated with microhabitat use due to the functional basis of these traits [46]. In iguanian lizards, longer limbs are typically associated with increased sprint speeds [36,37] and are associated with perch diameter in some *Anolis* lizards [67]. We found that generalist and terrestrial *Sceloporus* species typically have longer limbs for their body size (figure 1C), and these species probably use running as their predominant means of predator escape [68]. Arboreal and saxicolous species may instead use crevices or shuttle to the opposite side of their tree or boulder [68], thus reducing the need to optimize sprint speed and perhaps favouring climbing ability. Arboreal and saxicolous morphs reveal variation in relative limb lengths (figure 1C), suggesting lability in this trait; investigating the relationship of limb lengths to climbing and sprinting abilities across *Sceloporus* ecomorphs will be an interesting next step. We also found that bunchgrass ecomorphs are morphologically similar to terrestrial ecomorphs and have comparable body sizes but exhibit significant reduction in limb length, foot length and fourth toe length similar to other semi-fossorial lizards (e.g. [69,70]; figure 1C). Unlike terrestrial sprinters, these species are known to duck into bunchgrass clusters for refuge rather than flee [26,71]. Thus, relative limb length appears to be a key trait differentiating *Sceloporus* ecomorphs, with some specialized morphs also revealing divergent foot morphology.

Beyond ecology–morphology associations, we found that some ecomorph classes—terrestrial and sand—evolved multiple times with low phenotypic divergence relative to time, exhibiting evidence of convergence. The bunchgrass group also showed reduced phenotypic divergence but has evolved only once and therefore represents morphological conservatism rather than convergence. We did not detect a signal of convergence among generalists, likely due to the variance in traits across species. The saxicolous category is the only one that appears to represent two distinct phenotypes—basal group saxicolous species are small bodied and small scaled, with relatively long limbs for their body size, while saxicolous species in the rapid radiation exhibit larger bodies, larger scales and variation in limb lengths. Our examinations of ecomorphological variation across the phylogeny underscore the mosaic pattern of phenotypic evolution in this group: some ecological groups are highly conserved (bunchgrass), some are highly convergent (sand, terrestrial), some are highly labile (generalist) and one class reveals two distinct morphological strategies for adaptation to distinct habitats (saxicolous; basal group species are primarily rock crevice dwellers, while rapid radiation species primarily use boulders).

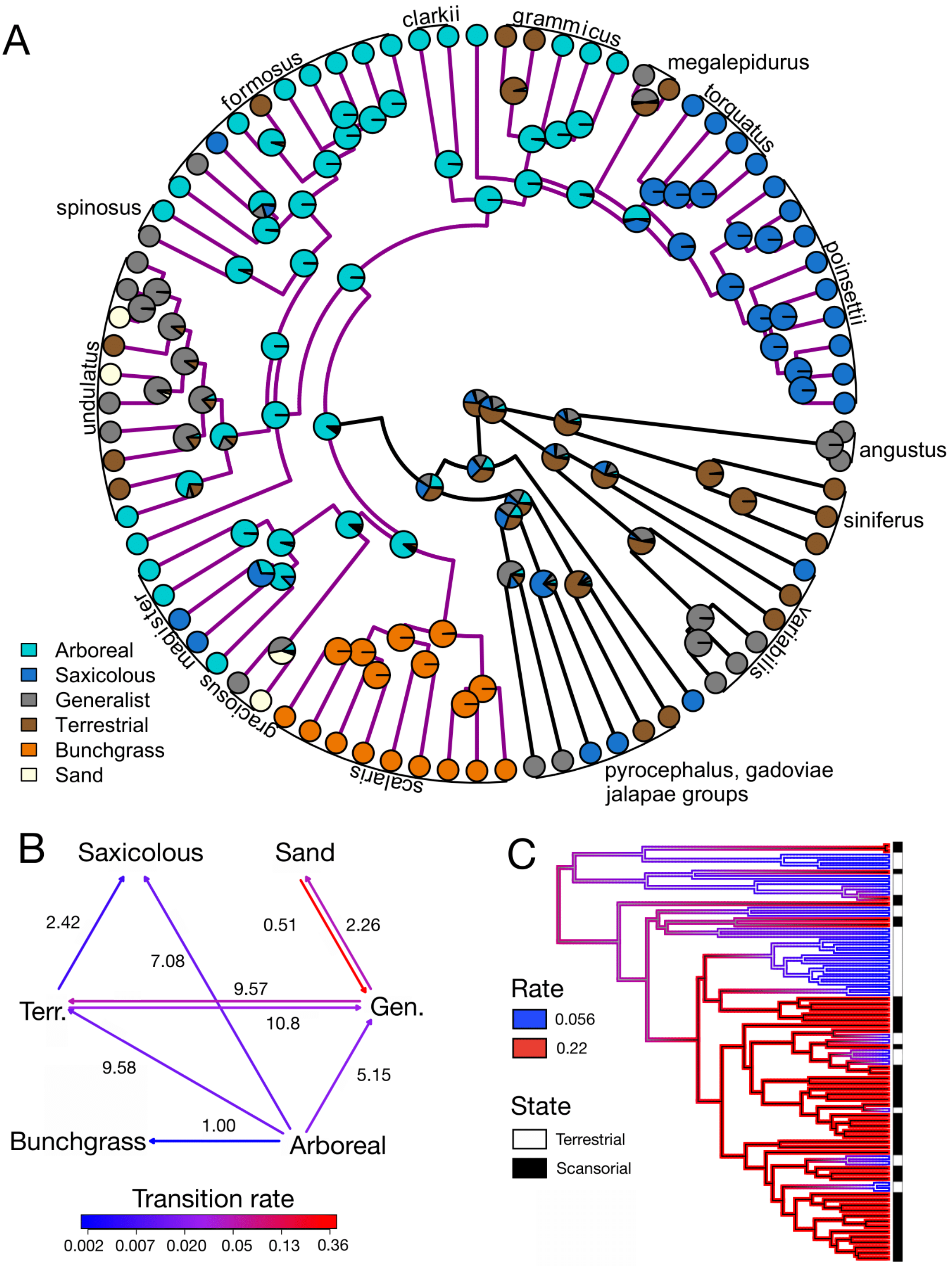

Figure 2. (A). Maximum likelihood ancestral character estimates for ecology are shown on a phylogeny of *Sceloporus* studied here. Tip colours correspond to ecological mode, and species groups are denoted with tip labels. (B) Transition rates between ecological modes. Arrows are coloured by transition rate, with red being faster, and labelled with estimated mean number of transitions between states. (C) Model-averaged speciation rates from our best-fit HiSSE model. Outer colours indicate speciation rate, with red being faster. Inner colours represent the ecological mode using the binary characterization.

(b) What are the dynamics of ecomorphological evolution?

We detected a moderate level of phylogenetic signal for morphology but a non-significant signal for ecology, suggesting that while morphology may be constrained by phylogenetic history in *Sceloporus*, ecology may be more labile. We found that the ancestral *Sceloporus* was most likely a terrestrial species and that arboreality evolved a single time at the base of the rapid radiation (~20–25 Ma). Arboreality then gave way to multiple other modalities, including a one-way transition to bunchgrass dwelling and the repeated evolution of saxicoly (figure 2A,B). This is consistent with results that larger body size evolved at the base of the rapid radiation and has been retained, as most scansorial species are large-bodied, including arboreal species and rapid radiation saxicolous species [22]. Our models of evolution revealed that body size evolved under different selective regimes for scansorial and terrestrial taxa. The relatively high value of α = 6.70 suggests both groups experienced strong selection but that trait variation (σ^2) was higher for scansorial taxa. Furthermore, the adaptive peaks differed, with scansorial

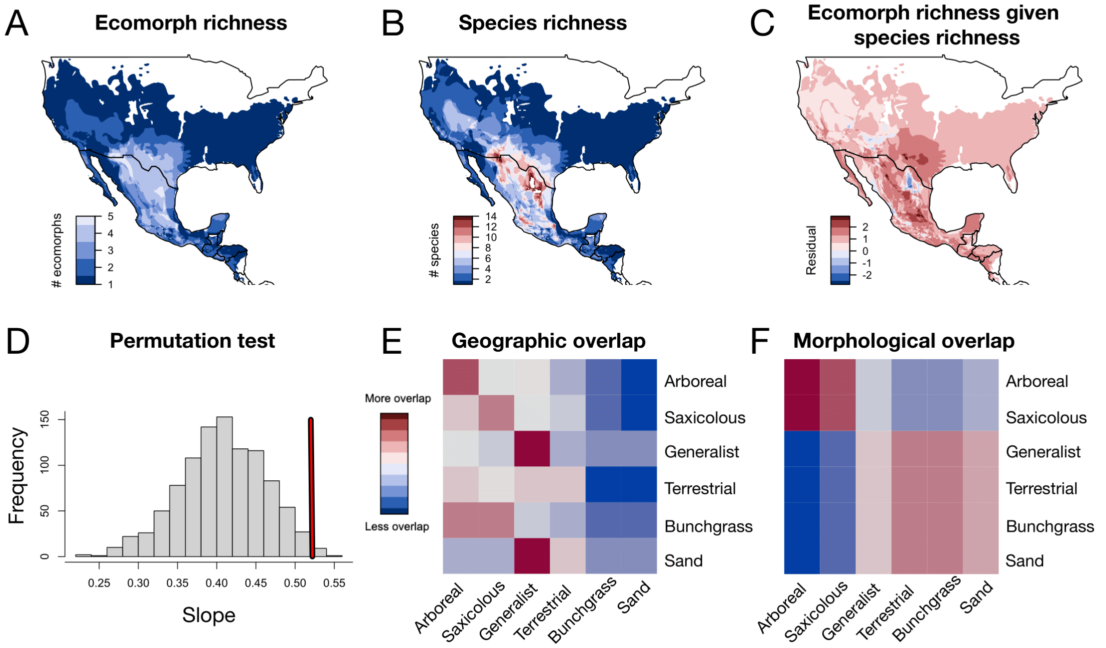

Figure 3. (A) Ecomorph richness peaks in the southwestern United States and Central Mexico. (B) Species richness also peaks in the same areas, with richness reaching 14 species per 5-minute grid cell in some areas. (C) Residuals of a regression of ecomorph richness on species richness reveal that across much of the range of the genus, *Sceloporus* ecomorphs are spatially overdispersed. (D) Distribution of slopes from our permutation test show that the observed distribution (ecomorph richness: species richness slope indicated by red line) is stronger than expected by chance. (E) Heatmap of geographic overlap between species by ecological group. (F) Heatmap of morphological overlap between species by ecological group.

Table 1. HiSSE model selection comparing ecology (terrestrial and scansorial) and parameter estimate results, including log-likelihoods, AIC, difference in AIC with minimum value (ΔAIC) and parameter estimates for speciation rate terrestrial (λ0), scansorial (λ1) and with hidden states (λA and λB). Other parameter estimates are not shown as they were not relevant to the goals of this study.

	logL	AIC	ΔAIC	λ_{0A}	λ_{1A}	λ_{0B}	λ_{1B}
null	−307.82	623.62	−9.36	0.0568	0.1005	—	—
hidden	−304.54	619.08	−4.82	0.1039	0.1039	0.0191	0.0191
ecology	−305.75	623.50	−9.24	0.0848	0.0848	—	—
ecology + hidden	−297.13	614.26	0	0.0557	0.2176	0	0.0203

taxa evolving towards larger body size relative to terrestrial taxa. Limb lengths as well showed different evolutionary optima for terrestrial and scansorial taxa. Our trait-dependent speciation analyses further revealed that speciation rates are faster in scansorial taxa (figure 2C). Thus, the transition to arboreality, a form of scansoriality, coincident with the rate shift at 20–25 Ma, may have been a key transition in *Sceloporus* that opened additional ecological and morphological space, allowing for faster speciation and the rapid accumulation of biodiversity.

Sceloporus evolved in the northern United States and Canada [72], probably invading Mexico only within the last 5 million years when the habitat became suitable [73]. Other lizards within the Nearctic guild are predominantly terrestrial (e.g. horned lizards, skinks, whiptails and night lizards) or saxicolous (e.g. collared lizards, rock lizards and desert iguanas). Arboreal lizards in this region include those in the genera *Urosaurus* (e.g. bush and tree lizards) and *Anolis*, the latter of which is found largely in the southern part of this range and arrived only in the Miocene [74]. Therefore, the arboreal niche where *Sceloporus* evolved was likely largely unoccupied and may have provided the initial opportunity for ecomorphological diversification. Arboreality has evolved many times in squamate reptiles [75] and could contribute to increased speciation by opening up new ecological space [76]. Shifts to open niche space, in this case arboreality in *Sceloporus*, can thus be key drivers of phenotypic novelty and even speciation.

Our findings that transitions between generality and terrestriality occurred frequently across the *Sceloporus* tree suggest these two states are especially labile. The fastest transition we detected occurred from sand back to generalist, suggesting the highly specialized sand ecomorphology may not be a successful long-term strategy given the limited availability of sand habitat (figure 3B). Of all the ecological modes, arboreality is the source of most transitions to other ecologies (figure 3C), again suggesting that the evolution of arboreal ecomorphology played a critical role in enabling adaptive diversification in this group.

(c) What is the spatial distribution of ecomorphological diversity?

We found evidence for spatial overdispersion of *Sceloporus* ecomorphs, suggesting that competitive exclusion plays a role in community assembly in this clade. Across the range of *Sceloporus*, species are unevenly distributed, with higher species richness occurring from Mesoamerica to Central America (figure 3B), broadly following the latitudinal diversity gradient, where diversity increases towards the tropics [77], and Rapoport's rule, where species at higher latitudes have larger ranges and less turnover [78]. Rivera *et al.* [22] showed that *Sceloporus* are phylogenetically clustered across the landscape and that heterogeneous environments, which can provide more opportunities for speciation, are positively associated with species richness. Some areas of very high species richness (e.g. north-central Mexico) are underrepresented with ecomorphs, given by negative residuals, which is likely an artefact of having only five possible ecomorphs that can co-occur in a given area, whereas species richness can reach 12 or even 14 (at the scale of our 5 arc-minute map). Tropical mountains with high species richness may offer additional microhabitat heterogeneity and niche space, such that species occupying the same ecomorph class in these regions may actually differ sufficiently in their ecologies to offset competitive overlap [79].

Furthermore, we found that ecomorphs may have different constraints on sympatry—while arboreal, saxicolous and generalist ecomorphs appear to co-occur readily, smaller ecomorphs such as the terrestrial, bunchgrass and sand ecomorphs are less likely to co-occur (figure 3E,F). This may be the result of allopatric speciation, especially within the *scalaris* clade, of which all members are bunchgrass ecomorphs and in which diversification appears tied to volcanism in the Trans-Mexican Volcanic Belt region [80]. However, bunchgrass ecomorph species are also the most ecologically and morphologically similar (figure 1C), and therefore constraints on limiting similarity may be higher. Similarly, the sand ecomorph species are the only *Sceloporus* in most parts of their specialized and restricted ranges (*S. arenicolus* in the Mescalero Sand Dune blowouts of New Mexico and Texas, *S. cowlesi* at White Sands, and *S. woodi* in the sandhill paleoislands of Florida) but do co-occur with terrestrial and generalist species in parts of their ranges. This echoes results found by Rivera *et al.* [22] that smaller species are more likely to co-occur with larger species (compared to small species) than expected by chance, whereas larger species had no such constraints and co-occurred with other large species readily. Many small-bodied species are also habitat specialists, which may be the underlying reason for their constraints on sympatry.

Of all ecomorph combinations, generalists occur most often with other generalists. This could be due in part to many of these species having larger ranges across temperate zones (e.g. *S. undulatus*, *S. occidentalis*, *S. graciosus* [23]) or because these species often exhibit lability in habitat use [36] such that they can offset their resource use in sympatry. The high degree of overlap between scansorial (arboreal and saxicolous) morphs may be a function of greater vertical space to partition, as in *Anolis* lizards [2,47,81]. Our use of aggregated polygons could overestimate community membership; however, the fact that our results support those found using occurrence data [22] suggest they are robust. Studies that continue to quantify closely related species' interactions, performance abilities and resource use in sympatry, and their relationships to morphology, will deepen our understanding of how interspecific interactions and phenotypic diversity shape patterns of co-occurrence.

5. Conclusion

Our results show that ecomorphological evolution is associated with speciation and co-occurrence in a diverse and widespread lizard radiation. We found that body size and relative limb and digit lengths differ between *Sceloporus* ecomorphs in ways consistent with functional differences in sprinting and climbing performance expected by their habitat utilization. The evolution of one of these ecomorphological forms, arboreality, is linked to an increase in speciation rate and led to further ecomorphological diversification, suggesting that some morphological shifts can precipitate the rapid accumulation of additional phenotypic novelty. Together, our results suggest that phenotypic evolution itself can create sufficient ecological opportunity, even without a shift in a lineage's geographic range or an environmental change in resource availability, to enable the rapid evolution of ecomorphological and species diversity.

Ethics. Permits for field-collected data were granted to EPW (AZGFD LIC#SP653941, SP404320, SP407158, SP808336, NMDGF #3780) and IJW (CA SC-8436). Animal care and field surveys were approved by the University of California Berkeley's Institutional Animal Care and Use Committee (Protocol AUP-2019-02-11797).

Data accessibility. Data and code supporting the conclusions of this paper are available on Dryad [82].

Supplementary material is available online [83].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. E.P.W.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; M.L.Y.: formal analysis, investigation, methodology, writing—review and editing; I.J.W.: funding acquisition, methodology, project administration, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. E.P.W. was supported by a Berkeley Fellowship (UC Berkeley), a Liu Fellowship (UC Berkeley), an NSF Graduate Research Fellowship (Grant #1752814) and an NSF Postdoctoral Fellowship in Biology (Award #2507670). M.L.Y. was supported by a Center for Population Biology Postdoctoral Fellowship from UC Davis. I.J.W. was supported by an NSF CAREER grant (Award #1845682).

Acknowledgements. This work would not have been possible without the help of collections managers and curators who went above and beyond to facilitate access to collections during the Covid-19 pandemic, including Carol Spencer at the MVZ, Emily Braker at UCM and Lauren Scheinberg at CAS. We thank UC Berkeley URAP and SPUR students Isabella Neidermair, Jiarui Wang, Maura Meijer, Annika Masaki and Coco Chen for their help in collecting morphological measurements. We thank the Wang lab at UC Berkeley for their valuable feedback on this manuscript.

References

1. Streelman JT, Danley PD. 2003 The stages of vertebrate evolutionary radiation. *Trends Ecol. Evol*. **18**, 126–131. (doi:10.1016/S0169-5347(02)00036-8)
2. Losos JB, Jackman TR, Larson A, Queiroz KD, Rodríguez-Schettino L. 1998 Contingency and determinism in replicated adaptive radiations of Island Lizards. *Science* **279**, 2115–2118. (doi:10.1126/science.279.5359.2115)
3. Bolnick DI, Lau OL. 2008 Predictable patterns of disruptive selection in stickleback in postglacial lakes. *Am. Nat*. **172**, 1–11. (doi:10.1086/587805)
4. Grant BR, Grant PR. 2003 What Darwin's finches can teach us about the evolutionary origin and regulation of biodiversity. *Bioscience* **53**, 965–975. (doi:10.1641/0006-3568(2003)053)
5. Arnold SJ. 1983 Morphology, performance and fitness. *Integr. Comp. Biol*. **23**, 347–361. (doi:10.1093/icb/23.2.347)
6. Pacala SW, Roughgarden J. 1985 Population experiments with the *Anolis* lizards of St Maarten and St Eustatius. *Ecology* **66**, 129–141. (doi:10.2307/1941313)
7. Schoener TW. 1974 Resource partitioning in ecological communities: research on how similar species divide resources helps reveal the natural regulation of species diversity. *Science* **185**, 27–39. (doi:10.1126/science.185.4145.27)
8. Pianka ER. 1974 Niche overlap and diffuse competition. *Proc. Natl Acad. Sci. USA* **71**, 2141–2145. (doi:10.1073/pnas.71.5.2141)
9. Schluter D. 2000 Ecological character displacement in adaptive radiation. *Am. Nat*. **156**, S4. (doi:10.2307/3079223)
10. Losos JB, Mahler DL. 2010 Adaptive radiation: the interaction of ecological opportunity, adaptation, and speciation. In *Evolution since Darwin: the first 150 years* (eds MA Bell, DJ Futuyma, WF Eanes, JS Levinton), pp. 381–420. New York, NY: Oxford University Press.
11. Nosil P, Reimchen TE. 2005 Ecological opportunity and levels of morphological variance within freshwater stickleback populations. *Biol. J. Linn. Soc*. **86**, 297–308. (doi:10.1111/j.1095-8312.2005.00517.x)
12. Refsnider JM, Des Roches S, Rosenblum EB. 2015 Evidence for ecological release over a fine spatial scale in a lizard from the White Sands formation. *Oikos* **124**, 1624–1631. (doi:10.1111/oik.02406)
13. Mahler DL, Revell LJ, Glor RE, Losos JB. 2010 Ecological opportunity and the rate of morphological evolution in the diversification of greater Antillean anoles. *Evolution* **64**, 2731–2745. (doi:10.1111/j.1558-5646.2010.01026.x)
14. Schluter D. 1988 Character displacement and the adaptive divergence of finches on Islands and continents. *Am. Nat*. **131**, 799–824. (doi:10.1086/284823)
15. Ford AGP, Rüber L, Newton J, Dasmahapatra KK, Balarin JD, Bruun K, Day JJ. 2016 Niche divergence facilitated by fine-scale ecological partitioning in a recent cichlid fish adaptive radiation. *Evolution* **70**, 2718–2735. (doi:10.1111/evo.13072)
16. Schluter D. 2000 *The ecology of adaptive radiation*. New York, NY: Oxford University Press. (doi:10.1093/oso/9780198505235.003.0010)
17. Wainwright PC, Smith WL, Price SA, Tang KL, Sparks JS, Ferry LA, Kuhn KL, Eytan RI, Near TJ. 2012 The evolution of pharyngognathy: a phylogenetic and functional appraisal of the pharyngeal jaw key innovation in labroid fishes and beyond. *Syst. Biol*. **61**, 1001–1027. (doi:10.1093/sysbio/sys060)
18. Yuan ML, Westeen EP. 2024 Decoupled evolution of ventral and dorsal scales in agamid lizards: ventral keels are associated with arboreality. *Biol. Lett*. **20**, 20240171. (doi:10.1098/rsbl.2024.0171)
19. Rundell RJ, Price TD. 2009 Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. *Trends Ecol. Evol*. **24**, 394–399. (doi:10.1016/j.tree.2009.02.007)
20. Webb CO, Ackerly DD, McPeek MA, Donoghue MJ. 2002 Phylogenies and community ecology. *Annu. Rev. Ecol. Syst*. **33**, 475–505. (doi:10.1146/annurev.ecolsys.33.010802.150448)
21. Hall WP. 2009 Chromosome variation, genomics, speciation and evolution in *Sceloporus* lizards. *Cytogenet. Genome Res*. **127**, 143–165. (doi:10.1159/000304050)
22. Rivera JA, Rich HN, Michelle Lawing A, Rosenberg MS, Martins EP. 2021 Occurrence data uncover patterns of allopatric divergence and interspecies interactions in the evolutionary history of *Sceloporus* lizards. *Ecol. Evol*. **11**, 2796–2813. (doi:10.1002/ece3.7237)
23. Roll U *et al*. 2017 The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nat. Ecol. Evol*. **1**, 1677–1682. (doi:10.1038/s41559-017-0332-2)
24. Leaché AD, Banbury BL, Linkem CW, de Oca ANM. 2016 Phylogenomics of a rapid radiation: is chromosomal evolution linked to increased diversification in north American spiny lizards (Genus *Sceloporus*)? *BMC Evol. Biol*. **16**, 16. (doi:10.1186/s12862-016-0628-x)
25. Warheit KI, Forman JD, Losos JB, Miles DB. 1999 Morphological diversification and adaptive radiation: a comparison of two diverse lizard clades. *Evolution* **53**, 1226–1234. (doi:10.1111/j.1558-5646.1999.tb04535.x)
26. Westeen EP, Martínez-Fonseca JG, Chen H, Wang IJ. 2023 Phenotypic diversity facilitates niche partitioning in a Sky Island assemblage of spiny lizards. *Biol. J. Linn. Soc*. **140**, 589–605. (doi:10.1093/biolinnean/blad077)
27. Laurent S, Pfeifer SP, Settles ML, Hunter SS, Hardwick KM, Ormond L, Sousa VC, Jensen JD, Rosenblum EB. 2016 The population genomics of rapid adaptation: disentangling signatures of selection and demography in white sands lizards. *Mol. Ecol*. **25**, 306–323. (doi:10.1111/mec.13385)
28. Wegener JE, Gartner GEA, Losos JB. 2014 Lizard scales in an adaptive radiation: variation in scale number follows climatic and structural habitat diversity in *Anolis* lizards. *Biol. J. Linn. Soc*. **113**, 570–579. (doi:10.1111/bij.12380)
29. Losos JB. 1990 Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecol. Monogr*. **60**, 369–388. (doi:10.2307/1943062)
30. Claunch NM *et al*. 2021 Body size impacts critical thermal maximum measurements in lizards. *J. Exp. Zool. A* **335**, 96–107. (doi:10.1002/jez.2410)
31. Rubalcaba JG, Olalla-Tárraga MÁ. 2020 The biogeography of thermal risk for terrestrial ectotherms: scaling of thermal tolerance with body size and latitude. *J. Anim. Ecol*. **89**, 1277–1285. (doi:10.1111/1365-2656.13181)
32. Adolph SC. 1990 Perch height selection by juvenile *Sceloporus* lizards: interspecific differences and relationship to habitat use. *J. Herpetol*. **24**, 69. (doi:10.2307/1564291)
33. Vitt LJ, Zani PA. 1996 Organization of a taxonomically diverse lizard assemblage in Amazonian Ecuador. *Can. J. Zool*. **74**, 1313–1335. (doi:10.1139/z96-147)
34. Losos JB. 1994 Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. *Annu. Rev. Ecol. Syst*. **25**, 467–493. (doi:10.1146/annurev.es.25.110194.002343)
35. Losos JB, Warheitt KI, Schoener TW. 1997 Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature* **387**, 70–73. (doi:10.1038/387070a0)
36. Sinervo B, Losos JB. 1991 Walking the tight rope: arboreal sprint performance among *Sceloporus* occidentalis lizard populations. *Ecology* **72**, 1225–1233. (doi:10.2307/1941096)
37. Losos JB, Sinervo B. 1989 The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *J. Exp. Biol*. **145**, 23–30. (doi:10.1242/jeb.145.1.23)
38. Reilly SM, Delancey MJ. 1997 Sprawling locomotion in the lizard *Sceloporus clarkii*: quantitative kinematics of a walking trot. *J. Exp. Biol*. **200**, 753–765. (doi:10.1242/jeb.200.4.753)
39. García-Rosales A, Ramírez-Bautista A, Stephenson BP. 2019 Comparative morphology and trophic ecology in a population of the polymorphic lizard *Sceloporus minor* (Squamata: Phrynosomatidae) from central Mexico. *PeerJ* **7**, e8099. (doi:10.7717/peerj.8099)
40. Oufiero CE, Gartner GEA, Adolph SC, Garland T. 2011 Latitudinal and climatic variation in body size and dorsal scale counts in *Sceloporus* lizards:a phylogenetic perspective. *Evolution* **65**, 3590–3607. (doi:10.1111/j.1558-5646.2011.01405.x)

41. Revell LJ. 2012 phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol*. **3**, 217–223. (doi:10.1111/j.2041-210x.2011.00169.x)
42. Meiri S. 2018 Traits of lizards of the world: variation around a successful evolutionary design. *Glob. Ecol. Biogeogr*. **27**, 1168–1172. (doi:10.1111/geb.12773)
43. Olberding JP, Herrel A, Higham TE, Garland T. 2016 Limb segment contributions to the evolution of hind limb length in phrynosomatid lizards. *Biol. J. Linn. Soc*. **117**, 775–795. (doi:10.1111/bij.12709)
44. Heimes P. 2022 *Lizards of Mexico part 1: iguanian lizards*. Frankfurt, Germany: Edition Chimaira.
45. Ballinger RE, Congdon JD. 1996 Status of the bunch grass lizard, *Sceloporus scalaris*, in the Chiricahua mountains of southeastern Arizona. *Bull. Md. Herpetol. Soc*. **32**, 67–69.
46. Foster KL, Garland T Jr, Schmitz L, Higham TE. 2018 Skink ecomorphology: forelimb and hind limb lengths, but not static stability, correlate with habitat use and demonstrate multiple solutions. *Biol. J. Linn. Soc*. **125**, 673–692. (doi:10.1093/biolinnean/bly146)
47. Williams EE. 1972 The origin of faunas: evolution of lizard congeners in a complex island fauna: a trial analysis. In *Evolutionary biology* (eds T Dobzhansky, MK Hecht, WC Steere), pp. 47–89. Boston, MA: Springer. (doi:10.1007/978-1-4684-9063-3_3)
48. Venables WN, Ripley BD. 2002 *Modern applied statistics with S*. New York, NY: Springer.
49. Arbuckle K, Bennett CM, Speed MP. 2014 A simple measure of the strength of convergent evolution. *Methods Ecol. Evol*. **5**, 685–693. (doi:10.1111/2041-210x.12195)
50. Arbuckle K, Minter A. 2015 Windex: analyzing convergent evolution using the wheatsheaf index in R. *Evol. Bioinform*. **11**, 11–14. (doi:10.4137/EBO.S20968)
51. Borges R, Machado JP, Gomes C, Rocha AP, Antunes A. 2019 Measuring phylogenetic signal between categorical traits and phylogenies. *Bioinformatics* **35**, 1862–1869. (doi:10.1093/bioinformatics/bty800)
52. Pagel M. 1994 Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. Lond. B* **255**, 37–45. (doi:10.1098/rspb.1994.0006)
53. Blomberg SP, Garland T, Ives AR. 2003 Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717–745. (doi:10.1111/j.0014-3820.2003.tb00285.x)
54. Beaulieu J, O'Meara B. In press. OUwie: analysis of evolutionary rates in an OU framework. *R package version 2.10*. See https://CRAN.R-project.org/package=OUwie.
55. Butler MA, King AA. 2004 Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *Am. Nat*. **164**, 683–695. (doi:10.2307/3473229)
56. Paradis E, Schliep K. 2019 Ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**, 526–528. (doi:10.1093/bioinformatics/bty633)
57. Huelsenbeck JP, Nielsen R, Bollback JP. 2003 Stochastic mapping of morphological characters. *Syst. Biol*. **52**, 131–158. (doi:10.1080/10635150390192780)
58. Beaulieu JM, O'Meara BC. 2016 Detecting hidden diversification shifts in models of trait-dependent speciation and extinction. *Syst. Biol*. **65**, 583–601. (doi:10.1093/sysbio/syw022)
59. Rabosky DL, Goldberg EE. 2015 Model inadequacy and mistaken inferences of trait-dependent speciation. *Syst. Biol*. **64**, 340–355. (doi:10.1093/sysbio/syu131)
60. Maddison WP, FitzJohn RG. 2015 The unsolved challenge to phylogenetic correlation tests for categorical characters. *Syst. Biol*. **64**, 127–136. (doi:10.1093/sysbio/syu070)
61. Davis Rabosky AR, Cox CL, Rabosky DL, Title PO, Holmes IA, Feldman A, McGuire JA. 2016 Coral snakes predict the evolution of mimicry across New World snakes. *Nat. Commun*. **7**, 1–9. (doi:10.1038/ncomms11484)
62. Bivand RS, Wong DWS. 2018 Comparing implementations of global and local indicators of spatial association. *Test* **27**, 716–748. (doi:10.1007/s11749-018-0599-x)
63. Yuan ML, Westeen EP, Wogan GOU, Wang IJ. 2022 Female dewlap ornaments are evolutionarily labile and associated with increased diversification rates in *Anolis* lizards. *Proc. R. Soc. B* **289**, 20221871. (doi:10.1098/rspb.2022.1871)
64. Shi JJ, Westeen EP, Katlein NT, Dumont ER, Rabosky DL. 2018 Ecomorphological and phylogenetic controls on sympatry across extant bats. *J. Biogeogr*. **45**, 1–11. (doi:10.1111/jbi.13353)
65. Pigot AL, Tobias JA. 2013 Species interactions constrain geographic range expansion over evolutionary time. *Ecol. Lett*. **16**, 330–338. (doi:10.1111/ele.12043)
66. R Core Team. 2021 R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
67. Kolbe JJ. 2015 Effects of hind-limb length and perch diameter on clinging performance in *Anolis* lizards from the British Virgin Islands. *J. Herpetol*. **49**, 284–290. (doi:10.1670/13-104)
68. Cooper WE, Avalos A. 2010 Escape decisions by the syntopic congeners *Sceloporus jarrovii* and *S. virgatus*: comparative effects of perch height and of predator approach speed, persistence, and direction of turning. *J. Herpetol.* **44**, 425–430. (doi:10.1670/09-221.1)
69. Brandley MC, Huelsenbeck JP, Wiens JJ. 2008 Rates and patterns in the evolution of snake-like body form in squamate reptiles: evidence for repeated re-evolution of lost digits and long-term persistence of intermediate body forms. *Evolution* **62**, 2042–2064. (doi:10.1111/j.1558-5646.2008.00430.x)
70. Camaiti M, Evans AR, Hipsley CA, Chapple DG. 2021 A farewell to arms and legs: a review of limb reduction in squamates. *Biol. Rev*. **96**, 1035–1050. (doi:10.1111/brv.12690)
71. Bock CE, Smith HM, Bock JH. 1990 The effect of livestock grazing upon abundance of the lizard, *Sceloporus scalaris*, in Southeastern Arizona. *J. Herpetol*. **24**, 445. (doi:10.2307/1565072)
72. Lawing AM, Polly PD, Hews DK, Martins EP. 2016 Including fossils in phylogenetic climate reconstructions: a deep time perspective on the climatic niche evolution and diversification of spiny lizards (*Sceloporus*). *Am. Nat*. **188**, 133–148. (doi:10.1086/687202)
73. Rivera JA, Lawing AM, Martins EP. 2020 Reconstructing historical shifts in suitable habitat of *Sceloporus* lineages using phylogenetic niche modelling. *J. Biogeogr*. **47**, 1–12. (doi:10.1111/jbi.13915)
74. Glor RE, Losos JB, Larson A. 2005 Out of Cuba: overwater dispersal and speciation among lizards in the *Anolis carolinensis* subgroup. *Mol. Ecol*. **14**, 2419–2432. (doi:10.1111/j.1365-294X.2005.02550.x)
75. Miller AH, Stroud JT. 2021 Novel tests of the key innovation hypothesis: adhesive toepads in arboreal lizards. *Syst. Biol*. **71**, 1–14. (doi:10.1093/sysbio/syab041)
76. Bars-Closel M, Kohlsdorf T, Moen DS, Wiens JJ. 2017 Diversification rates are more strongly related to microhabitat than climate in squamate reptiles (lizards and snakes). *Evolution* **71**, 2243–2261. (doi:10.1111/evo.13305)
77. Hillebrand H. 2004 On the generality of the latitudinal diversity gradient. *Am. Nat*. **163**, 192–211. (doi:10.1086/381004)
78. Stevens GC. 1989 The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Nat*. **133**, 240–256. (doi:10.1086/284913)
79. Janzen DH. 1967 Why mountain passes are higher in the tropics. *Am. Nat*. **101**, 233–249. (doi:10.1086/282487)
80. Bryson RW, García-Vázquez UO, Riddle BR. 2012 Relative roles of neogene vicariance and quaternary climate change on the historical diversification of bunchgrass lizards (*Sceloporus* scalaris group) in Mexico. *Mol. Phylogenet. Evol*. **62**, 447–457. (doi:10.1016/j.ympev.2011.10.014)
81. Losos JB. 2009 *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles*. Berkeley, CA: University of California Press. (doi:10.1525/california/9780520255913.001.0001)
82. Westeen E, Yuan M, Wang I. 2025 Ecomorphology is associated with speciation and co-occurrence in *Sceloporus* lizards. [Dataset]. Dryad Digital Repository. (doi:10.5061/dryad.z8w9ghxrm)
83. Westeen EP, Yuan ML, Wang IJ. 2025 Supplementary material from: Ecomorphology is associated with speciation and co-occurrence in Sceloporus lizards. Figshare. (doi:10.6084/m9.figshare.c.8172460)