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SYNTHESIS

Community phylogeographic patterns reveal how a barrier filters and structures taxa in North American warm deserts

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Abstract

Aim: The study of biogeographic barriers is instrumental in understanding the evolution and distribution of taxa. With the increasing availability of empirical datasets, emergent patterns can be inferred from communities by synthesizing how barriers filter and structure populations across species. We assemble phylogeographic data across a barrier and perform spatially explicit simulations, quantifying spatiotemporal patterns of divergence, the influence of traits on these patterns, and the statistical power needed to differentiate diversification modes.

Taxon: Vertebrates, Invertebrates, Plants

Location: North America

Methods: We incorporate published datasets, from papers that match relevant keywords, to examine taxa around the Cochise Filter Barrier, separating the Sonoran and Chihuahuan Deserts of North America, to synthesize phylogeographic structuring across the communities with respect to organismal functional traits. We then use simulation and machine learning to assess the power of phylogeographic model selection.

Results: Taxa distributed across the Cochise Filter Barrier show heterogeneous responses to the barrier in levels of gene flow, phylogeographic structure, divergence timing, barrier width, and divergence mechanism. These responses correlate with locomotor and thermoregulatory traits. Many taxa show a Pleistocene population genetic break, often with introgression after divergence. Allopatric isolation and isolation by environment are the primary mechanisms structuring genetic divergence within taxa. Simulations reveal that in spatially explicit isolation with migration models across the barrier, age of divergence, presence of gene flow, and presence of isolation by distance can confound the interpretation of evolutionary history and model selection by producing easily confusable results. We re-analyze five empirical genetic datasets to illustrate the utility of these simulations despite these constraints.

Main Conclusions: By synthesizing phylogeographic data for the Cochise Filter Barrier, we show that barriers interact with species traits to differentiate taxa in communities over millions of years. Identifying diversification modes across the barrier for these taxa remains challenging because commonly invoked demographic models may not be identifiable across a range of likely parameter space.

KEYWORDS
biogeographic barrier, comparative phylogeography, functional traits, genetic diversity, isolation by distance, isolation with migration, neural net, isolation with migration

1 | INTRODUCTION

Biogeographic barriers, which separate taxa and restrict gene flow via unsuitable habitat or impeded dispersal, have shaped the fields of evolutionary biology and ecology (e.g., Simpson, 1940; Lomolino et al., 2004). The study of barriers has led to development of theory in species concepts (e.g., Mayr, 1942; de Queiroz, 2005), island biogeography (e.g., Janzen, 1967; MacArthur & Wilson, 1967), hybridization (e.g., Hoskin et al., 2005), and taxonomy (e.g., Helbig et al., 2002). The unifying factor across these topics is that the barrier itself is directly or indirectly linked to the process that generated the pattern of interest. For example, in island biogeography, the oceanic barriers are the primary cause of island dynamics, whereas in hybridization, the existence of a biogeographic barrier is often implied in separating taxa before secondary contact. Understanding the mechanisms that produce these patterns has been a major focus in historical biogeography, and efforts to understand these mechanisms have expanded with the increasing number and complexity of phylogeographic studies (see Garrick et al., 2015).

Phylogeography has the dual aim of characterizing how genetic diversity is distributed across the landscape and proposing the temporal framework for when this diversity formed (Avise et al., 1987). In addition, phylogeographic approaches aim to infer the processes that have promoted genetic diversity across the landscape (Avise et al., 2016). Early studies provided insight into the distribution of genetic variation within species and between species complexes that often coincided with geographic features or environmental gradients (e.g., Kozak et al., 2006; Taberlet & Bouvet, 1994). The extension of phylogeographic approaches with advances of molecular dating yielded insight into the timing of divergence between populations (e.g., Arbogast et al., 2002; Fouquet et al., 2010; Matos et al., 2016). Further advancements in DNA sequencing technology and statistical modeling allowed researchers to better identify the patterns and processes associated with biogeographic barriers (Hickerson et al., 2010). However, the study of species diversification across barriers has been hampered by conceptual and logistical challenges. One such challenge is that although many taxa might show phylogeographic structure that is concordant with a barrier, this does not indicate that the barrier itself caused genetic differentiation. For example, processes such as speciation over environmental gradients (Nosil, 2008; but see Bierne et al., 2013), behavioral selection (Zhang et al., 2012) or abundance troughs (Barton & Hewitt, 1981; Barrowclough et al., 2005) could all produce similar patterns. Alternatively, previous barriers and changes in habitat could be the mechanisms of structure, rather than what appears to be the barrier in the present (e.g., river capture; Tagliacollo et al., 2015).

A second challenge is that a barrier may cause differentiation in some taxa, but it may not affect the entire biota at once; this is known as a barrier being semi-permeable or having filters (Simpson, 1940). Filters are hypothesized to be mediated by organismal traits such as morphology (Dick et al., 2008; Hanson et al., 2012), reproductive isolation (Christe et al., 2016; Provost et al., 2018), physiology and niche (Castoe et al., 2007; Edwards et al., 2018), or population demographics and drift (Carnicer et al., 2012). The mechanisms potentially underlying filter barriers are numerous, possibly barrier and taxon specific, and likely not mutually exclusive. Identifying which traits are important for causing isolation requires knowing which taxa are and are not separated at a barrier, where the barrier is relative to phylogeographic breaks between populations, and what functional traits are correlated with differentiation across the filter. To illuminate the role of filter barriers in diversification, and the mechanisms causing it, an understanding of the processes of differentiation and variation in the context of communities is required.

Advances in demographic modeling have enabled phylogeographers to distinguish between alternative modes of population differentiation (e.g., Gutenkunst et al., 2009; Gravel, 2012). Many of these approaches must manage computation expense while maximizing the information used (e.g., full likelihood or Bayesian methods) or alternately running quickly using approximate methods but requiring large amounts of summary statistics that may not use all of the data collected (e.g., ABC or approximate likelihood; Hickerson et al., 2006; Jackson et al., 2017). New approaches allow testing demographic models on multiple taxa simultaneously (Satler & Carstens, 2017; Xue & Hickerson, 2017) and incorporating species abundances (Overcast et al., 2019). A common outcome of demographic analyses is overwhelming support for isolation with migration models (Nosil, 2008; Carstens et al., 2017; but see Cruickshank & Hahn, 2014), which has two important implications. First, support for isolation with migration over pure allopatry challenges the view that differentiation is a discrete event. Second, filtering dynamics of barriers are likely more complex than recognized if gene flow continues to occur across them after isolation. Although detecting the timing and magnitude of gene flow is critical to understand barrier dynamics, using demographic model selection to do this can be difficult as models can often be indistinguishable (Roux et al., 2016). Furthermore, most models assume that populations are panmictic, despite the prevalence of isolation by distance (IBD), and violating the assumptions of the model may compromise inference (Battey et al., 2020). Accounting for IBD in models is now relatively straightforward using the suite of recently developed spatially explicit methods (e.g., Bradburd et al., 2018; Currat et al., 2019), especially when combined with sophisticated statistical analyses like machine learning (although challenges do remain to separate IBD from processes like isolation by environment; see Sexton et al., 2014).

Machine learning approaches relieve some of the statistical and computational burdens of demographic model selection by processing large amounts of data unconstrained by assumptions like data normality (Ripley, 1996). As such, they are able to use and learn from the entirety of large datasets, in contrast with ABC approaches, and can be less computationally expensive than likelihood frameworks. One type of machine learning that is particularly powerful, but underused, in evolutionary biology is supervised machine learning because it can incorporate what is already known about the data when making inferences and allows for the modeling of many alternative simulations (Schrider & Kern, 2018). A notable subtype of supervised machine learning that has risen to prominence in recent years is that of artificial neural networks, so named due to their resemblance to human brain neurons (Hopfield, 1982). Neural networks are excellent at learning complex patterns within labeled datasets and can be trained on a broad range of data types beyond numerical matrices, for example, sound files (e.g., Sprengel et al., 2016), still images (Allken et al., 2019), or video (Fan et al., 2016). These data, however, must be labeled with some form of output—it is this label that the neural network is ultimately being trained to predict. The structure of a basic neural network is typically tripartite and consists of (a) a layer of input nodes, which handle the data directly; (b) one or more layers of intermediate "hidden" nodes; and (c) output nodes, which generate predictions (Zell, 1994). Each layer is connected via a series of mathematical functions which take input from the previous layer's nodes and output the new result to be used in subsequent layers. The specific mathematical functions that connect nodes are known as weights, and these weights are what the neural network optimizes via an iterative process, comparing the actual label associated with the data to the predicted one output by the machine learning model (Zell, 1994). Given their utility and flexibility with respect to the kinds of data that they can learn from, supervised machine learning algorithms such as artificial neural networks can be used in demographic model selection (Schrider & Kern, 2018), giving the modern phylogeographer a powerful toolkit for estimating the evolutionary histories of their study groups.

Here, we use an important biogeographic barrier to understand how biodiversity accumulated in North America Warm Deserts across, the Cochise Filter Barrier (CFB; Figure 1). We explore the community-wide impact of a barrier on genetic differentiation within species, which traits mediate phylogeographic structure, and what analytical tools have been used to estimate those impacts. The CFB is a well-studied environmental and physical barrier that corresponds to a known transition zone between two biotas (Remington, 1968; Swenson & Howard, 2005) that divides the Sonoran and Chihuahuan Deserts of North America. Dynamic geological and ecological factors created this barrier, although the timing of the formation of the deserts is disputed (Wilson & Pitts, 2010). The southern region of the CFB dates back to the uplift of the Sierra Madre Occidental during the Oligo-Miocene, whereas the northern region formed during the Plio-Pleistocene glacial cycles (Van Devender, 1990; Holmgren et al., 2007) and the uplift of the Colorado Plateau (Spencer, 1996). Xeric habitat connecting the deserts was ephemeral during the Plio-Pleistocene, with glacial advances repeatedly replacing arid lands with forests (Thompson & Anderson, 2000; Hafner & Riddle, 2011). This would have created desert refugia east and west of the CFB. Environmental gradients also exist between the hotter, wetter Sonoran Desert and the cooler, dryer Chihuahuan Desert, including elevational and vegetational differences and a high-elevation grassland plain between the two (Shreve, 1942; Reynolds et al., 2004; Figure 1). Interactions among the environment, landscape, and organisms gave rise to the region's biodiversity; some taxa are continuously distributed with no evidence of differentiation, while others show strong phylogeographic structure across the CFB (e.g., Zink et al., 2001; Riddle & Hafner, 2006). In addition, there are many species that are endemic to a single desert (e.g., the saguaro cactus, *Carnegiea gigantea*; Hutto et al., 1986), supporting the idea that the CFB is acting as a filter of taxa. The barrier is not one sharp break; rather, the biota is thought to turn over approximately between 112 and 108°W longitude (Pyron & Burbrink, 2009; Hafner & Riddle, 2011). The CFB is also associated with the Western Continental Divide (Castoe et al., 2007), a major hydrological and elevational separation between western and eastern North America. Despite this, there is no quantitative estimate of the position and width of the barrier across taxa. Without understanding this, it is difficult to infer whether taxa have all been impacted by the same filter and which organismal traits may have been selectively advantageous for crossing the barrier and maintaining gene flow. It is also unclear when divergence happened, with estimates of population divergence ranging from the Miocene through the Pleistocene (e.g., Myers et al., 2017), or whether dispersal occurred after lineage formation. Knowing when and where taxa diversify can lead to inferences on the processes that cause the initial divergence between populations, as well as further insights on post-divergence gene flow and the impact of IBD within structured lineages.

We describe the diversity in genetic structure in taxa across the CFB. Synthesizing what phylogeographic analyses have been used to understand the system (e.g., divergence dating and estimates of gene flow), we examine which taxa are separated at the CFB, where the separation is, and when divergence occurred. Because discrepancies in the location, age, and width of the barrier across taxa can illuminate the filtering mechanisms that structure organisms, we examine the consistency of these metrics in the biota of this region. Furthermore, we ask if variation in functional traits corresponds to the presence of phylogeographic structure. Under a dispersal limitation hypothesis, the vagility of organisms should be correlated with how much phylogeographic structure they display. A barrier should have a stronger impact on less vagile organisms. Under a thermoregulatory hypothesis, we expect that the ability of an organism to regulate their body temperature should be correlated with phylogeographic structure if the barrier has more strongly influenced taxa during periods of cooling during the Pleistocene. For example, ectotherms may be more affected by environmental filters and more likely to experience reduced gene flow in the face of spatiotemporal climatic changes if behavioral adaptations are less efficient than endothermic adaptations (e.g., Buckley et al., 2012). We simulate genomic data under competing diversification scenarios across the CFB to determine whether genomic datasets and demographic models can further clarify how diversification proceeded. Furthermore, we test for support for these competing demographic models using machine learning and five previously published empirical datasets. We aim to describe how synthesizing across empirical, theoretical, and simulated phylogeographic studies can lead to novel insights about the mechanisms of divergence across biogeographic barriers.

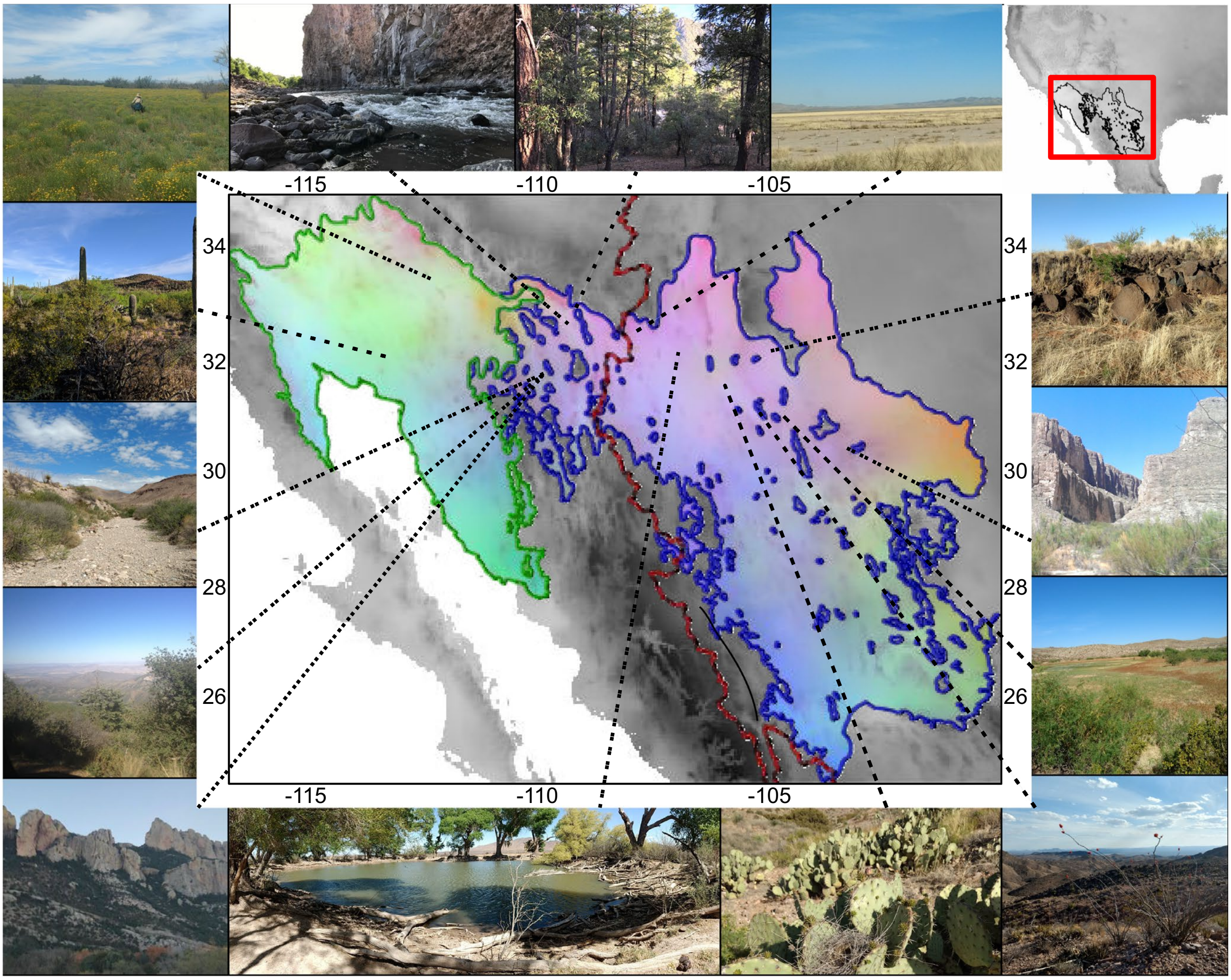

FIGURE 1 Examples of habitat and climatic variation in the Sonoran and Chihuahuan Deserts. Center shows Sonoran and Chihuahuan desert outlines in green and blue, respectively (Olson et al., 2001), and the dotted red line indicates the Western Continental Divide. Colors represent results of a PCA of climatic variables (see Appendix S1), with the first three principal components mapped to green, red, and blue channels of the image, respectively. More green indicates hotter summer temperatures. Redder indicates more variable temperatures across the year. More blue indicates more summer precipitation. Areas outside of the deserts are the same principal components converted into grayscale. Top right shows the section of North America that the center region displays. Photographs around the map show representative habitats across the region, with a line leading to the point on the map where the photograph was taken

2 | MATERIALS AND METHODS

2.1 | Characterizing phylogeographic breaks across the CFB

Understanding the filtering mechanisms operating on taxa distributed across barriers requires understanding where phylogeographic breaks are and which taxa are impacted. To quantify the patterns and frequency of modes of divergence across the CFB, we synthesized genetic patterns from published phylogeographic studies with inter- and intraspecific sampling across the CFB. To find published studies, we used the following Google Scholar search terms in March 2017: "Cochise Filter Barrier phylogeography," "Cochise Filter Barrier genetics," "Cochise Filter Barrier," and "Sonoran Desert Chihuahuan Desert phylogeography." We additionally supplemented this list with references from previous studies on the CFB (Riddle & Hafner, 2006; Pyron & Burbrink, 2009; O'Connell et al., 2017) that did not explicitly use these keywords. Studies which did not include phylogeographic data were excluded.

We recorded the publication date of each study, data type (e.g., single-locus, SNP, etc.), and number of loci. Finally, we characterized each taxon based on their type of locomotion (following Burbrink et al., 2016) and type of thermoregulation (endo- vs. ectothermic) to assess whether these traits are associated with the degree of population structuring across the barrier. We also quantified elevational preference (lowland, montane, or both) to control for elevational differences on diversification. To assess the effects of traits on divergence times, we performed generalized linear mixed modeling

(GLMMs) via the ‘lme4’ package version 1.1–21 (Bates et al., 2014) in R version 3.6.1 (R Core Team, 2019) with and without accounting for taxonomy and elevation (see Appendix S1 for supplementary analyses). GLMMs and similar models are extensions of the more typical linear models, with two specific modifications: (a) GLMMs, due to being mixed models, are able to specify both fixed and random effects, so as to better model unobserved variation in underlying data as well as to account for non-independence in the data; and (b) GLMMs, due to being generalized models, can process data that are non-normal (see Stroup, 2012).

For each taxon, we examined if a specific mode of diversification across the barrier was implicated by the authors of the respective studies (i.e., allopatry, ecological, hybridization, sexual selection, or polyploidy). Next, we assessed whether there was phylogeographic structure across the CFB, when structure arose, and if populations were reciprocally monophyletic with respect to individual loci when tree-based methods were used. Because of the ambiguity in the placement of the CFB we chose to characterize whether there was a phylogeographic break between 118 and 99°W longitude, a much larger range than previously thought (Pyron & Burbrink, 2009; Hafner & Riddle, 2011; Myers et al., 2019). In addition, we assessed the width of the contact zone for each taxon by taking the localities of specimens used in each study, or if specimen information was not available, by assessing placement of specimens on maps present within the figures of the study. We ignored other biogeographic breaks known to occur within the species' ranges. Missing data for variables not estimated for a given taxon were coded as ambiguous.

To determine when phylogeographic structure formed, we categorized the divergence time between populations by epoch: Pleistocene (2.58 Ma to 11.7 Ka), Pliocene (5.33 Ma to 2.58 Ma), Miocene (23.0 Ma to 5.33 Ma), or overlapping two epochs. We separated dates by epoch to allow broad comparisons in divergence across the community. Some studies suggested epochs of divergence between populations without explicit estimates of the divergence date, which we noted. When applicable, we included the full range of error around a divergence date estimate. In addition, to assess whether taxa were monophyletic with respect to the CFB, we visually assessed gene trees present in the study, if tree-based methods were used. Finally, we assessed whether gene flow across the barrier was explicitly estimated. If gene flow was not estimated, we considered individuals who show admixture in clustering analyses as a proxy for gene flow; we recognize that a high coefficient of ancestry could result from incomplete lineage sorting of ancestral polymorphisms. We then recorded whether gene flow was present, absent, or ambiguous.

2.2 | Simulation of discrete population structure and IBD

From our assessment of the literature across the CFB, two patterns were consistently found: discrete phylogeographic structure, or IBD without a discrete transition between populations. However, it is possible that both of these patterns are simultaneously observable in empirical population genetic data (Bradburd et al., 2018) and could be distinguished using a simulation-based approach. We used the program SLiM 3.1 (Haller & Messer, 2019) to build models that explored how the processes of allopatric isolation and speciation with gene flow interact to generate divergence across a biogeographic barrier.

First, we simulated four demographic models, which varied by genetic structure and introgression: (a) a single population model, in which only one panmictic population exists across the entire region, (b) a pure isolation model, in which two populations exist but no gene flow is allowed between them, (c) an isolation with migration model, with two populations and gene flow continuously between the populations, and (d) a secondary contact model, with gene flow allowed during the final 1000 generations of the simulation (Figure 2). We chose 1000 generations of the simulation to represent late-Holocene secondary contact. These four models represent different underlying processes of diversification that are commonly tested for in phylogeographic studies, and with them we evaluated how gene flow and divergence across the CFB varied.

Second, we simulated the presence of IBD to test whether it would impede our ability to determine phylogeographic structure. When IBD was implemented in a model, simulated individuals could only mate and produce offspring with their nearest neighbors. In isolation with migration models, gene flow could only occur between individuals close to the contact zone. In contrast, if IBD was not implemented, individuals could choose any other member of the population to produce offspring with, irrespective of geographic distance. These models were spatially explicit with respect to both the environment that individuals were simulated on and mate choice and production of offspring (see Appendix S1 for complete simulation methods).

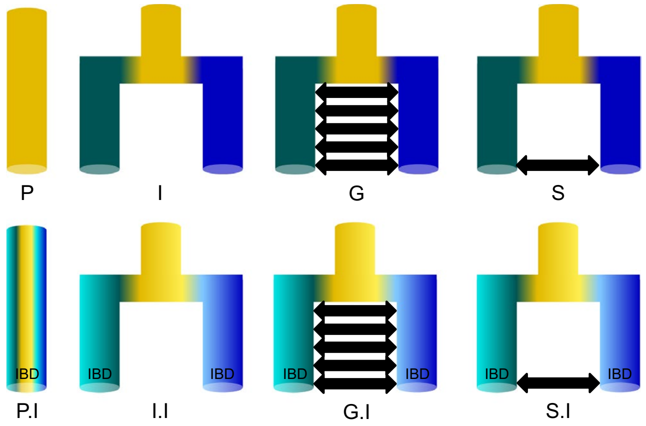

FIGURE 2 Visualization of the eight models simulated. Colorful tubes indicate populations. Arrows indicate gene flow. Color gradients within tubes indicate the presence of IBD, while solid-colored tubes indicate no IBD. P: Single population (“panmixia”) without IBD. P.I: Single population with IBD. I: Isolation without IBD. I.I: Isolation with IBD. G: isolation with migration (“gene flow”) without IBD. G.I: isolation with migration with IBD. S: Secondary contact without IBD. S.I: Secondary contact with IBD

We simulated four different lengths of time: 6000, 21,000, 120,000, and 1,000,000 generations. These approximately correspond to the mid-Holocene, last glacial maximum, last interglacial optimum, and mid-Pleistocene, assuming a generation time of one year. We chose to use different time frames to (a) test if we could tell apart the different models when divergence times were short, and (b) investigate divergence times that could have taken place during major environmental shifts in the CFB region and reflect variation in the divergence dates found in our review of empirical analysis (see Results). This gave 32 simulation regimes in total, which were all combinations of the four demographic models, presence/absence of IBD, and four time frames.

We selected parameter values for the models based on empirical estimates and suggested practices (Table 1; Nam et al., 2010; Provost et al., 2018). We used an ecological niche model (ENM) to provide the landscape under which all demographic models were simulated. This is coarse-scale resolution, solely to generate a scenario where the area between the deserts is not as suitable as the area within the deserts. To do this we used an ENM of Bell's Vireo (*Vireo bellii*), a species that has known population structure across the CFB (Klicka et al., 2016), which was built from GBIF data (GBIF.org, 2017; see Appendix S1 for details on ecological niche modeling). We assumed that the niches of the simulated taxa were static through time. From the simulated genetic data, we calculated 33 summary statistics using the R package 'POPGENOME' (Pfeifer et al., 2014; Table S1.2). These include statistics known to be correlated with particular aspects of demographic histories (e.g., Tajima's D, Tajima, 1989; haplotype diversity, Stumpf, 2004). We chose to use 11 of these summary statistics which were non-collinear and present results from these 11, but we include results from all 33 in the Appendix.

2.3 | Machine learning framework

We performed model selection across demographic regimes by building a neural network using 'SCIKIT-LEARN', a Python module specifically for machine learning (Pedregosa et al., 2011). Model selection was performed so that we could tell whether the demographic model generating the data could be accurately detected. We analyzed each of the time periods together, as well as separately. The inputs were the 11 summary statistics outlined above (see Appendix S1 for details on the machine learning framework). The network outputs a 3x1 matrix where each value in the matrix was the predicted population structure, predicted IBD value, and predicted divergence time. To evaluate the model performance, we calculated accuracy, precision, recall, and the F-score. Accuracy is the percentage of correctly identified positives. Precision is the number of true positives over the number of positives identified (i.e., true and false positives). Recall is the number of true positives over the number of actual positives (i.e., true positives and false negatives). The F-score is the weighted average of precision and recall.

To evaluate the performance of our machine learning models on empirical data, we acquired previously published genetic data for four species of snake (*Crotalus atrox*, *Crotalus scutulatus*, *Pituophis catenifer*, and the *Lampropeltis getula* complex [between *L. splendida*/*L. californiae*]; Myers et al., 2019) and one species of bird (Cardinalis cardinalis, Provost et al., 2018). All species had used reduced representation sequencing and had generated hundreds to thousands of individual loci, which we analyzed individually for all five taxa. In addition, we analyzed all five taxa by concatenating individual loci into one single supergene and ran analyses on this concatenated locus. We chose this double-pronged approach to investigate the variation in estimates among individual loci, as well

Gens.	Dataset	Precision	Recall	F-score	Acc. (P)	Acc. (I)	Acc. (A)
6000	Training	0.68	0.68	0.68	0.71	0.95	*n/a*
6000	Validation	0.24	0.25	0.24	0.28	0.84	*n/a*
6000	Test	0.23	0.23	0.23	0.28	0.83	*n/a*
21,000	Training	0.74	0.74	0.74	0.79	0.94	*n/a*
21,000	Validation	0.30	0.30	0.30	0.35	0.86	*n/a*
21,000	Test	0.32	0.33	0.32	0.37	0.87	*n/a*
120,000	Training	0.83	0.83	0.83	0.85	0.97	*n/a*
120,000	Validation	0.42	0.42	0.42	0.47	0.88	*n/a*
120,000	Test	0.39	0.39	0.39	0.47	0.86	*n/a*
1,000,000	Training	0.74	0.73	0.72	0.76	0.95	*n/a*
1,000,000	Validation	0.57	0.55	0.52	0.62	0.88	*n/a*
1,000,000	Test	0.65	0.65	0.64	0.72	0.87	*n/a*
All	Training	0.49	0.48	0.48	0.60	0.92	0.83
All	Validation	0.23	0.23	0.22	0.39	0.85	0.68
All	Test	0.24	0.24	0.23	0.40	0.86	0.67

TABLE 1 Model performance. Accuracies were calculated for phylogeographic structure alone (P), IBD alone (I), and ages alone (A) when applicable. "Gens." = generations. "Acc." =accuracy

as to assess the overall pattern. FASTA files were converted into VCF files using all empirical sites, including monomorphic ones and ones with missing data. Those VCF files were then converted into ms-formatted files. We then used those genetic data to calculate the summary statistics mentioned above, so as to give predicted demographic information for each taxon.

To ensure that the empirical data and simulated data were as similar as possible, we took our existing simulations and converted them to include nucleotide base pairs (rather than 0/1 ancestral/derived states only) as well as 50% missing data. To simulate nucleotide base pairs, we randomly assigned the ancestral and the derived states to one of A, C, T, or G, without assigning them both the same value. To obtain 50% missing data, we randomly selected sites within individuals and removed them.

We found that our simulation framework would not calculate summary statistics for all of the empirical data, which we suspected was due to too much missing data. In particular, calculations of haplotype counts and minor allele frequencies failed (see Table S1.2). Because of this, we chose to re-train our neural network without the eight summary statistics that were impacted, while also including the simulated data that had nucleotides and missing data added (see Appendix S1). We found that there were no qualitative performance differences between the neural network with the 33 original summary statistics and the neural network with the 25 that resulted after the eight were removed (see Appendix S1 for classification information). We assumed a 3-year generation time for the snake species (after Ernst & Ernst, 2003) and a 1-year generation time for the bird species (after Provost et al., 2018).

3 | RESULTS

3.1 | Biota around CFB shows variability in evolutionary histories

We found 300 published studies from our search terms, which we narrowed down to 99 studies comprising 68 taxa (species complexes of 1–6 species) in 39 families and 19 orders (Asterales, Caryophyllales, Cucurbitales, Pinales, Araneae, Coleoptera, Hymenoptera, Orthoptera, Scorpiones, Anura, Squamata, Testudines, Galliformes, Passeriformes, Piciformes, Artiodactyla, Carnivora, Chiroptera, and Rodentia; Table S1.3; see Appendix S2 for data sources). Phylogeographic inference was performed using a range of data including mitochondrial, chloroplast, and nuclear loci, microsatellites, allozymes, restriction fragment length polymorphisms, and reduced representation data generated via high-throughput sequencing (e.g., RADseq). Some taxa had descriptions of spatial variation based on phenotypic assessments, but all but one species had genetic data to reinforce those inferences. Seventeen taxa were supported using next-generation sequencing data.

The majority of the taxa (~60%) showed evidence for phylogeographic structure across the CFB (Figure S1.1). Of the 68 taxa examined, 41 showed structure (with 36/41 monophyletic), 13 showed no structure, and the remainder had unclear results where it was ambiguous whether there was structure. Divergence times were estimated in 27 of the structured taxa and ranged from the Miocene to the Pleistocene with no clear temporal congruence across species. Of these, 11/27 were in the Pleistocene alone, with an additional eight overlapping the Pleistocene and other epochs and the remaining eight restricted to the Miocene and/or Pliocene. The remaining 14 taxa that were found to have structure were not explicitly dated, but for five of those taxa the Plio-Pleistocene glacial cycles are cited as being a major driver of divergence.

Just under half of the taxa overall (32/68) had an explicit estimate of gene flow (Table S1.3, Figure S1.1). Of these, 5/32 had no gene flow across the CFB, 13 had gene flow, and the rest had ambiguous results. Seventeen species were structured and had gene flow estimated, which resulted in 3/17 with no gene flow, 7/17 with gene flow, and 7/17 with ambiguous results. Allopatry was the primary mode of speciation proposed, with isolation-by-environment secondary. Some of the studies that found support for gene flow (and thereby isolation with migration or secondary contact) concluded that pure allopatric speciation was taking place. Of the 55/68 taxa that had clear or ambiguous splits across the CFB, allopatric speciation was the mode of speciation proposed for 19 taxa, with an additional five identifying allopatry with another mode of speciation, including hybrid speciation, polyploidy, and sexual selection (Table S1.3). Another 12 declared isolation-by-environment alone (often with the influence of IBD) as the main driver; all these taxa had support from next-generation sequencing data and were from the same study (Myers et al., 2019). The remaining 19 taxa did not have inferred modes of speciation. There appears to be a temporal bias in the interpretation of these results: only recent papers (2004–2019, median 2017) suggested isolation-by-environment as the main driver, while older papers overwhelmingly suggested allopatry either alone (1986–2018, median 2005) or with another mechanism (1996–2014, median 2005).

The location and width of the contact zone varied between species and also varied with respect to the divergence times and locomotor types (Figure 3; Figures S1.2 and S1.3). The total extent of the barrier ranged from 118.3 to 99.5°W longitude, or an 18.8° longitude width. Of the 36 species for which we could estimate where the barrier was, 24/36 overlapped 108.6°W, the maximum number of species to overlap. The zone of overlap for over 50% of the taxa (18 or more species) ranged from 109.3 to 105.6°W. The contact zone widths for each taxon ranged from 0.3 to 11.2°W.

The overall width of the contact zone at the barrier varied with respect to divergence time (Figure S1.2). Width peaked for taxa who diverged in the Pliocene (16.9°) decreasing as divergence dates get both older (7.4–7.7°) and younger (8.2–9.3°). The contact zone width also varied with respect to locomotion type (Figure S1.3; see Appendix S1). Walking taxa spanned the entire range of 18.8°. For the other locomotion types, the largest-to-smallest width is crawling, jumping, flying, sessile, and swimming taxa (12.7–3.0°). In addition, locomotion type and structure co-varied (Figure 4). Flying species had the lowest percent of taxa with structure (8/17, ~47%). All

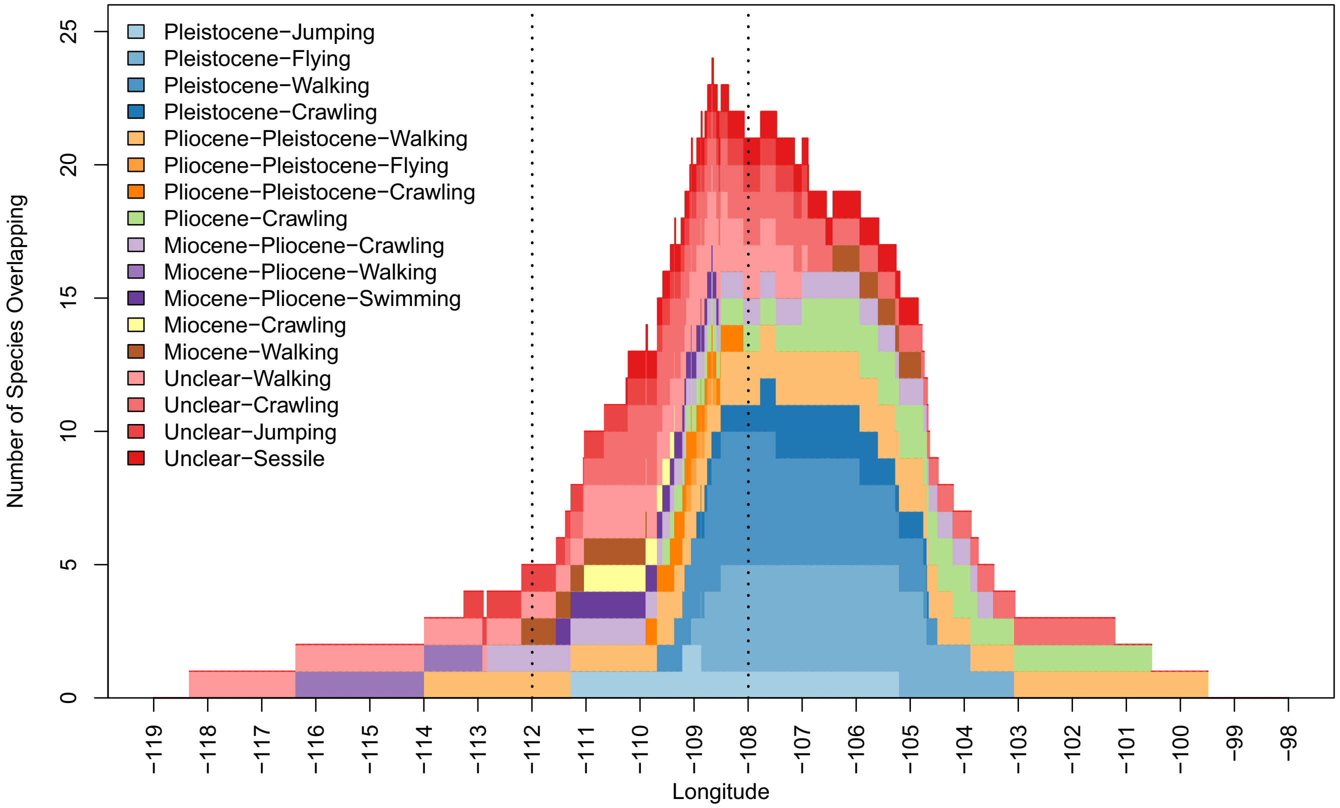

FIGURE 3 The width of the Cochise Filter Barrier (CFB) contact zone for taxa varies by the timing of divergence and the type of locomotion. Colors correspond to unique combinations of divergence and locomotion. Hues represent divergence times (Pleistocene, Pliocene, Miocene, Unclear, etc.) and shades represent locomotion types (Crawling, Flying, Walking, etc.). X-axis shows the longitudinal range, Y-axis shows the number of species that overlap a given longitude. Vertical dotted line shows previously estimated boundary of CFB (Pyron & Burbrink, 2009). See also Figures S1.2 and S1.3

swimming and jumping taxa (*N* = 1; *N* = 3) had structure. Of the rest, walking species had the highest percentage of taxa with structure (19/27, ~70%) followed by crawling (10/16, ~63%) and sessile species (2/4, 50%).

The influence of thermoregulation on population genetic divergence appears to be less clear than the influence of locomotion (see Appendix S1). A higher proportion of ectotherms were found to have structure (27/40, ~68%) than endotherms (14/28, 50%), but the difference was not significant ($\chi^2 = 2.11$, $p = 0.15$). Ectotherms also showed older divergences; all of the taxa whose divergences overlapped the Miocene were ectothermic (Figure S1.4) and of the remaining, proportionately fewer endotherms diverged in the Pliocene (2/9, ~22%) than the Pleistocene (14/27, ~52%). It is possible that this was an artifact of how divergence dating was performed across these groups with respect to variable substitution rates. Both thermoregulation and locomotion are significant predictors of divergence date (thermoregulation $R^2 = 0.14$, $p = 0.0078$, locomotion $R^2 = 0.25$, $p = 0.025$), although not when they were both in the same regression ($R^2 = 0.31$, thermoregulation $p = 0.060$, locomotion $p = 0.088$). They were still significant when accounting for elevational preference, taxonomy, or both simultaneously (range $R^2 = 0.14–0.34$, thermoregulation $p = 0.0054–0.014$; locomotion $p = 0.013–0.047$). Of the taxa examined, 34 were found in lowlands, 10 were montane, and the remainder were found in both; however, elevational preference was not a significant predictor of divergence time (with and without taxonomy $p = 0.57$).

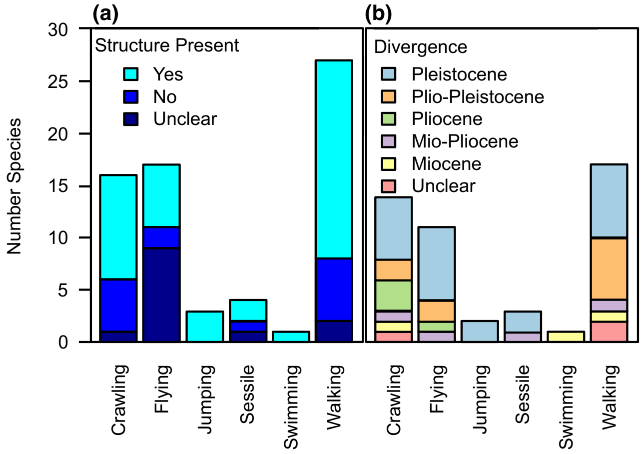

FIGURE 4 The presence of phylogeographic structure and divergence time across the Cochise Filter Barrier varied based on the locomotion type. X-axis: locomotion type. Y-axis: number of species per category. Colors describe the presence/absence of phylogeographic structure (a), or the divergence time (b)

3.2 | Accuracy of machine learning classification varies with age and phylogeographic history

After calculating summary statistics, removing duplicate simulations that produced the exact same statistics within the same model time, and eliminating collinear variables, we had 26,131 unique sets of summary statistics across the 32 models. The number of summary statistic sets per model varied based on the number of generations each model ran for (6,000 generations: 834–1099 sets per model; 21,000: 1011–1200; 120,000: 1100–1100, 1,000,000: 80–100). Generally, younger runs were more likely to produce duplicate results.

The neural network varied in accuracy (Table 1, Table S1.4), but was consistently precise at classifying whether models had IBD, less good (but consistent) at classifying the number of generations after divergence, and inconsistent at classifying the true demographic model. When the network was asked to classify if IBD was present, it did so with high accuracy regardless of how many generations after divergence or how many summary statistics were used (92–100% for training, 81–89% for validation/testing), and overfitting appeared to be slight (Table 1, Table S1.4; Figure S1.5). Similarly, when the network classified the number of generations since divergence, it did so with 83–85% accuracy in training, depending on how many summary statistics were used, and 66–68% in validation/testing. When models were misclassified, it was always to a similar number of generations (e.g., 21,000 generation runs were confused with 6000 and 120,000 generation runs, but never 1,000,000 generation runs; Figure S1.5). The differences in training and validation/testing suggest slight overfitting. Finally, neural network accuracy for classifying phylogeographic models was much more variable with a lot of overfitting (61–94% training, 28–62% validation/testing). Accuracy was positively associated with the number of generations after divergence models were run for, with those that ran for longer having higher ability to differentiate between models (Table 1, Table S1.4).

When examining performance across models (Figure 5), IBD had similar misclassification rates irrespective of the number of generations since divergence and phylogeographic structure simulated. The exception was for models run for 1,000,000 generations after divergence. Here, the single population with IBD models had high (worse than random) misclassification rates. Otherwise, models run for 6000–120,000 generations tend to have higher misclassification rates, although the trend was reversed for secondary contact models, which have lower misclassification rates. Phylogeographic structure was also more highly misclassified in models with a short number of generations since divergence, irrespective of IBD. Some models are classified worse than random based on age: isolation with IBD models (6000 generations), and isolation with migration both with (21,000 generations) and without IBD (6000 generations, 21,000 generations).

We examined which misclassifications were most common with respect to the number of generations modeled since divergence (Figure 6, Figure S1.6). From a phylogeographic structure perspective (irrespective of IBD), across all ages of divergence, single population models were likely to be misclassified as isolation with migration models and vice versa. Likewise, isolation models were likely to be misclassified as secondary contact models and vice versa. In models that were run for 1,000,000 generations since divergence, misclassifications between isolation/secondary contact and isolation with migration/single population were the only misclassifications that occurred. However, as the number of generations since divergence decreased, more kinds of misclassifications arose. In models run for 120,000 generations after divergence,

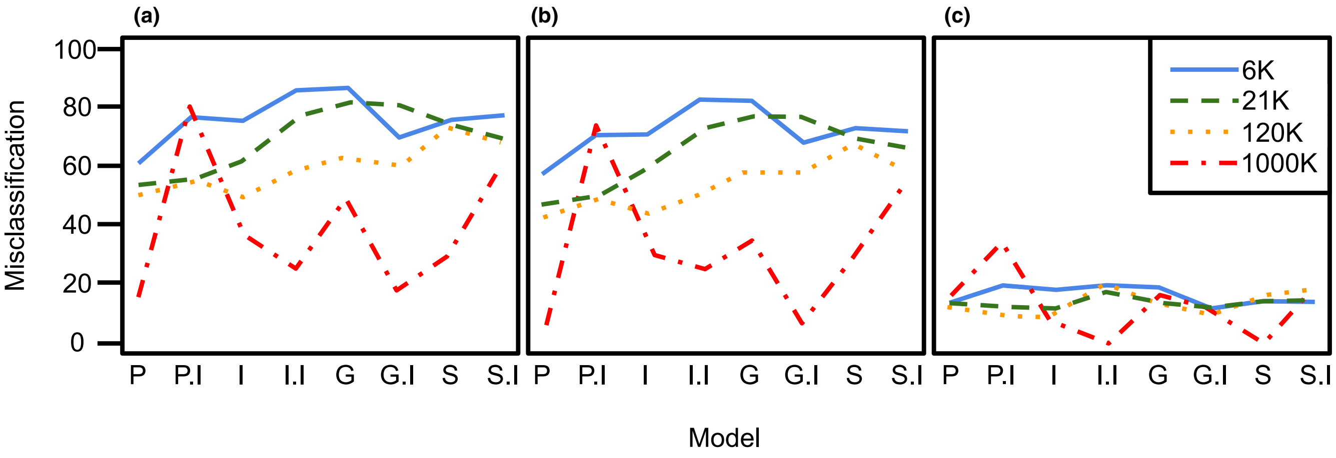

FIGURE 5 Neural networks classified models with older divergences much better than models with younger divergences. (a) Misclassification rates for the overall models. (b) Misclassification rates for only the phylogeographic models. (c) Misclassification rates for only IBD. Model values on the x-axis correspond to models in Figures 2 and 6. Y-axis shows misclassification rate, with higher values indicating poorer model performance. Lines of different colors and dash types differentiate the generations simulated, from 6,000 (6 K) to 1,000,000 (1000 K) generations. P: Single population ("panmixia") without IBD. P.I: Single population with IBD. I: Isolation without IBD. I.I: Isolation with IBD. G: isolation with migration ("gene flow") without IBD. G.I: isolation with migration with IBD. S: Secondary contact without IBD. S.I: Secondary contact with IBD

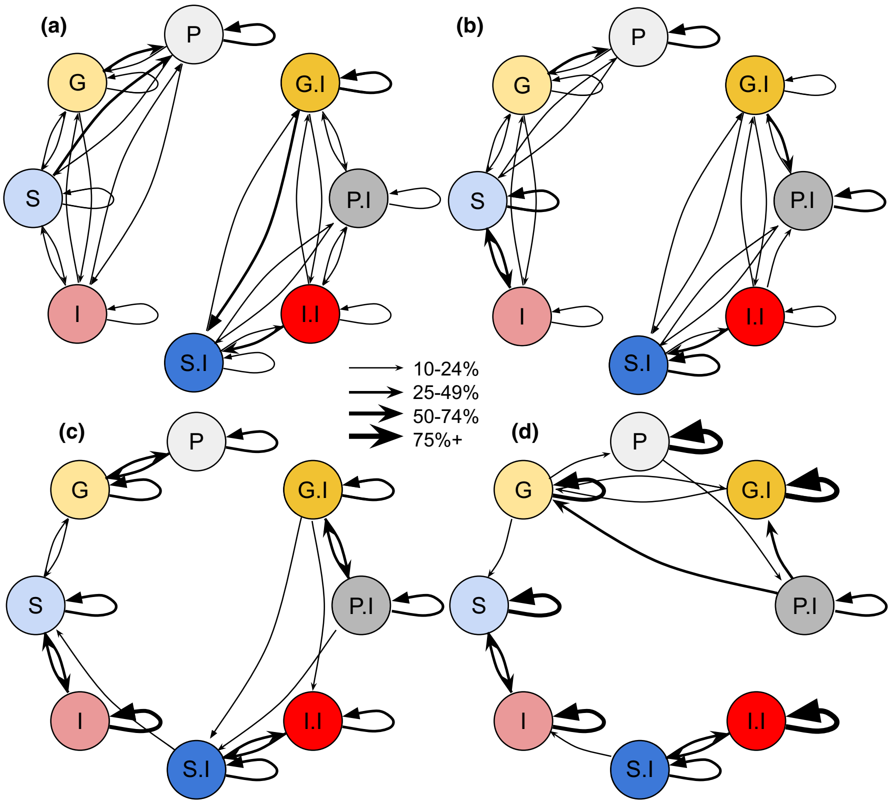

FIGURE 6 Overall model classifications are easily confused at young ages but improve with older ages. Arrows begin at the true model and end at the assigned model. Line thickness of arrows indicates the percentage of time those assignments are made. Assignments under 10% are omitted for clarity. Demographics include single panmictic populations ("P," grey), isolation with migration or gene flow ("G," yellow), secondary contact ("S," blue), and isolation ("I," red). Suffix of ".I" after demography indicates that IBD is present. (a) 6000 generations. (b) 21,000 generations. (c) 120,000 generations. (d) 1,000,000 generations. Models with IBD are on the right, models without IBD are on the left

isolation with migration and secondary contact were frequently misclassified, as were single population and secondary contact. All models were confusable in younger divergences, with confusion greatest in models run 6000 years after divergence. This reveals that even in lineages with old divergences, single population and isolation with migration models are hard to tell apart, as are isolation and secondary contact models. However, the younger a divergence was, and the less time for genetic differences to accumulate, the easier it was to confuse in all types of models. When considering misclassifications simultaneously between IBD and phylogeographic structure models, in older models we generally found that when models are misclassified between having IBD and not having IBD, it tends to be within the same model type (i.e., isolation with migration with IBD to isolation with migration without IBD) or between those models that were already identified as similar when not considering IBD (i.e., secondary contact with IBD to isolation without IBD).

3.3 | Classification of empirical data using a trained neural network

The re-trained neural network (see Appendix S1) was run on genomic data for four species of snake (*Cr. atrox*, *Cr. scutulatus*, *L. splendida-californiae*, and *P. catenifer*) and one species of bird (*Ca. cardinalis*). Analyzing all available data for each species as a single concatenated supergene, our machine learning algorithm predicted that *Cr. atrox*, *Cr. scutulatus*, *P. catenifer*, and *Ca. cardinalis* were best explained by a secondary contact model without IBD effects and for a time since divergence of 1,000,000 generations with relative probabilities greater than 99% for each (Figure 7). After accounting for generation time, this would suggest an early-Pleistocene to late-Pliocene divergence time. Of these species, *Cr. atrox* and *Ca. cardinalis* showed strong support for structure across the CFB, whereas *Cr. scutulatus* and *P. catenifer* have conflicting results, and show gene flow and/or IBD across the barrier (Castoe et al., 2007; Myers et al., 2017; Myers et al., 2019; Provost et al., 2018; Schield et al., 2018). Cardinalis cardinalis additionally has previous estimates for low levels of gene flow across ~991,000 years of divergence (Provost et al., 2018). *Lampropeltis splendida-californiae* also showed a pattern of secondary contact without IBD effects with relative probabilities of over 99%; however, this species was best predicted with 6000 generations since population isolation. The relative probability of *L. splendida-californiae* having 6000 generations since isolation was 75%, with all remaining probability showing that the best model was 21,000 generations since isolation, suggesting a divergence in the late Pleistocene. This is inconsistent with previous work based on mtDNA, which suggests that *L. splendida-californiae* diversified across the CFB from 750,000 to 3,440,000 years ago (Myers et al., 2017; Pyron & Burbrink, 2009). We report the results of the individual loci for these four snake species in the supplementary material (see Appendix S1). Generally, there was a large amount of variation, with nearly every combination of demographic history, IBD presence or absence, and generation time since isolation being present in at least one locus (Figure 7).

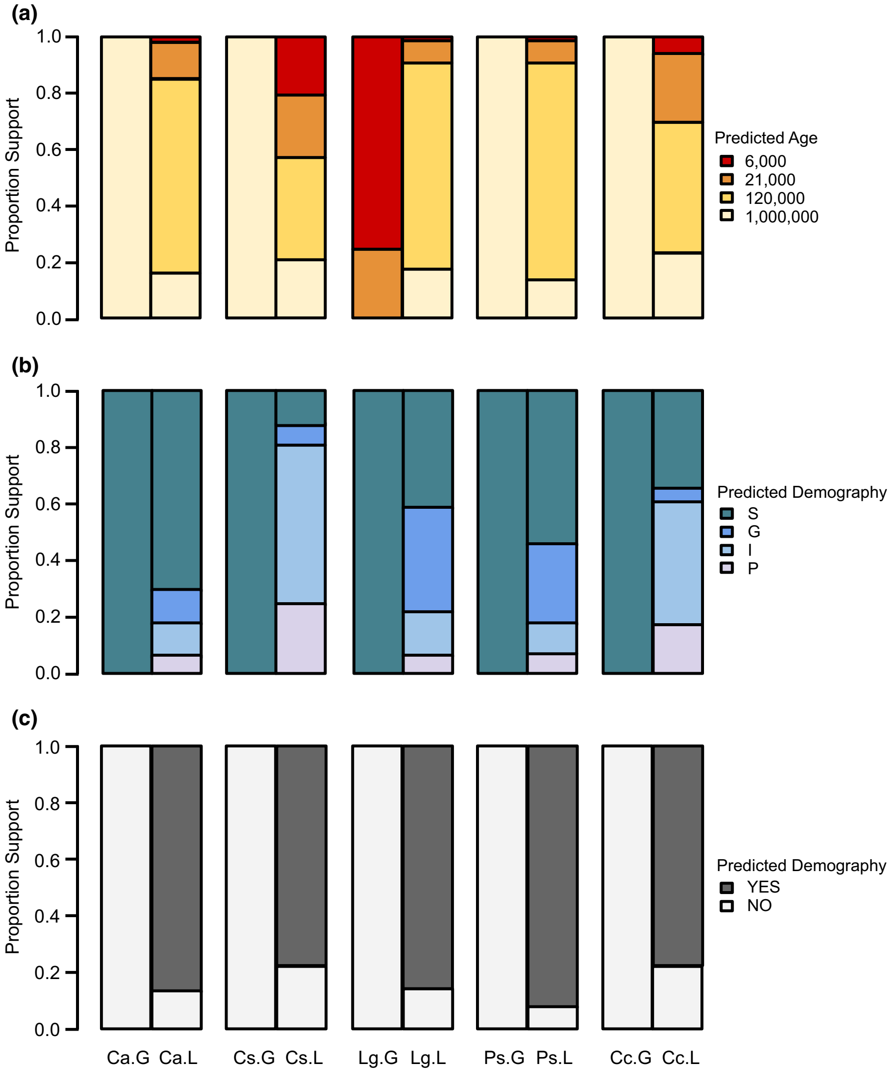

FIGURE 7 Predicted support for empirical species' divergence time in number of generations (a), demographic history (b), and presence or absence of isolation by distance (c). Y-axis shows the relative proportion of support for each value, with different colors showing different values. X-axis shows species: *Crotalus atrox* ("Ca"), the *Lampropeltis getula* complex or *L. splendida-californiae* ("Lg"), *Pituophis catenifer* ("Pc"), *Cr. scutulatus* ("Cs"), and cardinalis cardinalis ("Cc"), where suffix of ".G" and ".L" indicate the data analyzed are a supergene or individual loci, respectively (i.e., "Ca.G" = *Crotalus atrox* supergene). Demographic codes in (b) include single panmictic populations ("P"), isolation with migration or gene flow ("G"), secondary contact ("S"), and isolation ("I")

4 | DISCUSSION

We found that the communities of organisms that are co-distributed across the CFB show a wide amount of variation in their phylogeographic histories. However, some commonalities emerge. Many of the taxa surveyed show a Pleistocene divergence time. Ectotherms are more likely to diverge across the CFB than endotherms, and similarly, more vagile organisms are less likely to diverge. Leveraging machine learning, we used five exemplar datasets and predicted their demographic histories from simulated and empirical genetic data. All five species are generally predicted to have had a long period of genetic isolation, often with recent secondary contact. However, individual loci show that within species there is a high degree of variation in predicted phylogeographic histories. Divergence throughout the region appears, therefore, to be a combination of forces, ranging from allopatric isolation to ecological speciation, and combining empirical and simulation methods gives us a viable way forward for diagnosing how population structure and diversification proceed across this landscape.

Moving beyond descriptive narratives of landscape change generating biodiversity and understanding how taxa interact with barriers represent major challenges of biogeographic research. We used the Sonoran and Chihuahuan Deserts as an exemplar system for characterizing genetic differentiation among two regions, quantifying the temporal and spatial dynamics in phylogeographic structuring associated with a filter barrier. The range in divergence times and phylogeographic break locations in taxa distributed across the deserts reflects the semi-permeability of the CFB. The variability of molecular data used in this synthesis was not suitable for a formal test of simultaneous divergence (e.g., Hickerson et al., 2006), but the wide disparity of divergence times suggests taxa have been diverging across the CFB for millions of years (Myers et al., 2017). Locomotive and thermoregulatory traits help to explain this variation, suggesting that organisms that are more vagile and less dependent on external temperatures (i.e., endotherms) may be better at evading the impacts of the barrier, and selective pressures both on movement and on environmental tolerances might determine which taxa diverge. Divergence in allopatry was typically invoked as the main mode of differentiation across the CFB, but we found evidence of all other processes in addition to allopatry (i.e., ecological divergence, polyploidy, hybrid speciation, and sexual selection). Fully understanding how the CFB filters the taxa that are co-distributed across it necessitates a deeper understanding of the mechanisms causing differentiation more broadly in the region. Using simulations and model selection approaches can help illuminate those mechanisms via rigorous hypothesis testing and replication, which we have illustrated in our empirical work herein. These methods offer promise by more accurately identifying modes of differentiation, but the modeled scenarios can be difficult to distinguish. Nevertheless, simulation methods contextualize empirical results and show the utility of genomic-scale data in uncovering phylogeographic histories, allowing us to understand how organisms might be expected to diversify under different known conditions.

4.1 | The communities around barriers are influenced by a multitude of forces

Biogeographic barriers are typically viewed as abrupt transitions between two biotas, but our analysis showed the conditions in which this view does not hold. The entities identified as biogeographic barriers may represent a combination of forces that generated the contemporary distributions of taxa, which have a wide longitudinal range of phylogeographic breaks across the CFB after accounting for uncertainty. Most species have ranges that overlap ~109–106°W, a shift eastward from the ~112–108°W that was conventional in the literature (although very few species do not overlap the original distribution). This uncertainty may have numerous causes. First, barriers can be ephemeral over time, for example, due to river capture events (Tagliacollo et al., 2015), sea-level changes (Elias et al., 1996), or major climatic shifts (possibly including the CFB; Holmgren et al., 2007). Additionally, organisms have the capacity to disperse, which can retain or reintroduce gene flow and connectivity across barriers (Brandley et al., 2010). Population genetics theory also predicts that even in the absence of a barrier, phylogeographic structure can arise due to simple density troughs, where abundances are low and dispersal out of these troughs fails (Barrowclough et al., 2005; Barton & Hewitt, 1981). Finally, within the CFB, numerous studies lack individuals from the transition zone and therefore it is possible that incomplete sampling may be a culprit for the observed differences between taxa. Contact zone widths cannot be estimated without carefully collected transects through a region. Fortunately, targeted sampling across the CFB will resolve this discrepancy, especially with the addition of genome-level sampling. In our analyses here, we used all individuals to calculate summary statistics, but future work could subset individuals and create a sensitivity analysis to understand biases that could arise from incomplete sampling.

4.2 | Locomotion and thermoregulation as filters

Our results show the expected relationship between locomotion type and how organisms respond to the barrier. We found that flying organisms are less likely to have diverged across the barrier. Flying organisms can have higher dispersal ability, allowing them to potentially bypass any filtering mechanisms of a biogeographic filter barrier, and previous work has shown that flying organisms tend to show less genetic differentiation than taxa with other locomotive modes (Medina et al., 2018). The contact zone at the barrier also has a smaller estimated width for flying taxa than those with other forms of locomotion. Under an assumption where flying confers higher dispersal, it is counterintuitive that they should show a narrow range for the CFB, unless dispersal is unable to counteract the strength of the filters operating or the degree of environmental changes are relatively stronger than the effects of organismal traits. Flying organisms have a higher proportion of Pleistocene divergences relative to other epochs even after accounting for elevation, which has been found across other biogeographic barriers (e.g., Bacon et al., 2015). It is unclear whether the Pleistocene climatic shifts themselves caused diversification or if other processes drove diversification during this epoch. Alternatively, flying species may be able to more easily find suitable habitat across the barrier relative to other taxa, which would weaken the impact of the CFB. This would explain both the shallow divergences and the narrow width. In addition, some taxa are clearly under-sampled (e.g., sessile plants) or less abundant in desert habitats (e.g., fishes), which may explain the discrepancies. Increasing sampling of organisms with different forms of dispersal could clarify the trends identified here.

Ectothermic taxa appear more likely to diversify across the CFB than endothermic taxa, although the patterns are not significant. As ectothermic organisms are reliant on external temperature regulation (Boyko, 2014), it is feasible that any environmental changes could disproportionately affect them compared to endotherms. Under this assumption, Pleistocene climate change would have been an effective filter on ectotherms. Alternatively, local adaptation could be a stronger process in ectotherms relative to endotherms, which would explain divergence under an ecological-speciation hypothesis (Nosil, 2012). If so, finding the traits that are most important in driving this adaptation, perhaps body size or dispersal ability as mediated by physiology, would be key.

This work reveals the impact of locomotive mode and physiology on population genetic divergence across a biogeographic barrier. From this baseline, future studies could explore other traits that may mediate species diverge across this and other barriers. For example, microhabitat preferences, body size, diet, or interspecific interactions could be driving the pattern in addition to the traits we identified here. The relative width of the contact zone for a taxon could change through time as species-specific traits interact with the properties of the barrier, for example, whether it allows frequent or infrequent dispersal (see Pyron & Burbrink, 2009), is long-lived or ephemeral, and/or relocates through time. Both of these conditions are presumably the result of selection over long periods of time, whereas more stochastic forces could be at play in the short term. In addition, it is unclear which traits enhance and reduce dispersal through the CFB across time periods; the region experienced dramatic environmental changes across the range of divergences found here. Overall, phenotypic traits could be important for determining why multiple co-distributed taxa are concordant or discordant with respect to their phylogeographic histories (Zamudio et al., 2016).

One issue that remains to be resolved is when taxa are endemic to only one side of the CFB—for example, Saguaro Cactus, Sidewinder, Tiger Rattlesnake, Gila Woodpecker, and Costa's Hummingbird on the Sonoran side of the barrier, and Grey-banded Kingsnake, Rock Rattlesnake, and Golden-Fronted Woodpecker on the Chihuahuan side. These taxa could have been unable to cross the barrier initially, were once co-distributed but have since been extirpated (or speciated) on one side, or experienced competitive exclusion. Distinguishing between these scenarios would likely require fossil or paleoecological evidence (e.g., packrat middens; Betancourt et al., 1990; Van Devender, 1990) depending on the age of the taxon. Our work only assessed taxa that were co-distributed across the barrier and had individuals collected on each side, but understanding why organisms are endemic to only one desert would improve knowledge of what factors make the CFB a filter barrier. Do particular traits cause organisms to be unable to pass through the CFB, or is it perhaps competition between organisms with similar niches or even close relatives? These questions will need to be resolved to fully understand how the community in the Sonoran and Chihuahuan Deserts has assembled through time.

4.3 | Genome-level data can clarify phylogeographic patterns

Using machine learning methods on large, simulated datasets, combined with empirical and theoretical studies, allows for testing between phylogeographic models with numerous parameters of interest. For example, the divergence mechanisms in Australian honeyeaters are ambiguous in empirical data but may be resolvable using a simulated approach (Toon et al., 2010). Our simulations here are only a subset of model parameter space and larger genomic regions, population growth, and selection could be considered (Carstens et al., 2013; Ewing & Jensen, 2016). Likewise, we do not account for changes in parameter space over time (e.g., population size, mutation rate, and environmental factors). Demographic expansions and contractions in effective population size cause changes in the impact of genetic drift, and many phylogeographic studies find these changes in concordance with genetic structure (e.g., Charruau et al., 2011; Smith et al., 2011). Changes in habitat suitability over time can lead to these demographic changes; fortunately, spatially explicit methods can incorporate these changes via the addition of paleoclimate suitability models, which now extend back to the Pliocene (Brown et al., 2018; Dowsett et al., 2016).

The neural network approach we used here allows for direct estimation of the model power and model identifiability in test data, which can be leveraged when analyzing both simulated and empirical datasets. Validation schemes indicate how well a model performs on known simulationsEAM was supported through the Peter Buck models, giving estimates of error and describing which models have problems with identifiability. Furthermore, once neural networks such as ours are trained, almost no additional computation time is required to classify further data; it only needs to be trained once. Expanding on a neural network approach, for instance, to classify more empirical species, is computationally trivial, and the more a neural network is used after it is trained, the more computationally efficient it becomes.

The identifiability of our models was high when classifying IBD and number of generations. However, at young divergence times, our method struggled to tell apart different models, implying that differences between isolation and secondary contact are inscrutable at shallow-divergence histories. The difficulty in identifying models is well known with certain summaries of genomic data, for example, when using the site frequency spectrum effective population size is hard to estimate, especially when it has been dynamic over time (Lapierre et al., 2017; Terhorst & Song, 2015), and the presence of ancient population structure can erroneously appear as current gene flow (Eriksson & Manica, 2014). If these tenets also hold for additional summary statistics, they must be accounted for in future work. Nevertheless, this serves to reinforce that biologically similar models tend to be confused with one another (e.g., Roux et al., 2016). Further work will require additional testing as to the impact of model selection on different biological scenarios.

We validated our simulated models by using previously published data. We acknowledge that the simulation framework developed herein is a coarse scale meant to illustrate the utility of neural networks in classification of demographic histories across an exemplar biogeographic filter barrier. Although the neural networks trained with simulated and empirical data were similar in terms of performance, they were not entirely the same due to the differences in the underlying summary statistics used. Any modifications of the summary statistics require the neural network to be re-trained, as non-analogous data will not be classified correctly. Future researchers using similar frameworks must make sure that their machine learning models are trained with data that match the empirical data of interest as closely as possible to alleviate these issues.

Overall, we found variation between the previous empirical estimates of demographic history in the five species and our predicted values. Generally speaking, the predicted demographics from our neural network (Pleistocene, secondary contact, or pure isolation, with IBD) are close to the actual estimates for these five taxa and are in line with the frequently confused models from the simulations (e.g., Figure 6). The discrepancies between these two estimates of demographic history of these five taxa could be because of differences in the methodology used. Complex evolutionary histories are difficult to detect, and examining loci individually we see that there are potentially many interacting and conflicting signals in the genomes of these organisms. Despite these discrepancies, the fact that our estimates were close to previous ones and were computationally fast suggests that using similar frameworks is a viable method of determining phylogeographic history in actual systems.

5 | CONCLUSION

In conclusion, we synthesized phylogeographic studies across an exemplar barrier, examining how biogeographic filters affect communities. Among all species, gene flow, phylogeographic structuring, and timing of divergence all varied substantially. The location of the barrier and width of the contact zone are related to locomotion and thermoregulation, irrespective of phylogeny and elevational preferences. Simulations and machine learning allowed us to quantify spatiotemporal evolutionary histories, finding numerous aspects of demography including gene flow and isolation by distance are major confounding variables. Overall, barriers interact with traits of species to cause heterogeneous differentiation, but identifying the exact causes remains challenging.

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KLP and BTS conceived and planned the study. KLP performed all simulation, machine learning, and statistical analyses with input from BTS and EAM. All authors contributed to the literature review process. KLP wrote the manuscript and all authors contributed to editing and revising the work.

DATA AVAILABILITY STATEMENT

All data used to perform the analyses in this study are available in the Appendix or stored on Dryad (https://doi.org/10.5061/dryad.8931zcrq8).

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BIOSKETCH

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Authors contribution: KLP and BTS conceived and planned the study. KLP performed all simulation, machine learning, and statistical analyses with input from BTS and EAM. All authors contributed to the literature review process. KLP wrote the manuscript and all authors contributed to editing and revising the work.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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