

Genetic variability and the ecology of geographic range: A test of the central-marginal hypothesis in Australian scincid lizards

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Abstract

For many species, both local abundance and regional occupancy are highest near the centre of their geographic distributions. One hypothesis for this pattern is that niche suitability declines with increasing distance from a species geographic centre, such that populations near range margins are characterized by reduced density and increased patchiness. In these smaller edge populations, genetic drift is more powerful, leading to the loss of genetic diversity. This simple verbal model has been formalized as the central-marginal hypothesis, which predicts that core populations should have greater genetic diversity than edge populations. Here, we tested the central-marginal hypothesis using a genomic data set of 25 species-level taxa of Australian scincid lizards in the genera *Ctenotus* and *Lerista*. A majority of taxa in our data set showed range-wide patterns of genetic variation consistent with central-marginal hypothesis, and eight of 25 taxa showed significantly greater genetic diversity in the centre of their range. We then explored biological, historical, and methodological factors that might predict which taxa support the central-marginal hypothesis. We found that taxa with the strongest evidence for range expansion were the least likely to follow predictions of the central-marginal hypothesis. The majority of these taxa had range expansions that originated at the range edge, which led to a gradient of decreasing genetic diversity from the range edge to the core, contrary to the central-marginal hypothesis.

KEYWORDS

Australia, central-marginal hypothesis, ddRAD, genetic variation, historical demography, lizards

1 | INTRODUCTION

Whether they are big or small, species geographic ranges can be divided into core and edge populations. Verbal models from macroecology and population genetics predict that patterns of population abundance, individual fitness, and genetic diversity should differ across core and edge populations (Brown, 1984; Sagarin & Gaines, 2002), which can then contribute to the formation of range limits (García-Ramos & Kirkpatrick, 1997; Gaston, 2003).

At the centre of their range, species are hypothesized to be optimally adapted for the habitat, allowing them to maintain large, interconnected populations characterized by high local abundance (Brown, 1984; Sagarin & Gaines, 2002). Moving away from the centre, the habitat becomes more marginal, leading to decreased reproductive output (Angert, 2006; Gaston, 2009; Pigott & Huntley, 1981). Or, favourable habitat may become increasingly patchy towards the range edge, leading to depression of regional abundance relative to range centres. Populations towards

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the edge thus become smaller and more disconnected. Further, because these smaller populations are likely more subject to genetic drift and the swamping effects of gene flow from the range centre (Hoffmann & Blows, 1994; Kirkpatrick & Barton, 1997), they are less able to adapt to local, marginal conditions (Bridle & Vines, 2007; Emery et al., 2011; Lenormand, 2002). Thus, in the range centre, where populations are large and connected, populations will show high levels of genetic diversity and low levels of genetic differentiation (Eckert et al., 2008; Mayr, 1970). Conversely, small and isolated edge populations will exhibit low levels of genetic diversity and high levels of genetic differentiation. These expectations for how population abundance and genetic diversity vary across the range have been formalized as the abundant-centre and central-marginal hypotheses, respectively (Brown, 1995; Eckert et al., 2008).

Despite their intuitive appeal, both the abundant-centre and central-marginal hypotheses have mixed support in the literature (as reviewed in Dallas et al., 2017; Lira-Noriega & Manthey, 2014; Pennington et al., 2021; Pironon et al., 2017). This mixed support has a few potential explanations. First and foremost, the biological assumptions underpinning these hypotheses might be wrong—for example, perhaps niche suitability does not decline towards a range edge (Helmuth et al., 2002), perhaps population abundance does not vary predictably with niche suitability (Dallas et al., 2017; Dallas & Hastings, 2018), perhaps gene flow is not asymmetric between central and marginal populations (Kottler et al., 2021). Additionally, some have argued that geographic definitions of range core versus edges are irrelevant (Martínez-Meyer et al., 2013). Rather, core versus edge populations should be defined by how well they reflect the idealized environmental conditions for a species (Weber et al., 2017). Ecological distance from core environmental conditions might then better predict patterns of abundance and genetic diversity than geographic distance. Further, methodological issues—such as testing core-edge transects that span latitudinal and elevational gradients (Guo, 2012) or defining core versus edge populations for complex range geometries—can also complicate studies of the abundant-centre and central-marginal hypotheses.

Another possible confounding factor is demographic history, because it can also affect how genetic diversity is distributed across a range (Hewitt, 1999). One notable example is range expansions. As a species range expands, individuals disperse out of founding populations and establish new populations through repeated population bottlenecks (DeGiorgio et al., 2009; Excoffier et al., 2009). These serial founder effects lead to reduced levels of genetic diversity along the expanding range edge, high structure among populations, and clines in allele frequency centred on the origin of the expansion (Peter & Slatkin, 2013; Slatkin & Excoffier, 2012). Thus, both the central-marginal hypothesis and range expansions should lead to reduced genetic diversity and increased genetic differentiation in edge populations. These shared expectations can make it difficult to disentangle the effects of historical versus current demography on patterns of genetic diversity across a species range (Duncan et al., 2015).

In this study, we address this challenge by combining inference of historical demography and estimation of current genetic patterns to test the central-marginal hypothesis across 25 species-level taxa of Australian scincid lizards in the genera *Ctenotus* and *Lerista*. These taxa are largely codistributed (Figure 1, Appendix S1) and thus experienced the same biogeographic dynamics. Further, range limits in Australia generally do not correspond to sharp physical barriers or steep environmental gradients but rather seem to track subtler features of a relatively flat and gradually changing physiography (James & Shine, 2000; Pianka, 1972). Because of this, Australian taxa are somewhat of a “best case” scenario for detecting central-marginal structure. Here, using a final data set of 457 individuals and an average of 17K loci, we tested the predictions of the central-marginal hypothesis by determining if genetic diversity declines with distance from the range centre. Then, we fit demographic models of population growth and range expansion to our data to determine which historical demographic processes might be structuring genetic diversity. Finally, given the equivocal support for the central-marginal hypothesis in our data set, we determine which biological, historical, or methodological factors—if any—predict whether or not we recover support for the central-marginal hypothesis. To our knowledge, our study is the largest test yet of the central-marginal hypothesis using original data. Thus, our study represents an opportunity to determine the generality of this hypothesis.

2 | MATERIALS AND METHODS

2.1 | Sampling and genetic data collection and analysis

To determine how genetic diversity varies across geographic ranges, we initially analysed genetic data from 923 individuals from 142 nominal species across two species-rich genera of Australian scincid lizards: *Ctenotus* and *Lerista*. Samples were selected to span the geographic range of species (Figure S2); more individuals were sampled from broad-ranging than narrow-ranging species (r of sample and range size: 0.78, p -value = $1.29\text{e-}28$).

Genetic data from these individuals were previously published in Singhal, Huang, et al. (2018) and Singhal et al. (2017). Full details on data collection and analysis are available in these studies; we briefly summarize the approach here. We first collected genetic data using double digest restriction-site associated DNA sequencing (ddRADseq; Peterson et al., 2012). Then, we assembled reads using RAINBOW version 2.04 (Chong et al., 2012). Like many squamate species (Leaché & Fujita, 2010; Singhal, Hoskin, et al., 2018), nominal species in *Ctenotus* and *Lerista* often comprise multiple, cryptic lineages (Prates et al., 2022; Rabosky et al., 2014; Singhal, Huang, et al., 2018). Accordingly, we first delimited putative operational taxonomic units (OTUs) across these genera. For each genera, we first identified homologous loci across all individuals by using VSEARCH version 1.11.1 with a 80% clustering (Rognes et al., 2016). Then, we concatenated homologous loci with <40% missing data and used

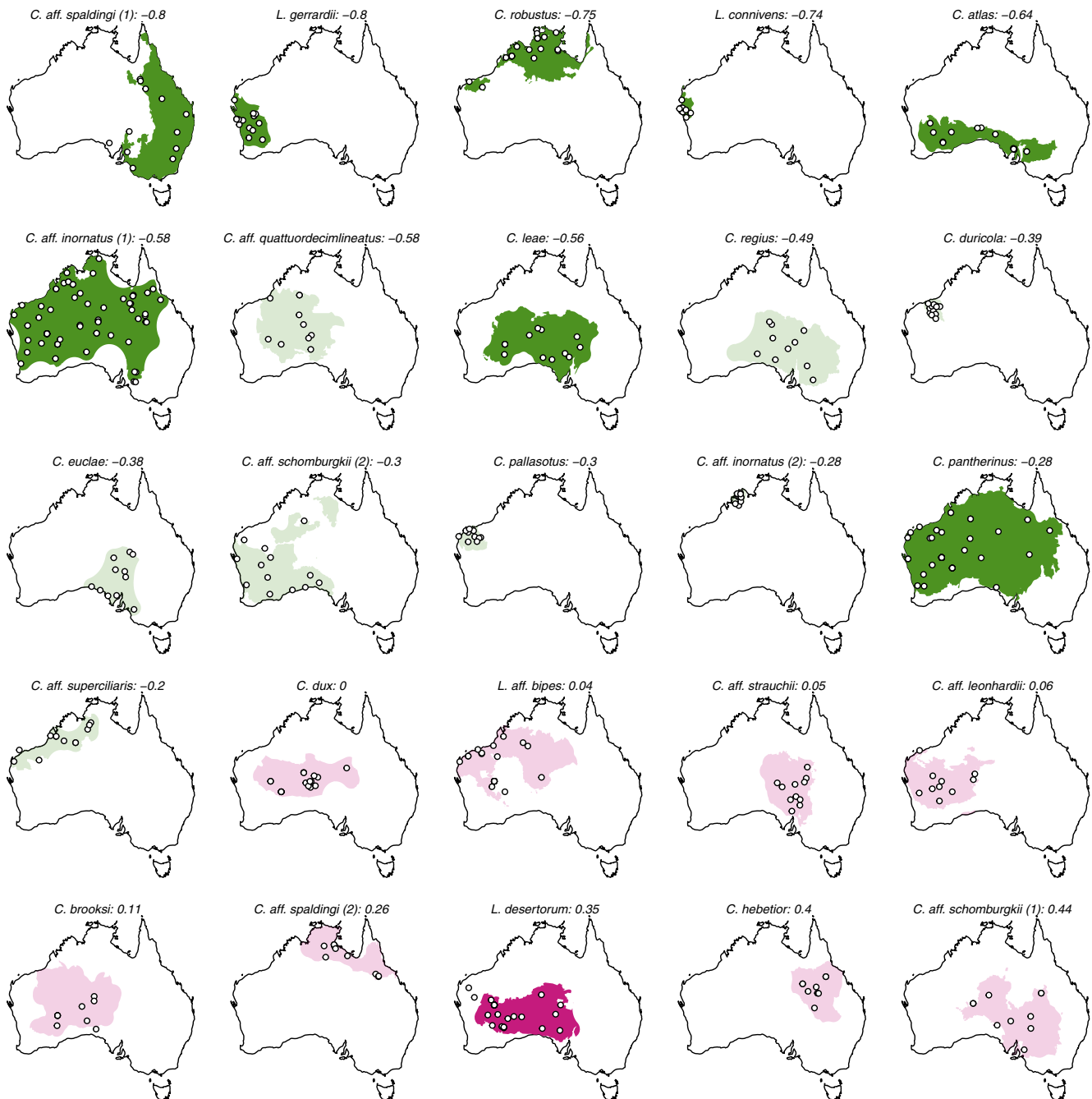


FIGURE 1 Range maps and sample localities (circles) for the 25 taxa included in this study; taxa are ordered by the magnitude of the correlation between distance to range centre and genetic diversity. Correlations are reported next to taxa names. Colour of range indicates if a taxa shows a decline in genetic diversity with increased distance from the range centre, as expected by the central-marginal hypothesis (green: yes; magenta: no). Opacity indicates if the correlation between distance and diversity is significant (dark: significant, light: nonsignificant). While these taxa are found throughout Australia, the majority (76%) are found primarily in Australia's desert biome. We were thus able to test the central-marginal hypothesis across a set of somewhat codistributed taxa.

the concatenated alignment to infer a phylogeny using RAXML version 8.2.0 (Stamatakis, 2014). We inferred an ultrametric tree from this phylogeny using the penalized likelihood approach implemented in TREEPL with $\lambda = 0.1$ (Smith & O'Meara, 2012). Finally, we delimited OTUs using GMYC, which is a coalescent-based method that infers where coalescent branching switches from within-species to between-species patterns. We applied the single-threshold model

in GMYC to this ultrametric tree (Fujisawa & Barraclough, 2013), thus delimiting putative OTUs. We confirmed OTU identity by determining (1) if the OTU spans a cohesive geographic range, (2) if OTUs form monophyletic mitochondrial groups, and (3) if patterns of genetic divergence across geographic space approximated a continuous isolation-by-distance pattern. Of the 151 resulting OTUs, we only retained OTUs sampled for ≥ 10 individuals. Our final data set

consisted of 25 OTUs and an average of 18.3 individuals sampled per OTU (Table S1).

For each OTU, we created a reference genome by selecting homologous loci across all individuals within that OTU using `VSEARCH` with a $\geq 95\%$ similarity search. We then aligned reads to the reference genome using `BWA` version 0.7.12 (Li, 2013) and called variant and invariant sites using `SAMTOOLS` version 1.2.1 (Li et al., 2009). All resulting variant sets were filtered to only include sites with $\geq 10\times$ coverage and ≥ 20 quality.

Using these filtered variant sets, we first determined how the number of sampled loci affected the stability of genetic diversity estimates. To do so, we subsampled 100, 500, 1000, 2000, 5000, and 10,000 loci, creating five bootstraps per subsample (Holmes & Grundler, 2022). For each variant set, we estimated genetic diversity per individual (π ; Tajima, 1983). These bootstrap analyses suggest that a minimum of 1000 loci are required for stable estimates of genetic diversity (Figure S2). Accordingly, we removed all individuals for which we sampled fewer than 1000 loci and then calculated genetic diversity. Our estimates of genetic diversity were measured for an average of 2.6 Mb sites across 17K independent loci per individual; sites had an average coverage of $43\times$ and 99% of sites had quality >100 . Thus, although we only sampled one individual at most geographic localities, each individual provided an estimate of deme-level patterns of variation (Nazareno et al., 2017).

2.2 | Testing for diversity and distance correlations

Testing the central-marginal hypothesis requires estimates of geographic ranges for a species. For most Australian squamate species, accurate ranges do not exist. Thus, we constructed species ranges based on occurrence data from museum databases based on an approach outlined by Rabosky et al. (2016). We inferred these ranges in previous studies (Singhal et al., 2017; Singhal, Huang, et al., 2018); we briefly summarize the approach here. First, using occurrence data per species, we defined an alpha-hull polygon across all the points. Then, using 22 environmental variables (19 BioClim variables, an aridity index, elevation, and actual evapotranspiration; Fick & Hijmans, 2017; Title & Bemmels, 2018), we inferred environmental niche models (ENM) per species. The geographic range was then defined as the intersection between the alpha-hull polygon and the ENM. To generate geographic ranges per OTU, nominal species ranges were then either combined or split, reflective of OTU delimitations.

For each individual in an OTU, we measured their location relative to the range centre using both geographic and climatic measures of distance. Climatic distance is a crude proxy for ecological distance, because it neglects important sources of environmental variation—such as substrate and vegetation composition—that probably influence range structure. For geographic distance, we measured distance from the range centroid (`RGEOS` version 0.5-3; Bivand & Rundel, 2017). We additionally measured distance from edge and the ratio of the centre distance to the range radius (geosphere

version 1.5-10; Hijmans et al., 2017). For climatic distance, we used two approaches. First, per OTU, we randomly sampled 1000 points within each range. We then extracted climatic data at each point across the 19 BioClim variables and summarized the data using a scaled and centred principal component (PC) analysis. We defined the climatic centroid as the mean value of the first six PC axes and calculated Euclidean distances of each individual to this centroid (Lira-Noriega & Manthey, 2014). Second, we used an approach based on identifying the niche centroid through `NTBOX` version 0.6.0 (Osorio-Olvera, Lira-Noriega, et al., 2020; Osorio-Olvera, Yañez-Arenas, et al., 2020). For each OTU, we randomly sampled 70% of the occurrence records to train the model and retained the remaining 30% to test model fit. We extracted climatic data across the 19 BioClim variables for the training data set, calculated correlations across variables, and dropped variables with correlations >0.80 . We then fit a niche model to the training data set, testing whether including the top two, three or four climatic variables in the final model fit the data best. The resulting niche model is defined as a minimum volume ellipsoid, and its centre is the climatic centroid of the range (Osorio-Olvera, Lira-Noriega, et al., 2020; Osorio-Olvera, Yañez-Arenas, et al., 2020). We then calculated individual distances to the centroid using Mahalanobis distances.

The central-marginal hypothesis predicts that genetic diversity should decline with greater distance from the range centre. We tested this prediction by calculating the strength and significance of the correlation between genetic diversity and each given measure of geographic and climatic distance using a Spearman's correlation (Figure 1). Additionally, we explored the possible joint effects of genetic and climatic distance on genetic diversity. Per OTU, we built linear models in which we modelled genetic diversity as a function of both geographic distance (as measured by distance to range centre) and climatic distance (as measured by distance to PC climatic centroid).

2.3 | Demographic modelling

Demographic processes—most notably, range and population expansion—can also lead to a pattern of declining genetic distance across space. To determine if these processes affect patterns of genetic variation across the range, we conducted two separate analyses. First, we used `DADI` version 2.1.1 to fit three possible demographic models to the allele frequency spectrum for each OTU (Gutenkunst et al., 2009): a model with no population change, a model with exponential population growth, and a model with an instantaneous population change (Figure S3). Per OTU, we filtered all variant sites to retain only those sites with $>60\%$ complete data across individuals, randomly sampled one variant site per locus, and then inferred the unfolded allele frequency spectrum by polarizing variants with outgroup sequence. We used the most closely-related OTU for a given OTU as the outgroup. We then down-projected the allele frequency spectrum to the median number of chromosomes sampled across all sites. Model fitting was done across multiple

rounds, following an approach implemented by Portik et al. (2017). We identified the best fitting model using the likelihood ratio test implemented in DADI. Second, we tested for range expansion using RANGEEXPANSION version 0.9 (Peter & Slatkin, 2013). As a species expands, new populations will harbour a fraction of the diversity of the original source population, resulting in a gradient of genetic diversity across the range (DeGiorgio et al., 2009; Peter & Slatkin, 2013, 2015). Further, variants in these new populations should be at a higher frequency than in the source populations. The RANGEEXPANSION approach uses the clines in variant frequency to infer the strength of the range expansion event and its likely origin. We used the same variant set and outgroup polarization used for DADI as input files for RANGEEXPANSION. The RANGEEXPANSION approach allows individuals to be assigned to multiple regions of expansion; here, we assigned all individuals to the same region.

2.4 | Comparative analyses

Our test of the central-marginal hypothesis returned mixed results across OTUs (see Section 3). Accordingly, we used a multipredictor model-averaging approach (Burnham & Anderson, 2003) to explore three possible types of factors (and nine variables in total) that might determine whether or not an OTU meets the predictions of the central-marginal hypothesis. Here, as a response variable, we use the correlation between geographic distance to range centre and genetic diversity. First, we included biological factors: isolation-by-distance (IBD) slope and biome. How species diverge across geographic distance might affect the diversity-divergence correlation, with species that exhibit greater isolation over geographic space showing a stronger correlation. Accordingly, we included IBD slopes per OTU (previously estimated in Singhal, Huang, et al., 2018). Also, the different biomes of Australia have experienced dynamic histories that might differentially affect patterns of genetic diversity. In particular, species endemic to the deserts likely experienced rapid population growth and range expansion as the deserts expanded in the late Miocene-early Pliocene (Pepper & Keogh, 2021). We included biome as a factor by determining which biome the majority of an OTU's geographic range spanned (Olson et al., 2001). Second, we included historical factors given that historical demography can restructure genetic diversity across a range. We included the relative change in population size as inferred by DADI and the strength of the correlation between allele frequency clines and distance as estimated by RANGEEXPANSION. Third, we included methodological factors: range eccentricity, number of individuals sampled and sampling coverage, range size, and mean genetic diversity. The more eccentric a range is, the harder it is to comparably define distance from the range centre. We measured range eccentricity as the coefficient of variation of the distance of the range centre to a random sample of 100 points on the range edge. Further, better sampling might result in more power. Thus, we included the number of individuals sampled and sampling coverage as factors. We measured sampling coverage as the fraction of the range covered by sampling points buffered by

a 100km radius. Similarly, we might have greater power to identify correlations in species with larger geographic range areas or higher overall genetic diversity. Thus, we included both range size and mean genetic diversity as variables.

Across these nine factors, we created the full set of linear models and fit them to the data using phylogenetic linear models using NLME version 3.1 in R (Pinheiro, 2009). To control for phylogeny, we used an ultrametric tree previously published in Singhal et al. (2017). We calculated the relative importance of variables by summing the relative Akaike information criteria weights for all the models in which the variable appeared.

2.5 | Data analysis and visualization

All scripts for data analysis and visualization were written in R and Python3 and are available at https://github.com/singhal/central_marginal. Data visualization used the R packages GGPLOT2 and COWPLOT (Wickham, 2016; Wilke et al., 2021).

3 | RESULTS

Of the 25 OTUs we tested, 16 (or 64%) recovered the expected negative correlation between distance from range centre and genetic diversity (Figures 1 and 2). Eight of these 16 correlations were significant (Figure 3a, Table S2). Using climatic estimates of distance, 16 of the 25 OTUs had negative distance-diversity correlations, of which six were significant (Figure 3b, Table S2). Unexpectedly, OTU *Lerista desertorum* showed a significant positive correlation between geographic distance-diversity and *Ctenotus atlas* showed a significant positive correlation between climatic distance-diversity (Table S2). On average, for those taxa showing a significant central-marginal pattern, genetic diversity at the range edge was 11% less than at the core. For comparison, across any given taxon, minimum and maximum genetic diversity varied an average of 2.4-fold.

Results varied depending on how geographic distance and climatic distance were measured. Although alternate measures of geographic and climatic distance were correlated with our focal distance estimators ($r = .094-.627$; Figure S4), the proportion of tests recovering a significant correlation in the expected direction varied from 16%–20% across these alternate measures (Figure 4, Table S2).

Models that included both geographic and climatic distance as factors influencing genetic diversity had adjusted r^2 values ranging from .0–.8 (mean adjusted $r^2 = .2$). For only two OTUs were both geographic and climatic distance included as significant predictors (Figure S5).

Demographic analysis found that the two-epoch model best fit all 25 OTUs, in which population size instantly changed some time in the past (Figure S3). Current population size was inferred to be an average of 4.3× greater than ancestral population sizes (Figure 5a). Fourteen of the 25 OTUs showed significant evidence for range expansion (Figure 5b). The origins of the range expansion were

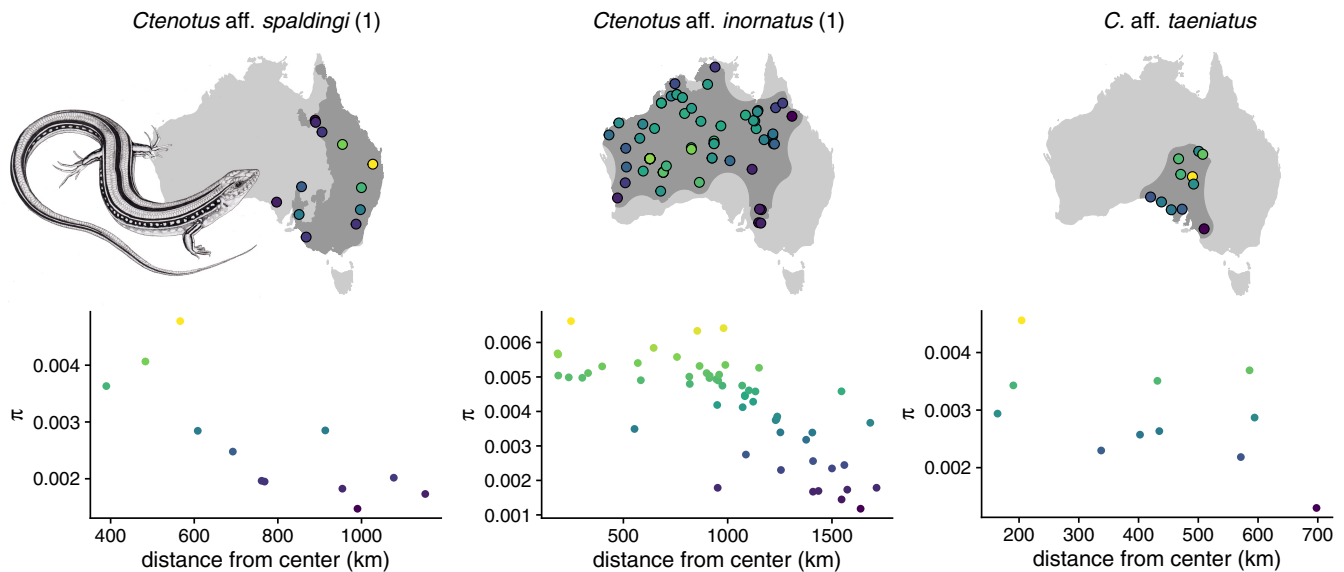


FIGURE 2 The relationship between genetic diversity and distance to range centre for three exemplar operational taxonomic units (OTUs). Two taxa showed a significant negative correlation (*Ctenotus aff. spaldingi* 1 and *C. aff. inornatus* 1), and one showed a nonsignificant negative correlation (*C. aff. taeniatus*). Our species delimitation approach occasionally split and lumped nominal species; for example, nominal species *C. taeniatus* and *C. euclae* have been lumped into the OTU *C. aff. taeniatus*. Shaded areas on maps indicate OTU geographic range and point colours vary based on genetic diversity. Drawing of *C. aff. spaldingi* 1 courtesy of M. Grundler (reused with permission from the University of Chicago Press).

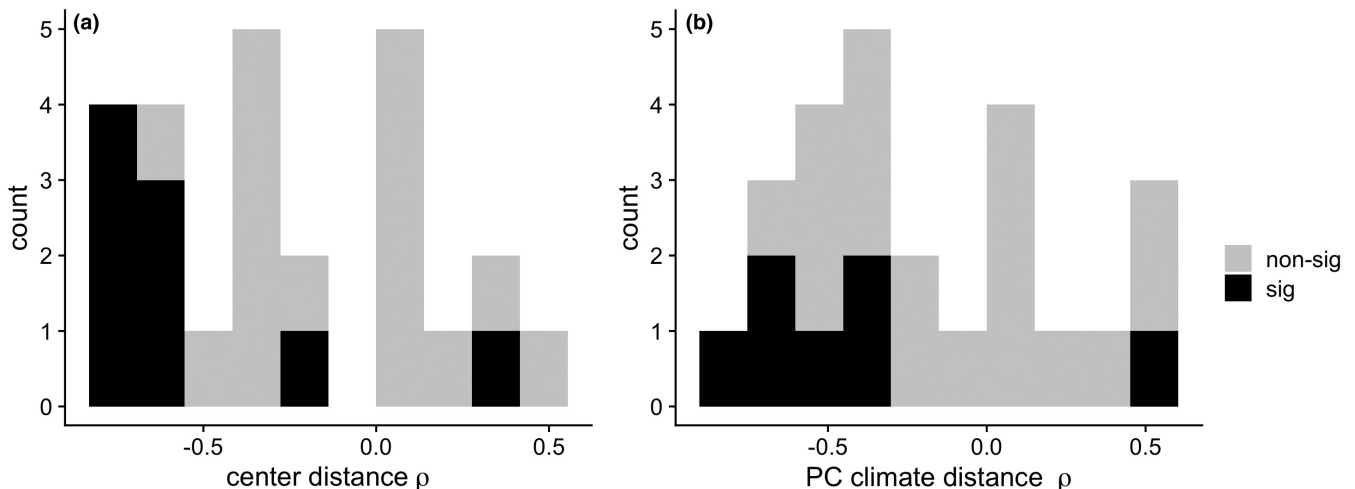


FIGURE 3 Spearman rank correlations (ρ) between genetic diversity and (a) geographic distance, as measured by the distance to range centre and (b) climatic distance, as measured by the distance to the principal component (PC) climatic centroid of the range ($n = 25$ operational taxonomic units [OTUs]). Fill colour indicates significance of correlation ($p < .05$). As expected under the central-marginal hypothesis, most correlations are negative though not all were significant.

generally inferred to be towards the edge of range; on average, the centre-edge distance ratio of origins was 0.81 (Figure S6).

We tested three sets of biological, historical, and methodological factors that might affect our ability to recover the central-marginal hypothesis. We found that a historical factor—the strength of the range expansion—was the best predictor of whether or not we recovered the central-marginal hypothesis (relative importance: 0.73; Figure 6a). Taxa with stronger evidence for a range expansion had more positive diversity-distance correlations and thus more strongly contradicted the predictions of the central-marginal hypothesis

(Figure 6b). The best overall model included strength of range expansion as the sole predictor of diversity-distance correlations and had an adjusted $r^2 = .2$.

4 | DISCUSSION

For the 25 species-level taxa for which we were able to test the central-marginal hypothesis, we found the expected negative correlation between genetic diversity and distance from range centre in

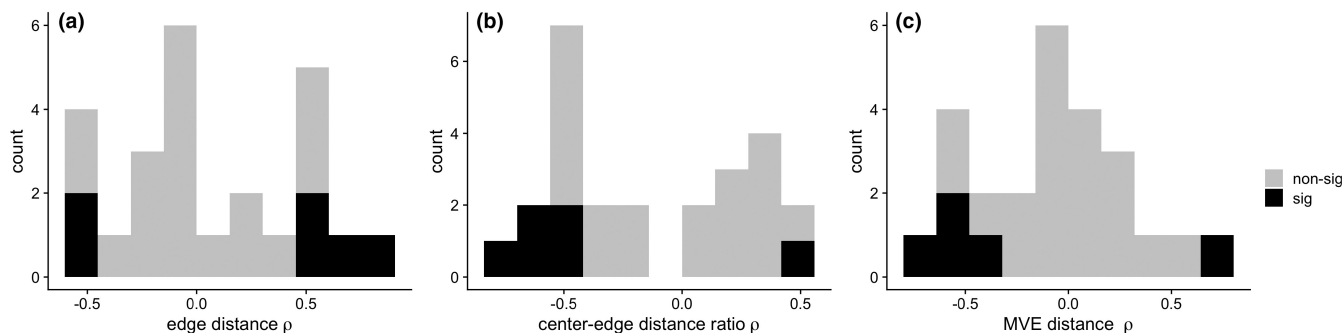


FIGURE 4 Spearman rank correlations (ρ) between genetic diversity and alternate measures of distance: (a) geographic distance, as measured by the distance to range edge, (b) geographic distance, as measured by the ratio of centre distance to range radius, and (c) distance from climatic centroid of range, as defined by the minimum volume ellipsoid (MVE). For the relationship shown in (a), we would predict to recover positive correlations under the central-marginal hypothesis; for the relationships shown in (b) and (c), we would predict negative. Fill colour indicates significance of correlation ($p < .05$). Across all metrics of distance, the majority of taxa showed support for the central-marginal hypothesis though the level of support varied.

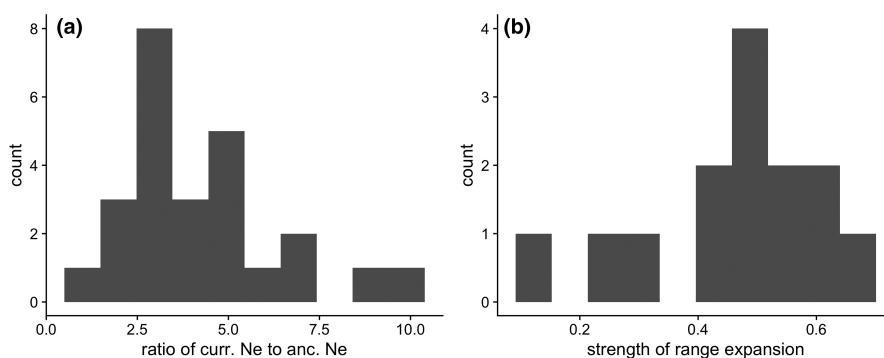


FIGURE 5 Demographic inference for OTUs included in this study. (a) Ratio of current effective population size (N_e) to ancestral N_e as inferred using *dadi*. All 25 OTUs best fit the two-epoch model, in which populations expanded instantly in the past (see Figure S3). (b) For the 14 OTUs that showed significant evidence for range expansion, we plot the strength of the range expansion, as measured by the correlation between allele frequency clines and geographic distance from the expansion origin.

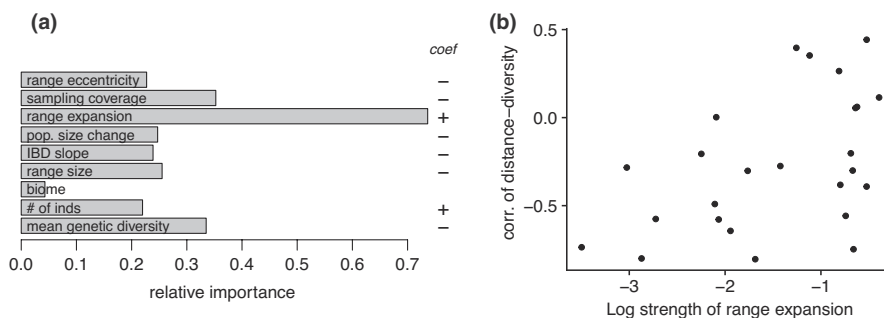


FIGURE 6 (a) Model fitting for nine variables that span three possible factors for whether or not we recover support for the central-marginal hypothesis in a given taxon: (1) biological factors: Isolation-by-distance (IBD) slope, biome; (2) historical factors: strength of range expansion, population size change; and (3) methodological factors: range eccentricity, sampling coverage, number of individuals sampled, range size, and mean genetic diversity. Shown are the relative importance of each variable and the sign of its coefficient. Range expansion was the best predictor of all tested variables. (b) Taxa that show stronger evidence for range expansion are more likely to exhibit a positive correlation between centre distance and genetic diversity, opposite to predictions from the central-marginal hypothesis.

16 taxa. This pattern was significant for eight taxa. Only one taxon provided significant evidence against the central-marginal hypothesis. As seen in other comparative tests of the central-marginal hypothesis and on the underlying abundant-centre hypothesis (Dallas

et al., 2017; Lira-Noriega & Manthey, 2014; Pennington et al., 2021; Pironon et al., 2017), we recovered support for the central-marginal hypothesis but with numerous exceptions and significant unexplained variability.

4.1 | Explanations for mixed support

All the empirical data collected thus far—including the present study—suggest that the central-marginal hypothesis is unlikely to hold uniformly across taxa (Eckert et al., 2008; Lira-Noriega & Manthey, 2014). Given this, the better question might be to explore which factors determine if a species shows patterns of genetic diversity congruent with the central-marginal hypothesis. Because of our comparative approach, we had the power to explore a set of three primary factors: biological, historical, and methodological.

First, the central-marginal hypothesis derives from the abundant-centre hypothesis. Both of these hypotheses make a number of biological assumptions, which while seemingly intuitive, might not hold in nature, thus leading to the rejection of these hypotheses. For example, the central-marginal hypothesis derives from the assumption that abundance is highest in the range core, but empirical data are equivocal (Gilman, 2005; Helmuth et al., 2002; Pironon et al., 2015; Santini et al., 2019). Unfortunately, we could not test this assumption by measuring how lizard abundance varies across the range. There are no shortcuts to estimating range-wide patterns of abundance in Australian desert lizards (Grundler et al., 2019), and obtaining abundance information for even single localities requires considerable time and resources (Pianka, 2014; Thompson et al., 2003).

Another assumption made by the central-marginal hypothesis is that the geographic and ecological core of the range are the same. But, ecological gradients do not necessarily follow simple patterns that correspond to a geographic range centre (Duncan et al., 2015; Pironon et al., 2015, 2017; Trumbo et al., 2016). We attempted to address this assumption by using climatic suitability as a proxy for niche suitability; we found weaker support for the central-marginal hypothesis using climatic versus geographic distance (Figure 3b). However, we estimated ecological distance solely using climatic variables, and many of the taxa (~70%) included in this study span arid biomes that are relatively climatically homogenous (James & Shine, 2000). For these taxa, climate might not define the marginality of habitats. Rather, broadscale aspects of vegetation structure and substrate might be more important determinants of geographic range limits in arid Australian lizards and might better define niche suitability (Pianka, 1972).

Our study thus shows the limitations of testing the central-marginal hypothesis without collecting detailed demographic and ecological data. In order to test the central-marginal hypothesis and the underlying abundant-centre hypothesis properly, an ideal study would directly measure the key variables of interest—for example, niche suitability, individual fitness, population abundance and density, genetic diversity, and genetic differentiation—across the geographic range. Only through such a holistic approach can properly test the generality of these hypotheses (compare with Dixon et al., 2013; Helmuth et al., 2002; Sexton et al., 2016; Yakimowski & Eckert, 2008).

Second, historical demographic shifts often redistribute genetic diversity across the range, either mimicking or obscuring a pattern of

declining genetic diversity from the range centre as expected under the central-marginal hypothesis (Eckert et al., 2008). In a nonequilibrium scenario, during range expansions, repeated serial founder events create gradients of allele frequencies and genetic diversity (DeGiorgio et al., 2009; Pierce et al., 2014; Provan & Maggs, 2012). If the origin of the expansion occurs near the centre of the range, then genetic diversity will decline from the centre to the edges of the range (DeGiorgio et al., 2009; Slatkin & Excoffier, 2012 but see Peter & Slatkin, 2013 which shows this can also occur due to edge effects).

Most of our focal taxa are arid distributed (Figure 1, Appendix S1), and the Australian arid zone has expanded dramatically since the Miocene (Pepper & Keogh, 2021). Given this biogeographic history, it is perhaps unsurprising that all of our taxa showed evidence for population expansion, and 14 of our 25 taxa showed evidence of range expansions (Figure 5b). Typically, range expansions are expected to generate patterns that mimic the expectations of the central-marginal hypothesis (Eckert et al., 2008). However, we found the opposite. Taxa that experienced range expansion more strongly contradicted the expectations of the central-marginal hypothesis (Figure 6b). Because these taxa mostly expanded from the range edge (Figure S6), these taxa exhibited a declining gradient in genetic diversity from the edge rather than the centre. Our study shows that the importance of considering historical demographic shifts when investigating current patterns of range-wide genetic diversity (Duncan et al., 2015; Moeller et al., 2011; Pironon et al., 2015; Wei et al., 2016).

Third, methodological issues—such as how geographic distance is measured, how centre-to-edge transects are constructed, and sampling effort—can affect support for the central-marginal hypothesis. The less round and more eccentric a range is, the harder it can be to determine which populations are core versus edge. Accordingly, how geographic distance is measured often matters (Sagarin et al., 2006; Santini et al., 2019; Yancovitch Shalom et al., 2020), though we find no strong evidence for its impact in our study. The three different metrics of geographical distance were only modestly correlated across our taxa ($r = .1-.62$, Figure S4), but most taxa still showed qualitatively consistent correlations across distance metrics (Table S2). Further, we found no evidence that more eccentric ranges were less likely to support the central-marginal hypothesis (Figure 6a).

Similarly, treating all range edges equivalently can confound tests of the central-marginal hypothesis (Sagarin et al., 2006), particularly if there are multiple peaks of population abundance (Dixon et al., 2013) or if ranges span elevational or latitudinal gradients (Connallon & Sgrò, 2018; Freeman & Beehler, 2018; Halbritter et al., 2015; Hampe & Petit, 2005). If the nature of the central-marginal hypothesis changes depending what range edge is considered, then collapsing range edges into a single transect—as we did in our study—could increase noise and decrease power to identify support for the hypothesis. Thus, although this represents a massive and perhaps unrealistic sampling effort, researchers would ideally test the central-marginal hypothesis across multiple linear transects from the range centre to the edge (Kennedy et al., 2020; Trumbo et al., 2016).

Finally, greater sampling can increase power, thus making it more likely the central-marginal hypothesis will be confirmed (Blackburn et al., 1999; Eckert et al., 2008; Lira-Noriega & Manthey, 2014). We found no evidence that sampling effort or sampling coverage affected support for the central-marginal hypothesis (Figure 6a). However, because we collected thousands of loci, we could treat each individual as a population (Nazareno et al., 2017), and we were thus able to measure distance as a continuous variable. In contrast, many studies compare patterns of genetic diversity after binning populations as either core or peripheral populations (Eckert et al., 2008; Yakimowski & Eckert, 2008). Had we binned populations, only four taxa would have supported the central-marginal hypothesis due to the corresponding reduction in effective sample size.

4.2 | Implications and future directions

Even though the abundant-centre and central-marginal hypotheses might not be as general as they were originally envisioned, these hypotheses remain compelling because they have clear implications for range limits and speciation. One hypothesis for why species have range limits is that boundaries form where species are no longer able to adapt to edge conditions (Hoffmann & Blows, 1994; Kirkpatrick & Barton, 1997; Polechová, 2018). In a world where ranges are shifting as a result of climate change, edge populations are perhaps most likely to be extirpated or swamped by gene flow (Hampe & Petit, 2005). Further, although edge populations are expected to have lower levels of genetic diversity overall, they are often genetically and phenotypically distinct from populations at the range core (Eckert et al., 2008), making their loss of particular concern for conservation aims. Thus, edge populations both help determine range limits and are particularly threatened as range limits shift.

Here, we find that many taxa have reduced genetic diversity at their edges, which supports the idea that limited variation hinders local adaptation in edge populations (Hoffmann & Blows, 1994). However, we measure an only modest reduction in genetic diversity (11%) between central and marginal populations. In other animal taxa (Eckert et al., 2008), 15 out of 18 taxa supported the central-marginal hypothesis, with a ~45% reduction in genetic diversity as measured by expected heterozygosity. Thus, relative to the spread in genetic diversity within taxon ranges (2.4-fold difference), reduction in genetic diversity in core populations seen in other species, and reduction in abundance expected in core populations, we see only a minor decline in genetic diversity. What consequence this decrease has for the potential of edge populations to adapt to changing environmental conditions—if any—is unclear.

Further, we only measured putatively neutral genetic variation, which may not correlate with genetic variation underpinning key adaptive traits (Pauls et al., 2013; Teixeira & Huber, 2021). To better explore the links between the central-marginal hypothesis and range limits, we should ideally sample quantitative trait loci and the traits

themselves (compare with Clark et al., 2021; Kennedy et al., 2020; Pennington et al., 2021; Pujol & Pannell, 2008).

In verbal models of species formation, edge or peripheral populations are often seen as engines of new species (Brown, 1957; Levin, 1970; Mayr, 1970). Peripheral populations are thought to be subject to different biogeographical and ecological conditions from the core populations. Thus, they might be more likely to split to form isolates that then evolve into new species (Bush, 1975). The central-marginal hypothesis predicts that peripheral populations should show greater genetic divergence than core populations (Dixon et al., 2013), which could further spur species formation at the edges. We could not robustly test these predictions because of sparse sampling, although we found some evidence that genetic divergence is greater between core-edge and edge-edge populations than core-core populations (Figure S7). Denser sampling would allow us to properly explore how the central-marginal hypothesis connects to speciation.

AUTHOR CONTRIBUTIONS

Sonal Singhal and Daniel L. Rabosky designed research, Sonal Singhal and John Wrath performed research, Sonal Singhal and John Wrath analysed data, Sonal Singhal and John Wrath wrote the manuscript, and all authors reviewed and finalized the final text.

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DATA AVAILABILITY STATEMENT

All data used in this study have been previously published in NCBI BioProjects PRJNA382545 and PRJNA476569; see Table S1 for NCBI SRA codes for each individual. Code used for data analysis and visualization is available at https://github.com/singhal/central_marginal.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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