

Genetic and Ecogeographic Controls on Species Cohesion in Australia's Most Diverse Lizard Radiation

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ABSTRACT: Species vary extensively in geographic range size and climatic niche breadth. If range limits are primarily determined by climatic factors, species with broad climatic tolerances and those that track geographically widespread climates should have large ranges. However, large ranges might increase the probability of population fragmentation and adaptive divergence, potentially decoupling climatic niche breadth and range size. Conversely, ecological generalism in large-ranged species might lead to higher gene flow across climatic transitions, increasing species' cohesion and thus decreasing genetic isolation by distance (IBD). Focusing on Australia's iconic *Ctenotus* lizard radiation, we ask whether species range size scales with climatic niche breadth and the degree of population isolation. To this end, we infer independently evolving operational taxonomic units (OTUs), their geographic and climatic ranges, and the strength of IBD within OTUs based on genome-wide loci from 722 individuals spanning 75 taxa. Large-ranged OTUs were common and had broader climatic niches than small-ranged OTUs; thus, large ranges do not appear to simply result from passive tracking of widespread climatic zones. OTUs with larger ranges and broader climatic niches showed relatively weaker IBD, suggesting that large-ranged species might possess intrinsic attributes that facilitate genetic cohesion across large distances and varied climates. By influencing population divergence and persistence, traits that affect species cohesion may play a central role in large-scale patterns of diversification and species richness.

Keywords: climatic niche breadth, geographic range size, isolation by distance, macroecology, speciation, species delimitation.

Introduction

Biologists have long recognized that species distributions vary along two interrelated axes: geographic range size, the extent of the world's area that a species occupies, and climatic niche breadth, the range of climatic conditions a species tolerates (Darwin 1859; Willis 1926; Hutchinson 1957). Range sizes can differ by orders of magnitude, as seen, for instance, in Amazonian frogs, African primates, and North American plants (Gaston 2003; Mittermeier et al. 2013; Morueta-Holme et al. 2013; Guillory et al. 2020). Likewise, climatic niche breadths vary extensively. Some species are found in a limited set of climatic conditions, as is the case of tropical mountaintop endemics (e.g., Strangas et al. 2019). Others can thrive across a range of climates, as illustrated by human-mediated invasives (e.g., Harper and Bunbury 2015). If tolerance to climatic factors is a primary limit on species ranges (Andrewartha and Birch 1960; Lee-Yaw et al. 2016), we might expect species with broader climatic tolerances to occupy larger geographic areas, all else being equal (Slatyer et al. 2013). In addition, large geographic ranges are presumably more likely to span broader climatic gradients than small ranges regardless of the factors behind range size (Sexton et al. 2009; Sizling et al. 2009). Therefore, differences in range size might both stem from and contribute to among-species variation in climatic niche breadth.

Empirical data are consistent with the expectation of a positive relationship between geographic range size and climatic niche breadth. As an illustrative example, figure 1A shows the significant relationship between these

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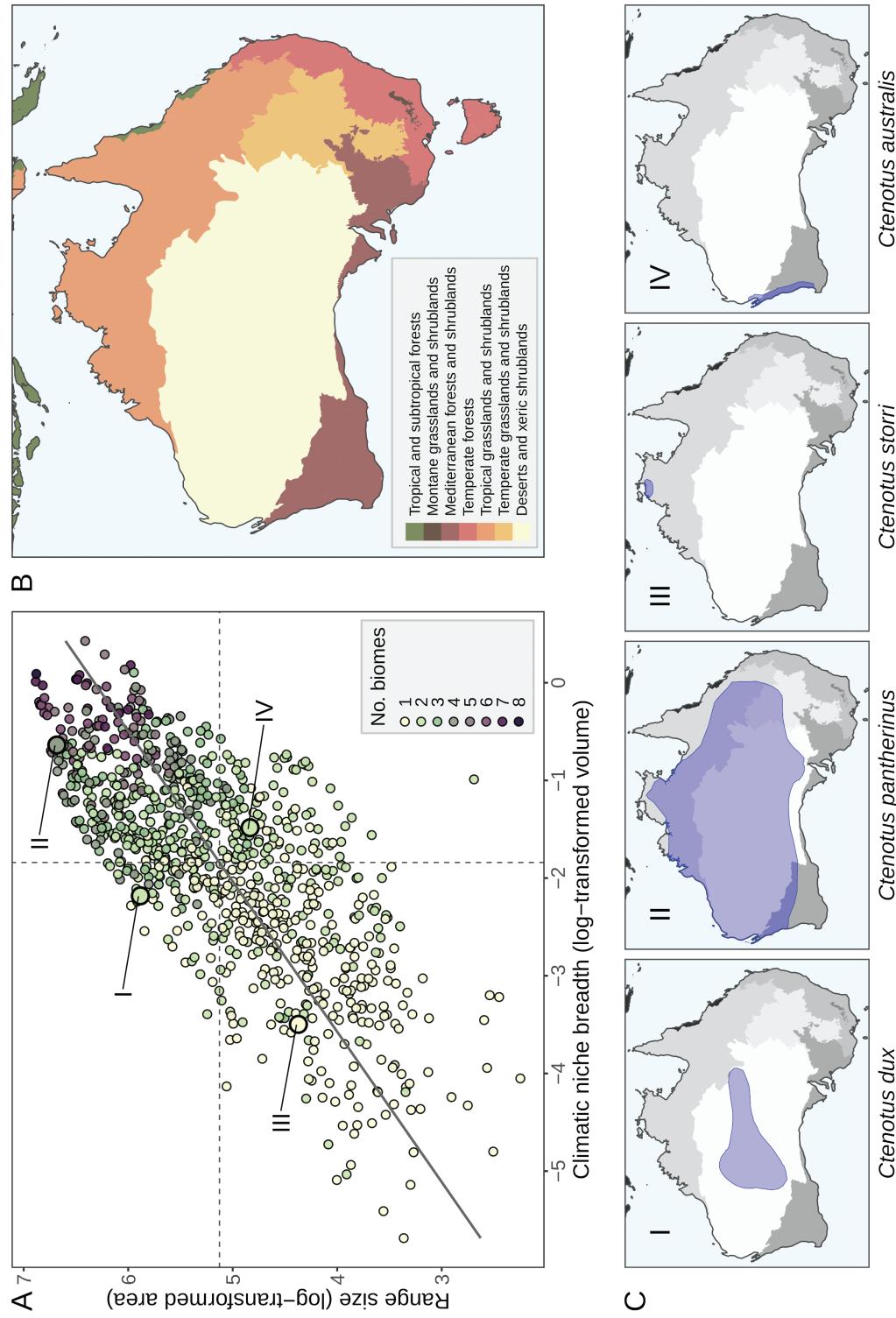


Figure 1: Variation in the spatial and climatic structure of taxon distributions. **A**, Relationship between geographic range size and climatic niche breadth in terrestrial Australian lizards and snakes ($n = 900$; $R^2 = 0.54$, $P < .001$) for currently recognized taxa. Range size corresponds to the spatial area occupied by a taxon per Roll et al. (2017). Climatic niche breadth corresponds to a hypervolume defined by four climatic variables that describe temperature and precipitation annual means and seasonality (see “Material and Methods”). The color of circles indicates the number of biomes occupied by each taxon. Roman numerals indicate representative *Ctenotus* lizard taxa that show different combinations of range size and climatic niche breadth, as follows: (I) large range size despite a relatively narrow climatic niche breadth, (II) large range and broad climatic niche, (III) small range and narrow climatic niche, and (IV) relatively small range given a broad climatic niche. Dashed lines indicate the mean value of each axis. **B**, Australia's biomes per Olson et al. (2001). **C**, Geographic distribution of the four representative *Ctenotus* taxa (I–IV) highlighted in **A** (per Roll et al. 2017). Taxon ranges indicated in blue. Biomes (indicated in grayscale) as in **B**.

two variables across 900 terrestrial Australian lizard and snake taxa (linear regression: $F_{1,898} = 1,064$, $R^2 = 0.54$, $P < .001$; for details on estimation, see “Material and Methods”). On one end of this relationship are taxa with large ranges and broad climatic niches, such as the scincid lizard *Ctenotus pantherinus*, whose distribution spans biomes that range from arid temperate deserts to tropical grasslands and shrublands (fig. 1B). On the other end are taxa with small ranges and narrow climatic niches, such as *Ctenotus storri*, restricted to tropical savannas in Australia’s Top End (fig. 1B). Even in closely related organisms within the same geographic theater—as illustrated by scincid lizards on the Australian continent—we find taxa that occur on opposite ends of the continuum defined by range size and climatic niche breadth, underlying the pervasiveness of this pattern.

This positive relationship between range size and climatic niche breadth (fig. 1) might be viewed as expected. For instance, it is consistent with the hypothesis that climatic tolerances are a primary driver of species range limits (Sexton et al. 2009; Slatyer et al. 2013; Lee-Yaw et al. 2016). On the other hand, the apparent commonness of large-ranged taxa (fig. 1) may be unexpected because large ranges spanning heterogeneous climates should be prone to fragmentation (Pigot et al. 2012). For instance, such ranges are susceptible to dissection by emerging geographic barriers (Rosenzweig 1995), favoring population divergence by genetic drift (Barraclough 2019). Even in continuously distributed species, dispersal limitation can lead to population differentiation via isolation by distance (IBD; Wright 1943; Irwin 2002). Additionally, spatial climatic gradients can promote genetic divergence through selection and local adaptation (Endler 1977; Bridle and Vines 2007; Schlüter and Conte 2009; Hohenlohe et al. 2010), leading to isolation by environment (Wang and Bradburd 2014). Given that these drivers of population divergence are more likely to affect large-ranged species, the empirical pattern depicted in figure 1A highlights a major issue: how do species, particularly those that span large areas or varied climates, remain cohesive in both genotype and phenotype?

One possibility is that species vary in their capacity for population connectivity, with large-ranged species being more resistant to the differentiating effects of geographic separation and spatial climatic gradients. Species cohesion across space has long been attributed to the homogenizing effects of population gene flow (Mayr 1963; Barker 2007; Barker and Wilson 2010). In turn, levels of gene flow may vary across species, as supported by studies reporting extensive variation in the degree of genetic IBD (Sexton et al. 2014; Singhal et al. 2018). We might expect large-ranged and ecologically generalized species to show lower IBD relative to small-ranged species because—all else being equal—a higher capacity to sustain population gene flow should de-

crease the likelihood of range splitting (Ackerly 2003). This capacity may stem, for instance, from intrinsic attributes that mediate dispersal (Ehrlich and Raven 1969) or population persistence and connectivity across climatic transitions (Ackerly 2003; Seebacher et al. 2012), leading to among-species variation in IBD. Under this model, the empirical pattern of a strong association between range size and climatic niche breadth (fig. 1A) might ultimately reflect species’ differential capacity to oppose the divergence of spatially separated populations in distinct climatic zones.

Comparative studies of distribution patterns and their potential climatic drivers have typically assumed that the underlying taxa are coherent and comparable units (Brown et al. 2014; González-Orozco et al. 2014; Zamborlini Saiter et al. 2016; Batista et al. 2020). However, many taxa once thought to be large ranged are now known to consist of divergent phylogenetic lineages. This pattern has been observed repeatedly in Australian squamates (Smith and Adams 2007; Rabosky et al. 2017; Potter et al. 2019), potentially complicating our interpretation of the relationship between range size and climatic niche breadth and our ability to compare these two variables across taxa (fig. 1). Traditionally, species delimitation has relied on organisms’ phenotypic attributes, yet the traits that diverge across species can be cryptic to humans (Zozaya et al. 2019). Conversely, high phenotypic variation among populations can complicate species delimitation, such that populations initially identified as multiple small-ranged taxa actually correspond to a single large-ranged polytypic species (Rabosky et al. 2014b). To properly understand the relationships between range size, climatic niche breadth, and IBD, the taxa must themselves be uniformly delimited. Studies of diversification dynamics have often recognized the need to delineate comparable evolutionary units (Smith et al. 2013; Ruane et al. 2014; Rabosky 2016; Singhal et al. 2018), yet macroecological analyses have rarely met this standard.

Here, we dissect the relationships between geographic range size, climatic niche breadth, and IBD in *Ctenotus*, a clade of lizards that occupies nearly all of Australia’s major biomes. *Ctenotus* includes about 100 species-level taxa that are broadly similar in morphological and life history traits (Cogger 2014). Therefore, we might expect them to have similar patterns of geographic, ecological, and genetic variation (Papadopoulou and Knowles 2016). However, whereas some of these taxa inhabit a relatively narrow set of climatic conditions within a single habitat type, others span climatically disparate forests, shrublands, grasslands, and deserts (Pianka 1969b, 1986). Australian *Ctenotus* occur in regions with little topographic variation, particularly in the extensive central arid zone (Pianka 1972; Pepper and Keogh 2021), which has likely minimized population isolation driven by geographic barriers (Potter et al. 2019). As a

result, these lizards are a promising system to investigate the relationships between range size, climatic variability, and genetic isolation on a continental scale.

Recent genetic assessments of *Ctenotus* have found deeply divergent phylogenetic lineages within morphology-defined taxa and rampant taxon paraphyly and synonymy (Rabosky et al. 2014b, 2017; Singhal et al. 2018). To ensure our study compared equivalent units, we first performed a detailed analysis to delimit operational taxonomic units (OTUs) based on genome-wide loci, which allowed us to assess the commonness (or rarity) of genetically cohesive units that span large areas and climatically heterogeneous regions. On the basis of the delimited OTUs, we estimate geographic range sizes, climatic niche breadths, and within-OTU IBD to address three questions. First, we ask whether the relationship between range size and climatic niche breadth is robust to OTU delimitation and taxonomic practice, thus assessing the extent to which previously reported patterns might have been influenced by limited comparability among the taxa considered. Second, we ask whether OTUs exhibit different levels of genetic isolation per unit of geographic distance, potentially reflecting variation in population gene flow and connectivity. We then proceed to test a core prediction from our hypothesis that species have differential capacities for cohesiveness in the presence of geographic and climatic heterogeneity: do large-ranged and ecologically generalized OTUs have weaker IBD relative to OTUs with small ranges and narrow climatic niches?

Material and Methods

A Note on Terminology

Throughout this article, we use “taxa” and “taxon” to refer to the nominal taxa currently recognized in *Ctenotus* taxonomy, most of which were defined according to morphological attributes. These taxa are taxonomic entities that may or may not correspond to “species” in an evolutionary sense. By “species,” we specifically refer to a conceptual category corresponding to separately evolving meta-population lineages (De Queiroz 1998, 2007). Applying this concept to taxonomic practice is often not trivial. Our approach employs OTUs, which we delimited on the basis of attributes expected to be present in true species (species criteria; see below). As such, these OTUs are our best approximation of species and can be understood as candidate species.

Climatic niche estimates should be interpreted as a measure of the realized climatic niche (i.e., the climatic envelope occupied by a taxon or OTU under constraints imposed by barriers to dispersal and biotic interactions; Jiménez et al. 2019). By contrast, the fundamental niche

is typically measured at taxonomic scales smaller than ours through ecophysiological experimentation (Lee-Yaw et al. 2016; but for a contestation of the biological reality of the fundamental niche concept, see Angilletta et al. 2019).

Geographic Range Size and Climatic Niche Breadth Estimation

To provide context for this investigation, we started by examining the relationship between range size and climatic niche breadth across the terrestrial Australian lizards and snakes, as currently recognized in taxonomy (fig. 1). For this analysis, we used the expert-derived taxon distribution polygons by Roll et al. (2017). We first generated 2,000 random points for each taxon, a number that evenly spanned the distribution of even the most widespread taxa while being computationally tractable. To obtain a similar spatial density of points across taxa with different range sizes, we used the speciesThin R package (Aiello-Lammens et al. 2015) to rarify these points, ensuring a minimum distance of 5 km between them. We then used the raster R package (Hijmans et al. 2015) to extract, from each resulting point, values of four bioclimatic variables (at a 30-arc-second resolution): annual mean temperature, temperature seasonality, annual precipitation, and precipitation seasonality, obtained from the CHELSA database (Karger et al. 2017). By focusing on only four variables that capture Australia’s major climatic regimes, we reduced niche dimensionality and the number of occurrence records needed for climatic niche estimation. On the basis of these data, we estimated a climatic hypervolume for each taxon. For this purpose, we used the multivariate kernel density estimation method of Blonder et al. (2014) as implemented in the hypervolume R package (Blonder et al. 2018). Following Blonder et al. (2014), we standardized the climatic variables across all points across taxa before hypervolume estimation by scaling values by their quadratic mean. With that, the resulting volumes are expressed in powers of quadratic means (i.e., a composite unit corresponding to the product of the climatic variable units; Blonder et al. 2014). We used these volumes as an estimate of climatic niche breadth. As a metric of range size for the Australian lizards and snakes, we used the area of each taxon polygon from Roll et al. (2017), expressed in square kilometers. Last, we extracted the number of biomes occupied by each taxon using the geospatial layer derived by Olson et al. (2001). We did not include taxa with ranges smaller than 20 km² ($n = 17$). These taxa, which generally occur in spatially restricted settings (e.g., islands) or are known solely from their type locality, often had a single point for climatic values, precluding hypervolume estimation.

We also used the approach described above to estimate climatic niche breadths for each delimited *Ctenotus* OTU (see below). To calculate each OTU's hypervolume, we extracted climatic information from the collection sites of individual samples (assigned to OTUs according to the delimitation results; see below). We used the sp R package (Pebesma and Bivand 2015) to estimate each OTU's range size (km^2) according to the area of a convex hull defined by the outermost collecting sites of individual samples, clipping hulls at the coastal outline of the Australian continent when needed.

Specimen Sampling

To delineate comparable evolutionary units and estimate IBD in *Ctenotus*, we used a double-digest restriction site-associated DNA (ddRAD) data set (Peterson et al. 2012). Data for most specimens (~75%) were generated by previous investigations of Australian scincid lizards (Singhal et al. 2017, 2018). For the newly sampled individuals, we obtained tissue samples through our fieldwork and loans from the Cornell University Museum of Vertebrates, Northern Territory Museum, Queensland Museum, South Australian Museum and its associated Australian Biological Tissue Collection, University of Michigan Museum of Zoology, and Western Australian Museum. The taxonomic identification of individuals was performed by the original collectors at the field or museum according to diagnostic morphological attributes.

Reduced-representation genomic data sets composed of divergent species can have high levels of missing data (Eaton et al. 2017), which might impair OTU delimitation. To minimize this issue, we assembled eight data sets corresponding to major *Ctenotus* clades, which mostly align with the traditional morphology-defined species groups in this genus (Storr et al. 1999): the *atlas*, *colletti*, *essingtonii*, *inornatus*, *leonhardii*, *pantherinus*, *schomburgkii*, and *taeniatus* clades. A ninth major clade, the *labillardieri* clade, was represented by four taxa with less than two samples each and was thus not included in OTU delimitation analyses. To inform the taxon composition of clades, we followed comprehensive molecular phylogenetic studies of scincids (Rabosky et al. 2014a; Singhal et al. 2017, 2018).

Sampling imbalance in genetic structure analyses can result in the artificial merging of undersampled groups and spurious grouping of intensely sampled localities (Puechmaille 2016; Lawson et al. 2018) and biased estimates of population genetic parameters (Battey et al. 2020). To minimize these issues, we limited the maximum number of samples per taxon per collecting site to five. Moreover, we did not include 18 taxa represented by just one or two samples after genetic filtering (see below). After these

steps and downstream filtering of single-nucleotide polymorphisms (SNPs; see below), 505 individuals representing 49 nominal *Ctenotus* taxa were included in the OTU delimitation analyses. However, to improve the inference of tree topology, phylogenetic analyses included samples from all nine *Ctenotus* major clades, including samples not used in delimitation analyses, totaling 722 samples from 75 species-level *Ctenotus* taxa.

Generation of Genetic Data

We extracted genomic DNA and generated ddRAD libraries following Singhal et al. (2017). Briefly, extractions were digested with the restriction enzymes EcoRI and MspI, and the resulting fragments were tagged with individual barcodes, polymerase chain reaction amplified, multiplexed, and sequenced on an Illumina HiSeq or NovaSeq platform (with pooling adjusted for platform read output). We used the ipyrad version 0.9.57 pipeline (Eaton and Overcast 2020) to demultiplex and assign reads to individuals according to sequence barcodes, allowing no nucleotide mismatches from individual barcodes. The number of paired-end reads ranged from ~100,000 to ~27 million per sample, with a read length of 100 base pairs. Owing to computational time constraints, only the forward reads (R1) were used in downstream analyses. We used ipyrad to perform de novo read assembly (minimum clustering similarity threshold = 0.90), align reads into loci, and call SNPs. A minimum Phred quality score (33), sequence coverage (6 times), read length (35 bp), and maximum proportion of heterozygous sites per locus (0.5) were enforced while ensuring that variable sites had no more than two alleles within an individual (i.e., a diploid genome). Newly generated demultiplexed raw sequence data were deposited in the Sequence Read Archive (BioProject PRJNA755251).

We used ipyrad to assemble an initial data set for each clade where each ddRAD locus was present in at least 60% of the sampled individuals. We extracted SNPs from these loci and removed those with a minimum allele frequency lower than 0.05 to improve inferences of population genetic structure and history (Linck and Battey 2019) and minimize spurious SNPs that result from sequencing errors (Ahrens et al. 2018). To ensure independence of SNPs, we then extracted a single SNP per locus. After these filtering steps, individuals with data for less than 50% of the final SNPs were excluded from downstream OTU delimitation analyses. We performed filtering using VCFtools version 0.1.16 (Danecek et al. 2011) and custom R scripts. Data used in all analyses have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.jm63xsjbq>; Prates et al. 2021). Computer scripts used to prepare and filter the data and perform all analyses are available through GitHub (<https://github.com/ivanprates/Ctenotus>

_species_cohesion) and Zenodo (<https://doi.org/10.5281/zenodo.5258926>).

Estimating Comparable Evolutionary Units

To compare geographic range sizes, climatic niche breadths, and genetic IBD in *Ctenotus*, we first defined comparable OTUs. We refrain from implementing coalescent-based delimitation approaches because they are computationally intractable for data sets as large as ours. Instead, we considered three sources of evidence widely used to support species delimitation (Mayr 1963; Dobzhansky 1971; Cracraft 1987; De Queiroz 1998; Mallet 2013, 2020): (1) the composition of genotypic groups from a genetic clustering approach, (2) the historical relationships between samples from a phylogenetic analysis, and (3) geographic distribution patterns (see below). We then compared the resulting OTUs with morphology-defined *Ctenotus* taxa based on the original identification of sampled individuals.

To perform genotypic clustering, we used sparse non-negative matrix factorization (sNMF), a method that is robust to departures from traditional population genetic model assumptions (Frichot et al. 2014). We ran sNMF based on the unlinked SNP data for each major *Ctenotus* clade separately using the R package LEA (Frichot and François 2015). To infer the best-fit number of clusters (K), we compared the fit of schemes under $K = 1\text{--}20$, with 50 replicates for each K . The K value that led to the lowest cross-entropy value across replicates was considered the best-fit K . We then ensured that samples assigned to the same cluster grouped in genotypic space. For that purpose, we performed a principal component analysis on the unlinked SNP data using the LEA R package and inspected biplots of the first four principal components.

To evaluate whether the inferred genotypic clusters correspond to phylogenetic lineages, we examined their correspondence with clades within *Ctenotus*. For that purpose, we performed phylogenetic inference under maximum likelihood for the entire *Ctenotus* genus using RaxML-HPC version 8.2.12 (Stamatakis 2014) through the CIPRES Science Gateway (Miller et al. 2010). We used the GTRCAT model of nucleotide evolution and estimated node support based on 100 bootstrap replicates. We included six representatives from other scincid clades as out-groups, namely, *Eremiascincus fasciolatus*, *Lerista bipes*, and *Lerista ips*. The final phylogenetic data set was composed of 83,083 SNPs, each present in at least 50% of the samples. We also used the resulting phylogeny (fig. S1; figs. S1–S7 are available online) to account for the historical relationships between OTUs when testing for associations between range size, climatic niche breadth, and population genetic isolation (see below). For that, we made the tree ultrametric based on penalized likelihood using the ape R package (Paradis et al. 2004)

and randomly sampled one individual per OTU. To visualize phylogenetic trees, we used the ape (Paradis et al. 2004), ggtree (Yu et al. 2017), and phytools (Revell 2012) R packages.

Quantifying Population Isolation and Testing for Relationships with Range Size and Climatic Niche Breadth

We tested whether OTUs with larger distributions and broader climatic niches show lower genetic isolation levels across their distribution relative to OTUs with narrow ranges and niches. To do so, we compared patterns of genetic IBD based on F_{ST} , a metric of genetic differentiation (Weir and Cockerham 1984; Weir and Hill 2002). Within each delimited OTU, we estimated pairwise F_{ST} between individuals based on the unlinked SNP data using the BEDASSLE R package (Bradburd et al. 2013). To calculate a matrix of geographic distances, we used the fossil R package (Vavrek 2011). We then estimated the slope of the relationship between genetic distances ($F_{ST}/(1 - F_{ST})$) and geographic distances for each OTU (hereafter, “IBD slopes”). We used these IBD slopes as an estimate of spatial genetic isolation within each OTU and thus as a proxy of cohesion across geographic space. Specifically, we considered a less pronounced IBD slope to indicate lower genetic isolation and thus higher cohesion over an OTU’s range. To determine whether the relationship between genetic and geographic distances was statistically significant for each OTU, we used multiple matrix regression with randomization in R (Wang 2013) employing 1,000 permutations. We then tested whether IBD slope varies as a function of range size and climatic niche breadth across the *Ctenotus* clade by implementing linear regressions in R. We also accounted for the historical relationships between OTUs in these analyses by implementing phylogenetic generalized least squares under Brownian motion ($\lambda = 1$) using the caper R package (Orme et al. 2013).

The number of samples available varied across OTUs (mean = 10.3, range = 3–37). For instance, of 48 OTUs used for IBD slope estimation, six were represented by three or four samples, a number that emerged automatically from our delimitation process (and thus could not be anticipated). Because our sampling strategy aimed to span a broad spatial area and include taxa collected only infrequently, we did not exclude OTUs represented by fewer samples from our analyses. Instead, we directly assessed whether the relationship between IBD slope and range size might have been affected by sample size. For that purpose, we performed an analysis of covariance (ANCOVA) with IBD slope as a dependent variable, range size as an independent variable, and the number of samples per OTU as a covariate.

Another potential confounding factor in these analyses is that species with large (or small) ranges might be concentrated in biomes that lead to lesser (or greater) IBD. To examine whether the relationship between IBD slope and range size is the same across biomes (as per Olson et al. 2001), we implemented another linear model in R with IBD slope as a dependent variable, range size as an independent variable, and the most frequent biome where a species occurred as a factor.

Estimates of population genetic differentiation (such as F_{ST}) might be affected by levels of within-population genetic diversity (Charlesworth 1998; Cruickshank and Hahn 2014). Additionally, genetic diversity is expected to be higher in populations with larger effective sizes (Charlesworth 2009; Lanfear et al. 2014), which might be the case of our large-ranged delimited OTUs. Therefore, we examined the potential associations between IBD slope, range size, and expected heterozygosity (a standard metric of genetic diversity) across the *Ctenotus* clade using linear regressions. To estimate expected heterozygosity based on the SNP data, we used the adegenet package in R (Jombart 2008). Last, to assess how delimitation schemes may affect estimates of IBD, range size, and climatic niche breadth, we compared OTU-based estimates with estimates for the corresponding taxa to which individuals within each OTU were originally assigned according to morphological attributes.

Results

Delimitation of Comparable Evolutionary Units

The overwhelming majority of the currently recognized *Ctenotus* taxa were described according to morphological characters. Our analyses indicate that 24 of 49 of the taxa included in our OTU delimitation analyses correspond to distinct genetic pools and are thus likely to represent separately evolving units. However, we also found evidence of both unrecognized diversity and taxonomic oversplitting within *Ctenotus*. As an illustration of the former, figure 2 presents OTU delimitation results for the *schomburgkii* clade (for results for the other seven major *Ctenotus* clades, see figs. S2, S3). In this group, samples originally assigned to the taxon *C. schomburgkii* formed two major genotypic clusters (light and dark blue in fig. 2) that are reciprocally monophyletic, have adjacent geographic distributions in central versus southwestern Australia, and show no evidence of admixture—a pattern consistent with evolutionary independence. Similarly, we inferred *C. strachanii* samples to correspond to two nonsister clades, each corresponding to a geographically coherent genotypic cluster in central and eastern Australia (yellow and light green in fig. 2, respectively). We found multiple OTUs within morpholog-

ically defined taxa in most of the major *Ctenotus* clades (fig. S2). As expected, the number of OTUs inferred within taxa increased with taxon range size ($F_{1,37} = 6.93, R^2 = 0.14, P = .01$; fig. S4).

In other cases, OTU delimitation analyses suggested that multiple nominal taxa may correspond to the same genetic pool. For instance, in the *schomburgkii* clade, samples assigned to *C. eutaenius* and *C. euclae* composed a single major genetic group (pink in fig. 2; see also fig. S2). In some instances, this pattern results from taxon misidentification, particularly among taxa with a subtle or unclear morphological diagnosis. For example, several individuals originally identified as *C. brooksi* clustered with samples attributed to *C. eutaenius* and *C. euclae*. Misidentification appeared particularly common in the *inornatus* clade, previously found to show rampant phenotypic parallelism and high levels of intraspecific trait variability (fig. S2; Rabosky et al. 2014b).

In total, delimitation analyses inferred 53 genetically and geographically coherent OTUs across the 49 nominal taxa included in delimitation analyses. Of these OTUs, 48 were represented by three or more climatically unique collecting sites, allowing climatic niche estimation. These uniformly delimited putative species were used in downstream analyses to quantify climatic niche breadths, range sizes, and genetic isolation over geographic space.

Relationship between Geographic Range Size and Climatic Niche Breadth

The range sizes and climatic niche breadths seen in the delimited *Ctenotus* OTUs spanned nearly the entire range seen in the Australian squamates as a whole (fig. 3). Even after accounting for potentially cryptic species within *Ctenotus*, widely distributed OTUs were common. This result supports that species that span large areas and varied climates are not artifacts from unrecognized diversity under the current taxonomy but a real biological pattern.

The positive relationship between range size and climatic niche breadth was statistically significant across OTUs ($F_{1,46} = 59.4, R^2 = 0.55, P < .001$) and remained so after accounting for phylogenetic autocorrelation ($F_{1,46} = 32.5, R^2 = 0.4, P < .001$). OTUs with large ranges invariably had broader climatic niches. The number of biomes occupied by an OTU generally increased with range size and climatic niche breadth (fig. 3). However, certain OTUs with broader niches were restricted to a single biome, reflecting the apparent climatic diversity within some biomes (Pepper and Keogh 2021). These findings seem to contradict the possibility that large ranges merely result from tracking narrow sets of climatic conditions that span large geographic areas.

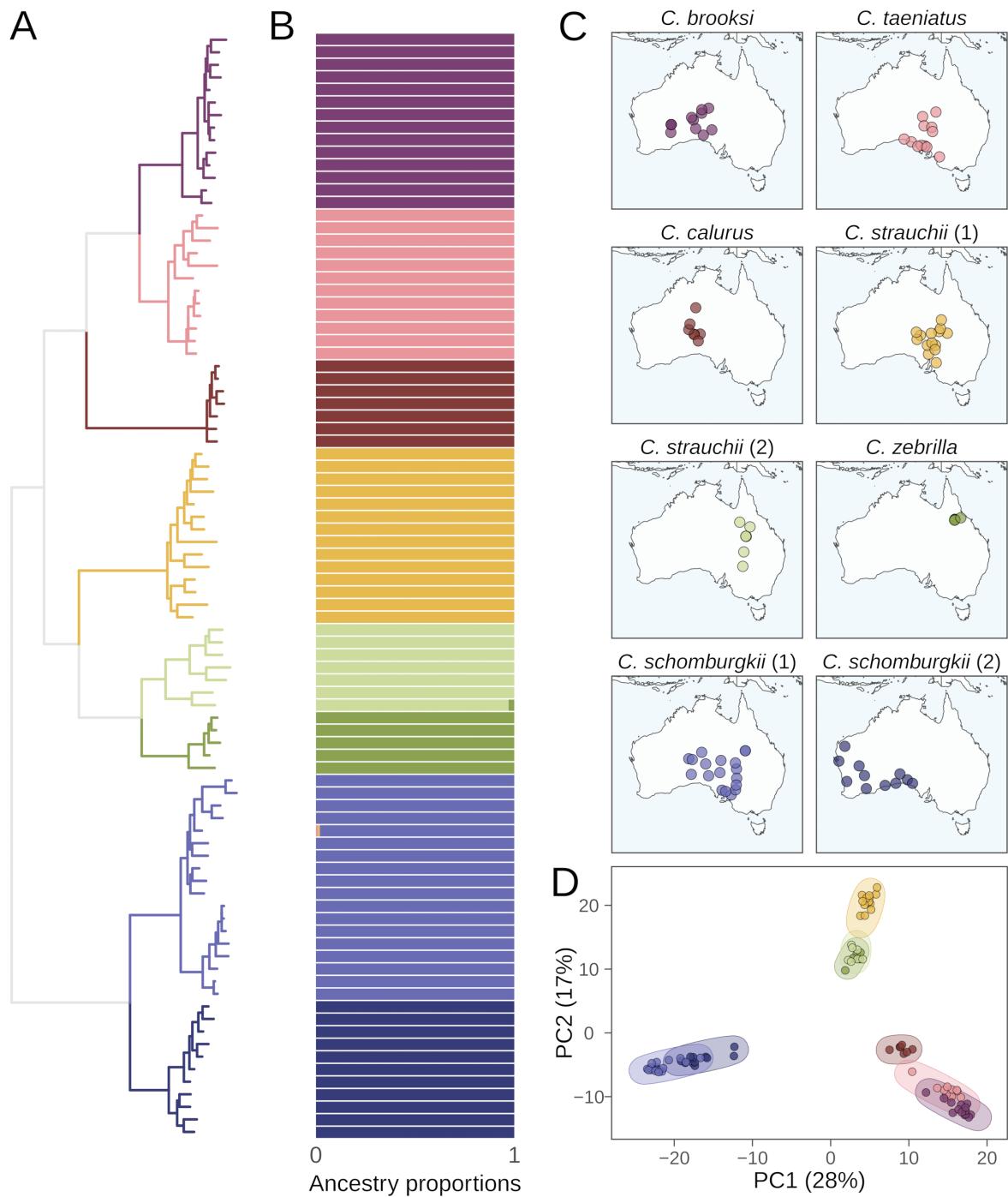


Figure 2: Operational taxonomic unit (OTU) delimitation in this study, as illustrated by *Ctenotus schomburgkii* and allied taxa. *A*, Phylogenetic relationships inferred under maximum likelihood and all double-digest restriction site-associated DNA single-nucleotide polymorphisms (SNPs). *B*, Ancestry proportions and assignment of sampled individuals to major genetic groups based on the unlinked SNP data. *C*, Geographic distributions of inferred genetic groups. Labels above maps indicate species-level taxa assigned to the majority of each OTU's samples. *D*, Sample clustering in genotypic space based on a principal component analysis of the SNP data. The plot shows PC1 and PC2; groups further separate along PC3 and PC4 (see fig. S3). Results for the other seven major *Ctenotus* clades included in the OTU delimitation analyses are presented in figure S2.

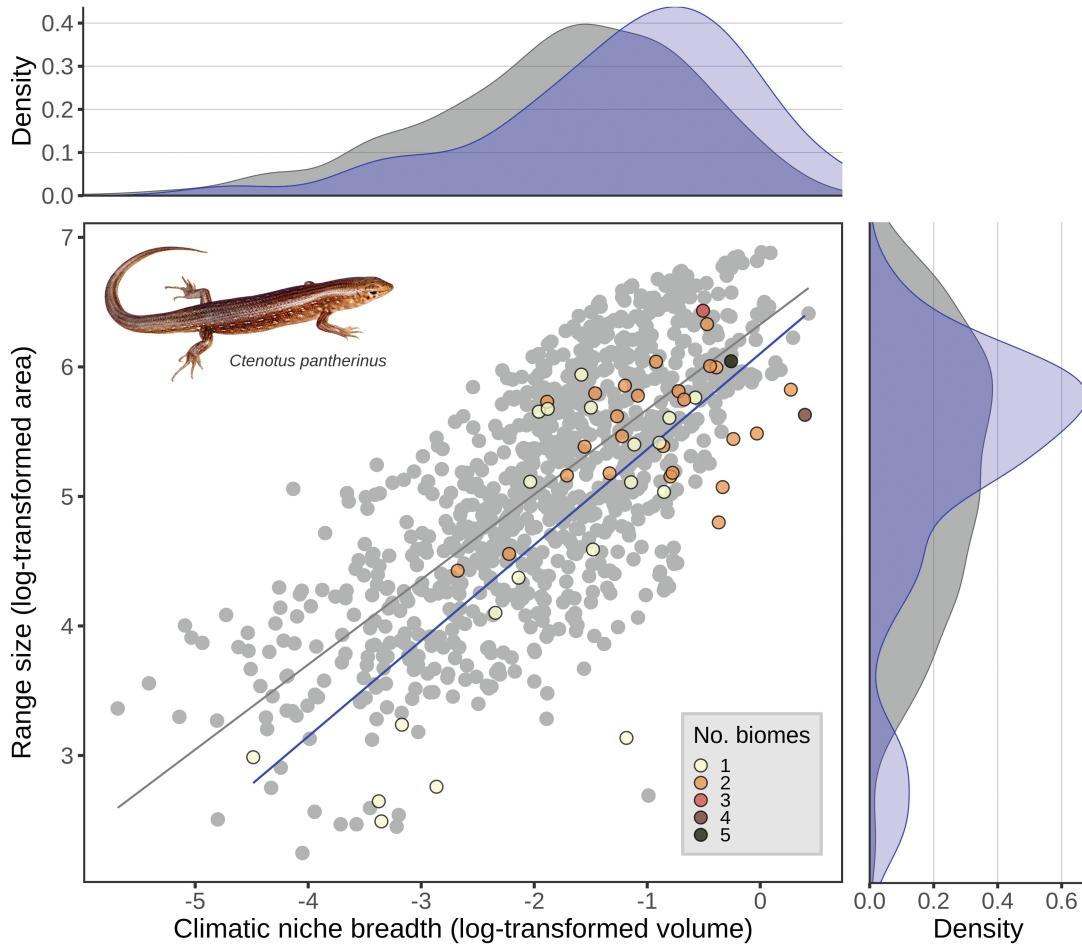


Figure 3: Relationship between geographic range size and climatic niche breadth in *Ctenotus* lizards based on the delimited operational taxonomic units (OTUs; $n = 48$). The blue line and colored circles correspond to estimates for *Ctenotus* OTUs, with circle color indicating the number of biomes where an OTU occurs. The gray line and circles indicate estimates for 900 Australian lizard and snake taxa (from Roll et al. 2017, the same data presented in fig. 1A). Density plots show the corresponding range of climatic niche breadth (top) and range size (right) values. Even after accounting for cryptic diversity and variation in taxonomic practice, there is a positive relationship between range size and climatic niche breadth ($R^2 = 0.55$, $P < .001$).

Patterns of Isolation by Distance

Pairwise F_{ST} estimates reveal a pattern of increasing genetic distance with geographic distance in 46 of 48 *Ctenotus* OTUs. This positive relationship was statistically significant in 30 OTUs ($P < .05$; multiple matrix regression with randomization). Despite this consistent pattern of genetic IBD, the slope of this relationship varied substantially across OTUs (figs. 4, S5).

Across *Ctenotus* OTUs, levels of genetic isolation by geographic distance—as described by the slope of IBD—decreased with increasing range sizes ($F_{1,46} = 32.5$, $R^2 = 0.4$, $P < .001$; fig. 5A) and niche breadths ($F_{1,46} = 12.8$, $R^2 = 0.2$, $P < .001$; fig. 5B). After accounting for phylogenetic autocorrelation, these negative relationships remained

statistically significant for range size ($F_{1,46} = 30.7$, $R^2 = 0.39$, $P < .001$) but not climatic niche breadth ($F_{1,46} = 3.4$, $R^2 = 0.05$, $P = .07$). These results suggest generally lower genetic isolation over the landscape in OTUs that span large areas and varied climates relative to small-ranged and climatically less diverse OTUs.

When accounting for the effect of biome in the relationship between IBD slope and range size or climatic niche breadth (fig. S6), we found that the interactions between biome and both range size ($F_{2,41} = 2.3$, $P = .12$) and niche breadth ($F_{2,41} = 0.7$, $P = .51$) were not significant. After removing the nonsignificant interaction terms, there was a significant effect of both range size ($F_{1,43} = 31$, $P < .001$) and niche breadth ($F_{1,43} = 13.2$, $P < .001$) on IBD slope but no effect of biome ($F_{3,43} = 1.5$, $P = .22$).

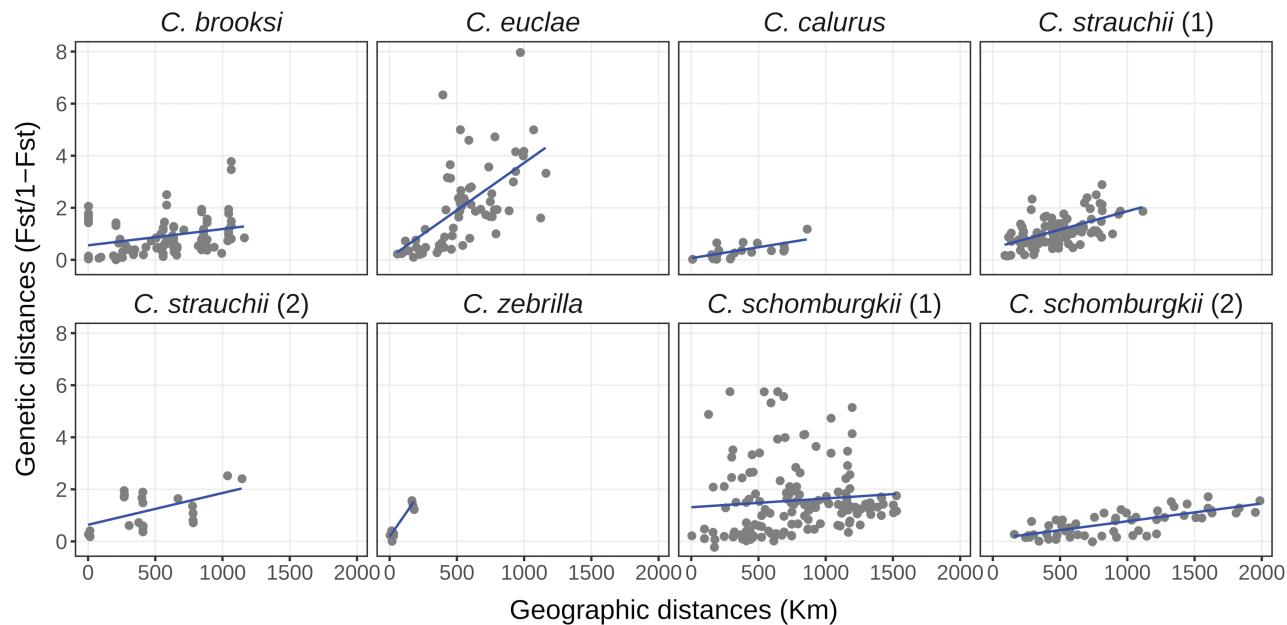


Figure 4: Relationship between genetic isolation and geographic distance, illustrated by operational taxonomic units (OTUs) in the *Ctenotus schomburgkii* clade (fig. 2). Pairwise F_{ST} based on the single-nucleotide polymorphism data was used as an estimate of within-OTU genetic isolation. To facilitate comparison, axes span the same range of values across plots. More pronounced slopes indicate higher isolation by distance between individuals within an OTU. Results for the other seven major clades of *Ctenotus* are presented in figure S5.

These results support that the relationships between IBD slope and range size or climatic niche breadth are not driven by consistent differences in IBD among biomes.

We found no association between expected heterozygosity and range size ($F_{1,46} = 3.88, R^2 = 0.06, P = .06$), suggesting no consistent differences in genetic diversity

levels across small- and large-ranged OTUs (fig. S7). Additionally, we found no association between IBD slope and expected heterozygosity ($F_{1,46} = 3, R^2 = 0.04, P = .09$), supporting that variation in the strength of IBD across OTUs does not simply reflect variation in genetic diversity levels (fig. S7).

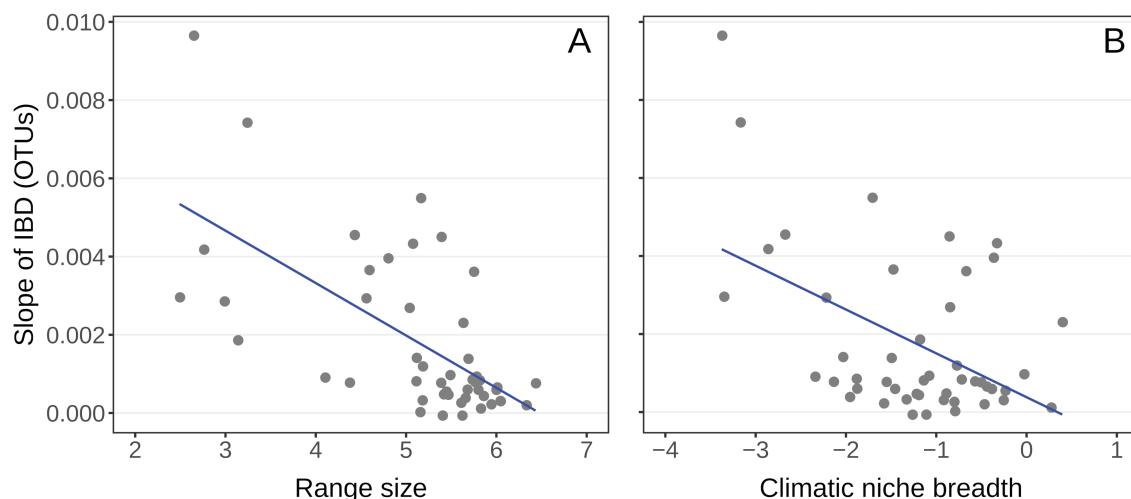


Figure 5: Predictors of genetic isolation by distance (IBD) levels across all *Ctenotus* operational taxonomic units (OTUs; $n = 48$). Lower IBD slopes indicate lower genetic IBD within a given OTU. *A*, Within-OTU IBD slopes are negatively correlated with range size ($R^2 = 0.4, P < .001$). *B*, These IBD slopes are also negatively correlated with climatic niche breadth ($R^2 = 0.2, P < .001$).

An analysis of the relationship between IBD slope and range size including the number of samples per OTU as a covariate found no significant effect of sample size ($F_{2,45} = 15.89, P = .94$). By contrast, range size continued to have a significant effect on the slope of IBD ($P < .001$), confirming that the negative association between those two variables cannot be explained by variation in the number of samples among OTUs.

Effects of Species Delimitation on Macroecological Estimates

Species delimitation scheme affected estimates of range size, climatic niche breadth, and IBD (fig. 6). For all three metrics, estimates based on the morphologically defined taxa to which individuals were originally assigned resulted in both higher and lower values relative to estimates based on the delimited OTUs. Taxon-based range sizes and climatic niche breadths (fig. 6A, 6B) spanned the same range of values as OTU-based estimates. By contrast, taxon-based IBD slopes were up to 10 times as high as OTU-based estimates (fig. 6C).

Discussion

Few studies have applied a standardized scheme to address the impacts of inconsistent species delimitation on macroecological patterns. Therefore, reported patterns of geographic range variation have typically relied on unstated assumptions about the comparability of the underlying units (e.g., Letcher and Harvey 1994; Blackburn and Gaston 1996; Waldron 2007; Slatyer et al. 2013; Zagmajster et al. 2014; Cardillo 2015; Pie and Meyer 2017). Using a uniform approach to delimit OTUs in *Ctenotus* lizards, we confirmed that range variation does not simply reflect heterogeneous species delimitation. The OTUs showed extensive variation in range size and climatic niche breadth, which spanned the same range of values we estimated for the (largely morphology-defined) Australian lizard and snake taxa as a whole. Even under this uniform delimitation scheme, large-ranged and ecologically generalized OTUs were common.

Additionally, our results provide little support for the hypothesis that large ranges result from narrow climatic envelopes that spread over extensive geographic areas (James and Shine 2000; Ackerly 2003). Instead, OTUs with larger ranges generally had broader climatic niches and often occurred in multiple biomes. These large-ranged and ecologically diverse OTUs typically had relatively weaker genetic IBD, which suggests a possible mechanism for the observed relationship between range size and climatic niche breadth. In particular, species with attributes that facilitate popu-

lation connectivity should be able to maintain coherent ranges across large areas. In contrast, species that cannot maintain such connectivity will tend to fragment into smaller units. Under this model, the pattern of strong coupling between range size and climatic niche breadth (figs. 1, 3) might ultimately originate from species traits that oppose the genetic differentiation of spatially separated populations in distinct climatic zones.

Effects of Species Delimitation on Macroecological Patterns

To assess the relationship between range sizes, climatic niche breadths, and IBD, we first delimited comparable OTUs—a step that is rarely part of macroecological analyses. To achieve this goal, we relied on three species criteria widely employed in delimitation studies: (1) that conspecific individuals tend to share derived genetic variants and thus form a monophyletic group; (2) that conspecifics comprise a cohesive genetic pool, sharing strongly correlated genome-wide allele frequency patterns; and (3) that conspecifics span a coherent and mostly continuous geographic area, allowing population gene flow (Mayr 1963; Dobzhansky 1971; Cracraft 1987; De Queiroz 1998; Mallet 2013, 2020). Many of the OTUs we delimited under these expectations correspond to long-recognized *Ctenotus* taxa, primarily described according to morphological attributes (e.g., Storr 1973, 1975, 1988; Ingram 1979; Horner 2009). However, our results also highlight cases that may require additional investigation of taxon limits and composition. In some instances, genotypic clustering analyses grouped samples that composed distinct clades and were initially assigned to different taxa according to morphology, as was the case of *C. euclae* and *C. taeniatus*. In other cases, OTU pairs corresponded to a single taxon, as seen in *C. schomburgkii* (fig. 2). These intrataxon OTUs were geographically coherent and formed distinct clades and genotypic clusters. They may also correspond to known phenotypic breaks within taxa, as is the case of *C. schomburgkii*, where the OTUs that emerged from our analyses may correspond to known color morphs (Storr et al. 1999; Wilson and Swan 2017).

Employing a uniform framework to outline OTUs affected some downstream inferences of macroecological variables. OTU-based estimates of range size and climatic niche breadth were both greater and less than estimates based on the taxa to which individuals were originally assigned (fig. 6). Taxon-based estimates of IBD were up to 10 times as high as OTU-based estimates, a pattern consistent with lumping of different species under the same taxon name. These findings support that incomplete delimitation and variation in taxonomic practice can influence estimates

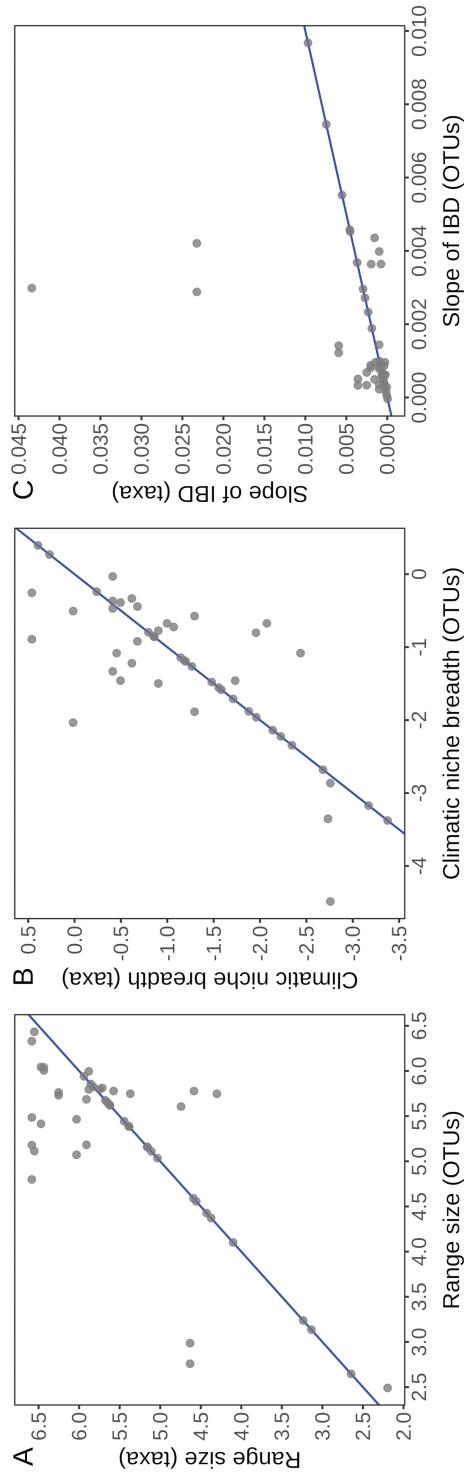


Figure 6: Effect of the delimitation scheme on estimates of range size (A), climatic niche breadth (B), and isolation by distance (IBD) slope (C). Each plot compares estimates based on the delimited OTUs (horizontal axes) versus the corresponding morphology-based taxa to which individuals were originally assigned (vertical axes). The blue lines correspond to identical values on both axes (i.e., $x = y$). Taxon-based estimates were both overestimated (points above the lines) and underestimated (points below the lines) relative to OTU-based estimates.

of species richness and turnover, ecological niches, and population genetic differentiation. We note, however, that these effects are likely clade specific, reflecting the status of the associated taxonomic knowledge (Melville et al. 2021; Moura and Jetz 2021).

Extrinsic and Intrinsic Drivers of Range Size and Climatic Niche Breadth Variation

Both extrinsic and intrinsic factors could generate the range size variation seen in *Ctenotus* and other taxa (Gaston 2003; Sexton et al. 2009; Slatyer et al. 2013). One potential extrinsic factor is geographic barriers to dispersal (Sheth et al. 2020), long recognized to limit species distributions (Wallace 1854; Darwin 1859). However, macroecological studies have noted that taxon range limits in *Ctenotus* cannot be readily attributed to landscape features that might limit dispersal (Pianka 1969a), in agreement with an apparent pattern of idiosyncratic range limits among our delimited OTUs (fig. S2). Accordingly, Australia generally lacks major physiographic features that might limit dispersal by terrestrial vertebrates in obvious ways, particularly in its vast and largely featureless central arid zone (Pianka 1972; James and Shine 2000; Pepper and Keogh 2021). In addition to such barriers, current species ranges may have been influenced by historical shifts in habitat distributions (Graham et al. 2006; Carnaval and Moritz 2008; Prates et al. 2016). However, while information on *Ctenotus* is lacking, studies of many Australian taxa have found idiosyncratic responses to Plio-Pleistocene climate change (Byrne et al. 2011; Potter et al. 2018; Pepper and Keogh 2021). This situation contrasts with other world regions where major transitions in the composition of regional species pools (or phylogenetic lineages) overlap with landscape features, such as mountains and rivers, or the presumed distributions of past habitats (e.g., Hewitt 2000; Graham et al. 2009; Oliveira et al. 2017).

Range sizes might also be influenced by extrinsic environmental factors. For instance, species with narrow climatic niches might acquire large distributions by tracking geographically widespread climates (Ackerly 2003). It has been suggested that such tracking might account for the high richness of *Ctenotus* assemblages in the arid zone, given the larger size of this biome relative to others (James and Shine 2000). Contrary to this hypothesis, we found that large-ranged OTUs mainly have broad climatic niches (fig. 3). While the range limits of certain OTUs roughly align with the climatic transitions that correspond to Australian biome boundaries (González-Orozco et al. 2014), several OTUs span multiple biomes, and both widely distributed OTUs and narrowly distributed OTUs occur within any given biome (fig. S2). These patterns suggest that spa-

tial climatic transitions are insufficient to explain the extensive range size and climatic niche breadth variation seen in *Ctenotus* lizards.

Another extrinsic environmental factor that might limit species distributions is biotic interactions. Several studies of *Ctenotus* have focused on the contribution of interspecific competition to ecological assemblage structure. For instance, regional co-occurrence of 14 or more *Ctenotus* taxa in Australia's arid zone has been attributed to divergence in diet, time of activity, habitat, and microhabitat use (Pianka 1969b; Rabosky et al. 2011). Competition-driven character displacement was invoked to explain assemblage-wide overdispersion in ecologically relevant traits in *Ctenotus* (and other lizard clades) at a local spatial scale (Rabosky et al. 2007, 2011). However, assemblage-wide trait diversity is nearly constant at a broader regional scale (Rabosky et al. 2007), and possible links between competition and taxon distributions remain unclear. How other types of biotic interactions—such as predation, parasitism, and hybridization with closely related species (Ricklefs 2010)—affect distribution patterns in *Ctenotus* is yet to be determined.

Among-species variation in range size and niche breadth might also be influenced by intrinsic organismal factors (Sheth et al. 2020). One example is traits that affect dispersal, invoked to explain range size variation in birds, bats, and insects, for instance (Böhning-Gaese et al. 2006; McCulloch et al. 2017; Luo et al. 2019). In *Lerista*, the clade sister to *Ctenotus*, taxa show varying degrees of limb reduction, which, in turn, predict some of the variance in range size (Lee et al. 2013). Limb reduction across *Lerista*, *Ctenotus*, and closely related clades is also associated with higher IBD (Singhal et al. 2018), suggesting that traits that mediate dispersal capacity may impose limits to range size by constraining gene flow across regions. Organismal traits might also contribute to among-species variation in climatic niche breadth. For instance, physiological studies of ectothermic organisms have reported among-population variation in thermal performance curves matching local climates (Wilson 2001; Gaitán-Espitia et al. 2014; Llewelyn et al. 2016; Kosmala et al. 2018). Last, the range of conditions where a species can occur is influenced by behavioral traits. For instance, lizards can adjust basking frequency and microhabitat use to local temperatures (Adolph 1990; Navas 2002), thus bypassing the need for adaptation (Buckley et al. 2015). Variation in thermal behavior has been reported among closely related taxa, which can range from thermoregulators to thermoconformers (Huey et al. 2009; Ibargüengoytía et al. 2010). Unfortunately, these types of data are largely lacking for *Ctenotus*, preventing a test of which phenotypic attributes may contribute to range size and climatic niche breadth variation. To fill these gaps, future studies will benefit from gathering information on

morphophysiological and behavioral variation across this diverse clade.

Evolutionary Causes and Consequences of Species Cohesion

Our finding of many large-ranged OTUs poses the question of what factors maintain species cohesion over large geographic distances. We found that large-ranged OTUs have shallower IBD slopes relative to OTUs with smaller ranges, consistent with the hypothesis of a higher capacity (or propensity) for cohesion in large-ranged species. This pattern might indicate that range size is primarily determined by dispersal, under the premise that IBD variation tracks differences in dispersal capacity across species (Wright 1943; Sexton et al. 2014). However, it is also possible that both range size and IBD are independently determined by species' climatic tolerances, such that species with broad tolerances might be able to persist across a range of environmental conditions without the ensuing disruption of gene flow. This combination of broad tolerances with sustained gene flow might be achieved through phenotypic plasticity and even local adaptation, as long as the behavioral and morphophysiological traits under selection (and their underlying genes) are unrelated to reproductive isolation (Ackerly 2003; Seebacher et al. 2012). By allowing populations to persist in varied conditions while remaining interconnected, factors that broaden species-level environmental tolerances may play a central role in species cohesion over large areas.

The potentially central role of gene flow in species cohesion has long been recognized (Mayr 1963; Barker and Wilson 2010). Nevertheless, other factors may buffer species from genetic (and phenotypic) change (Ehrlich and Raven 1969; Barker 2007), some of which may disproportionately affect species with large ranges. For instance, these species might have larger effective population sizes, resulting in less genetic divergence from drift (Excoffier and Ray 2008). However, we found no relationship between range size and heterozygosity, which is expected to scale with effective population size (Lande and Barrowclough 1987). Conversely, larger population sizes also increase the effectiveness of selection and thus the potential for adaptation (Charlesworth 2009; Lanfear et al. 2014). It is currently unknown whether populations of large-ranged *Ctenotus* species show genetically determined adaptations to local climates. Nevertheless, our finding of relatively lower IBD in OTUs with broad climatic niches suggests that spatial climatic gradients do not constrain population genetic connectivity. Accordingly, whereas local adaptation can sometimes contribute to reproductive isolation (Sobel et al. 2010; Nosil 2012), there is increasing evidence that this process rarely leads to speciation between para-

patic populations (Seehausen et al. 2014). Instead, locally adapted populations can sustain high gene flow levels even when the genomic regions that underpin adaptive phenotypes become markedly differentiated (Feder et al. 2012; Harrison 2012).

Our finding of extensive variation in IBD across OTUs has implications for our understanding of speciation and extinction over macroevolutionary timescales. If certain species are more prone to range fragmentation, they may have a greater probability of diversifying into multiple new species (Rabosky 2016). By affecting speciation probability, variation in species cohesion might influence evolutionary diversification and regional species richness. In this view, relative cohesiveness would be similar to other emergent species-level traits that lead to differential species proliferation (or "species selection") through its impact on speciation and extinction rates (Arnold and Fistrup 1982; Jablonski 2008). For instance, levels of genetic structure correlate with speciation rates in birds, although much variation in speciation remains unexplained (Harvey et al. 2017). By contrast, the strength of IBD did not predict speciation rate variation across the sphenomorphine lizard clade (in which *Ctenotus* is nested), though this association might be hard to identify at this narrow phylogenetic scale (Singhal et al. 2018). Establishing direct links between species cohesion and evolutionary diversification can also be complicated by the expected higher extinction rate of isolated populations, for instance, due to small population sizes (Harvey et al. 2019; Prates and Singhal 2020). Whether isolated populations will complete speciation or go extinct might be context dependent, as determined, for instance, by long-term habitat persistence tied to climatic stability (e.g., Carnaval et al. 2014; Dynesius and Jansson 2014). A synthetic understanding of the population-level controls on macroevolutionary dynamics is likely to require further investigations of the intrinsic and extrinsic factors that influence species cohesion through evolutionary time.

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Statement of Authorship

I.P., S.S., and D.L.R. conceived and designed the study. S.S. and D.L.R. supervised the study. S.S., C.M., S.C.D., and D.L.R. acquired funding. C.M., S.C.D., and D.L.R. provided resources. S.S., M.R.M.-R., M.R.G., and D.L.R. designed data collection. S.S., M.R.M.-R., and M.R.G. collected data. I.P. wrote computer scripts and prepared figures. I.P., S.S., and D.L.R. analyzed data and drafted the manuscript. I.P., S.S., M.R.M.-R., M.R.G., C.M., S.C.D., and D.L.R. edited the manuscript.

Data and Code Availability

Data used in all analyses have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.jm63xsjbq>; Prates et al. 2021). Newly generated demultiplexed raw DNA sequence data have been deposited in the Sequence Read Archive (BioProject PRJNA755251). R and UNIX shell scripts used to prepare and filter the data and perform all analyses are available through GitHub (https://github.com/ivanprates/Ctenotus_species_cohesion) and Zenodo (<https://doi.org/10.5281/zenodo.5258926>). A copy of the supplemental material is available at Zenodo (<https://doi.org/10.5281/zenodo.5258928>).

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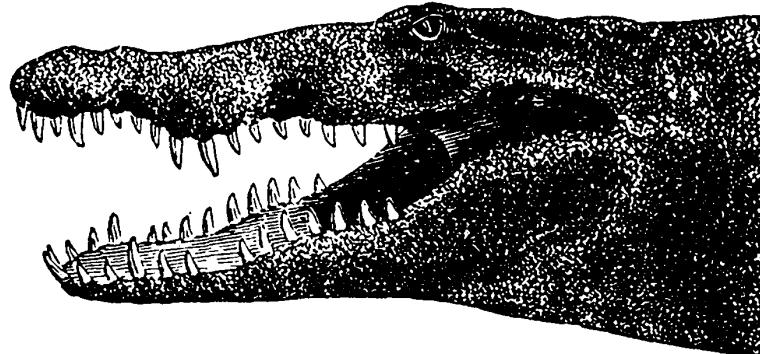
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"In the warm, placid waters of tropical streams whose banks are bordered by reedy marshes and forests of perpetual green, is the home of the crocodile. About the middle of the day numbers may be seen lying lazily on the banks enjoying the heat, their polished scales shining in the sunlight, and all looking the very picture of tropical languor and repose." From "The Crocodile in Florida" by Wm. T. Hornaday (*The American Naturalist*, 1875, 9:498–504).