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RESEARCH ARTICLE

Implications of barrier ephemerality in geogenomic research

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Abstract

Aim: Previous population genetic and phylogeographical studies have shown how generation time and dispersal affect population divergence in the presence of a vicariant barrier. More recently, speciation genomic studies have revealed that selection and recombination can be equally impactful. Here, we test how the interaction of these factors shapes the divergence expected in response to an ephemeral barrier and compare these results to empirical literature using the Baja California peninsula as a test case.

Location: Global.

Taxon: Diploid eukaryotes.

Methods: We forward simulated population genomic data with CDMetaPOP and SLiM by varying dispersal rate, mutation rate, generation time, selection pressure and recombination in the presence and then removal of a physical barrier. We tested which factors affect the divergence signal (measured as F_{ST}). We compared simulation results to empirical literature that included 147 records of generation times and 78 divergence estimates from population genomic studies.

Results: Population differentiation not only occurred due to the presence of a barrier under lower dispersal abilities but also emerged as a result of low dispersal among structured populations without a barrier. Divergent selection strengthened differentiation, which is supported by empirical data. Barrier removal quickly eroded the divergence signal (~500 generations) for high-dispersing species, but low dispersal species retained divergence after gene flow resumed. In the empirical data, generation times varied by four orders of magnitude and dispersal by three orders of magnitude.

Main Conclusions: Divergence can arise without vicariant barriers, it may not produce a tight co-divergence peak in absolute time, and co-divergence may not imply a common cause of divergence. Deeper integration of geologic, climatic and genomic data (i.e. geogenomics) may help clarify origins of divergence in physically complex settings.

KEYWORDS
earth-life science, comparative phylogeography, community evolution, genomics, population genetics, speciation

1 | INTRODUCTION

Comparative phylogeography deals in the structuring of genetic variation and relatedness of individuals across geography, with particular focus on the response of co-distributed species to landscape features such as topographic barriers or climatic differences (Avise, 2000; Avise et al., 1987, 2016; Edwards et al., 2022). However, many studies reveal organisms' responses are highly heterogeneous, particularly in the age or amount of divergence associated with landscape barriers. Examples of this include the Cochise Filter Barrier in North America (Provost et al., 2021), where nearly 70 taxa vary in divergence from the Miocene to the Pleistocene (i.e. 23–0.01 Mya), the climatic/ecological Dahomey Gap in Ghana where the divergence times of 20 amphibian and reptile species vary in magnitude by a 20-fold difference (Leaché et al., 2020), and genetic divergence on the Baja California peninsula in Mexico where divergence ages of over 80 species range from 15.3 to 0.6 Mya (Dolby et al., 2015; Leaché et al., 2007). A deep literature from population genetics shows several intrinsic biological factors affect the rate of coalescence among lineages (Charlesworth, 2009; Meirmans & Hedrick, 2011; Rosenberg & Nordborg, 2002), but these factors have not been fully integrated into predictions about how barrier conditions can produce heterogeneous divergence signals among different species. For example, the impacts of selection and recombination on species divergence have not been adequately tested in barrier settings.

Many factors influence the time to coalescence of populations. Effective population size (Ne) affects the rate of differentiation in the absence of gene flow (Charlesworth et al., 2003; Gaggiotti et al., 2009). Populations with higher mutation rates can reach mutation–drift equilibrium faster without gene flow (Ryman & Leimar, 2008), affecting rates of incomplete lineage sorting. Dispersal ability affects the amount of gene flow restricted by the barrier (barrier permeability; Lavinia et al., 2019; Smith et al., 2014), and connectivity between subpopulations can affect the rate to reach equilibrium for isolated populations (Landguth et al., 2010). Furthermore, divergent selection pressure can accelerate and strengthen divergence by increasing the frequency of differentially adapted alleles (Chen et al., 2010), with recombination subsequently breaking up linked alleles (Stapley et al., 2017). Other factors such as pre-existing population structure, habitat preference and mating system can also shape population divergence (Harvey et al., 2017; Wakeley, 2000; Whiteley et al., 2004). Coalescent time is useful because it can be used to compare divergence across species of different generation times while also controlling for effective size, but coalescence age must be placed on an absolute time-scale to assess geologic/climatic hypotheses about whether barrier events shaped divergence. This reconciliation of coalescent and absolute time depends on generation time (Amos & Harwood, 1998; Endler, 1982; Langergraber et al., 2012), which varies non-randomly across organismal groups (Martin & Palumbi, 1993).

Together, these intrinsic biological factors exert direct and interactive effects on the accumulation of population divergence following geological/barrier event(s) that may produce a heterogeneous 'co'-divergence signal. This poses a clear challenge within comparative phylogeography, as these factors vary across species and can obscure cause–effect relationships between landscape events and genetic divergence. Many analytical tools based on coalescent models and summary statistics have been developed to test shared signals of divergence or population histories (e.g. Huang et al., 2011; Oaks, 2019). However, population genetic processes and theory have yet to be fully integrated to understand the mechanisms producing heterogeneous responses to barrier isolation into deep time-scales, across species with varying life-history traits, and with the complexities of eukaryotic genomes (Dolby et al., 2022; Edwards et al., 2022). Speciation genomic studies have increasingly shown genomic linkage and selection play a pivotal role in genome-wide patterns of divergence (Ravinet et al., 2017; Samuk et al., 2017). We expand on prior work (Landguth et al., 2010) by testing how these factors affect expectations of genetic divergence and by comparing simulations to extensive data from empirical literature.

We define a physical barrier as any environmental, geologic or climatic feature that may limit gene flow in the absence of differential selection pressure (Caplat et al., 2016). Such barriers include topography, river networks, habitat discontinuities, landmass isolation due to marine incursions, climate heterogeneity and other climatic events (e.g. Dolby et al., 2019; Machado et al., 2018; Zuckerberg et al., 2020). In particular, we simulated ephemeral barrier settings, which are ideal to test divergence predictions because the limited duration should exploit differences in divergence rate across taxa. Many physical barriers on Earth's landscape are ephemeral (they only occur for a limited period of time). Examples of ephemeral barriers (Table S1) include temporary flooding of land through sea level changes (Dolby et al., 2020), fragmentation and then rejoining of habitat due to climatic changes (e.g. glacial cycles, Hewitt, 2004) and dynamic tectonic processes such as vertical changes in the landscape, as in the case of the emergence of the Panamanian Isthmus (Bacon et al., 2015). Gene flow is expected to resume once a barrier disappears *if* reproductive isolation has not completed, in which case the signal of genetic divergence is expected to fade.

Here, we use two forward simulation approaches to assess the impact of selection, recombination, mutation rate, dispersal and generation time on the divergence signal produced in ephemeral barrier settings and compare these results to empirical literature. We specifically asked:

1. How long does it take for a barrier to generate a divergence signal comparable to population or species-level divergence observed in empirical literature?
2. How do different biological features such as mutation rate, dispersal ability and generation time affect the rate of divergence accumulated in the presence of a barrier?
3. Assuming reproductive isolation is not reached, does the divergence signal attenuate when the barrier is removed, and how do biological factors affect this rate?

4. How do divergent selection pressure and recombination affect the rate of divergence accumulation and attenuation during the presence and removal of a barrier?

By comparing simulated and empirical data, we show that divergence rates are highly heterogeneous and different phylogeographic histories can result in the same pattern of divergence. Resolving these histories in some settings—such as the Baja California peninsula—may require strategic integration of geologic, climatic and genomic data, as provided by a geogenomic approach (Baker et al., 2014; Dolby et al., 2022).

2 | MATERIALS AND METHODS

We used two forward simulation genetic approaches to assess how long it takes for a physical barrier to generate a signal of genetic differentiation. Simulations allow the testing of hypotheses and assumptions about the settings under which earth processes affect evolutionary patterns (Epperson et al., 2010). We simulated SNP data consistent with whole genome sequence (WGS) data and reduced representation methods (e.g. Restriction Site-Associated DNA sequencing, RADseq), which are most commonly used to study population structure and divergence (Andrews et al., 2016).

2.1 | Simulating barrier isolation

We modelled the spatial design of our simulations using a popular case study from the Baja California peninsula (Lindell et al., 2006) to simulate the effects of a barrier on genetic structure. Patterns of north–south genetic divergence have been observed on the peninsula in over 80 species (Dolby et al., 2015). Many authors attribute this pattern to an ephemeral seaway barrier crossing the middle of the peninsula (Figure 1a, Lindell et al., 2006; Riddle et al., 2000). But, alternative hypotheses include the stochastic or emergent effects of isolation by distance (Frantz et al., 2009; Meirmans, 2012; Perez et al., 2018), population isolation during Pleistocene glacial–interglacial cycles (Harrington et al., 2018; Valdivia-Carrillo et al., 2017), or adaptation to the different rainfall patterns (Dolby et al., 2015; Klimova et al., 2018). We modelled this barrier as 'complete' (impermeable to dispersal) and simulated the barrier with isolation by distance (IBD), as well as a null scenario with only IBD (no barrier).

We used CDMetaPop v1.0 (Landguth et al., 2017) to simulate 20 spatially explicit populations evenly distributed throughout the peninsula (~60 km average distance between populations, Figure 1a) and generated genetic data for 100 biallelic, unlinked SNPs. We used three different substitution rates representative of SNP loci for multicellular organisms (10^{-7}, 10^{-8} and 10^{-9} subs × site^{-1} × generation^{-1}; Lynch et al., 2016). Simulations included 'species' with low dispersal (LD) and species with high dispersal (HD), which was modelled as the probability of moving a determined distance per individual per generation using a negative exponential movement function (see Table 1 for details). Under this function, the probability of moving 10 km is 0.81 and 0.94 for LD and HD, respectively, while movement for 60 km (distance between populations) is 0.29 and 0.69 for LD and HD, respectively. Following Wright's island population structure model (Wright, 1951), population size was held constant at 500 individuals per population (5000 total individuals in the northern and southern groups each). Other variables in CDMetaPop such as type of mating, age or sex structure, phenotypic plasticity were not varied. Ten replicates per scenario were run for 10,000 generations each and genetic data were sampled every 500 generations; outfiles were converted for downstream analysis with a custom script in R 4.0.2 (R Core Team, 2020). Scripts are available in Supplementary Information.

2.2 | Simulating barrier isolation with adaptation

CDMetaPop allows easy parameterization of spatially explicit simulations but does not model genomic linkage between adaptive and neutral loci and therefore has limitations when modelling the emergent effects of differential selection on populations. Therefore, to explore the interactive effects caused by a barrier in addition to natural selection, we used SLiM v3.3.2 (Haller & Messer, 2019) following the methodology described by Moore et al. (2021). We simulated 60,000 bp of sequence per individual under a mutation rate of 10^{-8} for two groups (north and south) with 5000 individuals each, which is equivalent to CDMetaPop but without spatially substructured populations. For simulations with selection, the genome was divided into 10 coding and 10 non-coding regions that were each 3000 bp long; divergent selection was modelled by amino acid, where in population 1, the codons for proline, leucine and serine were positively selected and codons for glycine, alanine and arginine were selected against. In population 2, these selection conditions were inversed. In each scenario, the fitness cost was proportional to the number of unfit amino acids within an individual, with a fitness reduction of 0.5 per amino acid change; fitness was calculated per generation and scripts are available in Supplementary Information. Simulations were run with and without a recombination rate of 10^{-8} bp^{-1} × generation^{-1}. We performed 5000 initial generations of a panmictic population for standing variation to accumulate followed by 10,000 generations of isolation. For this, we simulated a complete barrier 'No Dispersal' (ND) (probability of migration = 0), a 'Low Dispersal' (LD) scenario (probability of migration = 3.9×10^{-5}) and a 'High Dispersal' (HD) scenario (probability of migration = 0.046). To make the two simulation approaches comparable, north–south gene flow for the SLiM simulations was calculated as the average migration rate between northern and southern populations based on the high/low dispersal scenarios of the CDMetaPop simulations. Migration rates between north and south groups were obtained from the cost–distance matrix and the movement function used

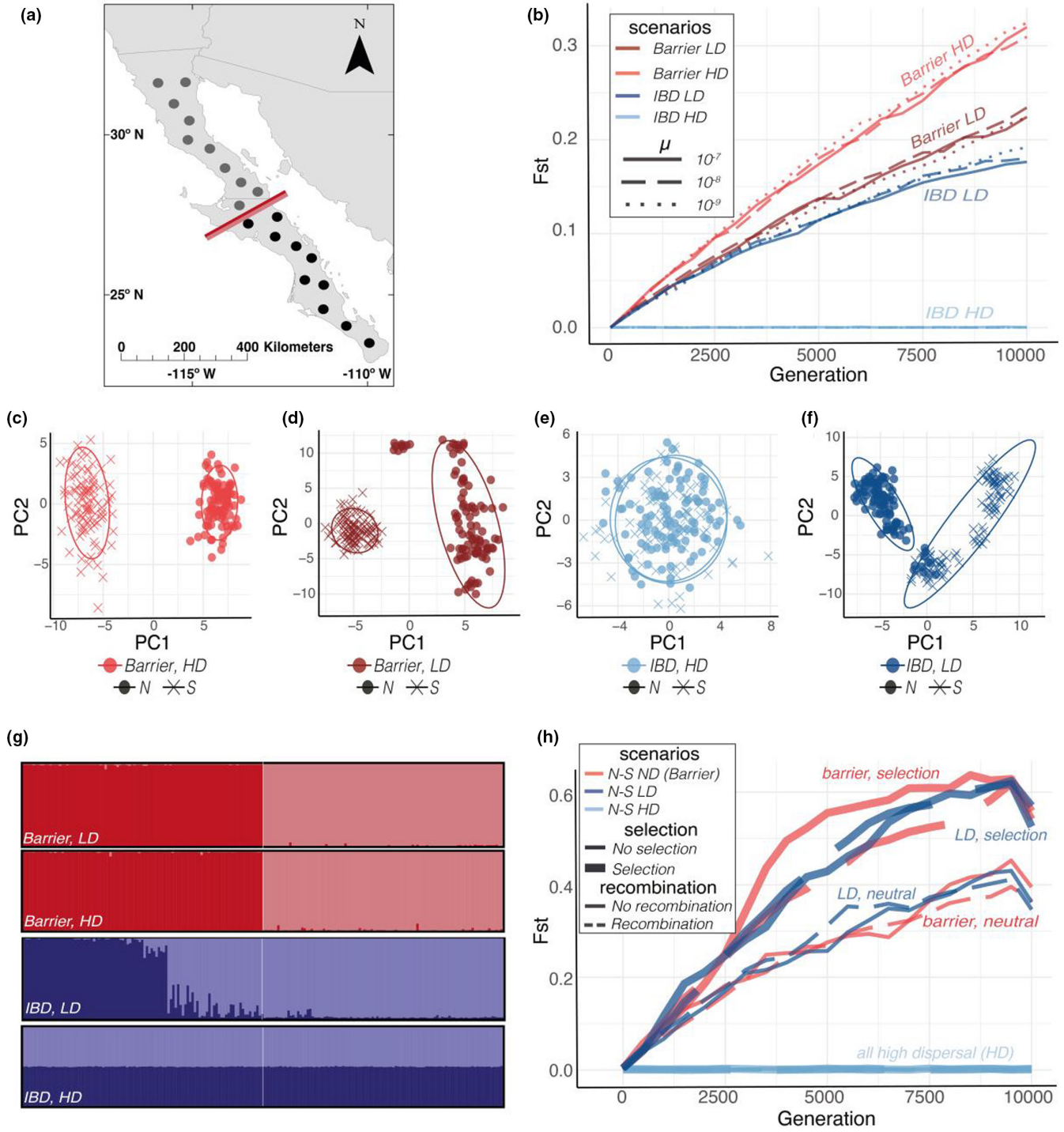

FIGURE 1 Genetic divergence from a barrier. (a) The populations (circles) for which genetic data were simulated along the Baja California peninsula in CDMetaPop (red lines denote location of the simulated barrier); divergence statistics were calculated by group (north, grey and south, black). (b) Average of 10 replicates for north–south genetic divergence measured as F_{ST} for barrier + IBD (red) versus isolation by distance alone (IBD, blue) under high dispersal (HD) and low dispersal (LD) and varying mutation rate (μ). (c–f) PCAs of genetic variation for one representative replicate (generations = 7500, $\mu = 10^{-8}$) in the presence (c, d) or absence (e, f) of a barrier. See Figure S2 for a PCA of all replicates. (g) Results for $K = 2$ from Structure analysis ($g = 7500$, $\mu = 10^{-8}$) aggregated over three replicates. (h) F_{ST} averaged over 10 replicates for north–south (N-S) groups in SLiM simulations. No dispersal (ND), low dispersal (LD) and high dispersal (HD) are shown; differential selection (thick lines) increases divergence in the presence of a barrier (red) and does not affect divergence under high dispersal (light blue). LD and barrier produce equivalent patterns.

TABLE 1 A summary of the simulation parameters used in CDMetaPop and SLiM. Distance is in kilometres and group refers to north or south, which in CDMetaPop each contained 10 spatially explicit populations

Software	CDMetaPOP		SLiM	
Simulation	**Barrier divergence**	**Barrier removal**	**Barrier divergence**	**Barrier removal**
Genetic data	100 unlinked SNPs	100 unlinked SNPs	60,000 bp of sequence	60,000 bp of sequence
Barrier scenarios	Barrier & IBD, No barrier IBD alone	No barrier IBD alone	Barrier; No barrier	No barrier
Number of populations	20	20	2	2
Population size	10,000 (500 per population)	10,000 (500 per population)	10,000 (5000 per group)	10,000 (5000 per group)
Probability of dispersal	$1\times10^{(-b\times\text{distance})}$	$1\times10^{(-b\times\text{distance})}$	HD: 0.046; LD: 3.9×10^{-5}	HD: 0.046; LD: 3.9×10^{-5}
Dispersal function parameters	HD: $b = 2.7\times10^{-3}$ LD: $b = 9\times10^{-3}$	HD: $b = 2.7\times10^{-3}$ LD: $b = 9\times10^{-3}$	—	—
Mutation rate	10^{-7}, 10^{-8}, 10^{-9}	10^{-7}, 10^{-8}, 10^{-9}	10^{-8}	10^{-8}
Selection	—	—	Neutral, divergent selection	Neutral, divergent selection
Recombination	—	—	10^{-8}; linkage	10^{-8}; linkage
No. replicates	10 each	10 each	10 each	10 each
Sample size used for statistics	200 (10 per population)	200 (10 per population)	200 (100 per group)	200 (100 per group)

in CDMetaPop. The resultant variant call files were used for downstream statistics based on a random sample of 100 individuals per group.

2.3 | Simulating barrier removal

To evaluate if and for how long the divergence is retained once a barrier is removed, we simulated 10,000 additional generations beginning with diverged populations (F_{ST} ~ 0.3) but now allowing gene flow. In CDMetaPop, we varied dispersal and mutation rate, and in SLiM, we varied the presence/absence of divergent selection pressure, recombination and dispersal rate to see how the interaction of these parameters affected attenuation (or not) of the divergence signal. Otherwise, parameterizations were the same as previous simulations (Table 1). Importantly, these simulations assume that reproductive isolation was not achieved during barrier isolation.

2.4 | Divergence analyses

We evaluated divergence between northern and southern groups for all simulations listed above. Nei's F_{ST} (Nei, 1973) was calculated in R using hierfstat v0.5-7 (Goudet, 2005) using a random sample of 200 individuals (10 per population grouped into north and south for CDMetaPop, 100 per group for SLiM). The F_{ST} index has some limitations such as its sensitivity to within-population variation (Meirmans & Hedrick, 2011) or bias due to population substructure (Ochoa & Storey, 2021). Despite these considerations, we chose F_{ST} because it is most reported in the literature to describe genetic differentiation (compared to alternative measures of absolute genetic distance such as Dxy or Da) and therefore allowed us to compare our simulations to empirical data. Furthermore, it adequately represents population structure when the mutation rates are low (Whitlock, 2011), and it is less sensitive to sample size when a large number of loci are analysed (Willing et al., 2012). We statistically compared F_{ST} values among scenarios, dispersal abilities, mutation rates, recombination and selection over number of generations by using a mixed linear model with glme v0.1.0 (Weerahandi & Yu, 2020) in R considering the replicate as a random variable and fitting the best distribution with the maximized restricted log-likelihood method. For the CDMetaPop simulations, we evaluated population structure with Structure v2.3.4 using the same 200-individual dataset as used for F_{ST} calculations, specifically choosing the 7500-generation time step and the 10^{-8} mutation rate (Pritchard et al., 2000). We ran three iterations per dataset over 100,000 MCMC iterations with a burn-in of 10,000 using admixture ancestry model with correlated allele frequencies and $K = 2$ to visualize the genetic structure across scenarios. Replicates were aggregated using clumpp v1.2.2, with the 'greedy' algorithm (Jakobsson & Rosenberg, 2007). We further visualized the genetic divergence on the same datasets with a principal component analysis (PCA) using the adegenet v2.1.4 package (Jombart, 2008) in R for each simulation independently. Since results were consistent, only one representative PCA was chosen for display.

2.5 | Effect of generation time on reconciling biological and geological time-scales

Population genetics and phylogeography often deal with relative or coalescent time (i.e. number of generations scaled by effective population size). Yet, understanding the effects of geological/climatic change on population divergence requires the translating between

relative time and geological time, and generation time is central to this conversion (Endler, 1982). To visualize this, we converted the F_{ST} results from the high dispersal/barrier simulations onto an absolute (i.e. geologic) time-scale assuming four generation times (0.02, 0.2, 2 and 20 years). Effective population size also affects this relationship (i.e. higher drift and faster coalescence in smaller populations); to account for its effect, we added the variability in time it would take to reach a given F_{ST} level considering a fivefold decrease and fivefold increase in Ne based on the relationships showed for Ne and G_{ST} in Leng and Zhang (2013). We used this relationship since Nei's F_{ST} is equivalent to G_{ST} under the infinite island model (Takahata & Nei, 1984).

2.6 | Empirical literature curation: Generation time and divergence level

To understand the variation in generation times expected in nature, we curated data from literature with the goal of surveying as wide a range of generation times as possible for multicellular eukaryotes. We recorded author-reported generation times in years, the genus and species and its broad taxonomic group (e.g. mammal, non-avian reptile, fish, bird, invertebrate, non-tree plants, trees). This resulted in 147 observations (Appendix S1). We compared generation time between taxonomic group with a generalized linear model (GLM) by using a log-link function for a Poisson distribution, and post hoc comparisons were done using the 'multcomp' library (Hothorn et al., 2008) in R. We tested for significant differences in variance among groups using a Bartlett test in R.

To compare divergence results from our simulations to values recorded in empirical literature, we curated data from studies published since 2015 that used whole genome data (RAD and WGS) to assess divergence across different taxonomic groups ($N = 78$; Appendix S2). We recorded the F_{ST} values, the author-reported relationship of groups (population-pairs or species-pairs), the sequencing method (RAD or WGS) and main driver of divergence reported by the authors (physical barrier, adaptation or *both* physical barrier and adaptation). We used GLMs in R with a Poisson distribution to compare between sequencing methods, level of divergence and driver of divergence for the F_{ST} values from this dataset.

3 | RESULTS

3.1 | Divergence produced by a physical barrier

Both simulation approaches showed that genetic divergence between northern and southern groups increased with the number of generations of isolation (Figure 1b,g) and there was low variation between replicates for each scenario (Figure S1). For CDMetaPop, no significant differences were detected between substitution rates, but a significant effect from dispersal was detected (Table S2). In the high dispersal scenarios, F_{ST} increased faster in populations isolated by a barrier (mean F_{ST}: 0.32; range: 0.26–0.38), but divergence was not produced by IBD only (Figure 1b). For the low dispersal scenarios, both barrier (mean F_{ST}: 0.23; range: 0.19–0.27) and IBD (mean F_{ST}: 0.18; range: 0.15–0.23) produced divergence (Figure 1b). PCA and STRUCTURE results showed a signal of divergence for a barrier in both high and low dispersal scenarios. The IBD signal for low dispersal showed a genetic gradation as expected (Figure 1c–f; Figure S2). For SLiM simulations, divergent selection amplified the divergence (mean F_{ST}: 0.55; range: 0.38–0.71 vs. mean F_{ST}: 0.36; range: 0.21–0.58) produced under barrier and low dispersal scenarios, but again no divergence was produced under high dispersal (Figure 1h; Table S3). The presence or absence of recombination significantly affected the rate of divergence (Table S3), but its influence was weaker than that of dispersal and selection. The barrier/no selection, low dispersal/no selection scenarios simulated in CDMetaPop and SLiM produced extremely similar results, suggesting the results from the two programs reflect consistent evolutionary processes and their results can be compared (Figure 1b vs. h).

3.2 | Decay of divergence upon barrier removal

Removal of the barrier and resumption of gene flow eroded population differentiation within ~500 generations under high dispersal, but the divergence signal was retained under low dispersal (Figure 2a; Table S4). Divergent selection increased divergence for the low dispersal scenarios upon barrier removal, whereas it did not affect the pattern nor rate at which the divergence signal decayed for high dispersal (Table S5; Figure 2b). A significant effect of recombination was also detected, mainly evident for low dispersal without selection (Figure 2b) where recombination decreased the rate of divergence, as expected.

3.3 | Generation times observed in literature

The 147 generation times recorded from the literature ranged from 0.02 to 100 years (Appendix S1). Trees presented significantly higher generation times compared with every other taxonomic group (Table 2; Table S6; Figure 4a). Non-tree plants showed significantly higher generation times than birds and invertebrates. Additionally, the variance in generation times significantly differed by taxonomic group (Table S7), with trees having the most variable generation times followed by reptiles and non-tree plants; invertebrates and birds showed shorter and less variable generation times (Table 2; Figure 4a).

3.4 | Divergence values observed in literature

Data curated from literature resulted in F_{ST} values for 78 pairs of population/species which ranged in F_{ST} values from 0 to 0.83 (Appendix S2). No significant difference in F_{ST} was detected between RAD and WGS

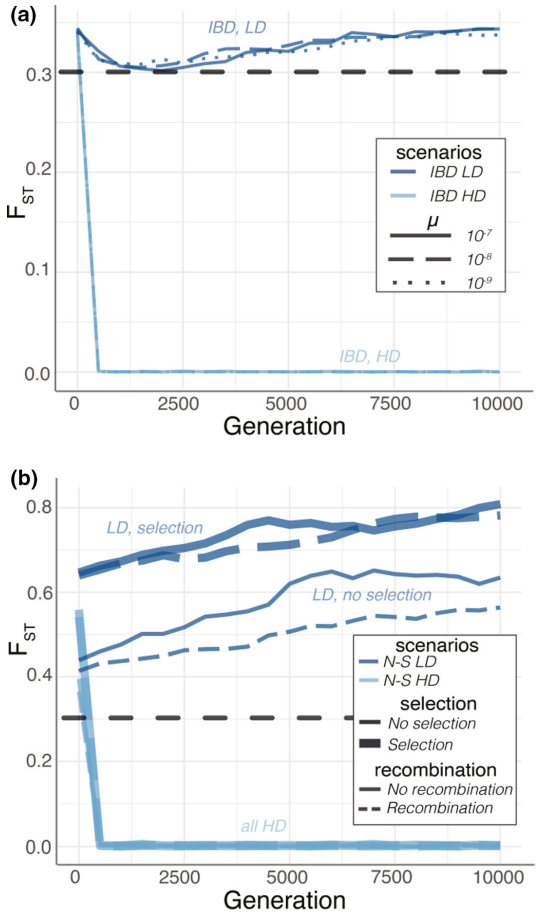

FIGURE 2 Genetic homogenization following barrier removal. (a) Results from CDMetaPop on genetic differentiation (F_{ST}) when a barrier is removed, assuming no reproductive isolation. Low-dispersal (LD, dark blue) individuals retain the divergence accumulated from IBD/barrier and do not homogenize, but the divergence signal quickly decays (within ~500 generations) for high dispersal (light blue). The dashed line represents the $F_{ST} = 0.3$ threshold for species-level divergence (from Figure 3). (b) Results from SLiM; low dispersal (LD) also retains divergence after barrier removal. Divergent selection between north and south groups (thick lines) does not affect the rate of signal decay when gene flow is resumed after barrier removal. Selection was modelled where the number of unfit amino acids proportionally decreased individuals' fitness and different amino acids were deleterious in the north versus the south (see Section 2).

(Table S8; Figure S3), so these studies were combined. Higher F_{ST} values were detected for the species-level divergence (mean = 0.32; Figure 3a; Table S9). A difference was not observed among driver of divergence (physical isolation vs. adaptation) when considered alone, but the combination of physical isolation and differential adaptation produced higher divergence. This result was not significant, perhaps due to low statistical power (Figure 3b; Table S10). Within this empirical F_{ST} dataset, for studies with divergence caused only by a physical barrier ($N = 9$), we calculated the number of generations that lapsed since divergence began based on barrier age and generation times reported in each study to compare to simulation results. While we did not detect a significant relationship between F_{ST} and number of generations

TABLE 2 Mean and standard deviation values of generation times per taxonomic group reported in empirical literature ($N = 147$)

Taxon	Mean generation time (years ± standard deviation)
Invertebrate	3.39 (±3.20)
Fish	8.15 (±5.27)
Reptiles	11.23 (±12.24)
Birds	5.13 (±3.31)
Mammals	12.17 (±10.28)
Non-tree plants	15.76 (±10.28)
Trees	50.08 (±37.28)

(Table S11), the inferred F_{ST} values from empirical literature at 10,000 generations were similar to the divergence reached in the simulations (Figure 3c), suggesting our simulated system is consistent with divergence values observed in nature.

3.5 | Generation time and the biological response to physical barriers

Converting the F_{ST} results from the high dispersal barrier simulations with CDMetaPop onto an absolute time-scale (average rate of F_{ST} change through generations of 3×10^{-5}/generation) illustrated how generation time is central to the divergence accrued on a geological time-scale (Figure S4). Despite potentially similar coalescence ages, species with longer generation times require longer *absolute* periods of isolation to reach equivalent differentiation to species with shorter generations. This extrapolation illustrates that species with a generation time of 20 years or higher (e.g. some trees, reptiles and mammals) would require over 100,000 years to reach species-level divergence based on the Ne of the simulations. In contrast, the same F_{ST} values can be reached in less than 1000 years for a species with a generation time of 0.2 years (e.g. many invertebrates and some fishes).

4 | DISCUSSION

Comparative phylogeography often expects that species will co-diverge when faced with a barrier to gene flow (Arbogast & Kenagy, 2001), and testing that hypothesis requires the reconciliation of evolutionary and geological time-scales. Using extensive simulations, we assessed intrinsic factors affecting the rate at which organisms accumulate and lose genetic divergence in response to an ephemeral barrier. Simulations used the Baja California peninsula, Mexico, as a case study because it hosts a noisy divergence signal hypothesized to be from an ephemeral seaway (Dolby et al., 2015; Leaché et al., 2007).

In this study, simulations show that dispersal ability and divergent selection mainly control the rate and magnitude of genetic divergence accumulated (Figure 1b,h). Surprisingly, there is almost no difference observed between populations isolated by

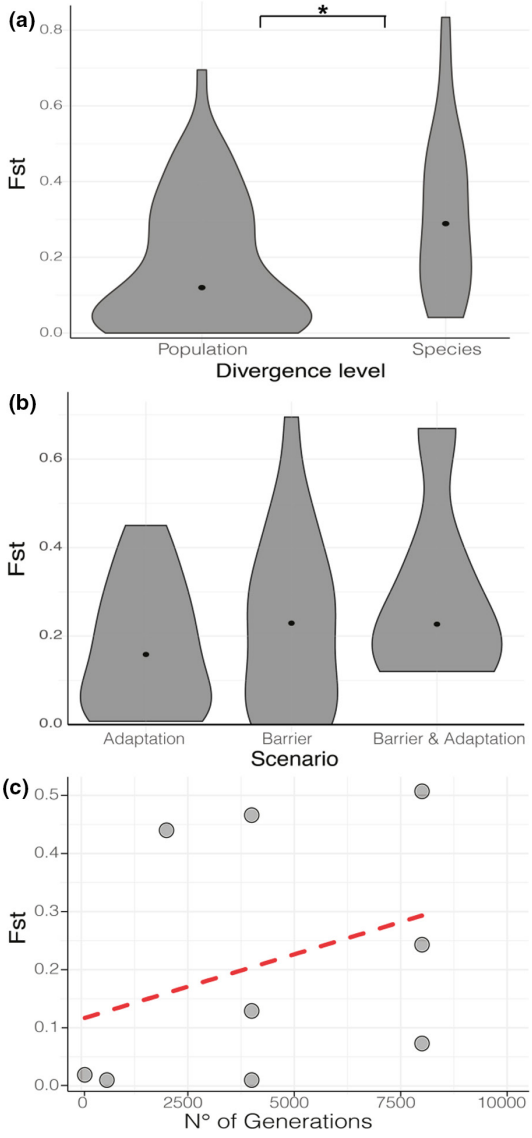

FIGURE 3 Empirical F_{ST} values. (a) Distribution of F_{ST} values observed in empirical literature ($N = 78$) for the population and species level of divergence (means are 0.178 and 0.318 respectively). (b) Distribution of F_{ST} values from literature ($N = 44$) where cause of divergence was specified (adaptation only, barrier only, combination of barrier *and* adaptation). (c) Relationship between F_{ST} and number of generations since divergence for studies from literature for species whose divergence is thought to be associated with a barrier of a known age ($p > 0.05$, $R^2 = 0.11$, Table S11; Appendix S2).

a physical barrier and those with low dispersal under isolation by distance without a barrier, particularly under divergent selection. This highlights that distinguishing the effects of a physical barrier on genomic divergence over geologic time would be easier in species with high dispersal. Starting with genetically diverged groups and assuming those groups were not reproductively isolated, divergence quickly erodes under high dispersal once a barrier is removed, but the signal is retained under low dispersal (Figure 2). Reconciling these results to geologic time depends on generation time (Figure 4; Figure S4), which we show from empirical literature varies by orders of magnitude and assorts non-randomly across organismal groups (Table 2). We therefore suggest to expect a large variation in observed divergence rates across a community subjected to a common physical barrier solely due to life-history traits. Results underscore why determining the cause of divergence based on divergence age may not always be accurate.

4.1 | Neutral controls on divergence

Genetic divergence increased through time when populations were isolated, as expected (Charlesworth et al., 2003; Wright, 1951). However, scenarios under low dispersal (modelled as two north–south groups or many populations with isolation by distance) produced similar levels of divergence to what was observed for a barrier scenario (Figure 1b,h). Previous literature shows that such emergent population structure can result under strong IBD (Frantz et al., 2009; Meirmans, 2012; Perez et al., 2018), especially under conditions of low dispersal and low effective population size (Irwin, 2002; Meirmans, 2012; Zink, 2002). In the presence of a barrier, F_{ST} increased faster and to higher values under high dispersal. Perhaps counterintuitive, this pattern is supported by population genetic literature that shows greater connectivity between subpopulations allows populations to sort alleles and reach equilibrium faster (Landguth et al., 2010; Whitlock, 2011). Conversely, under conditions of very low dispersal (VLD, probability of dispersing 10 km = 0.02), a strong deme-like population structure emerged and presence/absence of a barrier became inconsequential. Population structure was instead determined by founder events and high genetic drift occurring locally in the small, discreet populations (see SI for VLD results; Figure S5).

Substitution rates did not affect F_{ST} values (Table S2). However, higher mutation rates can increase the rate at which isolated populations reach equilibrium (Ryman & Leimar, 2008), so we may not have simulated enough generations to reach mutation–drift equilibrium, and thus underreport the effect of mutation rate. Or, the effect of mutation rate may have just been small relative to the different migration rates modelled (Ryman & Leimar, 2008; Takahata & Nei, 1984; Whitlock, 2011). We did not simulate differences in effective population size, but populations with smaller Ne experience stronger genetic drift and therefore should differentiate faster following the differential fixation/loss of alleles (Charlesworth et al., 2003; Leng & Zhang, 2013; Lowe & Allendorf, 2010). In the case of barriers (or glacial refugia), subdividing populations should accelerate the divergence rate due to reduced effective sizes in daughter populations. In the case of Pleistocene glaciations, this implies a fluctuating Ne as populations fragment and then re-merge in response to climate oscillations.

4.2 | Differential selection and divergence

The divergence observed under barrier and low dispersal conditions increased significantly when divergent selection was added

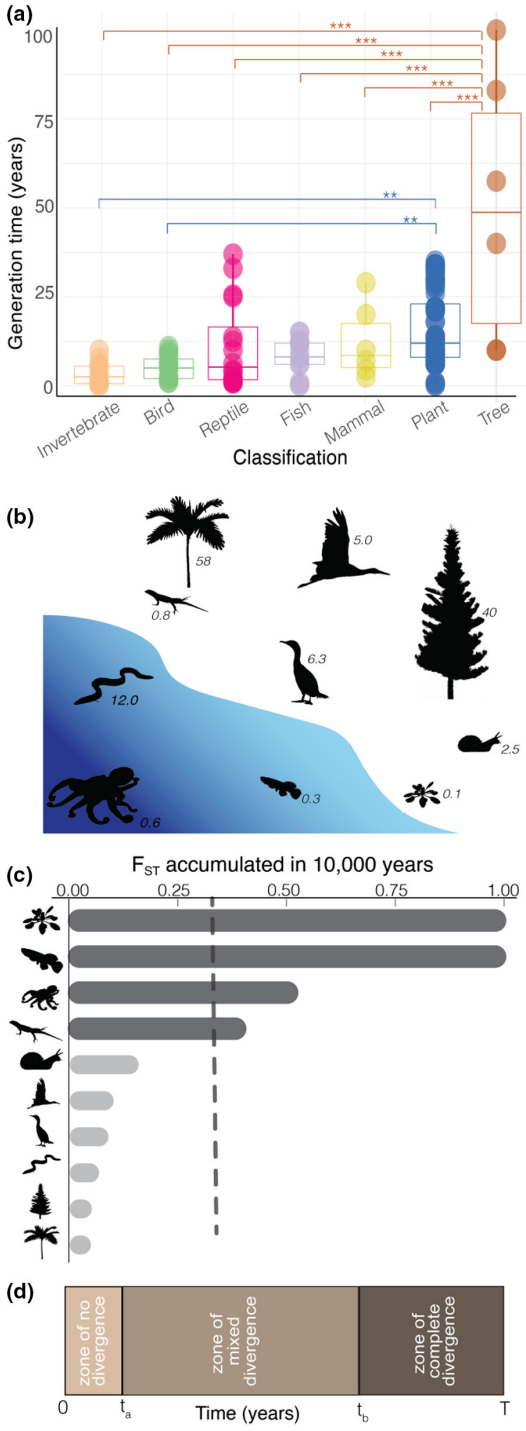

FIGURE 4 Generation time in communities. (a) Distribution of generation times based on literature ($N = 147$ studies; Appendix S1). (b) Cartoon of an ecological community composed of species with different generation times in years (italicized numbers). (c) Organisms in a community will accumulate F_{ST} at different rates. Assuming a barrier lasts 10,000 years, species with short generation time will reach higher divergence. Calculations assume the generation times listed for organisms in the cartoon above and rate of F_{ST} accumulation in panel b. (d) Concept diagram based on data from panels a–b and assuming identical Ne across all illustrated taxa, showing a window of absolute time under which isolation is expected to produce no species-level divergence for any member of a community ($t \leq t_a$) and a window where all populations will reach species-level divergence ($t \geq t_b$). In between is a zone of mixed divergence that depends on generation time.

(Figure 1h; Table S3). This is expected due to the high fitness costs of unfit amino acid changes in isolated populations (Yeaman & Otto, 2011) and is the basis for reinforcement and ecological speciation (Coyne & Orr, 2004). Our summary of empirical literature supports this result as reduced gene flow due to a barrier combined with divergent selection shows higher divergence than either one alone (Figure 3b), though this result was not statistically significant.

Divergent selection was not sufficient to produce divergence under high dispersal as gene flow swamped out differentially selected variants (Figure 1h; Yeaman & Otto, 2011). Effect of recombination (and therefore linkage) was statistically significant (Table S3) with recombination leading to lower divergence, although the divergence curves do not look appreciably different (Figure 1h). This result follows prevailing knowledge that linkage of differentially adapted sites increases population divergence (Chen et al., 2010). By simulating 60 kbp genomes, our results probably undervalue the effect of recombination relative to larger (Gbp) genomes.

4.3 | What happens when a barrier is removed?

Following barrier removal, under low dispersal, the effects of the barrier were retained (Figure 2; Irwin, 2002). In contrast, the resumption of gene flow under high dispersal conditions eroded population differentiation within ~500 generations. This supports population genetics theory which predicts that only one reproductively successful migrant per generation is sufficient to homogenize populations (Landguth et al., 2010; Lowe et al., 2017; Lowe & Allendorf, 2010). Therefore, for high-dispersing species, if reproductive isolation is not reached *quickly* during physical isolation, the divergence signal erodes quickly upon barrier removal while low-dispersing species retain the signal, yielding mixed species responses. When the barrier was removed but divergent selection was ongoing, divergence continued to accrue under low dispersal (Figure 2b). In settings where the presence of an historical ephemeral barrier is unknown, this could result in overestimating the role selection/adaptation played in producing or maintaining that divergence. Overall, the combined effects of ephemeral barrier, divergent selection, varying generation time and effective population sizes are expected to result in different amounts of divergence, which may translate into different age of divergence estimates.

4.4 | When does 'species-level' divergence occur?

The rapid erosion of divergence under high gene flow illustrates the importance of developing prezygotic isolation mechanisms during physical isolation. In nature, many 'good' species show signs of continued reproductive ability or ongoing gene flow. Examples include admixture among *Heliconius* butterflies in the Neotropics (Nadeau

et al., 2013) or hybrids between three species of *Gopherus* desert tortoises in North America, which are thought to be ~5 million years diverged (Edwards et al., 2016).

Empirical literature showed a mean F_{ST} of 0.32 for species-level divergence (Figure 3a), consistent with Roux et al. (2016) who reported species-level divergence of 0.02 for absolute divergence (Da), which correlates to F_{ST} values of 0.2–0.3 in their study (based on Figure S3 in Roux et al., 2016). While genetic differentiation does not have a linear correlation to the speciation process (Carstens et al., 2013; Hogner et al., 2012), we used this value (F_{ST} = 0.3) as a proxy to represent species-level divergence. With this assumption, simulations showed species-level divergence can occur within 10,000 generations of barrier isolation, especially under divergent selection (Figures 1h and 3b).

Differential adaptation contributes to reinforcement through Dobzhansky–Muller incompatibility, in which differentially adapted suites of alleles are incompatible in hybrids (Unckless & Orr, 2009). Low recombination can facilitate reinforcement by maintaining linked loci that contain suites of locally adapted alleles that are less fit in hybrids (Samuk et al., 2017). Supporting this, our results showed a significant effect of recombination rate on divergence, with non-recombining loci showing higher divergence (Figure 1h; Table S3). Changes in karyotype and genome reorganizations through large-scale translocations or inversions were not modelled but can also contribute to reinforcement (Faria & Navarro, 2010). Therefore, considering the whole landscape of the genome, beyond SNPs, may be important to determining whether reproductive isolation can be achieved during barrier isolation.

4.5 | Implications for divergence on the Baja peninsula, Mexico

The results from this study have several implications for how to interpret the noisy pattern of genetic 'co'-divergence on the Baja California peninsula (Dolby et al., 2015; Lindell et al., 2006; Riddle et al., 2000). First, results showed isolation by distance can produce the same divergence signal expected by a physical barrier in species with restricted dispersal, revealing there is no need for vicariant barriers to explain divergence on the peninsula. It may be that peninsulas and linear coastlines are particularly conducive for this phenomenon. Second, divergence is amplified under differential selection for low-dispersing species; along the arid Baja peninsula, there is a strong gradient in the annual amount and seasonality of precipitation (Avila-Lovera & Garcillán, 2021; Cab-Sulub & Álvarez-Castañeda, 2021), both controlled by the North American monsoon (Adams & Comrie, 1997; Higgins et al., 1999), which suggests differential adaptation may also be an important factor for interpreting this signal (Klimova et al., 2018). Importantly, species do not have the same physiology and niche constraints and therefore are not expected to be equally impacted by this gradient. Therefore, differing sensitivities to the selection regime could account for some variation in the magnitude of divergence, and under coalescence, the associated ages of divergence. Third, the divergence observed on the peninsula has been primarily shown with mtDNA data and several studies have shown cytonuclear discordance with this pattern (Bernardo et al., 2019; Lindell et al., 2005; Lindell et al., 2008). Our simulations with and without recombination illustrate how discordance can arise through linkage if there is selection on the mitochondrion and not on nuclear genes (Table S3). Finally, our simulations illustrate that generation time (Figure 4) and dispersal ability (Figure 1) drastically affect whether a species will show genetic divergence due to IBD or an ephemeral barrier. These factors together demonstrate that a pattern of genetic divergence, even when observed across dozens of species, does not necessitate a historical barrier *or* that the divergence has a common cause. It also tells us that even if arising from a common cause, the magnitude of divergence expected across members of a community is expected to vary widely. Therefore, understanding the drivers of divergence in some complex settings requires a new approach—the concerted study of both the geologic and climatic history paired with in-depth genomic analysis across organisms displaying variation in life-history traits. This geogenomic approach (Baker et al., 2014; Dolby et al., 2022) can define and characterize geological/climatic hypotheses—such as quantifying a monsoon gradient or characterizing historical barriers—and these hypotheses can be paired with predicted genomic effects, such as signatures of differential adaptation or whether age of divergence fits within the timeframe for a proposed barrier (as opposed to inferring barrier age from coalescence age and generation time).

4.6 | Community-level response to ephemeral barriers

While difficult to measure (Langergraber et al., 2012), generation times from literature ranged from 0.02 years to 100 years (Figure 4a), and their means and variances differed significantly among groups (Table 2). Considering additional variation in effective population sizes, the expected level of divergence resulting from a physical barrier is expected to vary by orders of magnitude across organisms subjected to the same barrier (Amos & Harwood, 1998; Endler, 1982). This means that generation time is central to how organisms in a community evolve at different rates under the same geological/climatic conditions (e.g. Leaché et al., 2020; Provost et al., 2021). Dispersal is another axis along which members of a community vary by orders of magnitude, from dozens of meters (*Chaetodipus* spp., *Dipodomys* spp., *Mus* spp., *Myodes glareolus* and many lizards; Munguia-Vega et al., 2013; Santini et al., 2013; Vercken et al., 2012) to tens of kilometres (e.g. *Populus* spp., *Acer rubrum*, *Corylus avellana*; Tamme et al., 2014); dispersal also tends to assort non-randomly by organismal group.

The fact that communities are constructed by organisms with greatly differing generation times and dispersal abilities implies that members of this community will respond at different rates and to different magnitudes to the same landscape features, made particularly acute in ephemeral barrier settings. While dispersal and extirpation

will alter the composition of the community over these time-scales, if we consider an ephemeral barrier lasting for 10,000 years, affected organisms with short generation times are expected to accumulate high (perhaps species-level) divergence, while organisms with longer generation times may reach only low divergence, assuming equivalent Ne (Figure 4b).

Importance of the speciation process to community ecology has been established (Vellend, 2010), as it is the sole process generating species de novo within a community. With the concept of a 'species pool', in which newly formed species are more likely to be ecologically similar to sister species (Taylor et al., 1990; Vellend, 2010), then it follows that species may perform ecological functions similar to their recently diverged congeners. If they also share similar generation times (the null expectation), then this provides a bridge to how generation time is likely to impact speciation rates within a community, and how uneven speciation rates in turn can feed back to affect community structure and function. This follows a longer time-scale view of species as individualistic (Gleason, 1926), and generation time as one more axis upon which members of a community vary. If we consider an axis of *absolute* time, it can be partitioned to highlight the segment where members of a community are expected to respond variably to the presence of a barrier based on generation time: the zone of mixed divergence (Figure 4c). This zone is where, based on generation time, some organisms can reach species-level divergence and others will not, assuming all else is equal. This mixed zone highlights potentially interesting and complex temporal dynamics where the time-scales of speciation, dispersal and extirpation overlap within a community. We can similarly identify durations of barriers which are likely too short to elicit any divergence ($t < t_a$), as well as those which are likely to impact divergence community-wide ($t > t_b$).

5 | CONCLUSION

Comparative phylogeography requires the reconciliation of geological and evolutionary time-scales and often expects species to co-diverge when faced with a barrier. Through simulations, we show that multiple phylogeographic histories can lead to the same divergence pattern and that species' responses to the same barrier will vary greatly based on dispersal ability and generation time. Addition of selection and absence of recombination will enhance divergence. To decipher the cause(s) of divergence in some settings requires more deeply integrated information between the geologic/climatic landscape and the genomic landscape (a geogenomic approach; Baker et al., 2014; Dolby et al., 2022). Combining simulations with empirical literature shows that organisms in a community will respond to the same physical barrier at different rates and magnitudes, as has likely occurred on the Baja California peninsula. This could perhaps manifest changes in community composition and function that are particularly relevant in settings with ephemeral barriers, where mixed divergence responses are expected.

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CONFLICT OF INTEREST

The authors have no conflicts to declare.

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DATA AVAILABILITY STATEMENT

Simulated datasets and scripts are bundled and available in an ASU Dataverse: https://doi.org/10.48349/ASU/IKNUHC. Empirical data curated for this paper are available in Appendices S1 and S2.

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BIOSKETCH

We are a group of evolutionary biologists interested in better understanding the role geologic and climatic processes play in the adaptation, evolution and diversification of life broadly. We work in the emerging area of geogenomics and have a long-standing interest in the evolution of warm deserts.

Author contributions: RA-D carried out all simulations; RA-D and SMB performed analyses; PA-A, MJS, BTW curated empirical data; RA-D, AM-V, GAD conceived of and wrote the study; AM-V and GAD supervised and provided resources. All authors revised the manuscript.

SUPPORTING INFORMATION

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