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META-ANALYSIS

Geographic barriers but not life history traits shape the phylogeography of North American mammals

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Abstract

Aim: Synthesize literature on genetic structure within species to understand how geographic features and species traits influence past responses to climate change.

Location: North America.

Time Period: We synthesized phylogeographic studies from 1978 to 2023, which describe genetic lineages that diverged during the Pleistocene (≥11,700 years ago).

Major Taxa Studied: Mammals.

Methods: We conducted a literature review to map genetic breaks in species distributions, then tested a set of geographic hypotheses (e.g., mountains, rivers) to explain their position by comparing break locations to a grid within each species' sampled range using logistic regression. We then conducted a meta-analysis using species-specific model estimates to ask if life-history traits explained variation in which barriers were most important in species' past response to climate change.

Results: Our findings reveal heterogeneity in both where North American mammal phylogeography has been studied and the density of genetic breaks across 229 species. We found relatively high concordance among carnivores, ungulates and lagomorphs, where breaks were associated with mountains, major water bodies and relatively even terrain. In contrast, we found high variability within rodents and shrews, and no evidence that intrinsic factors related to dispersal ability explained the importance of hypothesized barriers across all species.

Main Conclusions: Southern Mexico is a hotspot for genetic breaks that has yet to be integrated into the broader story of North American phylogeography. We show that mountains and major water bodies play particularly important roles as barriers, but substantial variation across species within orders suggests that there is more to the story besides shared climatic or phylogenetic histories. Thus, understanding the phylogeography of individual species will continue to be important given that our results suggest high variability in how species may respond to future global change.

KEYWORDS

biogeography, climate change, connectivity, dispersal, glacial refugia, lineage, Pleistocene, subspecies

1 | INTRODUCTION

Understanding the patterns and processes that shape the genetic structure of species (i.e., phylogeography; Avise, 2000) can be insightful for a diversity of disciplines, including ecology and conservation (Beheregaray, 2008). In phylogeographic studies, samples are collected across a species' range and patterns of genetic differences are quantified. Studies often discover that species contain multiple genetic lineages within their distribution, sometimes revealing cryptic biodiversity invisible via phenotypic comparisons (Malaney et al., 2017; Riddle & Jezkova, 2019). These genetic differences between lineages are sometimes so large as to warrant taxonomically splitting a species (Georges et al., 2018; Hewitt, 2001) and identifying isolated lineages can be grounds for increased conservation efforts (Gallego-García et al., 2023). Phylogeographic knowledge can also be used to uncover a species' recent evolutionary history, which in temperate regions typically describes how past cycles of glaciation influenced the dynamic distribution of genetic lineages (Avise, 2000; Hewitt, 2004). This knowledge of past responses to environmental changes can then be used to forecast how each lineage will respond to future climate change (D'Amen et al., 2013; Razgour et al., 2019; Williams & Blois, 2018).

While most phylogeographic studies focus on a single species, there has been long-standing interest in comparing genetic structure across co-distributed species (i.e., comparative phylogeography; Bermingham & Moritz, 1998; Avise et al., 2016). This community-level approach can identify phylogeographic "hotspots"—regions where genetic breaks exist for multiple species (Avise, 2000; Riddle, 2016). In temperate regions, one of the major drivers of concordance in genetic structure is shared refugia during Pleistocene glaciation. Many temperate species were isolated in multiple refugia during glaciation and then expanded their distributions as the planet warmed and glaciers retreated (Hewitt, 2004; Shafer et al., 2010). Some of these expanding lineages encountered geographic barriers to dispersal (e.g., mountain ranges or rivers), and remained isolated; in other cases, lineages came into secondary contact, yet genetic signatures of past separation remain. Although comparative phylogeography has revealed some shared patterns in genetic structure across species, there is a recognized need for more explicit testing of hypotheses that generate these patterns (McGaughran et al., 2022; Riddle & Jezkova, 2019).

Despite some shared patterns, there is often discordance in genetic structure among species that shared glacial refugia. At times, discordance can occur because different genetic markers were used to study each species (e.g., mitochondrial DNA vs. nuclear DNA), which can lead to different conclusions about the number and size of lineages (Riddle, 2016; Riddle & Jezkova, 2019). In other cases, discordance is likely a product of intrinsic factors (i.e., species-specific life history traits) influencing how species tracked newly available habitats and thus where resultant genetic breaks occur in contemporary populations (Papadopoulou & Knowles, 2016; Zamudio et al., 2016). For example, a species' dispersal ability would likely influence how quickly they expanded from refugia and the frequency of gene flow across genetic lineages in contact (Hewitt, 2004). Likewise, environmental tolerance would determine a species' persistence in new habitats (Pelletier & Carstens, 2016), and the influence of different types of barriers on dispersal and vicariance. Thus, both geographic and species traits are thought to influence phylogeography, but few comparative studies have integrated these hypotheses into a single framework, limiting our ability to use these lessons from past responses to climate change to prepare for the future.

North America is an ideal place to test comparative phylogeographic hypotheses because many studies have occurred on the continent. Studies are particularly rich in western North America, and several comparative studies have shown how the signatures of multiple glacial refugia (e.g., California, coastal Pacific Northwest) are reflected in the current genetic structure of the taxa that occur there (Cartens et al., 2005; Miller & Haig, 2010; Shafer et al., 2010). Although less extensive, investigations in eastern North America highlight a complex story of glacial refugia, physical barriers to dispersal, and taxa-specific patterns (Avise et al., 1987; Lyman & Edwards, 2022; Soltis et al., 2006). Yet, there has been little comparative work outside these regions and no synthesis of the phylogeography of the full continent, limiting our ability to fully understand what shapes the continent-wide genetic structure of North America.

Our goal was to better understand how geography and species traits interact to shape North American mammal phylogeography. We chose to focus on mammals because we hypothesized that they would have some degree of concordance in their responses to past climate change and many of their orders are well-studied in North America (Beheregaray, 2008; Riddle & Jezkova, 2019). Our first objective was to describe the current state of North American mammal phylogeographic research: which taxa have been studied, where have they been studied, and which genetic markers have been used. Our second objective was to map phylogeographic breaks within species' distributions using the literature. Our third objective was to test several competing hypotheses about where these breaks occur in North America. We hypothesized that breaks would be closer to barriers to dispersal, as these barriers would prevent mixing between lineages as they expanded out of glacial refugia. In line with Swenson and Howard (2005), we predicted that mountain ranges would be most aligned with phylogeographic breaks, but other barriers (e.g., rivers) could be important for smaller non-volant taxa. In addition, we predicted that genetic breaks would be aligned with the boundaries between ecoregions if each lineage had become specialized to a given habitat. After conducting this break analysis, our fourth objective was to conduct a meta-analysis on the results, asking whether species-level traits related to dispersal ability and habitat generalization explain variation in the importance of barriers. We predicted that the lineages of better dispersers and more generalist species would be less influenced by barriers and ecotones, respectively, such that their genetic breaks would be less likely to be close to these environmental features. Collectively, our results highlight how extrinsic and intrinsic factors shape the genetic structure of North American mammals, with implications for variation in how species will respond to future global change.

2 | METHODS

2.1 | Overview

We first conducted a comprehensive review of the North American terrestrial mammal phylogeographic literature, which we used to describe taxonomic and geographic representation as well as trends in the use of different genetic markers. We used this literature to identify and digitize phylogeographic breaks for as many species as possible. We tested several competing hypotheses that we predicted would explain where breaks occur by comparing their locations to a grid of points within each species' sampled range via logistic regression. Lastly, we asked whether life-history traits related to dispersal ability explained variation in the directionality and strength of our estimates by conducting a meta-analysis on the species-level effect estimates.

2.2 | Literature review

We curated our list of species from the American Society of Mammalogists' Mammal Diversity Database (Version 1.10, released December 2022). Species had to meet the following criteria to be included: (1) present in Canada, the United States, or Mexico (according to the database), (2) be primarily terrestrial (not marine) and (3) be extant. These criteria were met by 764 species. We conducted a literature search in the Web of Science Core Collection in the spring of 2023. For each species, we searched for titles, abstracts, or keywords which matched the following search string: TS=("Common name" OR "Scientific name") AND TS=("phylogeograph*"). We included alternative common or scientific names in the search when appropriate to include older papers published with outdated taxonomy. We scanned titles and abstracts and downloaded papers that seemed relevant for our project (Figure S1). We also used a snowball approach, where we scanned the literature cited sections of the first set of papers to pick up additional papers we may have missed in the search.

We reviewed each downloaded paper to create our phylogeographic database. In order to ensure papers were at a relevant phylogeographic scale, we only included papers which used samples from ≥25% of a given species' range within our focal countries. It was usually clear when sample coverage was above or below this threshold, but 12 species with 25%–30% coverage were judgement calls. We recorded the following data from each paper:

1. Approximate percentage of their North American range sampled.
2. Number of genetic lineages. We identified lineages using some combination of the following analyses within each paper: (1) highly supported monophyletic groups in a phylogenetic tree; (2) differentiated groups within a haplotype network; (3) well-supported genetic clusters within a Bayesian clustering analysis.
3. Time since each lineage diverged from its sister lineage (if available).

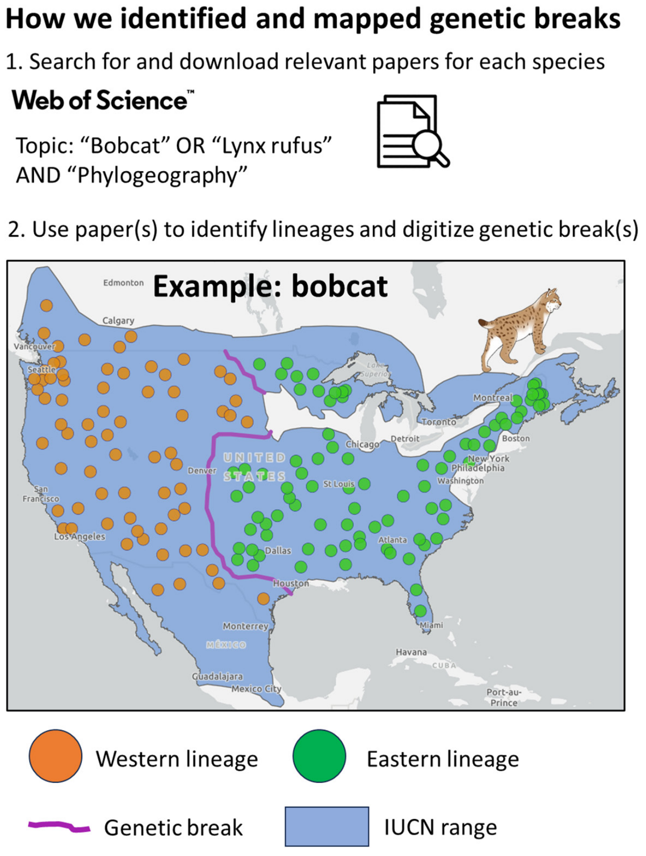

FIGURE 1 Example of how we searched for studies on the phylogeography of North American mammals and used these studies to digitize phylogeographic breaks. Here we show our search terms and the two lineages we identified for bobcat. The sample locations and genetic break lines are recreated from Reding et al. (2012), but we do not show all of their sampling locations for clarity.

4. Phylogeographic category (Pleistocene = ≥11,700 years ago, Holocene = <11,700 years ago).
5. Whether the lineages were visualized or described in enough detail to georeference (Figure 1)
6. Sample sizes for each lineage.
7. Genetic marker used: mitochondrial DNA, nuclear microsatellites or nuclear single nucleotide polymorphisms (SNPs).

2.3 | Drawing genetic breaks

We used our database of papers to georeference and draw phylogeographic breaks across species ranges (Figure 1). We found only one paper for most species (62%), while for the remainder of species, we used the paper with the best geographic coverage. If papers had similar geographic coverage, we used the more recent paper. We drew breaks in ArcGIS online using species range maps from IUCN (2023). A subset of species (8%) had papers that explicitly showed or described break locations (e.g., Reding et al., 2012; Yi & Latch, 2022), in which case we replicated inferred breaks. In most cases (68%), the paper showed maps of sampling locations with different colours or symbols representing different lineages (e.g., Lanier et al., 2015) and we drew breaks between these points. Similarly, some papers (10%) included polygons representing each lineage and we drew breaks between polygons (e.g., O'Neill et al., 2005). In other cases (10%), the paper described the location of the break as occurring along a physical feature (e.g., the Rocky Mountains, Rueness et al., 2003) or an established subspecies boundary (e.g., Decker & Ammerman, 2020). In any case, we only drew breaks in regions that were adequately sampled. For 9% of species, the range shown in the paper was not the same as the IUCN range, in which case we drew breaks following the paper even if they occurred outside the species' IUCN range.

2.4 | Testing genetic break hypotheses

We hypothesized that genetic breaks would be more likely to occur in areas that were geographic barriers (Table 1; Figure S4). Based on prior phylogeographic studies in North America (Swenson & Howard, 2005), we predicted that mountain ranges would be major physical barriers for many mammals, and we used a global layer of mountain range polygons from the United Nations Environment Program (UN Environment Programme, 2023) to represent these. Major water bodies have also been revealed as barriers to mammal dispersal (Soltis et al., 2006), so we used a layer of major rivers from Natural Earth Data (Natural Earth Data, 2023) to represent those. We supplemented these rivers with eight lakes >15,000 km^2 (the Great Lakes, Great Bear Lake, Great Slave Lake, and Lake Winnipeg) as well as the St. Lawrence River. We also included the waters between the southeastern Alaskan islands (from Vancouver Island up to Juneau) because these islands were glacial refugia during the Pleistocene (Shafer et al., 2010). We hypothesized that ecotones (boundaries between two ecoregions) could also be barriers if lineages were specialized to a certain ecoregion and became isolated from populations in other ecoregions. We used both level I (15 categories) and level II (50 categories) North American ecoregions from the United States Environmental Protection Agency (US Environmental Protection Agency, 2023). Lastly, we hypothesized that rugged terrain could be a barrier to dispersal because of the energetic costs of moving across complex terrain (Killeen et al., 2014; Nisi et al., 2022). We used a 1 km terrain ruggedness index from Amatulli et al. (2018), which is the mean of the absolute differences in elevation between a focal cell and its eight surrounding cells. While rugged areas are generally associated with mountains, there are parts of mountain ranges not necessarily very rugged (Figure S4).

2.5 | Genetic break analysis

To test the hypothesis that breaks were associated with barriers, we compared the locations of the breaks between genetic lineages with a series of background points. We extracted values associated with our hypotheses from along the genetic breaks by generating points every 10 km along each line. For comparison to the points along the genetic break, we created a grid of uniform background points across North America spaced approximately 20 km apart. We chose 20 km because it created similar distances between points as the breaks without generating an excessive amount of background points for computation. For both the genetic break and background points, we extracted four environmental variables: (1) distance to mountain range, (2) distance to large water bodies, (3) distance to ecoregion boundary and (4) terrain ruggedness (Table 1). All points within the mountain range polygon were given a distance value of zero. For each species, we clipped the gridded points to the species' IUCN range. If <75% of the species' IUCN range was sampled by the associated paper,

TABLE 1 Barriers to dispersal which we hypothesized would be aligned with where genetic breaks are within North American mammal ranges.

Hypothesis	Description	Units	Source
Distance to mountains	Distance to the nearest mountain range	km	UN Environment Programme
Distance to major water	Distance to the nearest major body of water. This was a combination of major rivers, lakes >15,000 km^2, the St. Lawrence River, and the waterway in southeastern Alaska between the mainland and islands	km	Natural Earth data (rivers and lakes)
Distance to ecoregion boundary	Distance to the nearest ecoregion boundary. We used both the Level I (15 categories) and Level II (50 categories) layers, but then model averaged for a single estimate	km	US Environmental Protection Agency
Terrain ruggedness	Relative flatness of the landscape (1 km resolution). Calculated based on differences in elevation among a given cell and the surrounding cells.	None	Amatulli et al. (2018)

then we clipped the range to only include the area that was sampled to represent the gridded data.

Given the variability in how lineages and breaks were presented in the literature (see "Drawing genetic breaks" above), we conducted a sensitivity analysis to determine how our approach influenced the covariate values we extracted along the breaks. To do this, we randomly jittered each point along the break by 50 km, a distance we chose as an estimate of the average uncertainty we had when drawing breaks. We then extracted covariate values at these new locations and compared the average values to the values from the actual breaks. We found that that this introduced noise had little influence on the values of our covariates; the average distance to barriers changed by 0.5%, while the average values of terrain ruggedness changed by 4%. We conclude that our approach, although somewhat ad-hoc, is robust to capturing the location of genetic breaks from the published literature.

We used species-level logistic regression models (1 = on break, 0 = background point) to quantify the difference in our environmental variables between the genetic breaks and the species range. For each species, we square-rooted the distance measures, then centered and scaled all variables to facilitate estimate comparison. We tested for significant correlations and found that distances to ecoregion I and II were often highly correlated (Pearson's $r > 0.9$). We considered choosing one of these ecoregions, but an exploratory comparison revealed that there were not clear patterns in which levels better explained the data across taxa. As a result, we fit separate global models using each ecoregion and used AIC-based model-averaging to generate weighted estimates and confidence intervals (Dormann et al., 2018). We fit logistic regression models for each species using glmmTMB (Brooks et al., 2017). Models for 17 species (16 rodents, 1 rabbit) failed to converge—likely because breaks were short (thereby generating too few points along them). We summarized our estimates by order and considered estimates to be significant if their 95% confidence intervals did not overlap zero. We assessed model performance by calculating the area under the curve (AUC) using the pROC package (Robin et al., 2011), which assessed how well the model can distinguish between two classes (break vs. background in our case). We also checked if the number of background points influenced the uncertainty in our estimates by doubling and halving them and rerunning our models. Estimate uncertainty was not substantially different in either case (Muff et al., 2020), which makes sense given presence-background regression approximates a Poisson process as the density of background points increases (Warton & Shepherd, 2010). We conducted all spatial and statistical analyses in R version 4.2.2.

2.6 | Trait-based meta-analysis

We hypothesized that species-level life history traits could explain variability in the directionality and importance of environmental factors on genetic breaks (Table 2). Although some life history traits are likely conserved across orders, others exhibit substantial variation within orders, motivating this species-level analysis. For example, the mass of North American carnivores we analyzed varies from 0.1 kg (American ermine; *Mustela richardsonii*) to 241 kg (brown bear; *Ursus arctos*). Our first prediction was that species with better dispersal ability would be less likely to have genetic breaks closer to our hypothesized barriers. We predicted that the genetic breaks of (1) larger species and (2) species that disperse farther distances would be less likely to be associated with mountains, major water, and ecoregion boundaries (Whitmee & Orme, 2013). Additionally, we distinguished between terrestrial and (3) flying taxa (e.g., bats), because terrestrial barriers present less of a barrier to volant species. We also included a hypothesis related to montane habitats, where we predicted that (4) species whose ranges were dissected by mountains (i.e., lowland associated) would be more likely to have genetic breaks closer to mountains. Finally, we included (5) habitat breadth (number of suitable habitats), which even within orders can vary from habitat specialists (e.g., fisher, *Pekania pennanti*) to cosmopolitan generalists (e.g., red fox, *Vulpes vulpes*). We sourced these mammal life history traits from the COMBINE database (Soria et al., 2021; Table 2), which integrates data from previously published sources (e.g., PanTHERIA) and interpolates missing values.

For each of our hypothesized barriers (e.g., mountain ranges), we conducted a species-level meta-analysis using the estimates from our genetic break analysis. We used the metafor package (Viechtbauer, 2010) to jointly model the estimates while propagating uncertainty via standard errors and fit a global model with all of our life history traits as predictors (Table 2). For a given hypothesis, our model was specified as:

TABLE 2 Species-level life-history traits we hypothesized would explain variation in the directionality and importance of estimates from our break analysis.

Hypothesis	Definition from COMBINE metadata	Data type
Adult mass g	Body mass of an adult individual in grams	grams
Dispersal km	The distance an animal travels between its place of birth to the place where it reproduces in kilometres. Though ultimately dropped from analysis because it was correlated with mass ($r = 0.75$)	km
Terrestrial volant	The species is capable of powered flight and spends a significant amount of time flying in the air	0 or 1
Dissected by mountains	Dissected by mountains source	0 or 1
Habitat breadth *n*	Number of distinct suitable level 1 IUCN habitats	Integer

$$y_i = \beta_0 + \beta_1 \times \text{mass}_i + \beta_2 \times \text{habitat}_i + \beta_3 \times \text{volant}_i + \beta_4 \times \text{mtn\_sp}_i + u_i + \epsilon_i$$

where y_i is the observed effect size on species *i*, β_0 is the overall mean effect size (intercept), $\beta_{1,2,3,4}$ are the coefficients for the fixed effects, u_i is a random effect propagating the standard error for the effect size associated with species *i*, and ϵ_i is residual error. We tested for correlations among our predictors and found that body size and dispersal distance were significantly correlated (Pearson's $r = 0.75$); dispersal distances for bat species were absent so we dropped dispersal distance from the models. We considered predictors significant if 95% confidence intervals did not overlap zero.

3 | RESULTS

We reviewed the phylogeographic literature for 764 North American mammal species and found 396 relevant papers (Figure S1). Only 30% of species ($n = 229$) had at least one paper, and we found substantial variation in how well orders were represented (Figure 2). For example, even-toed ungulates and carnivores were well-represented (~60% of species had at least one paper), while bats and shrews were underrepresented (~15%). Rodents had the most species represented ($n = 77$), but this was only 34% of all rodents in North America. Geographically, we found that more studies occurred in western North America, particularly in mountainous regions (Figure 2). Regions with less studies included northeastern Canada, western Alaska, and the south-central United States. In terms of trends in genetic markers (Figure 2), mitochondrial DNA has remained the most common for the last 30 years, though nuclear DNA (i.e., microsatellites) was nearly as common in the last 10 years. SNPs have also been used since 2015, though they are still only represented in ~10% of papers during that period. There has also been a general declining trend in the number of publications since 2014.

Of the 229 species with at least one phylogeographic paper, 146 (64%) had at least one genetic break, while the rest (83) only exhibited one identified lineage (Figure S2). Of the 146 species with breaks (i.e., multiple lineages), 129 (88%) of the breaks were dated to the Pleistocene or later (≥11,700 ya; hereafter "Pleistocene"; Figure S3), 11 (8%) were from the Holocene (<11,700 ya), 6 (4%) had breaks from both time periods, and 6 (4%) were not dated. Of the 129 from the Pleistocene, 115 were sampled sufficiently enough for us to map the genetic breaks between lineages. Rodents represented over half of these species ($n = 77$), but other orders were also fairly well represented (Figure 2). Breaks were distributed across

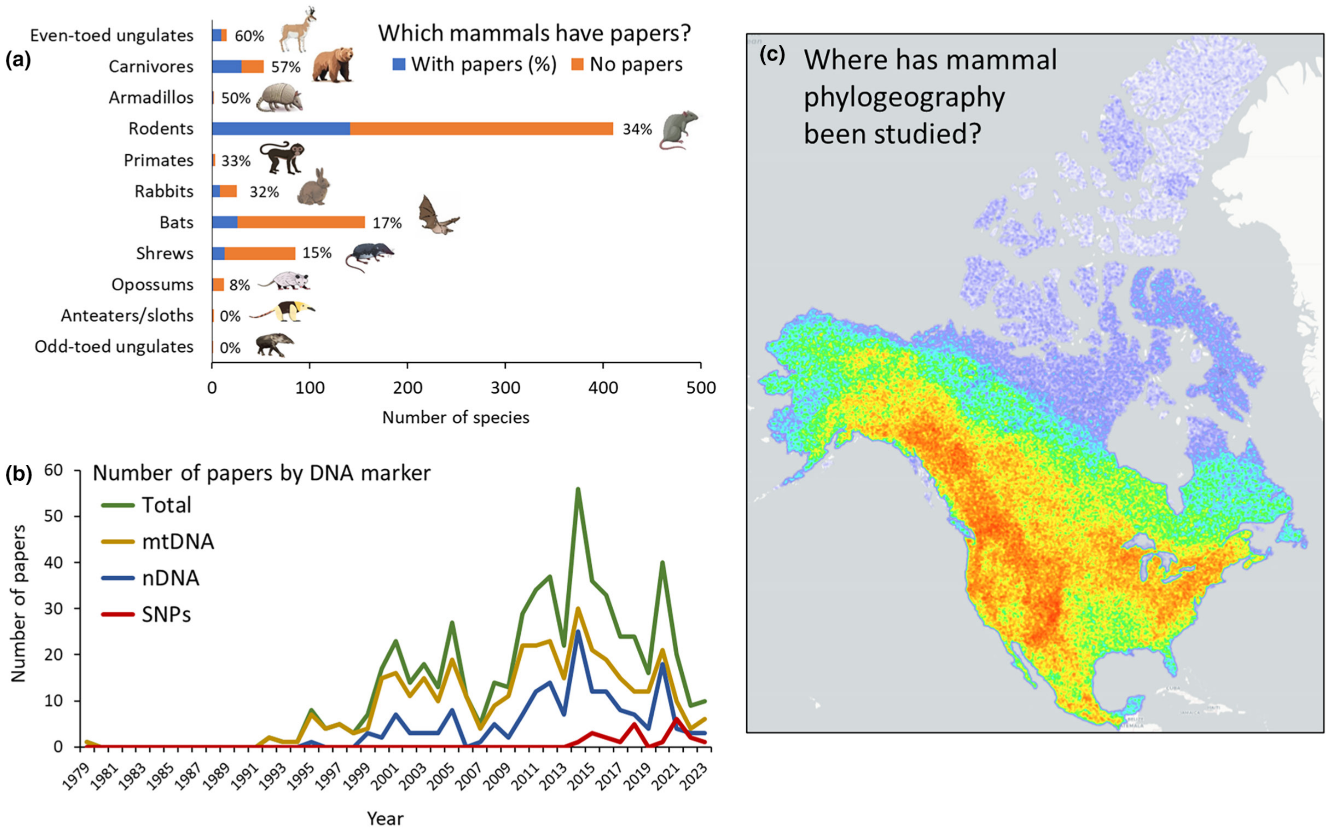

FIGURE 2 A summary of taxonomic and geographic representation as well as the DNA markers used to study North American mammal phylogeography. In (a) we show the percent of species (by order) with at least one phylogeography paper. In (b) we show the count of papers on North American mammal phylogeography through time by DNA marker type. Total is a sum of the other three lines (mtDNA = mitochondrial; nDNA = nuclear; SNP = single nucleotide polymorphisms). In (c) we show density of species ranges (or portions of ranges) that have been included in phylogeographic studies.

North America, but density was highest in the west—particularly along the mountains of southern Mexico, the Rocky Mountains, and the Pacific coast (Figure 3).

3.1 | Genetic break analysis

We estimated the effects of spatial covariates on break locations for 98 species. All species but one (salt-marsh harvest mouse, *Reithrodontomys raviventris*) had at least one significant estimate, suggesting that our hypotheses explained breaks fairly well at the species-level. For example, breaks for American black bear (*Ursus americanus*) were closer to mountains, closer to major water bodies, and in less rough terrain. Another example is snowshoe hare (*Lepus americanus*), where breaks were closer to mountains, closer to water, and in more rough terrain. There was variation in the predictive power of our models, where 32% of species had high AUC scores (0.8–0.9), and the remainder had lower scores (0.7–0.8) that still suggested good predictive power. The species with the top five best and worst AUC scores were all rodents, with no clear pattern related to range-size or break length.

Across species, we found substantial variability in the directionality and effect from each of our hypothesized barriers to dispersal (Figure 4). Distance to water had the largest median effect (estimate = −0.21), where breaks tended to be closer to water (Figure 4b). Breaks also tended to be in less rough terrain (−0.16), closer to mountains (−0.15), and slightly closer to ecoregion boundaries (−0.08). There was also variability within most orders, where some species' estimates were significantly positive, some were significantly negative, and some overlapped zero (Figure 4c). In contrast, results for Lagomorpha ($n = 4$) were all consistent, with breaks occurring closer to mountains (mean estimate [95% confidence intervals] = −1.7 [−2.6: −0.7]), closer to water (−0.51 [−0.68: −0.34]), and in less rough terrain (−0.25 [−0.40: −0.11]; Figure 4c). The breaks of most ungulates and carnivores also followed this same pattern of being closer to mountains (−0.68 [−0.88: 0.47]; −0.42 [−0.61: −0.24]), closer to water (−0.51 [−0.68: −0.34]; −0.66 [−0.88: −0.45]), and in less rough terrain (−0.37 [−0.55: −0.19]; −0.33 [−0.55: −0.12]). Bat breaks were further from water compared to their ranges (0.57 [0.27: 0.87]). For shrews, breaks tended to be in less rough terrain (0.43 [−0.82: −0.05]) but otherwise mean estimates were close to zero. For rodents, uncertainty in our mean estimates was high—likely because there were so many species ($n = 63$, 62% of our dataset) with large variability in responses.

3.2 | Trait-based meta-analysis

Using the estimates we generated in the previous objective, we tested if species-specific life-history traits (Table 2) explained variation in our estimates. We found that none of our hypothesized traits significantly predicted the importance of geographic barriers across species (Figure 5).

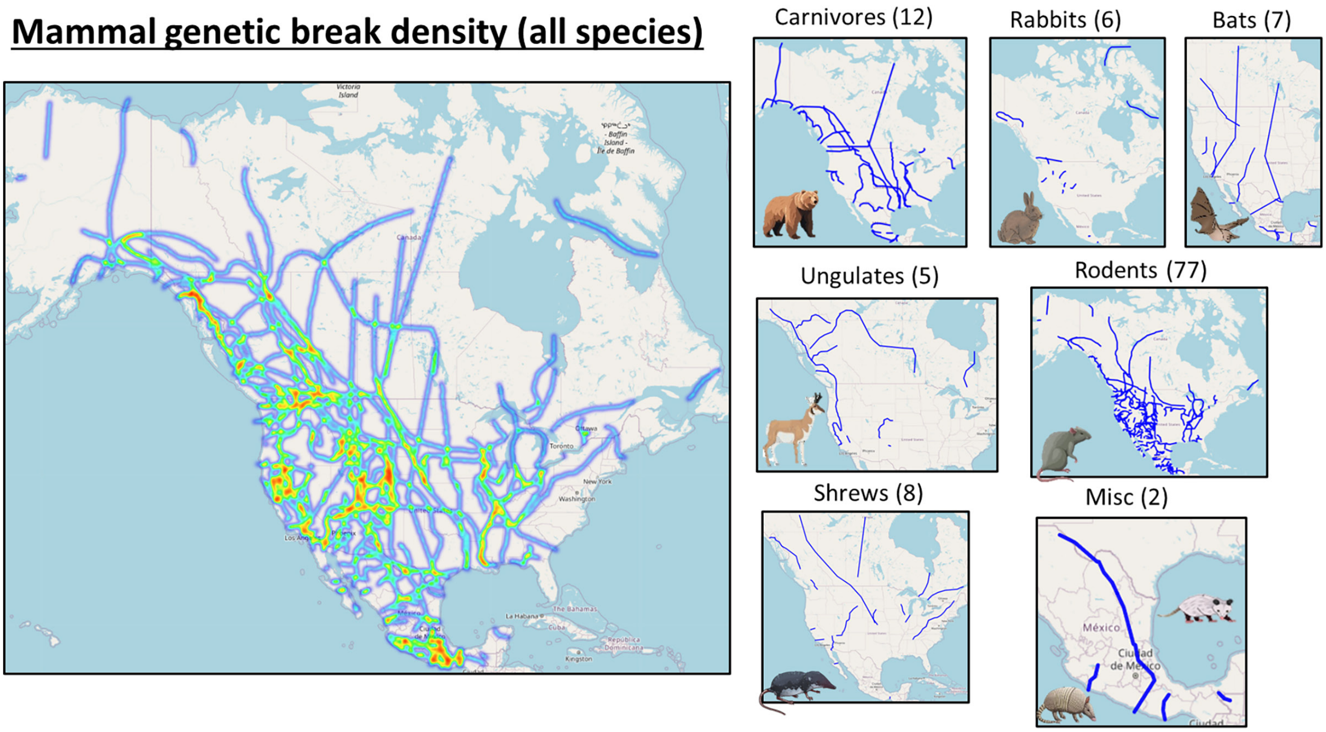

FIGURE 3 Maps of where phylogeographic breaks were for 115 North American mammals. In the main panel, we show the density of breaks across all species. In the smaller panels, we show these breaks for each order, including the number of species in parentheses. The "Rabbits" order includes all lagomorphs. The "Misc" order is the nine-banded armadillo (*Dasypus novemcinctus*) and the Tehuantepec grey mouse opossum (*Tlacuatzin canescens*).

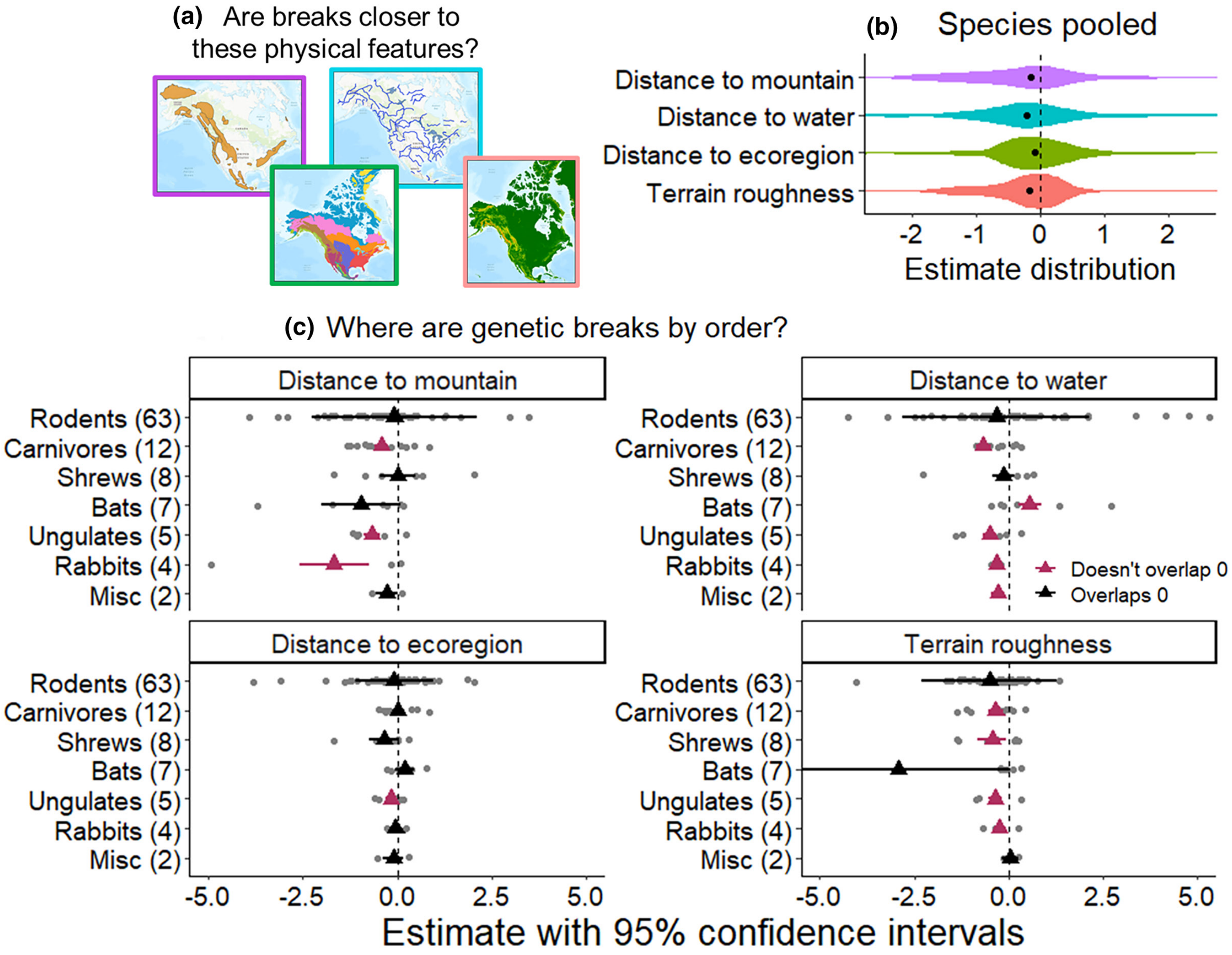

FIGURE 4 Variability in estimates from our analysis of where genetic breaks are for 99 mammals in North America. In (a) we show the spatial data we used to test our hypotheses (mountain ranges, major water bodies, ecoregions (level I), and terrain roughness. In (b) we show the distribution of estimates for each hypothesis across all species, with the black dot indicating the mean value. In (c) we show the estimates for each species (circles), as well as the mean value with 95% confidence intervals (black triangle). The "Rabbits" order includes all lagomorphs. The "Misc" order is the nine-banded armadillo and the Tehuantepec grey mouse opossum.

4 | DISCUSSION

Understanding the processes which shaped the current genetic structure of species gives unique insight into how their populations might respond to future global change (McGaughran et al., 2022). Using the available information on North American mammal phylogeography, we mapped genetic breaks for individual species, determined which barriers they were most associated with, then asked to what extent intrinsic factors predict the most important movement barriers. Geographically, we found that there was greater overlap of genetic breaks in western North America, particularly in mountainous regions. Yet, when we explicitly tested if breaks were associated with mountains, we found mixed support for this hypothesis, suggesting mountains are barriers to movement for some species but not others (Soltis et al., 2006). We found relatively high concordance among carnivores, ungulates and lagomorphs—their breaks were associated with mountains, major water bodies and relatively even terrain. In contrast, we found the most variability within the rodent, shrew and bat orders, suggesting that the extrinsic factors that shape their genetic structure are not widely shared or occur on much smaller scales than our analysis could capture. Similarly, we found no evidence that intrinsic factors related to dispersal ability explained the importance of our hypothesized barriers. Collectively, our findings suggest that although there is concordance for some orders, the combination of large variability across (closely related) species and a lack of support for our dispersal hypotheses mean that species-specific studies will continue to be needed to predict how species will respond to global change.

Our results highlight several established phylogeographic hotspots for North American mammals, and one which has received relatively little attention in the literature. Similar to a previous comparative analysis (Shafer et al., 2010), our findings support the existence of a glacial refugium off the coast of southeastern Alaska, where populations inhabiting the islands have genetically diverged

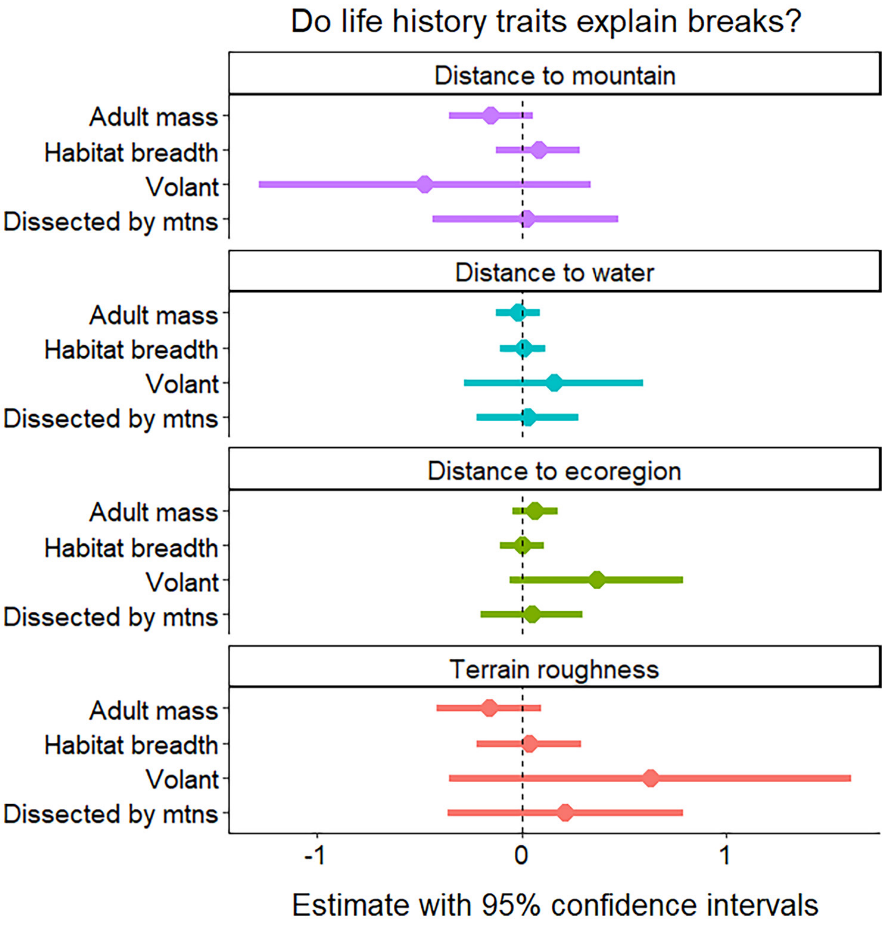

FIGURE 5 Results from our meta-analysis of whether life history traits explain variation in genetic breaks for North American mammals. We curated data from the COMBINE database (Soria et al., 2021). The dissected by mountains variable is whether or not a species' range is dissected by mountains.

from mainland populations. We found this pattern across taxa, including for mule deer (*Odocoileus virginianus*), brown bear, black bear, southern montane shrew (*Sorex monticolus*) and North American red squirrel (*Tamiasciurus hudsonicus*). Similarly, a hotspot of genetic breaks in northern California supports the existence of a glacial refugium in this region, as well as the Sierra Nevada mountains acting as a barrier to dispersal for some species. We also found high overlap generally following the Rocky Mountains, from Colorado up into western Canada. Most of these species were rodents (e.g., silky pocket mouse, *Perognathus flavus*; North American red squirrel), but carnivores (bobcat, *Lynx rufus*; red fox), and one bat (little brown myotis, *Myotis lucifugus*) also had genetic breaks in this region. We also identified a hotspot in southern Mexico along the Sierra Madre del Sur mountains and Isthmus of Tehuantepec, which has yet to be integrated into the broader story of North American phylogeography. Despite relatively few studies occurring in the region, we found that many species shared genetic breaks here, and all mammalian orders (except lagomorphs) had at least one species represented. Further, some of the species with breaks in this region are mountaintop specialists (e.g., painted spiny pocket mouse, *Heteromys pictus*), and therefore low elevation areas in the region would likely be barriers to their dispersal (Ornelas et al., 2013; Sullivan et al., 2000). Perhaps, this variation in life-history, combined with mountains in eastern North America (i.e., the Appalachians) not aligning with many genetic breaks, explains the variation in how important we found mountains to be overall.

One of our core findings was the amount of variation in the strength and directionality of our estimates of barrier effects, even within orders. Our novel analysis allowed us to quantify multiple factors at the same time, and revealed significant spatial associations for the location of phylogeographic breaks of nearly all species, although there was little consistency in these across species. This was particularly true within rodents, where we found virtually no patterns in the association between break locations and our hypothesized barriers shared among the species studied. This likely (at least partially) reflects the diversity within rodentia, both in terms of the number of species represented in our dataset and high functional and ecological diversity (Riddle & Jezkova, 2019). We also found few significant effects across species within the shrew and bat orders, perhaps again reflecting ecological diversity within these orders (Peixoto et al., 2018). However, we did find that bat genetic breaks tend to be further from major water, which makes sense given water would not be a barrier to their dispersal. In contrast, we found that larger-bodied species (carnivores, ungulates and lagomorphs) shared similar general patterns in where their genetic breaks were, suggesting that mountains and major waterways are more likely to be barriers for species within these orders. In contrast to our hypothesis, we also found that these orders tended to have breaks in less rugged terrain, which could have at least two explanations. First, some of these species are forest-associated (e.g., grey fox, *Urocyon cinereoargenteus*;

Reding et al., 2021) and therefore more open habitats like the Great Plains and deserts (which tend to be relatively flat) could serve as barriers. Second, many of these species have large ranges which overlap with regions of high terrain ruggedness; if their breaks are in relatively flat areas, then this would likely result in this pattern even if terrain ruggedness was not directly responsible. Regardless, future comparative studies could similarly test if rugged terrain is associated with the locations of genetic breaks.

Given the concordance among these relatively large-bodied species, we expected to find some evidence that body size, dispersal ability, or other intrinsic traits were related to the importance of our extrinsic hypotheses. However, none of these variables were significant within our models. This result was surprising given other studies have shown that dispersal ability explains some variation in the phylogeography of a variety of taxa, including bats (Morales et al., 2016), salamanders (Pelletier & Carstens, 2016) and beetles (Roe et al., 2011). Indeed, species traits have been hypothesized to be an important (and traditionally overlooked) factor explaining discordance in genetic structure among codistributed species (Papadopoulou & Knowles, 2016). Yet perhaps these patterns disappear when analysing a diverse class of species at a continental scale. Likewise, variation across species could be a function of the wide temporal range of when genetic breaks formed—species whose lineages have been separated for longer could be more associated with static barriers (i.e., mountains), compared to more dynamic barriers (like water bodies and ecoregions). It is also possible that the dispersal metrics in large trait databases are not an accurate proxy of their ability to colonize new habitats, or that other species-specific factors are important which we did not explore. For example, species interactions have been hypothesized to shape phylogeography, leading to stronger concordance among species who closely interact (McGaughran et al., 2022). Regardless, our findings here suggest that dispersal ability and habitat generalization do not broadly explain the variation in how North American mammals responded to past change. We therefore expect to find similar levels of variation in how species respond to future climate change as well (Williams & Blois, 2018).

However, our findings do shed some light on specific regions where mammals may be most constrained in their ability to respond to future climate change. For example, western mountains likely act as barriers to gene flow, and interventions like assisted migration could be needed to help species survive the pace of modern climate change (Twardek et al., 2023). Although large portions of these ranges run north–south (and thus would not be a harsh barrier to northward range expansion), the confluence of the Rocky Mountains and the Cascade Range near the border of the United States and Canada could be a strong barrier to dispersal. This could also be true for alpine specialists, where warming temperatures shrink their suitable habitat and potentially isolate populations between warmer lower elevations. In our context, this could be happening to mammals in the mountains of southern Mexico or species such as pika (*Ochotona princeps*, *Ochotona collaris*), who have received considerable attention within climate change research (Schmidt et al., 2021; Smith et al., 2019). This pattern was particularly pronounced for American pika, as Galbreath et al. (2009, 2010) showed that genetic breaks align with lower elevation areas between mountain ranges, including between the Rockies and Cascades, the Cascades and the Sierra Nevadas, and between smaller ranges in Utah and Colorado.

Our findings also highlight several important facets of the current status of North American mammal phylogeography. First, in line with other global reviews (Riddle, 2016; Riddle & Jezkova, 2019), we found a taxonomic bias in how well represented taxa were in the phylogeographic literature. Perhaps unsurprisingly, carnivores and ungulates were best represented, likely reflecting a general pattern of more attention on these larger and charismatic species (Dos Santos et al., 2020). Relative to the number of species, bats and shrews were particularly underrepresented, highlighting two orders which phylogeographers should prioritize in future work. Part of this variation in representation could be explained by a geographic bias in where research occurs (Di Marco et al., 2017)—there are many species of bats, rabbits, shrews, and opossums only found in Mexico but not yet studied phylogeographically. The gulf coast (Texas to Florida) is also relatively underrepresented by mammal phylogeographic studies, despite containing hypothesized refugia and established contact zones between lineages (Lyman & Edwards, 2022; Soltis et al., 2006; Swenson & Howard, 2005). There are likely additional genetic breaks within these underrepresented regions that we missed, which future studies could investigate.

We also tracked trends in the use of popular genetic markers because these decisions can influence phylogeographic conclusions. In line with a global review of phylogeography (Riddle, 2016), we found that mtDNA-based studies have remained more common than nDNA, but the gap has narrowed in the last 15 years. mtDNA is generally considered to be a suitable first approximation of the genetic structure of a species but it has limitations, including containing a small portion of the heritable information from a species and only capturing information from maternal lineages (Riddle & Jezkova, 2019). For these reasons (and differences in mutation rates), phylogeographers often find “cyto-nuclear discordance” when comparing the genetic structure of a species using mtDNA and nNDA (Blois & Arbogast, 2006; Vonhof et al., 2015). This seemed to be particularly common for bats in our data set (3/9 species), perhaps reflecting strong sex differences in gene flow, incomplete lineage sorting, or homoplasy. More broadly, we found that the phylogeography of 50% of the species in our dataset was based on mtDNA only, highlighting ample opportunity for comparison with nDNA. Our results also suggest that the growth of North American mammal phylogeographic research has slowed and may be declining. This seems to be the case with the field as a whole in the last 15 years (McGaughran et al., 2022), perhaps reflecting a decline in the number of unstudied species with easily-attainable genetic data.

Taken together, our findings show that there is heterogeneity in both where mammal phylogeography has been studied in North America, as well as the density of genetic breaks across 229 species with good sampling coverage. As previous studies have highlighted (Ornelas et al., 2013; Swenson & Howard, 2005), we show that mountains play particularly important roles in shaping phylogeography, both acting as barriers to dispersal for low-elevation species, but also as sky islands for high-elevation specialists. Major water bodies seem to separate lineages for ungulates, carnivores, and lagomorphs, but are not barriers for bats because they can fly over them. Yet ecotones (boundaries between ecoregions) were generally not aligned with genetic breaks, suggesting that lineage isolation does not necessarily lead to habitat specialization. Despite these patterns, we found quite large variation across species within orders, indicating that there is more to the story besides shared climatic or phylogenetic histories. But we also did not find support for our hypotheses that species-specific intrinsic traits related to dispersal and environmental tolerance explain variation in our estimates (Papadopoulou & Knowles, 2016; Zamudio et al., 2016). This suggests that there are other potential traits which explain variation better (e.g., community interactions) or there are patterns at smaller spatial or taxonomic scales not captured by our broad approach. But there is still much to learn—we were only able to find phylogeographic data for 30% of North American mammals, with some orders and regions poorly represented. Indeed, understanding the phylogeography of individual species will continue to be important given our results suggest that there may be high variability in how species respond to future global change.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Metadata, code and shapefiles are available on Figshare. Data we recorded from each study and data we synthesized for each species using these studies: https://figshare.com/s/7a58e7a1b6b3c647b4d2.

Shapefiles of genetic breaks and IUCN ranges for each species. We include both breaks dated to the Pleistocene and breaks dated to the Holocene: https://figshare.com/s/1fa446cbb00bad232db3.

Code used in our break analysis and species trait analysis: https://figshare.com/s/36bf9c11338c35a9a5e7.

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BIOSKETCH

This paper is one piece of a larger effort to model the relative abundance of mammals across North America where we will test how genetic lineages influence responses to the environment.

SUPPORTING INFORMATION

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

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