

1 **Title**

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

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11 Running title: Genetic variation across lizard ranges

12 **Abstract**

13 For many species, both local abundance and regional occupancy are highest near the center of
14 their geographic distributions. One hypothesis for this pattern is that niche suitability declines
15 with increasing distance from a species geographic center, such that populations near range
16 margins are characterized by reduced density and increased patchiness. In these smaller edge
17 populations, genetic drift is more powerful, leading to the loss of genetic diversity. This simple
18 verbal model has been formalized as the central-marginal hypothesis, which predicts that core
19 populations should have greater genetic diversity than edge populations. However,
20 demographic shifts over time can generate a similar pattern. For example, in species with
21 expanding ranges, populations at the range edge experience serial founder effects, creating a
22 gradient of declining genetic diversity from the range core to edge. Testing the central-marginal
23 hypothesis properly thus requires us to consider the confounding role of historical demography.
24 Here, we account for the role of history in testing the central-marginal hypothesis using a
25 genomic dataset of 25 species-level taxa of Australian skink lizards (genus: *Ctenotus* and
26 *Lerista*). We found support for the central-marginal hypothesis in 16 of our 25 taxa, of which
27 eight taxa recovered significant support. Unexpectedly, species with the strongest evidence for
28 range expansion were the least likely to follow predictions of the central-marginal hypothesis.
29 The majority of these species had range expansions that originated at the range edge, which
30 led to lower genetic diversity at the range edge compared to the core, contrary to the
31 central-marginal hypothesis.

32 **Keywords**

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

34 Introduction

35 Whether they are big or small, species geographic ranges can be divided into central core
36 population and edge populations. As predicted by verbal models from macroecology and
37 population genetics, patterns of population abundance, individual fitness, and genetic diversity
38 should differ across core and edge populations (Brown, 1984; Sagarin & Gaines, 2002), which
39 can then contribute to the formation of range limits (García-Ramos & Kirkpatrick, 1997; Gaston,
40 2003). At the center of their range, species are hypothesized to be optimally adapted for the
41 habitat, allowing them to maintain large, interconnected populations characterized by high local
42 abundance (Brown, 1984; Sagarin & Gaines, 2002). Moving away from the center, the habitat
43 becomes more marginal, leading to decreased reproductive output in populations (Angert, 2006;
44 Gaston, 2009; Pigott & Huntley, 1981). Populations thus become smaller and patchier. Further,
45 because these smaller populations are likely more subject to genetic drift and the swamping
46 effects of gene flow from the range center (Hoffmann & Blows, 1994; Kirkpatrick & Barton,
47 1997), they are less able to adapt to these local, marginal conditions (Bridle & Vines, 2007;
48 Lenormand, 2002). Thus, in the range center, where populations are large and connected,
49 populations will show high levels of genetic diversity and low levels of genetic differentiation
50 (Eckert, Samis, & Loughheed, 2008; Mayr, 1970). Conversely, small and isolated edge
51 populations will exhibit low levels of genetic diversity and high levels of genetic differentiation.
52 These expectations for how population abundance and genetic diversity vary across the range
53 have been formalized as the abundant-center and central-marginal hypotheses, respectively
54 (Brown, 1995; Eckert et al., 2008).

55 Despite their intuitive appeal, both the abundant-center and central-marginal hypotheses have
56 mixed support in the literature (as reviewed in Dallas, Decker, & Hastings, 2017; Lira-Noriega &

57 Manthey, 2014; Pennington, Slatyer, Ruiz-Ramos, Veloz, & Sexton, 2021; Pironon et al., 2017).

58 This mixed support has a few potential explanations. Some have argued that geographic

59 definitions of range core versus range edges are irrelevant (Martínez-Meyer, Díaz-Porras,

60 Peterson, & Yáñez-Arenas, 2013). Rather, core versus edge populations should be defined by

61 how well they reflect the idealized niche conditions for a species (Weber, Stevens, Diniz-Filho, &

62 Grelle, 2017). Ecological distance might then better predict patterns than geographic distance.

63 Others have suggested that patterns at range edges might be variable depending on which

64 edge is considered, particularly when range edges fall across latitudinal and elevational

65 gradients (Guo, 2012). Further, the complexity of many ranges' geometries might make it

66 difficult to define core versus edge populations.

67 Another possible confounding factor involves demographic history, which can also affect the

68 distribution of genetic diversity across a range (Hewitt, 1999). One notable example is range

69 expansions. As a species range expands, individuals disperse out of founding populations and

70 establish new populations through repeated population bottlenecks (DeGiorgio, Jakobsson, &

71 Rosenberg, 2009; Excoffier, Foll, & Petit, 2009). These serial founder effects lead to reduced

72 levels of genetic diversity along the expanding range edge, high structure among populations,

73 and clines in allele frequency centered on the origin of the expansion (Peter & Slatkin, 2013;

74 Slatkin & Excoffier, 2012). Thus, both the central-marginal hypothesis and range expansions

75 should lead to reduced genetic diversity and increased genetic differentiation in edge

76 populations. These shared predictions can make it difficult to disentangle the effects of historical

77 versus current demography on patterns of genetic diversity across a species range (Duncan,

78 Crespi, Mattheus, & Rissler, 2015).

79 In this study, we address this challenge by combining inference of historical demography and
80 estimation of current genetic patterns to test the central-marginal hypothesis across 25
81 species-level taxa of Australian scincid lizards in the genera *Ctenotus* and *Lerista*. These
82 species are largely co-distributed (Fig. S1) and have likely experienced many of the same
83 biogeographic dynamics and historical shifts. Further, range limits in Australia generally do not
84 correspond to hard biogeographic boundaries but seemingly track more subtle features of a
85 relatively flat and gradually changing physiography (James & Shine, 2000; Pianka, 1972).
86 Because of the absence of sharp physical barriers or steep environmental gradients, Australian
87 taxa are somewhat of a "best case" scenario for detecting central-marginal structure. Thus, our
88 study allows us to test the central-marginal hypothesis across a fairly similar set of taxa in a
89 similar environment. First, using a final dataset of 457 individuals and an average of 17K loci,
90 we test the predictions of the central-marginal hypothesis by looking for patterns of declining
91 genetic variation with respect to distance from range center. Then, we fit demographic models of
92 population growth and range expansion to our data to determine which historical processes
93 might be structuring genetic diversity. Finally, given the mixed support for the central-marginal
94 hypothesis in both our dataset and other datasets, we determine which demographic, intrinsic,
95 and extrinsic factors — if any — predict whether or not we recover support for the
96 central-marginal hypothesis.

97 **Methods**

98 *Sampling and Genetic Data Collection & Analysis*

99 To determine how genetic diversity varies across geographic ranges, we initially analyzed
100 genetic data from 923 individuals from 142 nominal species across two species-rich genera of

101 Australian scincid lizards: *Ctenotus* and *Lerista*. Samples were selected to span the geographic
102 range of species (Fig. S2); more individuals were sampled from broad-ranging species than
103 narrow-ranging species (r of sample and range size: 0.78, p -value = $1.29\text{e-}28$).

104 Genetic data from these individuals were previously published in (Singhal, Huang, et al., 2018;
105 Singhal et al., 2017). Full details on data collection and analysis are available in these studies;
106 we briefly summarize the approach here. We first collected genetic data using double digest
107 restriction-site associated DNA sequencing (ddRADseq; Peterson, Weber, Kay, Fisher, &
108 Hoekstra, 2012). Then, we assembled reads using Rainbow v2.04 (Chong, Ruan, & Wu, 2012).
109 Like many squamate species (Leaché & Fujita, 2010; Singhal, Hoskin, Couper, Potter, & Moritz,
110 2018), nominal species in *Ctenotus* and *Lerista* often comprise multiple, cryptic lineages (Prates
111 et al., in press.; Rabosky, Hutchinson, Donnellan, Talaba, & Lovette, 2014; Singhal, Huang, et
112 al., 2018). Accordingly, we first delimited putative operational taxonomic units (OTUs) across
113 these genera. For each genera, we first identified homologous loci across all individuals by
114 using VSEARCH v1.11.1 with a 80% clustering (Rognes, Flouri, Nichols, Quince, & Mahé,
115 2016). Then, we concatenated homologous loci with <40% missing data and used the
116 concatenated alignment to infer a phylogeny using RAxML v8.2.0 (Stamatakis, 2014). We
117 inferred an ultrametric tree from this phylogeny using the penalized likelihood approach
118 implemented in TreePL with $\lambda=0.1$ (Smith & O'Meara, 2012). Finally, we delimited OTUs using
119 GMYC, which is a coalescent-based method that infers where coalescent branching switches
120 from within-species to between-species patterns. We applied the single-threshold model in
121 GMYC to this ultrametric tree (Fujisawa & Barraclough, 2013), thus delimiting putative OTUs.
122 We confirmed OTU identity by determining (1) if the OTU spans a cohesive geographic range,
123 (2) if OTUs form monophyletic mitochondrial groups, and (3) if patterns of genetic divergence
124 across geographic space approximated a continuous isolation-by-distance pattern. Of the 151

125 resulting OTUs, we only retained OTUs with ≥ 10 individuals for further analysis. Our final
126 dataset consisted of 25 OTUs and an average of 18.3 individuals per OTU (Table S1).

127 For each OTU, we created a reference genome by selecting homologous loci across all
128 individuals within that OTU using VSEARCH with a $\geq 95\%$ similarity search. We then aligned
129 reads to the reference genome using bwa v0.7.12 (Li, 2013) and called variant and invariant
130 sites using samtools v1.2.1 (Li et al., 2009). All resulting variant sets were filtered to only include
131 sites with $\geq 10\times$ coverage and ≥ 20 quality.

132 Using these filtered variant sets, we first determined how the number of sampled loci affects the
133 stability of genetic diversity estimates. To do so, we subsampled 100, 500, 1000, 2000, 5000,
134 and 10000 loci, creating five bootstraps per subsample (Holmes & Grundler, in review). For
135 each variant set, we estimated genetic diversity per individual (π ; Singhal et al., 2017; Tajima,
136 1983). These bootstrap analyses suggest that a minimum of 1,000 loci are required for stable
137 estimates of genetic diversity (Fig. S3). Accordingly, we removed all individuals for which we
138 sampled fewer than 1,000 loci and then calculated genetic diversity. Our estimates of genetic
139 diversity were measured for an average of 2.6 Mb sites across 17K independent loci per
140 individual. Thus, although we only sample one individual at most geographic localities, each
141 individual provides an estimate of deme-level patterns of variation (Nazareno, Bemmels, Dick, &
142 Lohmann, 2017).

143 *Testing for diversity and distance correlations*

144 Testing the central marginal hypothesis requires estimates of geographic ranges for a species.
145 For most Australian squamate species, accurate ranges do not exist. Thus, we constructed
146 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, Huang, et al., 2018; Singhal et al., 2017); 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, species ranges were then either combined or split, dependent on OTU delimitations.

For each individual in an OTU, we measured their location in the range as a function of both geographic and bioclimatic estimates of distance. Bioclimatic estimates of distance might serve as crude proxies for ecological divergence across a species' range, although they likely neglect important sources of ecological variation, such as substrate composition and vegetation structure. For geographic distance, we measured distance from the range centroid, as estimated (rgeos v0.5-3; Bivand & Rundel, 2017). We additionally measured distance from edge (geosphere v1.5-10; Hijmans, Williams, Vennes, & Hijmans, 2017) and the ratio of the center distance to the range radius. 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 these data using a scaled and centered 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 the R package ntbox v0.6.0 (Osorio-Olvera et al., 2020; Osorio-Olvera, Yañez-Arenas, Martínez-Meyer, & Peterson, 2020). For each OTU, we randomly sampled 70% of the occurrence records for use to train the model and retained the remaining 30% to test the

171 fit of the model. We extracted climatic data across the 19 BioClim variables for the training
172 dataset, calculated correlations across variables, and dropped variables with correlations >0.80 .
173 We then fit a niche model to the training dataset, testing whether including the best 2, 3 or 4
174 climatic variables in the final model fit the data best. This niche model is defined as a minimum
175 volume ellipsoid; its center was the climatic centroid of the range (Osorio-Olvera et al., 2020).
176 We then calculated individual distance to the centroid using Mahalanobis distances.

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

185 *Demographic modeling*

186 Demographic processes — most notably, range and population expansion — can also lead to a
187 pattern of declining genetic distance across space. To determine if these processes affect
188 patterns of genetic variation across the range, we conducted two separate analyses. First, we
189 used dadi v2.1.1 to fit three possible demographic models to the allele frequency spectrum for
190 each OTU (Gutenkunst, Hernandez, Williamson, & Bustamante, 2009): a neutral model with no
191 population change and two models of population expansion, one with exponential growth and
192 one with an instantaneous population change (Fig. S4). Per OTU, we filtered all variant sites to
193 retain only those sites with $>60\%$ complete data across individuals and then inferred the

194 unfolded allele frequency spectrum by polarizing variants with outgroup sequence. We used the
195 most closely-related OTU for a given OTU as the outgroup. We then down-projected the allele
196 frequency spectrum to the median number of chromosomes sampled across all sites. Model
197 fitting was done across multiple rounds, following an approach implemented by (Portik et al.,
198 2017). We identified the best fitting model using the likelihood ratio test implemented in dadi.
199 Second, we tested for range expansion using the R package rangeExpansion (Peter & Slatkin,
200 2013). As a species expands across the range, new populations will harbor a fraction of the
201 diversity of the original source population, resulting in a gradient of genetic diversity across the
202 range (DeGiorgio et al., 2009; Peter & Slatkin, 2013, 2015). Further, variants in these new
203 populations should be at a higher frequency than in the source populations. The
204 rangeExpansion approach uses the clines in variant frequency to infer the strength of the range
205 expansion event and its likely origin. We used the same variant set and outgroup polarization
206 used for dadi as input files for rangeExpansion. The rangeExpansion approach allows
207 individuals to be assigned to multiple regions of expansion; here, we assigned all individuals to
208 the same region.

209 *Comparative analyses*

210 Our test of the central-marginal hypothesis returned mixed results across OTUs (see *Results*).
211 Accordingly, we used a multipredictor model-averaging approach (Burnham & Anderson, 2003)
212 to explore four possible sets of factors (and seven variables in total) that might determine
213 whether or not an OTU meets the predictions of the central-marginal hypothesis. Here, as a
214 response variable, we use the correlation between distance to center and genetic diversity.
215 First, we considered sampling effort, because better sampled species might be more likely to
216 exhibit stronger patterns. Thus, we included the number of individuals sampled as a factor.

217 Similarly, we might have greater power to identify correlations in species with larger geographic
218 range areas or higher overall genetic diversity. Thus, we included both range size and mean
219 genetic diversity as variables. Second, how species diverge across geographic distance might
220 affect the diversity-divergence correlation, with species that exhibit greater isolation over
221 geographic space showing a stronger correlation. Accordingly, we included estimates of the
222 slope of isolation-by-distance (previously estimated in Singhal, Huang, et al., 2018). Third, the
223 different biomes of Australia have experienced dynamic histories that might differentially affect
224 patterns of genetic diversity. In particular, species endemic to the deserts likely experienced
225 rapid population growth and range expansion as the deserts expanded in the late Miocene-early
226 Pliocene (Pepper & Keogh, 2021). We included biome as a factor by determining which biome
227 the majority of a OTU's geographic range spanned (Olson et al., 2001). Fourth, we included two
228 variables from our demographic analyses, given that historical demography leaves an imprint on
229 genetic diversity. We included the relative change in population size as inferred by dadi and the
230 strength of the correlation between allele frequency clines and distance as estimated by
231 rangeExpansion.

232 Across these seven factors, we created the full set of linear models and fit them to the data
233 using phylogenetic linear models using nlme v3.1 in R (Pinheiro, 2009). To control for
234 phylogeny, we used an ultrametric tree previously published in (Singhal et al., 2017). We
235 calculated relative importance of variables by summing the relative Akaike information criteria
236 weights for all the models in which the variable appeared.

237 *Data visualization and analysis*

238 All scripts for data visualization and analysis were written in R and Python3 and are available at
239 https://github.com/singhal/central_marginal. Data visualization used the R packages ggplot2
240 and cowplot (Wickham, 2016; Wilke, 2016).

241 **Results**

242 Of the 25 OTUs we tested, 16 (or 64%) recovered the expected negative correlation between
243 distance from range center and genetic diversity. Eight of these correlations (32%) were
244 significant (Fig. 2A, Table S2). Using estimates of distance from the climatic center, 16 of the 25
245 OTUs had negative distance-diversity correlations, of which six were significant (Fig. 2B, Table
246 S2). Unexpectedly, OTU *Lerista desertorum* showed a significant positive correlation between
247 geographic distance-diversity and *Ctenotus atlas* showed a significant positive correlation
248 between climatic distance-diversity (Table S2). On average, for those species showing a
249 significant central-marginal pattern, genetic diversity at the range edge was 11% less than at the
250 core. For comparison, across any given species, minimum and maximum genetic diversity
251 varied 2.4-fold.

252 As other studies have shown (Sagarin, Gaines, & Gaylord, 2006; Santini, Pironon, Maiorano, &
253 Thuiller, 2019; Yancovitch Shalom et al., 2020), how geographic distance and ecological
254 distance are measured matter. Although alternate measures of geographic and ecological
255 distance were correlated with our focal distance estimators ($r = 0.094 - 0.627$; Fig. S5), the
256 proportion of tests recovering a significant correlation in the expected direction varied from 16 -
257 20% across these alternate measures (Fig. 3, Table S2).

258 Models that included both geographic and climatic distance as factors influencing genetic
259 diversity had adjusted r^2 values ranging from 0.0 - 0.8 (mean adjusted $r^2=0.2$). For only two
260 OTUs were both geographic and climatic distance included as significant predictors (Fig. S6).

261 Demographic analysis found that the two-epoch model best fit all 25 OTUs, in which population
262 size instantly changed some time in the past (Fig. 4, S4). Current population size was inferred to
263 be an average of 4.3× greater than ancestral population sizes (Fig. 4A). Fourteen of the 25
264 OTUs showed significant evidence for range expansion (Fig. 4B). The origins of the range
265 expansion were generally inferred to be towards the edge of range; on average, the center-edge
266 distance ratio of origins was 0.81 (Fig. S7).

267 We tested four sets of demographic, intrinsic, and extrinsic factors that might affect our ability to
268 recover the central-marginal hypothesis. We found that the strength of the range expansion was
269 the best predictor of whether or not we recovered the central-marginal hypothesis (relative
270 importance: 0.86; Fig. 5A). Species with stronger evidence for a range expansion have more
271 positive diversity-distance correlations and thus more strongly contradict the predictions of the
272 central marginal hypothesis (Fig. 5B). The best overall model included strength of range
273 expansion as the sole predictor of diversity-distance correlations and had an adjusted $r^2 = 0.2$.

274 **Discussion**

275 For the 25 species-level taxa for which we were able to test the central-marginal hypothesis, we
276 found the expected negative correlation between genetic diversity and distance from range
277 center in 16 taxa. This pattern was significant for 8 taxa. Across these 16 taxa, edge populations
278 only have 11% lower genetic diversity than central populations. Relative to differences in
279 expected abundance across a range (Brown, 1984), this decline in genetic diversity across the

range is fairly modest. Only one taxon provided significant evidence against the central-marginal hypothesis. Thus, our results mirror the patterns identified 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), which find support for the central marginal hypothesis but with numerous exceptions and significant unexplained variability.

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 these results, it is perhaps more interesting to identify the factors determining whether or not the central-marginal hypothesis is recovered in a given species. First, the central-marginal hypothesis derives from the abundant-center model, which implicitly assumes that the geographic core of a range is also the ecological core of the range. In other words, the center of the range is where individuals in a species have the most ideal conditions and the highest reproductive output (Brown, 1984). However, ecological gradients do not necessarily follow simple patterns that correspond to a geographic range center (Duncan et al., 2015; Pironon et al., 2017; Pironon, Villellas, Morris, Doak, & García, 2015; Trumbo et al., 2016). In such cases, taxa would exhibit a distance-diversity relationship only when distance is measured in ecological units. For our taxa, geographic and climatic distance were only modestly correlated ($r = 0.1 - 0.43$, Fig. S5), which suggests that geographic distance is not necessarily synonymous with climatic distance. Yet, when testing the central-marginal hypothesis using climatic distance, we do not see greater support for the hypothesis. Only 6 of 25 taxa follow predictions and have significantly negative correlations (Fig. 2B). These results suggest that

303 failure to recover the central-marginal hypothesis is not due to differences in geographic versus
304 climatic distance. However, we estimated ecological distance solely using climatic variables,
305 and many of the taxa included in this study span arid biomes that are relatively climatically
306 homogenous (James & Shine, 2000). Pianka (1972) suggested that broad-scale aspects of
307 vegetation structure and substrate are important determinants of geographic range limits in arid
308 Australian lizards. More nuanced estimates of ecological distance — particularly if they
309 encompass environmental variables that define range limits — could certainly result in different
310 patterns. Ultimately, however, the central-marginal hypothesis originates from the
311 abundant-center hypothesis. Instead of using ecological suitability as a proxy for population
312 density and a predictor of genetic diversity, directly measuring population density and
313 abundance itself might be appropriate (c.f. Dixon, Herlihy, & Busch, 2013; Sexton et al., 2016;
314 Yakimowski & Eckert, 2008). Unfortunately, there are no shortcuts to estimating range-wide
315 patterns of abundance in Australian desert lizards (Grundler, Singhal, Cowan, & Rabosky,
316 2019), and obtaining abundance information for even single localities requires considerable time
317 and resources (Pianka, 2014; Thompson, Withers, Pianka, & Thompson, 2003).

318 Second, how geographic distance is measured matters (Sagarin et al., 2006; Santini et al.,
319 2019; Yancovitch Shalom et al., 2020). Depending on range shape, alternate measures of
320 geographic distance can be markedly different. For example, take our taxa *Ctenotus* aff.
321 *spaldingi* (1), which has a long range that spans from north to south along the full Eastern coast
322 of Australia (Fig. 1). Our focal estimator of distance was distance from the range centroid. A
323 population that is due east of the range center could be at the edge of the range and still be
324 relatively close to the range center, whereas an equidistant population that is due north of the
325 range center would still be far from the edge range. The less round and more eccentric a range
326 is, the harder it can be to define an adequate metric for geographic distance. Further,

327 geographic ranges shift through time; populations might retain the (non-equilibrium) signature of
328 historical range movements such that present-day range position may not be reflective of
329 historical range structure that most influenced present-day genetic variability (Samis & Eckert,
330 2007). This likely explains why various metrics of geographical distance are only modestly
331 correlated ($r = 0.1 - 0.62$, Fig. S5) and could partially explain why the outcomes of our test of the
332 central-marginal hypothesis varies across species (Fig. 2A). Note that our estimate of range
333 center itself was fairly simplistic; defining range center itself can be fraught (Borregaard &
334 Rahbek, 2010). That said, most taxa showed qualitatively consistent correlations across
335 distance metrics (Table S2); significance levels however varied.

336 Similarly, treating all range edges equivalently can confound tests of the central-marginal
337 hypothesis (Sagarin et al., 2006), particularly if there are multiple peaks of population
338 abundance (Dixon et al., 2013) or if ranges span elevational or latitudinal gradients. Factors
339 structuring range limits often vary across northern versus southern edges and higher versus
340 lower elevations (Connallon & Sgrò, 2018; Freeman & Beehler, 2018; Halbritter, Billeter,
341 Edwards, & Alexander, 2015), which might then affect patterns of abundance. Further, historical
342 environmental changes, such as glacial cycles, often act differentially across range edges,
343 leading to “lagging” and “leading” edges that can further structure genetic diversity (Hampe &
344 Petit, 2005). If the nature of the central-marginal hypothesis changes depending what range
345 edge is considered, then collapsing range edges into a single transect could increase noise and
346 decrease power to identify support for the hypothesis. Thus, ideally, researchers would test the
347 central-marginal hypothesis across multiple linear transects from the range center to the edge
348 (Kennedy, Preziosi, Rowntree, & Feller, 2020; Trumbo et al., 2016). This represents a massive
349 sampling effort and would be simply untenable for many species, including those in our study.

350 Third, certain demographic histories can produce patterns that mimic those expected under the
351 central-marginal hypothesis (Eckert et al., 2008). For species at demographic equilibrium,
352 limited migration between populations combined with boundary effects at range borders can
353 result in a gradient of high genetic diversity at the range core and lower diversity at the edges
354 (Peter & Slatkin, 2013; Wilkins & Wakeley, 2002). In a non-equilibrium scenario, during range
355 expansions, repeated serial founder events create gradients of allele frequencies and genetic
356 diversity. If the origin of the expansion occurs near the center of the range, then genetic diversity
357 will decline from the center to the edges of the range (DeGiorgio et al., 2009; Slatkin & Excoffier,
358 2012 but see Peter & Slatkin, 2013) which shows this can also occur due to edge effects).

359 Numerous species across the tree of life show this pattern, presumably due to the effects of
360 range expansion (DeGiorgio et al., 2009; Pierce et al., 2014; Provan & Maggs, 2012). Most of
361 our focal taxa are arid distributed (Fig. S1), and in Australia, the arid zone has expanded
362 dramatically since the Miocene (Pepper & Keogh, 2021). Given this biogeographic history, it is
363 perhaps unsurprising that all of our taxa showed evidence for population expansion, and 14 of
364 our 25 taxa showed evidence of range expansions (Fig. 4). However, contrary to what has been
365 seen in other species, species that experienced range expansion more strongly contradict the
366 expectations of the central-marginal hypothesis (Fig. 5B). We inferred that most ranges
367 expanded from the range edge (Fig. S7); thus, we predict to see a declining gradient in genetic
368 diversity from the range edge rather than the range center. Thus, even though range
369 expansions can lead to patterns that mimic those expected under the central-marginal
370 hypothesis, in our study, species that experienced range expansions were the least likely to
371 show support for the central-marginal hypothesis. Our approach thus shows the promise of
372 using population genetic inference to disentangle historical and current demography (see also
373 (Duncan et al., 2015; Moeller, Geber, & Tiffin, 2011; Wei, Sork, Meng, & Jiang, 2016),

374 particularly when combined with retrodictions of past geographic range distribution (Pironon et
375 al., 2015).

376 Finally, testing the central-marginal hypothesis can be affected by sampling effort (Blackburn,
377 Gaston, Quinn, & Gregory, 1999). Previous meta-analyses have found mixed effects of
378 sampling effort on study outcomes (Eckert et al., 2008; Lira-Noriega & Manthey, 2014), but
379 greater sampling should allow more nuanced tests of the central-marginal hypothesis. For
380 example, many studies compare patterns of genetic diversity after binning populations as either
381 core or peripheral populations (Eckert et al., 2008; Yakimowski & Eckert, 2008). Here, because
382 we collected thousands of loci, we could treat each individual as a population (Nazareno et al.,
383 2017), and we were thus able to measure distance as a continuous variable. Binning
384 populations as core versus peripheral results in less granularity and also requires researchers to
385 arbitrarily define central vs. edge populations. Had we binned populations, only four species
386 would have supported the central-marginal hypothesis. While sample size did not affect the
387 likelihood of recovering the central-marginal hypothesis (Fig. 5A), even greater sampling would
388 allow us to test more complex models for how patterns of genetic diversity change across the
389 range, like humped or stepwise models (Freeman & Beehler, 2018; Miller, Bermingham, Klicka,
390 Escalante, & Winker, 2010; Yancovitch Shalom et al., 2020).

391 *Implications and future directions*

392 The abundant-centre and central-marginal hypotheses are compelling because they have clear
393 implications for range limits and speciation. One hypothesis for why species have range limits is
394 that boundaries form where species are no longer able to adapt to edge conditions (Hoffmann &
395 Blows, 1994; Kirkpatrick & Barton, 1997; Polechová, 2018). In a world where ranges are shifting
396 as a result of climate change, edge populations are perhaps most likely to be extirpated or

397 swamped by gene flow (Hampe & Petit, 2005). Further, although edge populations are expected
398 to have lower levels of genetic diversity overall, they are often genetically and phenotypically
399 distinct from populations at the range core (Eckert et al., 2008), making their loss of particular
400 concern for conservation aims. Thus, edge populations both help determine range limits and are
401 particularly threatened as range limits shift. Here, we find that many species have reduced
402 genetic diversity at their edges, which supports the idea that edge populations are perhaps less
403 able to evolve to their local conditions due to a lack of variability (Hoffmann & Blows, 1994).
404 However, the difference in genetic diversity between central and marginal populations is modest
405 compared to the variance in genetic diversity seen across the range. Further, we only measured
406 putatively neutral genetic variation, which may not correlate with genetic variation underpinning
407 key adaptive traits (Pauls, Nowak, Bálint, & Pfenninger, 2013; Teixeira & Huber, 2021). To better
408 explore the links between the central-marginal hypothesis and range limits, we should ideally
409 sample quantitative trait loci and the traits themselves (c.f. Clark et al., 2021; Kennedy et al.,
410 2020; Pennington et al., 2021; Pujol & Pannell, 2008).

411 In verbal models of species formation, peripheral populations are often seen as engines of new
412 species (Brown, 1957; Levin, 1970; Mayr, 1970). Peripheral populations are thought to be
413 subject to different biogeographical and ecological conditions from the core populations, simply
414 because of their geographical location. Thus, they might be more likely to split to form isolates
415 that then evolve into new species (Bush, 1975). The central-marginal hypothesis predicts that
416 peripheral populations should show greater levels of genetic divergence than core populations
417 (Dixon et al., 2013), which could further spur species formation at the edges. We cannot
418 robustly test these predictions because of sparse sampling, although we find some evidence
419 that genetic divergence is greater between core-edge and edge-edge populations than

420 core-core populations (Fig. S8). With denser sampling, we would be better able to explore how
421 the patterns of the central-marginal hypothesis connect to speciation.

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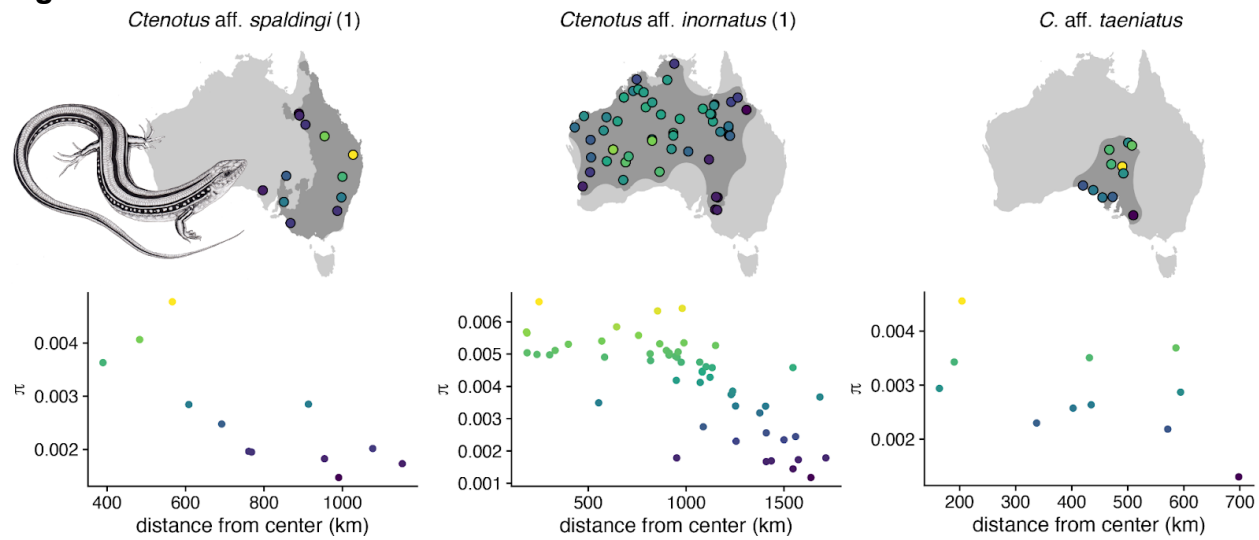
674 **Data Accessibility**

675 All data used in this study has been previously published (see Table S1 for SRA codes). Code
676 used for data analysis and visualization is available at
677 https://github.com/singhal/central_marginal.

678 **Author Contributions**

679 SS & DLR designed research, SS & JW performed research, SS & JW analyzed data, SS & JW
680 wrote the paper, and all authors reviewed and finalized the final text.

681 **Figures**



682 **Figure 1:** The relationship between genetic diversity and distance from range center for three
683 exemplar OTUs that showed a significant negative correlation (*Ctenotus* aff. *spaldingi* 1), a
684 significant negative correlation (*C. aff. inornatus* 1), and a non-significant negative correlation
685 (*C. aff. taeniatus*). Our species delimitation approach occasionally splits and lumps nominal
686 species; here, nominal species *C. taeniatus* and *C. euclae* have been lumped into the OTU *C.*
687 aff. *taeniatus*. Shaded areas on maps indicate OTU geographic range and point colors vary
688 based on genetic diversity. Drawing of *C. aff. spaldingi* 1 courtesy of M. Grundler (re-used with
689 permission from the University of Chicago Press).

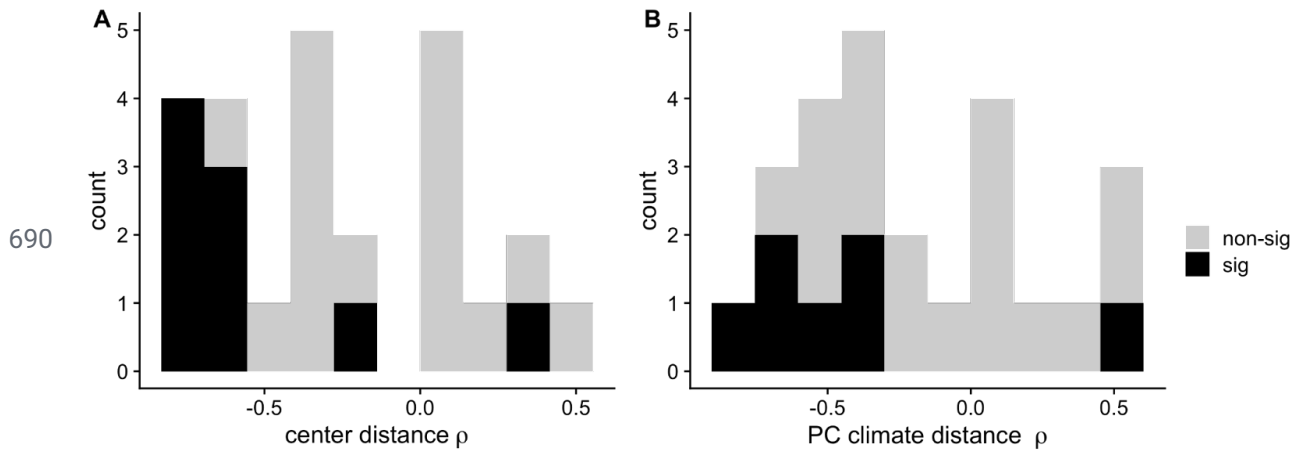
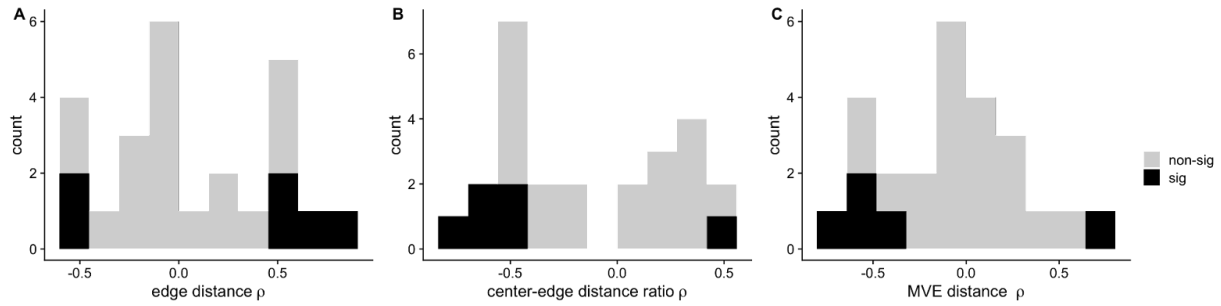
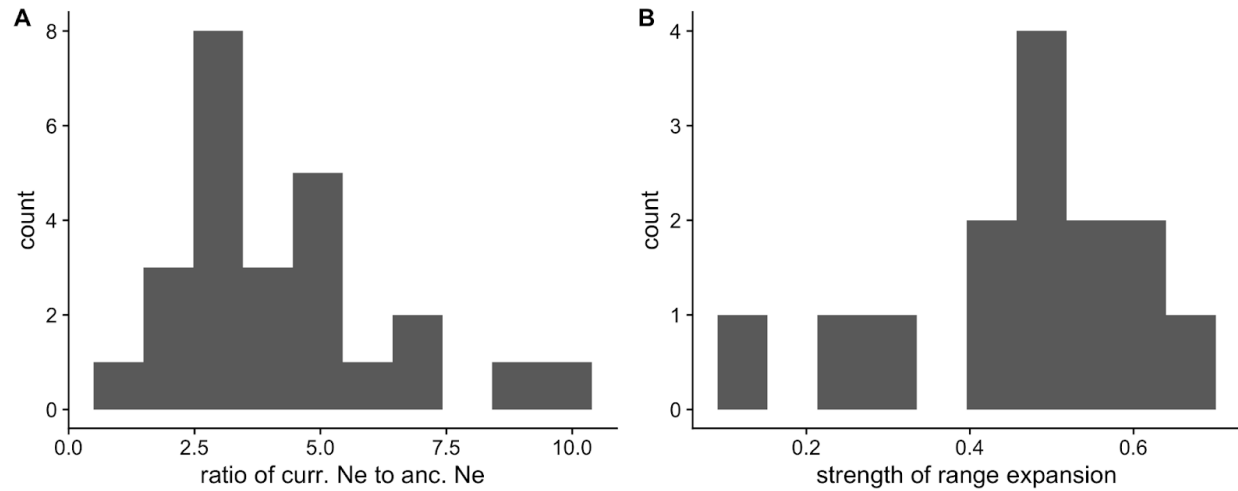


Figure 2: Spearman rank correlations (ρ) between genetic diversity and (A) geographic distance, as measured by the distance to range center and (B) climatic distance, as measured by the distance to the principal component (PC) climatic centroid of the range ($n = 25$ OTUs). Fill color indicates significance of correlation ($p < 0.05$). As expected under the central-marginal hypothesis, most correlations are negative though not all are significant.



696 **Figure 3:** Spearman rank correlations (ρ) between genetic diversity and alternate measures of
697 distance: (A) geographic distance, as measured by the distance to range edge, (B) geographic
698 distance, as measured by the ratio of center distance to range radius, and (C) distance from
699 climatic centroid of range, as defined by the minimum volume ellipsoid (MVE). For the
700 relationship shown in (A), we would predict to recover positive correlations under the
701 central-marginal hypothesis; for the relationships shown in (B) and (C), we would predict
702 negative. Fill color indicates significance of correlation ($p < 0.05$). Although the majority of
703 datasets follow expectations, patterns vary across alternative metrics of distance.



704 **Figure 4:** Demographic inference for OTUs included in this study. (A) Ratio of current effective
705 population size (N_e) to ancestral N_e as inferred using dadi. All 25 OTUs best fit the two-epoch
706 model, in which populations expanded instantly in the past (see Fig. S3). (B) For the 14 OTUs
707 that showed significant evidence for range expansion, we plot the strength of the range
708 expansion, as measured by the correlation between allele frequency clines and geographic
709 distance from the expansion origin.

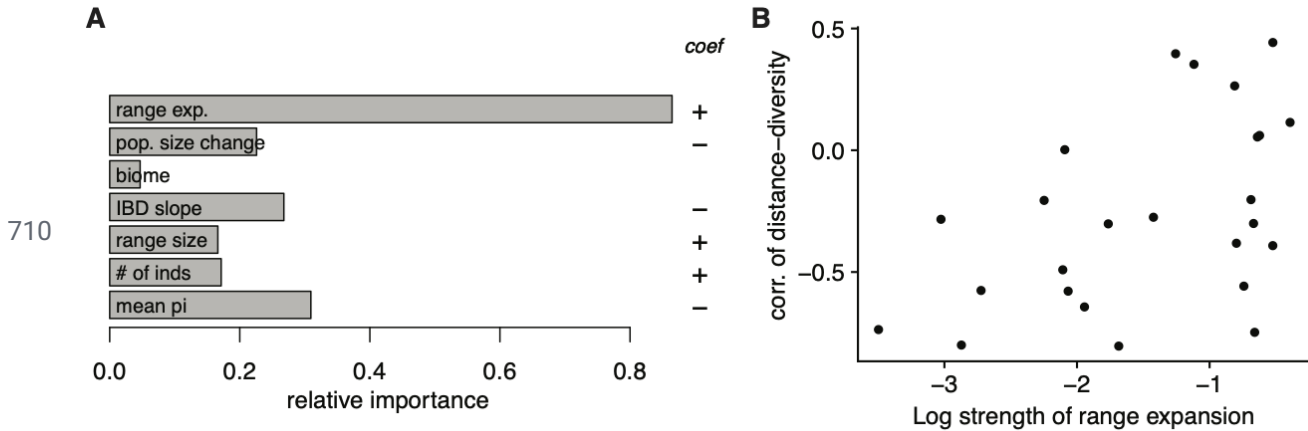


Figure 5: (A) Model fitting for seven variables that span four possible explanations for whether or not we recover support for the central-marginal hypothesis in a given taxon: (1) potential power-related factors: range size, number of individuals sampled, and mean genetic diversity for the OTU, (2) intrinsic factors: isolation-by-distance (IBD) slope, (3) extrinsic factors: biome, and (4) demographic factors: strength of range expansion, population size change. 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) Species that show stronger evidence for range expansion are more likely to exhibit a positive correlation between center distance and genetic diversity, opposite to predictions from the central-marginal hypothesis.