Latitudinal genetic diversity gradients steepen toward the poles

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Abstract

Latitudinal biodiversity gradients are among the best-described biogeographic patterns. However, there is little agreement on whether genetic diversity, the most fundamental level of biodiversity, is also latitudinally distributed. The confusion about the distribution of genetic diversity at biogeographic scales stems in part from the fact that genetic diversity gradients have been described for multiple types of genetic diversity, with good reasons to expect patterns to vary with the component of genetic diversity examined. Genome-wide diversity varies both within and across species. Thus, nuclear genetic diversity gradients might arise due to the existence of parallel latitudinal gradients within species, or due to species turnover and differences in species-level genetic diversity across latitudes. We used a compilation of nuclear genetic data from 100 mammal species across 1,426 locations to test for latitudinal genetic

diversity gradients using Bayesian hierarchical regressions. We detected no general latitudinal genetic diversity gradients within or across species. However, the direction of within-species genetic diversity gradients was associated with species attributes. Notably, the slopes of intraspecific latitudinal gradients became increasingly positive for species distributed at higher latitudes. Interactions between species-level and population-level processes appear to shape the biogeography of genetic diversity.

Keywords: latitudinal diversity gradient, biogeography, biodiversity, population genetics, macrogenetics, mammals

Introduction

The processes organizing global biodiversity gradients remain unresolved despite intensive study (Lawrence & Fraser, 2020; Pontarp et al., 2019). Comparing and contrasting patterns among different components of biodiversity across varying levels of organization can help to distinguish among competing hypotheses about their origins and maintenance. Genetic diversity is a fundamental component of biodiversity that represents the outcome of ecological and evolutionary processes acting on populations, and reflects populations' adaptive capacity. Despite considerable interest in understanding whether global patterns of genetic diversity covary with other biodiversity components such as species richness, functional, or phylogenetic diversity, evidence for a latitudinal gradient in genetic diversity is equivocal (De Kort et al., 2021; Gratton et al., 2017; Lawrence & Fraser, 2020; Miraldo et al., 2016; Schipper et al., 2008; Schumm et al., 2019). Generally, a lack of recognition that different expectations apply to various types of genetic diversity gradients has hindered progress in understanding the extent to which latitudinal biodiversity patterns are generalizable as well as the processes underlying their emergence and maintenance.

The challenge in relating genetic diversity patterns to other forms of biodiversity gradients is that it exists in many forms. Genetic diversity can be quantified for specific genes (e.g. mitochondrial cytochrome oxydase I, Miraldo et al., 2016; MHC genes, Yiming et al., 2021), organellar genomes, or across the nuclear genome (genome-wide genetic diversity, (De Kort et al., 2021; Lawrence et al., 2023; Schmidt, Dray, et al., 2022). Neutral, nuclear genome-wide diversity is the most informative type of genetic diversity for understanding universal mechanisms structuring biodiversity. This is because it reflects genetic drift and gene flow—neutral evolutionary processes that operate across the genome (Charlesworth & Charlesworth, 2010).

The strengths of genetic drift and gene flow are influenced by population size and dispersal, key ecological attributes of populations that are shaped by environments. Genetic drift and gene flow also influence population structure and genetic differentiation, which are the first steps of the speciation process. Thus, broad-scale, multispecies patterns of genome-wide genetic variation and differentiation can be readily incorporated into existing hypotheses about the processes maintaining latitudinal diversity gradients at the species level and above (Dowle et al., 2013; Lawrence & Fraser, 2020; Schmidt, Dray, et al., 2022), particularly those based on resource availability and diversification dynamics (Etienne et al., 2019; Mittelbach et al., 2007; Schmidt, Dray, et al., 2022; Schmidt, Muñoz, et al., 2022).

Until recently, genetic data suitable for estimating genome-wide diversity were not available at the broad geographic and taxonomic scales needed to assess latitudinal gradients of genetic diversity. Studies of genetic diversity gradients are highly heterogeneous in terms of marker type, genetic metrics, and methodology (Lawrence et al., 2023; Miraldo et al., 2016; Theodoridis et al., 2020; Yiming et al., 2021). Genome-wide diversity varies both within and across species. In mammals, genome-wide diversity at the species level is predictably associated with morphological, ecological, and life-history traits (Buffalo, 2021; Romiguier et al., 2014), while several historical and contemporary environmental and evolutionary factors also contribute to spatial patterns of genome-wide diversity within species.

Tests for latitudinal genetic diversity patterns rarely consider that genetic diversity can vary latitudinally and be statistically detectable in two ways (Fig. 1). First, species turnover and genetic diversity differences across species and latitudes could produce a gradient (Fig. 1a). Second, genetic diversity gradients might arise due to the existence of parallel latitudinal gradients across populations within species (Fig. 1b). For example, genetic diversity gradients

across species may correlate with latitudinal gradients in body size or range size that are associated with species-level genetic diversity (He et al., 2023; Romiguier et al., 2014). Interactions between latitudinally varying species characteristics and population-level processes may also shape intraspecific genetic diversity patterns, for example if latitudinal trait variation caused consistent latitudinal variation in population demographics (Dowle et al., 2013). Because they emerge from different processes, disentangling within- and across-species latitudinal genetic diversity gradients is necessary to achieve a more cohesive view of how biodiversity patterns may be maintained across levels of organization.

We used a compilation of nuclear genetic data from 59587 individuals sampled across 100 mammal species at 1426 locations to test for the presence of latitudinal genetic diversity gradients within and across species. We assessed two metrics of genome-wide genetic diversity, gene diversity and allelic richness, and additionally estimated contemporary effective population size which provides an estimate of the strength of genetic drift. We also tested for gradients in population differentiation. We used hierarchical Bayesian generalized linear regressions to test for latitudinal genetic diversity patterns across species (interspecific gradient), and within species (intraspecific gradients). Finally, given the wide variation in the strength and direction of within-species gradients, we performed a post-hoc analysis to assess whether species' attributes moderated latitudinal relationships.

Methods

Genetic data

We used a previously compiled database of publicly available microsatellite genotypes for terrestrial mammals to test for latitudinal relationships (Schmidt et al., 2025). In brief, these data

were compiled by programmatically querying DataONE (https://www.dataone.org/) and the Dryad Digital Repository (https://datadryad.org/) with a list of species names and the search term "microsat*" (e.g., *Tamias striatus* microsat*). Because we were interested in generally describing contemporary latitudinal patterns of genetic diversity, we applied the following filters to the database: removing sites located outside species' native ranges as identified by the authors of original works; removing hybrid species as identified by the original authors; removing historical samples where identified (pre-1900); and removing cosmopolitan, human-associated species (i.e., *Mus musculus*). Finally, we also excluded island sites due to specific processes that may cause systematic downward biases in island genetic diversity relative to the mainland independent of latitude (i.e., bottlenecks and reduced gene flow). The final database encompassed 100 mammal species, 1426 sample locations (sites) and 59587 individuals (Fig. 2). The median number of individuals sampled at each site was 23 (range 5 – 2444 individuals), and the median number of sample locations per species was 7 (range 1 – 82 sites).

To describe latitudinal patterns of genetic diversity and differentiation, we estimated four genetic metrics each at site and species levels using the *adegenet* and *hierfstat* packages in R (Goudet & Jombart, 2015; Jombart et al., 2017). First, we used two alternative metrics of genetic diversity: gene diversity and allelic richness. Gene diversity is the probability of sampling two different alleles in a non-random mating population (Nei, 1973). We estimated gene diversity at each site, and at the species level we estimated the overall gene diversity across all sites within each dataset. Allelic richness is a count of alleles in a sample of individuals standardized using sample-based rarefaction to account for variation in sample size across sites (El Mousadik & Petit, 1996). The genetic database only retains sites with a minimum of 5 sampled individuals, thus we rarefied allelic richness to a minimum of 10 alleles across the entire database to ensure

comparability. To estimate allelic richness at the species level, we grouped all individuals within a dataset into a single population and re-estimated allelic richness, retaining a 10-allele minimum for rarefaction because this was the smallest sample size across all datasets. We use *dataset* to refer to a single genotype file for one species of a given study (a unique combination of species and study).

Next, we estimated contemporary effective population size, a measure of the strength of genetic drift, using the linkage disequilibrium method implemented in NeEstimator v2 (Do et al., 2014). Contemporary effective population size measures signatures of genetic drift in the parental generation of sampled individuals at each locality. The linkage disequilibrium method performs well for small effective sizes, however returns estimates of infinity if too few individuals were sampled and sampling error overwhelms the signal of genetic drift, or if effective population sizes are very large (Waples & Do, 2010). We set estimates of infinity to NA and removed them from the final analysis. To estimate effective population size at the species level, we combined all individuals per dataset into a single population. Instead of a local effective population size, this species-level estimate is better considered as a metapopulation effective population size (Waples, 2025). Metapopulation effective population sizes reflect the outcomes of longer-term evolutionary demographic processes compared to local, contemporary effective population size (Waples, 2025).

Finally, we estimated genetic differentiation per site and overall population structure at the species level. At the site level we used population-specific F_{ST} (Weir & Goudet, 2017), which estimates how genetically differentiated sites are from a single common ancestor of all sites in the sample. Genetic differentiation is only estimable when at least two sites were sampled in original datasets, thus datasets with single populations were omitted from all F_{ST} analyses. We

144 estimated a species-level measure of population structure using G'_{ST} (Hedrick, 2005). G'_{ST} is a
145 variant of G_{ST} (Nei, 1973), which estimates F_{ST} for multiallelic markers. Maximum G_{ST} values
146 are set by the genetic diversity of subpopulations, and are thus not comparable across datasets or
147 species. G'_{ST} addresses this issue by rescaling G_{ST} to remove its dependency on the average
148 genetic diversity of subpopulations.

149

150 *Species attributes*

151 We obtained spatial distribution data for terrestrial mammals from the International Union for
152 the Conservation of Nature (IUCN, 2021). We filtered species range data to retain only regions
153 where species were recorded as extant, native, and resident. We identified the mid-range latitude
154 for each species by taking the latitude of the range centroid using the *sf* package (Pebesma, 2018;
155 Pebesma & Bivand, 2023).

156 We obtained species body mass (g) data from PanTHERIA (Jones et al., 2009) using the
157 *traitdata* package version 0.0.1 (RS-eco, 2022). We manually added body masses for species
158 missing data (6 species) using reference information from the Global Biodiversity Information
159 Facility (www.gbif.org/species).

160

161 *Analysis*

162 We used hierarchical Bayesian generalized linear models to test for interspecific and
163 intraspecific relationships between genetic metrics and latitude. We fit all models with *brms*
164 (Bürkner, 2017) using normally distributed priors (mean 0, SD 1) for fixed effects, and default

priors for all other parameters. To retain the same directionality for latitudinal relationships across hemispheres, we used absolute latitude in all models. We log-transformed effective population size, body mass and range size, and scaled and centered all predictor and response variables before analysis. All analyses were conducted in R Version 4.3.2 (R Core Team, 2023).

Interspecific gradients. We first tested for evidence of interspecific latitudinal gradients, which may emerge if species' genetic diversity, effective population size, or overall population structure were related to the latitudinal positions of their range. We fit a series of models regressing species' mid-range latitude on genetic metrics. We fit simple linear regressions with species-level estimates of gene diversity, allelic richness, effective population size, or population structure as the response variable. We did not have enough replication of species across studies to account for study-level variation with random effects, thus we took the median allelic richness and effective population size, and mean gene diversity or population structure in cases where one species had estimates from multiple studies.

Intraspecific gradients. We next tested for latitudinal genetic gradients within species using hierarchical linear regressions with site-level latitude as a predictor, incorporating random slopes and intercepts for species. Our genetic response variables included site-level measures of gene diversity, allelic richness, effective population size, and population-specific F_{ST}, resulting in a total of 4 models. In this model structure, random intercepts account for variation in the means of each genetic metric across species, and random slopes allow the relationship between genetic metrics and latitude vary per species. With this approach, we did not make assumptions about the strength or direction of latitudinal genetic patterns of individual species; we instead ask the extent to which latitudinal genetic relationships are consistently negative or positive across all species in the sample. An overall effect size of zero for latitude may therefore indicate that

genetic metrics for all species do not vary with latitude (all species-specific slopes near zero), or alternatively that the effect sizes for individual species relationships with latitude vary from negative to positive, effectively balancing out to a zero overall effect size.

Interactions with species-level variables. Our intraspecific hierarchical models suggested that species varied widely in the strength and direction (negative or positive) of latitudinal genetic diversity gradients. We therefore performed a post-hoc analysis to examine whether body mass, range size, or latitudinal range position may be factors moderating the direction of latitudinal patterns across species for each genetic metric. Body mass tends to vary latitudinally in mammals (Bergmann's Rule; see also He et al., 2023) and is correlated with several other important species traits in addition to genetic diversity, such as population density and life history. Range size, typically associated with body size, also tends to increase with latitude (Rapoport's Rule). Interactions with body size or range size may indicate that species' biological or ecological traits (such as temperature tolerance, dispersal capacity, or generalism) are related to the slopes of within-species gradients. Finally, we examined whether the latitudinal position of species ranges (mid-range latitude) influenced the slope of within-species gradients. Such a relationship would suggest that species' habitat preferences (e.g., polar, temperate, tropical) are associated with the slope of latitudinal gradients within species.

We included each species-level predictor (body mass, range size, mid-range latitude) and their interactions with site-level latitude as additional predictors in our intraspecific models. Interaction terms allowed the effect of site-level latitude to vary conditional on each species-level variable. We modeled each species-level variable separately for a series of three models per genetic metric. We log-transformed, scaled, and centered body mass and range size for comparability across models. We scaled and centered the absolute values of midrange latitude.

To better describe the conditional effects of latitude dependent on interaction terms with species-level variables, we assessed the probability that latitudinal relationships were negative or positive conditional on low and high values for body size, range size, and mid-range latitude. We did this using the hypothesis() function in *brms* to test whether the effect of latitude was greater or less than 0 while conditioned on body size, range size, or mid-range latitude being large (+1 SD) or small (-1 SD).

Sensitivity tests. We note that because some species in the database (31 species) were represented by multiple studies, using species as a random effect does not fully account for study-specific variation across datasets. However, a majority (69%) of species are from single studies and some studies include multiple species, making it infeasible to simultaneously account for species- and study-level variation with random effects in our models. One species, *Apodemus flavicollis*, had a markedly large effect size for gene diversity due to a study-level difference in this metric that was confounded with latitude. We thus performed a sensitivity test by coding these datasets as separate species (Apodemus_flavicollis1 and 2) in intraspecific models (with and without interaction terms). We additionally ran intraspecific models and interaction models using a genotype dataset-specific grouping factor (genotype file name) for random slopes and intercepts instead of species. Genotype dataset as a random effect uniquely identified each species-study combination. All model results were qualitatively similar. We report results from models with species-level random effects with *Apodemus flavicollis* coded as two species in the main text.

Results

Interspecific genetic diversity gradient

We did not detect strong evidence for latitudinal gradients across species for any genetic metric (Fig. 3a). Relationships between latitude and gene diversity, allelic richness, and effective population size all trended in a positive direction, but the probability of relationships being positive was below 90% for all models (Fig. 3a). We note that the number of sample locations per species increased with absolute latitude (Pearson's $r = 0.23$). Species-level genetic diversity and effective population size could tend to increase at high latitudes due to increased chances of sampling across multiple differentiated populations. This correlation between latitude and number of sample locations may result from the combined effects of higher data density in North America and Europe, and because species ranges tend to be larger at higher latitudes facilitating sampling greater numbers of sites. The number of sampled individuals was not correlated with absolute latitude at site or species levels.

Intraspecific genetic diversity gradients

We found no overall relationships between latitude and gene diversity, allelic richness, or population differentiation within species, however site-level effective population sizes tended to increase with latitude (Table 2, Fig. 3b). Inspection of species-specific slopes suggested that one species, *Apodemus flavicollis*, had a strongly negative relationship with latitude due to differing genetic diversity estimates from two studies conducted at different latitudes. For all intraspecific analyses, we present results from models with *A. flavicollis* datasets coded as separate species in the main text. We note that in additional sensitivity tests with genotype dataset as a random effect, latitude had a generally positive relationship with gene diversity, allelic richness, and effective population size. However, this was due to greater numbers of higher-latitude species being represented in multiple studies, giving higher-latitude species greater weight in estimates

of overall effects across species. Generally, species varied widely in their relationships with latitude across all models, with random slopes ranging from negative to positive (Fig. 3b).

Species-level variables as moderating factors

There were clear positive interactions between mid-range latitude, gene diversity and allelic richness; body mass, gene diversity and effective population size; and range size and allelic richness (Fig. 4). Interactions between latitude and species level traits were unrelated to genetic differentiation across all models (Fig. 4). Species with higher mid-range latitudes, larger body sizes, and larger range areas tended to exhibit more strongly positive latitudinal genetic diversity gradients (Fig. 4), while no strong trends were detectable for species with lower mid-range latitudes of smaller size with smaller ranges. Across all models and sensitivity tests, the effect of latitude conditioned on higher values of species level predictors (1 SD above the mean for mid-range latitude, body size, range area) remained positive (Fig. 4). Species-level characteristics thus accounted for some of the variation in the effect of latitude across species.

Discussion

We found no evidence for a straightforward, generalizable latitudinal gradient in genome-wide diversity within or across species that aligned with well-described gradients in species richness. However, integrating within- and across-species gradients yielded a marked pattern of increasingly positive within-species genetic latitudinal gradients toward the poles (Fig. 4). The direction of latitudinal genetic diversity gradients within species was more variable nearer the tropics, becoming more consistently positive in species distributed at higher latitudes. Though these interactive effects on genetic diversity (gene diversity and allelic richness) were most apparent for mid-range latitude, this pattern also generally held for body size and range size.

Populations of larger-bodied species and species with larger ranges tended to be more genetically diverse at higher latitudes within their range. Our results suggest that there may not be clear latitudinal gradients in genetic diversity *per se*; however, there is greater variety in the strength and direction of latitudinal gradients within species at lower latitudes that become more consistently positive with increasing latitude.

Reduced genetic diversity in populations nearer the poles, particularly in the northern hemisphere, is often a predicted outcome of glaciation as species expanded poleward following glacial retreat (Fonseca et al., 2023; Hewitt, 2000). Genetic diversity estimates from microsatellite data are unlikely to capture such historic patterns, instead primarily reflecting contemporary population demography. Across species, genetic diversity is generally better explained by species biology and ecology than historical demography (Romiguier et al., 2014). In general, spatial patterns of genetic diversity within species are complex and are likely not well-described by latitude alone (Schmidt, Dray, et al., 2022; Schmidt et al., 2023).

The intraspecific patterns we find suggest that larger, widely-distributed temperate species more consistently tend to have larger, more genetically diverse populations further from the equator while latitudinal demographic patterns for smaller, range-restricted tropical species are more unpredictable. Stronger latitudinal patterns toward the poles are potentially related to the tendency for range sizes to increase with latitude. Latitudinal gradients may be more statistically detectable for species with wider latitudinal range spans compared to species distributed across a narrower range of latitudes. However, there is no *a priori* expectation for gradients to become more consistently positive across species.

The clear relationships between the directionality of latitudinal gradients and species mid-range latitude suggest that intraspecific genetic diversity gradients may be partly related to species-

specific habitat suitability and the capacity of environments to support larger populations. Lower variability in the direction of latitudinal gradients indicates that spatial population structure is similarly shaped by the environment across species distributed at higher latitudes. Population demography in higher-latitude species is potentially more constrained by the types of environments capable of supporting large population sizes and connectivity nearer the poles, whereas low-latitude populations and species may exploit a greater variety of environments (e.g., by specializing to different habitats or resources) that shape population structure in a variety of ways that are not consistent across species. Latitudinal gradients in not only the mean, but variation of species' traits—including life history traits (Yanco et al., 2022) and mass-corrected field metabolic rate (Anderson & Jetz, 2005)—have been previously reported in terrestrial vertebrates, suggesting that a greater variety of physiological strategies are supported in environments with more stable resource availability year-round due to greater specialization and generally narrower niche widths (Yanco et al., 2022).

Differences in taxonomic practice and taxonomic uncertainty related to species definitions across latitudes may also affect the steepness of latitudinal biodiversity gradients (Freeman & Pennell, 2021). The lack of interspecific latitudinal patterns of population structure we find suggests there is no systematic bias in taxonomic practices tending towards lumping or splitting species across the species included here. We were primarily interested in characterizing genetic diversity gradients present in existing data, which are geographically biased toward North America and Europe. The dependence of the direction of within-species latitudinal gradients on species-level attributes makes clear that overall relationships between latitude and genetic diversity in multi-species analyses will strongly reflect the species composition of the sample. Indeed, we detected an overall positive effect of latitude in sensitivity tests with genotype-dataset specific random

effects (see Methods) because northern-hemisphere temperate species were more likely to be represented by multiple studies, increasing their weight in hierarchical models. The overall consistency of intraspecific latitudinal gradients in multispecies samples must therefore be interpreted with care. While we detected strong evidence for increasing gradient steepness toward the poles for temperate species, greater coverage is needed to fully assess whether uncertainty in gradient directionality at low latitudes is a general pattern or a product of smaller sample size.

Steepening intraspecific genetic diversity gradients that do not align with species richness patterns introduce conflicts for area-based conservation of genetic and species diversity (Kahilainen et al., 2014). Indeed, genome-wide genetic diversity is generally lower in areas of potential conservation interest from species or ecosystem perspectives, including mammalian and amphibian species richness hotspots (Schmidt, Dray, et al., 2022; Schmidt, Munshi-South, et al., 2022), and in transitional zones between biogeographic regions (Schmidt, Muñoz, et al., 2022). While tropical habitats harbor most of the world's species, higher-latitude populations may be reservoirs of genetic diversity and adaptive potential for temperate species. With greater focus on area-based conservation targets as set by Target 3 of the 2022 Montreal-Kunming Global Biodiversity Framework goal to protect 30% of land and seas by 2030 ('30x30' target; CBD, 2022), balancing priorities and consideration of how protected areas may differently serve biodiversity across genetic and species levels is necessary (Díaz et al., 2020).

Implications for processes underlying latitudinal species richness gradients

Processes hypothesized to contribute to latitudinal biodiversity gradients can be generally grouped into three categories, those dealing with resource availability and ecological limits, evolutionary rates, and evolutionary time. While our results do not directly support or refute any one set of hypotheses, they bear on the proposed population-level processes underlying patterns of biodiversity. Although these mechanisms often involve long-term diversification dynamics that may be largely uncoupled from the dynamics of populations (Singhal et al., 2018, 2022), the continued maintenance of latitudinal biodiversity patterns relies on the environmental and ecological drivers maintaining contemporary population processes that produce the gradients over longer periods of time.

Ecological limits hypotheses posit that greater resource availability and diversity of resources in the tropics can support more individuals, and thus larger communities of coexisting species potentially made up of larger populations with lower extinction probabilities (Wright, 1983). Though not a measure of abundance, neutral, nuclear genome-wide diversity can be related to population size through its relationship to genetic drift. Larger populations maintain higher genetic diversity because genetic drift erodes genetic diversity at a rate inversely proportional to the effective population size (Charlesworth & Charlesworth, 2010), which is generally positively correlated with abundance (Charlesworth, 2009).

Our results suggest that neither the size of local populations nor species-wide abundance consistently increase toward the tropics. Indeed, at the species level, poleward species had a slight tendency to be more genetically diverse and have larger species-level effective population sizes, though uncertainty surrounding these estimates was high (Fig. 3a). Further, while our results suggest larger population sizes at higher latitudes for species with poleward distributions, populations of larger-bodied mammals are typically less dense than those of smaller-bodied

mammals (Damuth, 1981; Jetz et al., 2004). Larger poleward populations may be spread across larger geographic areas, meaning fewer individuals per unit area. With no strong tendency for the population sizes of individual species to increase at lower latitudes, the total abundance of individuals within communities may be shaped by other processes that instead affect the number of species in communities (Storch et al., 2018).

Evolutionary rates hypotheses propose that diversification rates are higher in the tropics due to a combination of increased speciation and decreased extinction (Mittelbach et al., 2007). Because reduced gene flow and genetic divergence help initiate the speciation process, tests of evolutionary rates hypotheses typically predict that populations will be further genetically diverged at lower latitudes, over time culminating in more speciation. Potential underlying mechanisms vary, including greater availability and diversity of resources in the tropics creating more ecological opportunities for divergence and speciation, or relationships between higher temperature, faster mutation rates, and shorter generation times potentially leading to faster accumulation of genetic incompatibilities at lower latitudes (Allen et al., 2006; Lawrence & Fraser, 2020; Mittelbach et al., 2007). However, whether speciation rates in mammals increase, decrease, or are related to latitude is unclear (Rolland et al., 2014; Soria-Carrasco & Castresana, 2012; J. T. Weir & Schluter, 2007) though there is evidence for faster speciation rates at higher latitudes across vertebrate groups (Harvey et al., 2020; Rabosky et al., 2018; Weir & Schluter, 2007).

We did not detect consistent patterns of greater genetic divergence toward the tropics. Species with ranges nearer the tropics did not exhibit greater overall population structure (Fig. 3a), and intraspecific latitudinal gradients of genetic differentiation varied considerably across species (Fig. 3b). In general, the microevolutionary extent of population differentiation is decoupled

391 from speciation rates at macroevolutionary scales (Rabosky & Matute, 2013; Singhal et al.,
392 2018, 2022), as there are multiple steps between genetic divergence and successful speciation
393 (Yamaguchi et al., 2025). However, contemporary patterns of genome-wide genetic
394 differentiation and species richness tend to be geographically correlated in region- and taxon-
395 specific analyses, suggesting latitude alone may not capture general environmental patterns that
396 are relevant for both genetic divergence and complete speciation (Schmidt, Dray, et al., 2022;
397 Schmidt, Munshi-South, et al., 2022).

398 Evolutionary rates hypotheses based on ecological opportunities for speciation often rely on
399 natural selection to drive ecological divergence (Schluter, 2016). The strength of genetic drift,
400 quantified by effective population size, is inversely related to the efficiency with which natural
401 selection can spread beneficial alleles to facilitate genetic adaptation (Charlesworth &
402 Charlesworth, 2010). Due to this inverse relationship between genetic drift and selection
403 efficiency, patterns of effective population size are also relevant to evolutionary rates
404 hypotheses. Small and isolated populations may rapidly genetically diverge due to stronger
405 genetic drift, but at the same time have higher extinction risk due to demographic stochasticity
406 and genetic factors such as inbreeding (Lande, 1993). Larger populations with greater effective
407 population sizes may have the genetic diversity and capacity to respond to divergent selection
408 and persist long enough to speciate (Yamaguchi et al., 2025). Our finding of positive latitudinal
409 gradients in effective population size within species (particularly higher-latitude species)
410 suggests that selection may generally be more efficient, and populations may be more likely to
411 locally adapt, toward the poleward edge of their distributions. Simultaneously, smaller
412 populations toward the equatorward distribution edge may be more prone to neutral genetic
413 divergence due to drift.

414

415 *Reconciling latitudinal genetic patterns across markers and metrics*

416 The literature on latitudinal gradients in genetic diversity is substantial. Despite increased
417 interest in this question, particularly in the field of macrogenetics, there has been no empirical
418 consensus on whether such gradients exist (Gratton et al., 2017; Pereira, 2016; Schluter &
419 Pennell, 2017). Part of the reason for this is unclear terminology surrounding the types of
420 latitudinal genetic diversity gradients being quantified. For instance, *latitudinal gradients of*
421 *genetic diversity* may include latitudinal gradients in intraspecific mitochondrial genetic diversity
422 (Adams & Hadly, 2012; Clark & Pinsky, 2024), interspecific mitochondrial genetic diversity
423 (Fonseca et al., 2023), interspecific chloroplast genetic diversity (Fonseca et al., 2023),
424 mitochondrial genetic differentiation (Martin & McKay, 2004), multispecies averages of
425 mitochondrial genetic diversity (French et al., 2023; Manel et al., 2020; Miraldo et al., 2016;
426 Theodoridis et al., 2020), intraspecific nuclear genetic diversity (Clark & Pinsky, 2024; De Kort
427 et al., 2021; Lawrence et al., 2023; Schmidt, Dray, et al., 2022; Schmidt, Munshi-South, et al.,
428 2022), nuclear genetic differentiation (Eo et al., 2008), and gene-specific diversity
429 (mitochondrial cytochrome oxidase I and cytochrome b: French et al., 2023; Manel et al., 2020;
430 Miraldo et al., 2016; Theodoridis et al., 2020; MHC: Yiming et al., 2021).

431 Predictions may differ for the genetic diversity of local populations or genetic differentiation,
432 and also depend on whether such patterns are quantified at the population or species level. More
433 importantly, different genetic markers reflect distinct evolutionary processes that can be
434 considered holistically, but not interchangeably, in the broader context of understanding how
435 latitudinal biodiversity gradients are maintained (Schmidt & Garroway 2021). The evolution of
436 organellar genomes differs from the nuclear genome due to their distinctive biological properties:

437 they are uniparentally inherited, do not recombine, are gene-dense, and have different mutation
438 rates than the nuclear genome (Galtier et al., 2009). For example, ecological limits hypotheses as
439 applied to genetic diversity rely on a relationship between genetic diversity metrics and
440 population size. Neutral, nuclear genome-wide diversity can be related to population size through
441 its relationship to genetic drift and genome-wide effective population size. The same does not
442 necessarily hold for mitochondrial genetic diversity (Bazin et al., 2006; Galtier et al., 2009). The
443 mitochondrial effective population size is typically smaller than that of the nuclear genome. The
444 mitochondrial genome also primarily contains genes that are necessary for cellular respiration,
445 which means its diversity is significantly shaped by natural selection (Dowle et al., 2013; Galtier
446 et al., 2009). This muddies potential inferences about demographic processes. Gene-specific
447 latitudinal gradients enable the study of specific biological processes; for example, an
448 exploration of functional latitudinal gradients in the diversity of MHC II genes suggested higher
449 diversity and stronger selection nearer the equator, potentially related to the diversity and
450 prevalence of parasites and immune function (Yiming et al., 2021). Different types of genetic
451 diversity are not necessarily equally interpretable under the major macroecological and
452 macroevolutionary processes proposed to underlie global biodiversity patterns (Schmidt &
453 Garroway, 2021). The varied components of genetic diversity—neutral, functional, nuclear, and
454 organellar—are each distinct, complementary layers of latitudinal biodiversity gradients that are
455 more richly informative as a whole.

456

457 *Conclusions*

458 Unlike other biodiversity components, mammalian genome-wide genetic diversity does not
459 exhibit strong latitudinal gradients at the species or population levels. In notable contrast to

latitudinal patterns of mitochondrial genetic diversity, our findings build on an increasingly consistent lack of general gradient in genome-wide diversity across terrestrial vertebrates, marine and freshwater fish, and plants (Clark & Pinsky, 2024; De Kort et al., 2021; Lawrence et al., 2023). However, we characterize a pattern of steepening positive latitudinal gradients of intraspecific genetic diversity toward the poles. Latitudinal variation in the strength and direction of within-species diversity gradients captures an interplay between the longer-term, species-level processes determining suitable habitat and range position, and their underlying population dynamics. Although macroevolutionary and macroecological hypotheses for the origins and maintenance of latitudinal biodiversity gradients typically focus on long-term community and diversification dynamics, our results add a contemporary, population-level perspective to this long-held question.

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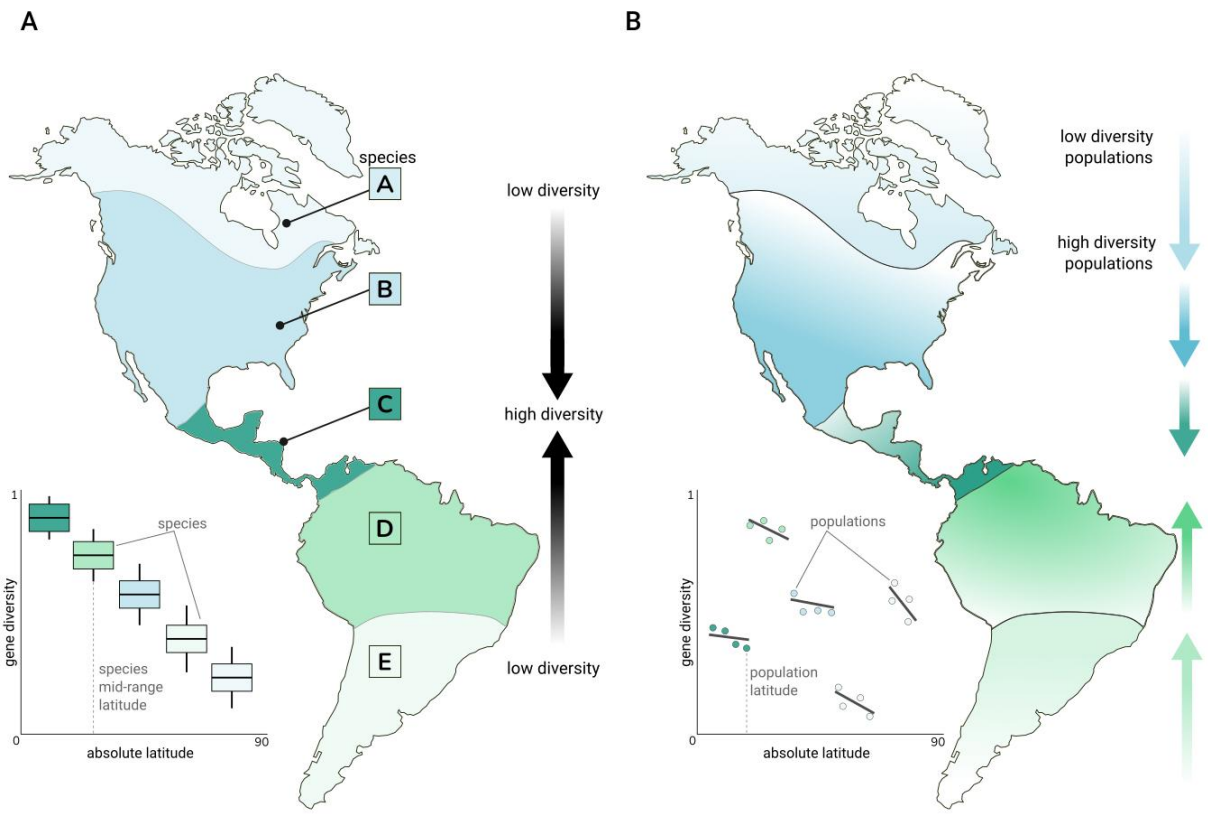


Figure 1. Conceptual figure depicting two types of statistically detectable genetic diversity gradients: interspecific (A) and intraspecific (B) latitudinal diversity gradients. (A) The ranges of species *A* – *E* have different latitudinal range positions. All species have variable levels of genetic diversity across their ranges, shown in boxplots. Interspecific gradients of genetic diversity would align with latitudinal gradients in other biodiversity components if species-level genetic diversity consistently decreased with latitude, i.e. if tropical species *C* and *D* had higher species-level genetic diversity than temperate species *A*, *B*, and *E*. (B) Species are distributed at different latitudes as in (A). Intraspecific gradients in genetic diversity would have an overall negative relationship with latitude if, within all species, populations at lower latitudes tended to be more genetically diverse than high latitude populations. Though depicted independently, inter- and intraspecific genetic diversity gradients are not mutually exclusive.

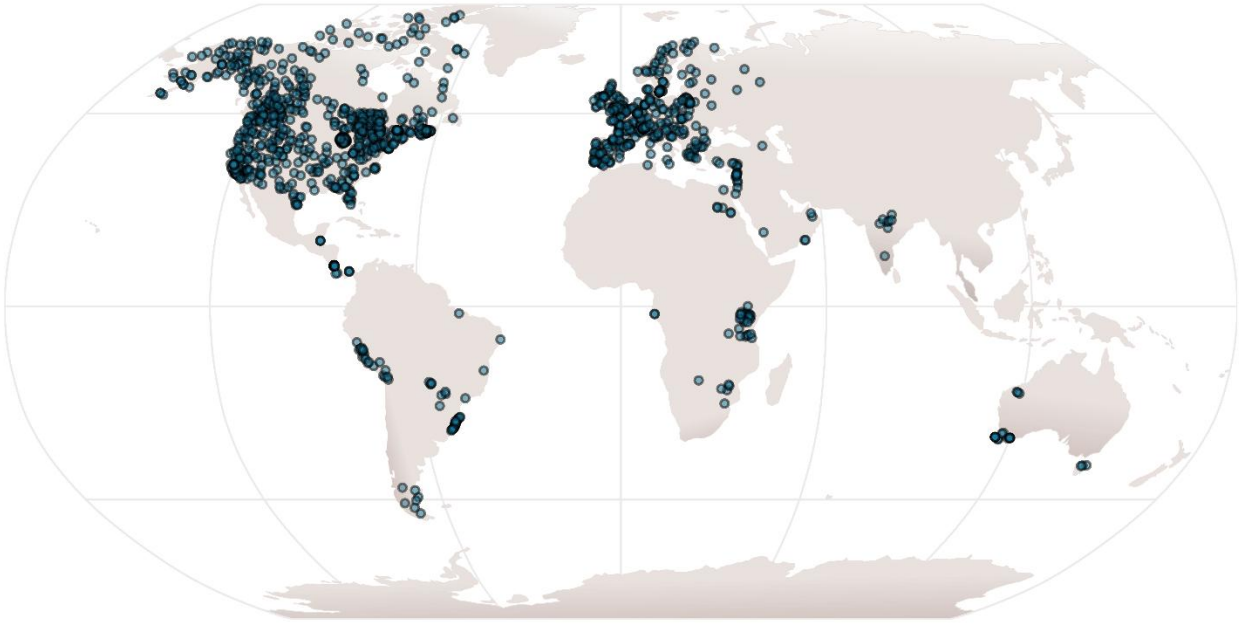
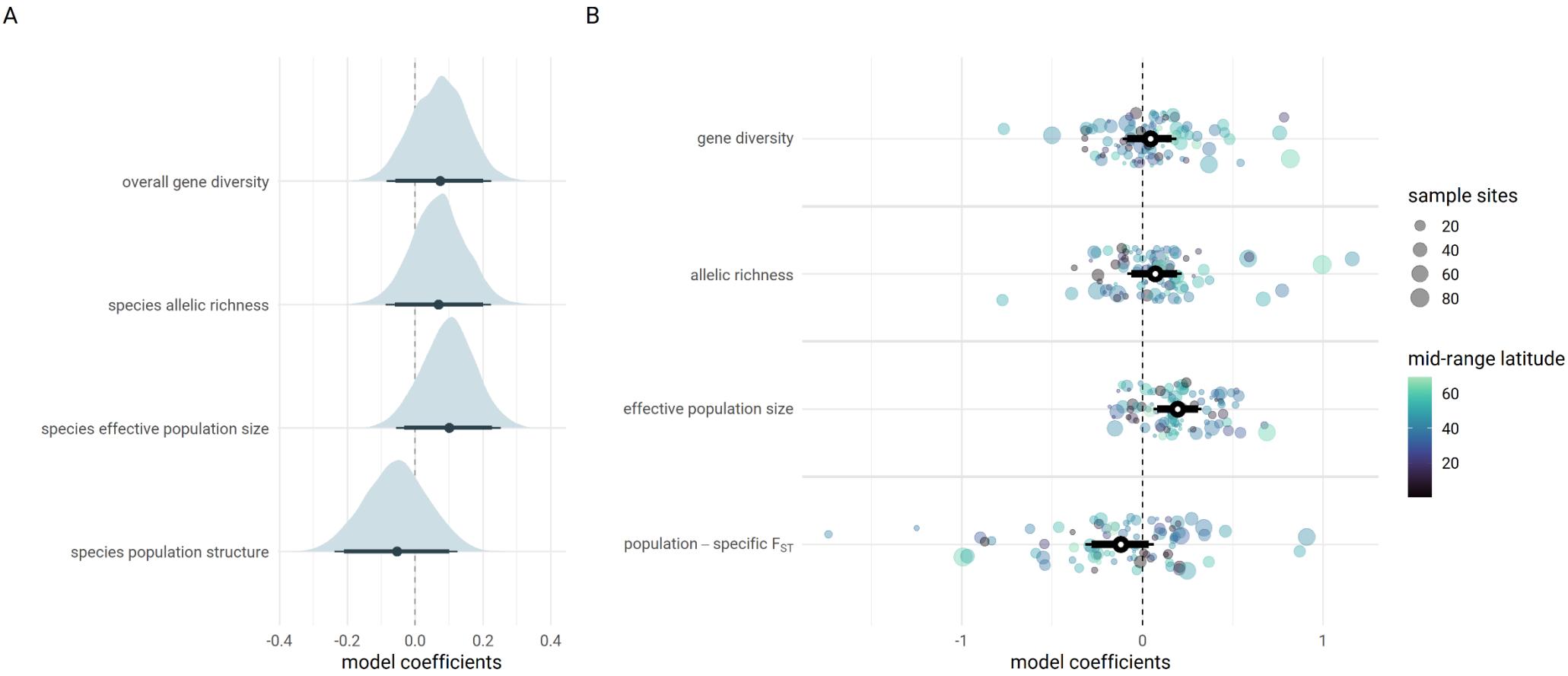


Figure 2. Map of sample locations. The data comprised 59587 individuals sampled across 100 mammal species at 1426 locations. Each point represents a site where multiple individuals were genotyped. The median number of individuals sampled at each site was 23 (range 5 – 2444 individuals), and the median number of sample locations per species was 7 (range 1 – 82 sites).



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742 **Figure 3.** Model results for interspecific (A) and intraspecific (B) genetic gradients. (A) Relationships between species' absolute mid-
743 range latitude and genetic metrics estimated at the species level. Points represent the effect of latitude flanked by 90 (bold lines) and
744 95% (narrow lines) credible intervals and posterior densities. Absolute latitude was not strongly related to any genetic metric at the

745 species level, suggesting there are no gradients in genetic diversity or differentiation across species. (B) Coefficient plot showing the
746 effect of absolute latitude on genetic metrics at the site level. Open circles show the estimated overall effect of latitude across all
747 species, with 90 and 95% credible intervals (bold and narrow lines, respectively). Colored circles represent species-specific effects of
748 latitude (i.e. random slope estimates). Circle diameter is proportional to the number of locations sampled for each species. Circle color
749 denotes species' absolute mid-range latitudes, with darker hues representing species with ranges nearer the tropics, and lighter hues
750 species with ranges nearer the poles. Only effective population size was consistently related to latitude across species, and generally
751 increased with latitude.

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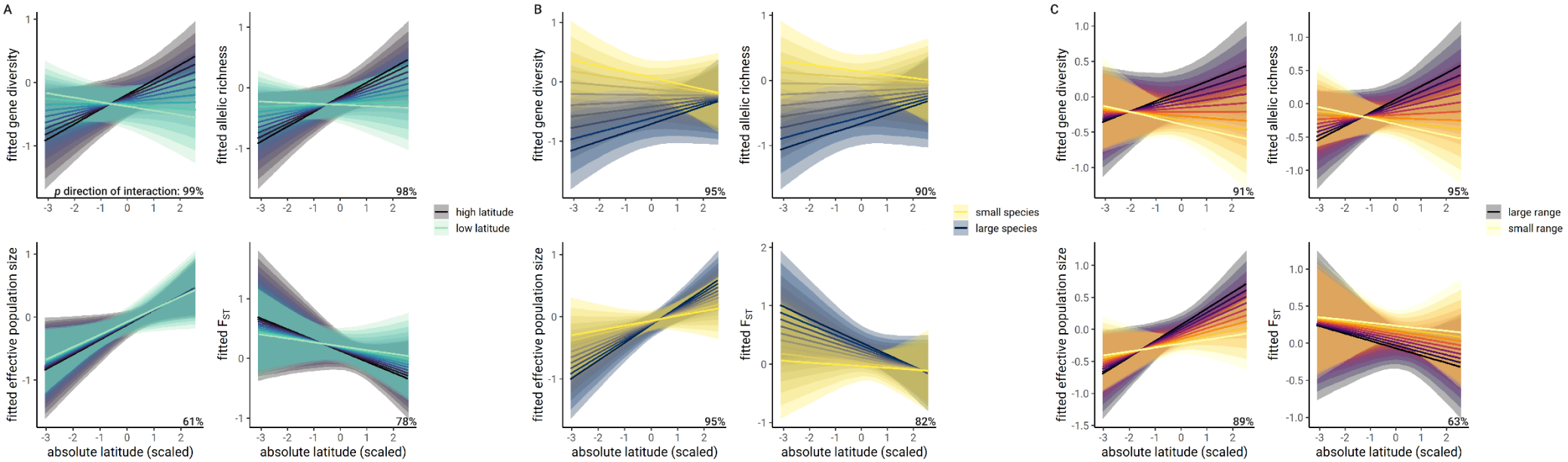

Figure 4. Interactive relationships between intraspecific latitudinal gradients and species-level attributes, including absolute mid-range latitude (A), log adult body mass (B), and log range area (C). Plots show predicted genetic metrics (y axes) based on regressions including interaction terms between latitude and species level attributes for different levels of each attribute. The probability of direction (the proportion of posterior draws with effects in the estimated direction) for the interaction term in each model is shown at the bottom right of all plots. Shaded regions represent 95% credible intervals. For gene diversity, allelic richness, and effective population size, relationships with latitude tended to become more strongly positive, indicating that these genetic metrics generally

760 increased towards the poles for species with higher mid-range latitudes, and larger body and range size while gradient direction was
761 more uncertain for smaller species with smaller ranges nearer the equator.

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