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Phylogeography of the Northern Alligator Lizard (Squamata, Anguinae): Hidden diversity in a western endemic

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Abstract

Western North America includes the California Floristic Province and the Pacific Northwest, biologically diverse regions highlighted by a complex topography, geology, climate and history. A number of animals span these regions and show distinctive patterns of dispersal, vicariance and lineage diversification. Examining phylogeographic patterns in the fauna of this area aids in our understanding of the forces that have contributed to the generation and maintenance of regional biodiversity. Here, we investigate the biogeography and population structure of the Northern Alligator Lizard (*Elgaria coerulea*), a wide-ranging anguid endemic to western North America. We sequenced two mtDNA fragments (ND2 and ND4) for 181 individuals across the range of the species and analysed these data with phylogenetic approaches to infer population and biogeographic history, and date major divergences within the taxon. We further used Bayesian clustering methods to assess major patterns of population structure and performed ecological niche modelling (ENM) to aid in our interpretation of geographic structure and diversification of *E. coerulea* lineages. Our phylogeographic examination of *E. coerulea* uncovered surprising diversity and structure, recovering 10 major lineages, each with substantial geographic substructure. While some divergences within the species are relatively old (Pliocene, 5.3–2.6 mya), most intraspecific variation appears to be of more recent origin (Pleistocene, 2.6 mya–11,700 ya). Current diversity appears to have arisen in the Sierra Nevada Mountains and spread west and north since the Pliocene. Finally, our ENMs suggest that much of the Coast Ranges in California provided ideal habitat during the Last Glacial Maxima (LGM) that has since contracted dramatically and shifted northwards, whereas significant portions of the Sierra Nevada were unsuitable during the LGM and have since become more suitable. Interestingly, *E. coerulea* shares a number of genetic boundaries with other sympatric taxa, suggesting common historical events and geomorphological features have shaped the biota of this region.

KEYWORDS

alligator lizard, biogeography, California, *Elgaria*, phylogeography, Pleistocene

1 | INTRODUCTION

A central goal of evolution is to understand how biodiversity is generated and maintained. At a landscape level, examining patterns of population differentiation across space can shed

light on the roles of geography, climate and history in driving or constraining diversification (Avice, 2000). California, and the west coast of the United States (US) in general, is an ideal arena for exploring spatial patterns of diversification because the region's complex topography, geology, climate

and history (Schoenherr, 1992) have allowed the assembly and maintenance of a variety of ecological communities (Olson et al., 2001; Schoenherr, 1992) in this biodiversity hotspot (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000). In addition, phylogeographic relationships have been examined for a diverse array of California flora and fauna, providing a wealth of biogeographic information on this region, as well as testable hypotheses of how the major landscape features and historical events may have shaped current patterns of diversity in the region (Calsbeek, Thompson, & Richardson, 2003; Chazmanolis & Caterino, 2007; Feldman & Spicer, 2006; Rissler, Hijmans, Graham, Moritz, & Wake, 2006; Schierenbeck, 2014).

One particularly unusual feature of this region is the distribution of montane forest and woodland habitat encircling the Great Central Valley (GCV), a historic grassland and wetland. This upland ring is created by the Coastal Ranges along the Pacific, the Sierra Nevada Mountains in California's interior, the Transverse Ranges in Southern California, and the Klamath-Siskiyou and Lower Cascade Mountains in Northern California. Animals associated with woodland and forest communities are bound to these mountain chains and thus distributed in a ring, or semi-ring, around the GCV. This unique arrangement of topography and habitat has given rise to interesting patterns of vicariance, dispersal and secondary contact around the GCV, including the textbook example of a ring species, *Ensatina eschscholtzii* (Kuchta & Wake, 2016; Kuchta, Parks, Mueller, & Wake, 2009; Moritz, Schneider, & Wake, 1992; Stebbins, 2003). To date, at least four major biogeographic scenarios have been proposed for woodland and forest associated species in this region (Figure 1): a northern origin (e.g., *E. eschscholtzii*; Stebbins, 1949; Moritz et al., 1992; Kuchta et al., 2009), a southern origin (e.g., the Southern Alligator Lizard (*Elgaria multicarinata*); Feldman & Spicer, 2006), a coastal origin (e.g., the California Newt (*Taricha torosa*); Kuchta & Tan, 2006) and a Sierra Nevada origin (e.g., Dusky-footed Woodrat (*Neotoma fuscipes*); Matocq, 2002). A noteworthy feature of these scenarios is that secondary contact is expected where formerly isolated populations (or lineages) come into contact at points around the ring, such that populations might either merge or further diverge through the evolution of reinforcing mechanisms (Coyner, Murphy, & Matocq, 2015; Kuchta & Wake, 2016; Matocq, Kelly, Phillips, & Maldonado, 2012). Regardless, these major patterns appear repeatedly across taxa (reviewed in Schierenbeck, 2014) and are important in assessing the spatial and temporal processes that have influenced diversification, as well as in understanding how communities have been assembled.

We test these biogeographical hypotheses in the Northern Alligator Lizard (*Elgaria coerulea*), a western native that exhibits a semi-ring distribution in California and along the west coast of the United States and Canada. This taxon has

largely been overlooked, yet should make an ideal subject for understanding the factors driving regional diversification and biogeography because the species displays low vagility, possesses strong habitat affinities and has a sizable range (Nussbaum, Brodie, & Storm, 1983; St. John, 2002; Stebbins, 2003). Thus, patterns of genetic structure and continuity in this taxon should reflect the historic and contemporary forces that have caused population fragmentation and connectivity (Avice, 2000).

Elgaria coerulea is a wide-ranging anguid lizard that occupies much of the California Floristic Province and Pacific Northwest. Throughout its distribution, *E. coerulea* is associated with cooler and generally more mesic forest communities (Nussbaum et al., 1983; St. John, 2002; Stebbins, 2003), ranging along the Pacific Coast, from Monterey Bay northward to British Columbia, and in the interior from the Sierra Nevada north where it bypasses the drier Colombia Plateau and extends eastward into Western Montana (Figure 2). Although alligator lizards (*Elgaria*) are typically absent from hot and arid environments, the Northern Alligator Lizard appears more cold tolerant than other western species (Telemeco & Addis, 2014; Telemeco et al., 2017). The taxon is capable of dealing with cooler temperatures than other sympatric lizards, displaying less physiological stress and remaining active at lower temperatures than even other *Elgaria* species (Telemeco & Addis, 2014). These traits allow *E. coerulea* to occupy high elevation sites, including subalpine and even alpine environs (Nussbaum et al., 1983; St. John, 2002; Stebbins, 2003).

The biogeographic scenario proposed for *E. coerulea* involves a northward expansion out of the Sierra Nevada Range around the GCV into the Coastal Ranges, with the Coastal Ranges serving as a corridor for both southward movement to Monterey Bay and northward movement into the Pacific Northwest (Peabody & Savage, 1958). This scenario, while plausible, has never been tested and does not take into account complexities of either the geologic assembly of the Coastal Ranges or the effects of climate-induced glaciation and changing habitat distribution through time. Thus, it is unclear if the "Out of Sierra Nevada" model holds, or if biogeographic patterns in *E. coerulea* are more consistent with those seen in other codistributed taxa (e.g., *Ensatina* salamander (*E. eschscholtzii*); the Sharp-tailed Snake (*Contia tenuis*); woodrat (*Neotoma fuscipes*)). In addition, morphological work suggests that two to four distinct lineages exist within *E. coerulea*. The taxon is quite morphologically variable, ranging substantially in size, body proportions, coloration and dorsal pattern across its range, with four subspecies currently recognized (Fitch, 1938; Stebbins, 2003) (Figure 2). However, a second morphological study using meristic and morphometric traits (Good, 1985) suggested only two morphological groups, designated as pattern classes because these groups lacked obvious diagnosable features, and instead

describe the groups' general morphometric trends. Good (1985) Pattern Class A referred to *E. coerulea* populations in the outer Coastal Ranges and in the Pacific Northwest,

whereas Pattern Class B referred to populations in the interior Coastal Ranges, Northern California and the Sierra Nevada. Both Fitch (1938) and Good (1985) suggested that

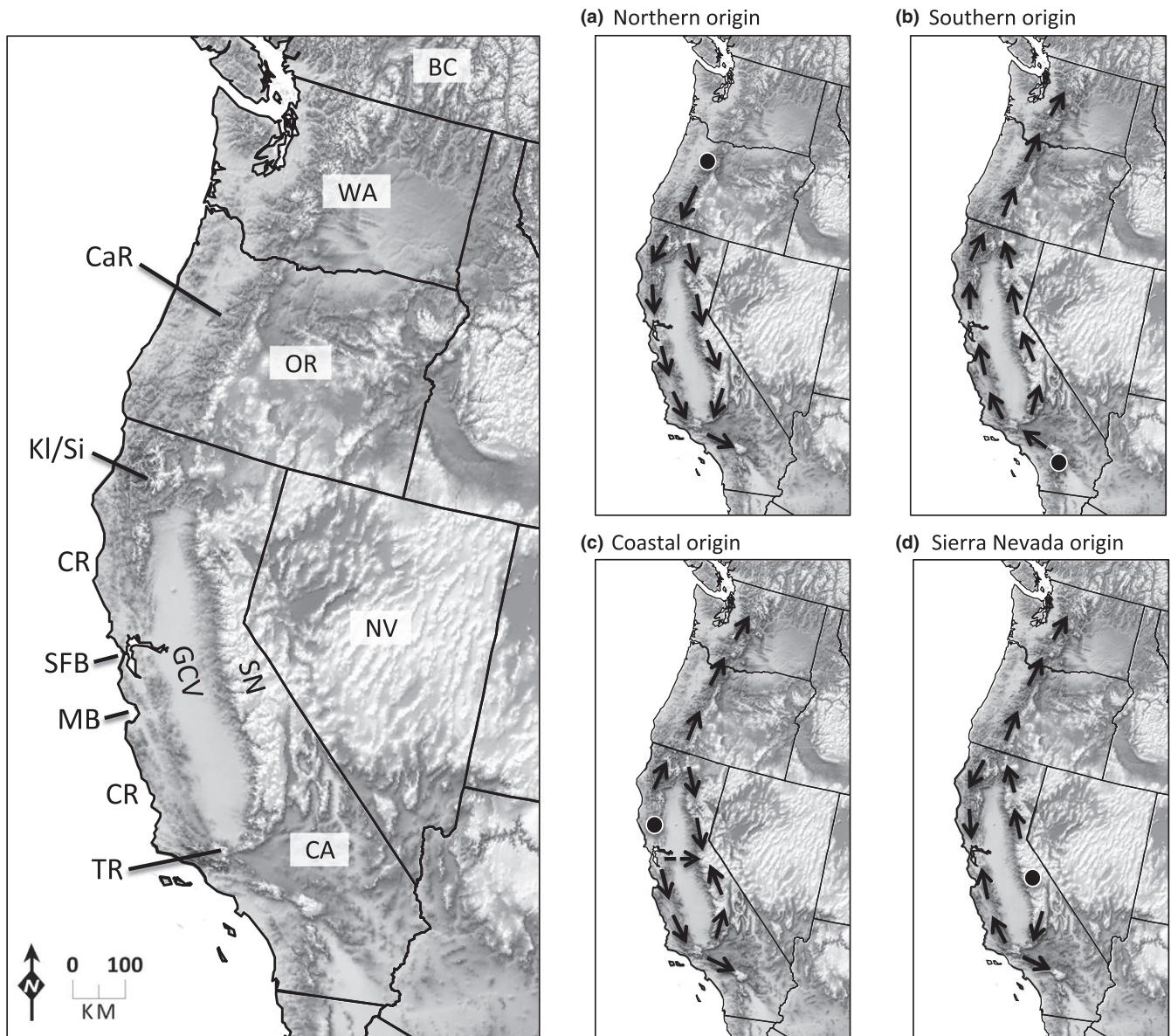


FIGURE 1 Major biogeographic patterns observed in woodland and forest animals distributed in a ring or semi-ring around the Great Central Valley (GCV) of California. Circles represent hypothesized areas of origin, and arrows represent dispersal from source populations. In most scenarios, secondary contact is expected where populations that have been spatially and temporally isolated come into contact at points around the ring. Note that the four models presented are over simplifications of actual patterns seen in taxa, and that some taxa actually display elements of more than one major scenario (e.g., *Ensatina*). (a) Northern origin and southern dispersal around the GCV; example taxon: plethodontid salamander *Ensatina eschscholtzii* (Kuchta & Wake, 2016; Kuchta et al., 2009; Moritz et al., 1992; Stebbins, 1949). (b) Southern origin and northern dispersal around the GCV; example taxa: anguid lizard *Elgaria multicarinata* (Feldman & Spicer, 2006), colubrid snake *Diadophis punctatus* (Fontanella, Feldman, Siddall, & Burbrink, 2008). (c) Coastal origin and movement north or south into the Sierra Nevada, sometimes including a “transvalley leak” (dashed arrow) across riparian corridors; example taxa: salamandrid newt *Taricha torosa* (Kuchta & Tan, 2006), and plethodontid salamander *Batrachospes attenuatus* (Martínez-Solano et al., 2007). (d) Sierra Nevada origin and movement north or south into the Coastal Ranges; example taxa: cricetid rodent *Neotoma fuscipes* (Matocq, 2002), and theraphosid spiders *Aphonopelma* sp. (Wilson, Gunnell, Wahl, & Pitts, 2013). The left pane shows the portion of Western North America considered, along with important regions and geographical features mentioned in the text: CA: California; NV: Nevada; OR: Oregon; WA: Washington; BC: British Columbia (Canada); TR: Transverse Ranges; CR: Coast Ranges; MB: Monterey Bay (sight of Monterey embayment); SFB: San Francisco Bay (sight of Golden Gate outlet); KI/Si: Klamath/Siskiyou Mountains; CaR: Cascade Range; GCV: Great Central Valley; SN: Sierra Nevada Range

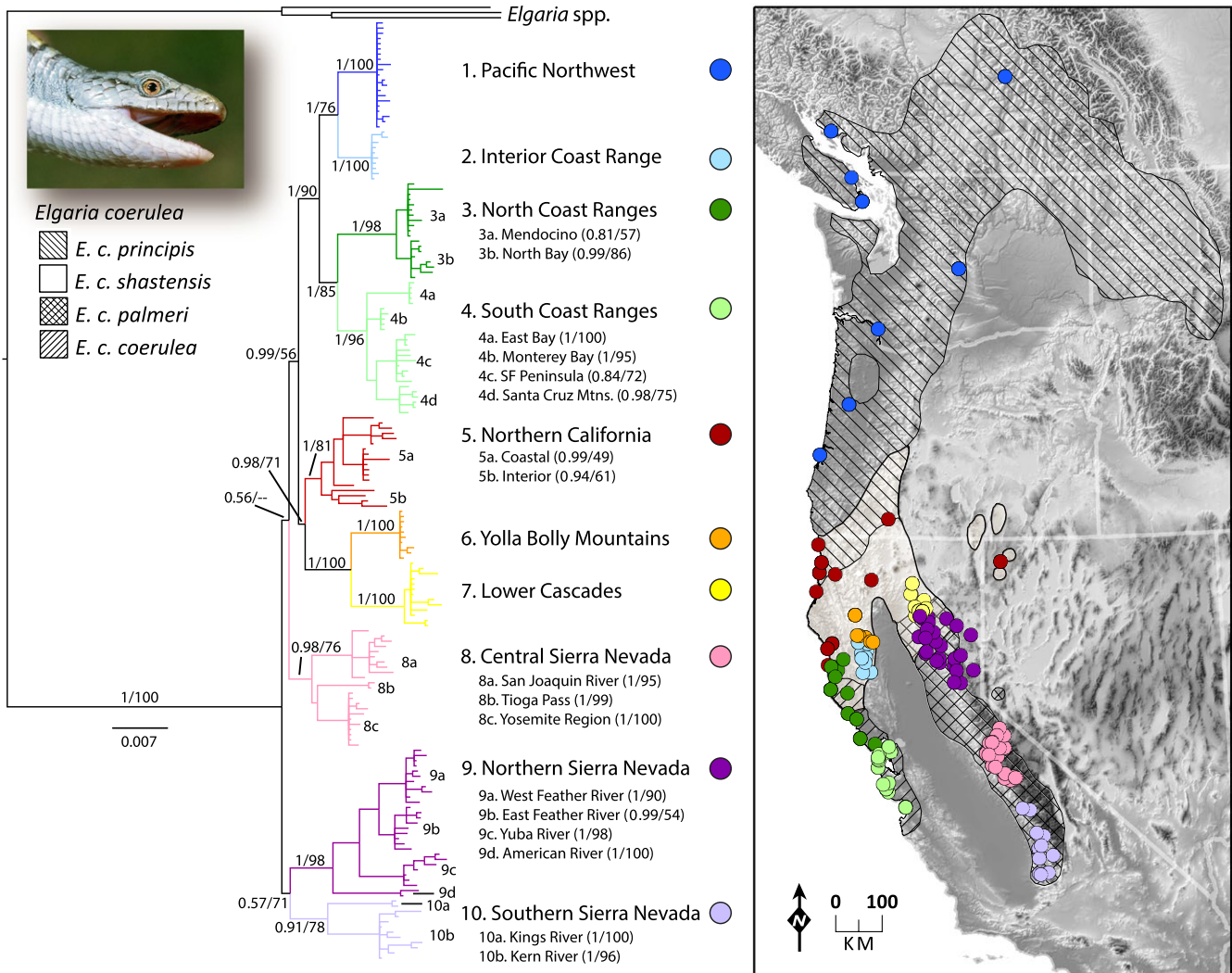


FIGURE 2 Phylogenetic relationships of *Elgaria coerulea* populations and the distribution of those lineages along the west coast of North America. The major mtDNA lineages are labelled and colour coded; branch lengths are proportional to distances from BI tree, and nodal support is given by posterior probability (Bayesian inference) and bootstrap proportions (maximum-likelihood), respectively. The map displays sampled localities, colour coded to match clade identity; major features discussed in the text are labelled; geographic subclades are numbered. Geographic distribution of *E. coerulea* (after Stebbins, 2003) with the approximate ranges of the four subspecies (after Fitch, 1938; Lais, 1976) mapped onto the sampling map. Photo courtesy of G. Nafis

the morphological groups were not reproductively exclusive, describing individuals that appear to be intergrades in areas where the different forms come into contact. Nevertheless, these geographically based groups suggest that populations may be well structured in *E. coerulea* and warrant further investigation.

Here, we examine the phylogeographic and population structure of *E. coerulea* to (a) test the plausibility of the previously proposed biogeographic scenarios (Figure 1); (b) compare biogeographic patterns in *E. coerulea* to other species that inhabit the California Floristic Region and Pacific Northwest; and (c) assess the role of climate in structuring clades using niche modelling and molecular dating.

2 | MATERIALS AND METHODS

2.1 | Sampling protocol

We sampled lizards from multiple distinct localities across the entire range of *E. coerulea*, including the distributions of the four subspecies and two pattern classes. We sampled 181 individuals from the major geographical regions the taxon occupies, including all four subspecies and intergrade zones (Table S1; Figure 2). For outgroups, we selected *Elgaria panamintina*, *Elgaria kingii* and *Elgaria paucicarinata*, based on previous *Elgaria* phylogenies (Conroy, Bryson, Lazcano, & Knight, 2005; Feldman & Spicer, 2006; Leavitt, Marion, Hollingsworth, & Reeder, 2017; Macey et al., 1999).

We attempted to gain both nuclear and mitochondrial perspectives on history and genetic structure of *E. coerulea* populations. However, our initial screens of over 20 single copy nuclear loci showed that our markers were invariant or uninformative (e.g., a single, uninformative substitution across the taxon). Thus, we conducted subsequent work using two, well-established, mitochondrial regions: a fragment of ND4 with associated tRNAs, and a fragment of ND2 with associated tRNAs (Leavitt et al., 2017).

2.2 | Laboratory protocols

We extracted tissue samples with a salt extraction protocol (Sambrook & Russell, 2001). We amplified our two regions of mtDNA with Polymerase Chain Reaction (PCR) under standard conditions, using primers ND4 [5-CACCTATGACTACCAAAGCTCATGTAGAAGC-3] and LEU [5-CATTACTTTTACTTGGATTGACCA-3] (Arèvalo, Davis, & Sites, 1994) for the ND4 fragment (55°C annealing temperature), and L4437/Metf.6 [5-AAGCTTTCGGGCCCATACC-3], H5574/ALAr.2 [5-CGCAAGTCTTACAGAAAC-3], and H5934/COIr.1 [5-AGRGTGCCAATGCTTTGTGRTT-3] (Crawford & Smith, 2005; Macey, Larson, Ananjeva, Fang, & Papenfuss, 1997) for the ND2 fragment (50°C annealing temperature or a touchdown protocol with annealing temperature dropping from 52 to 50°C). Note that we only used Metf6 and Alar2 for sequencing the ND2 gene fragment. We ran PCR reactions with an initial denaturing step of 2 min, then a denaturing step for 30 s, annealing step for 30 s, and an extension step for one minute (ND4) or one and a half minutes (ND2) for 35 cycles; with a final extension of 5 min. Our touchdown protocol dropped a degree after five cycles, 10 cycles, then ran at 50°C for the last 20 cycles. We cleaned PCR products with ExoSAP-IT (USB Corp.) and performed cycle sequencing reactions with Big Dye 3.1 Chemistry (Applied Biosystems Inc.). We sequenced all samples in both directions, cleaned cycle sequencing reactions with Sephadex columns (Amersham-Pharmacia) and ran sequences on an ABI 3730 Genetic Analyzer (Applied Biosystems Inc.) in the Evolutionary Genetics Laboratory, UC Berkeley.

2.3 | Alignment construction protocol

We edited and aligned sequences in Sequencher 4.8 (Gene Codes Corp.) and translated coding regions into amino acid sequences using MacClade 4.08 (Maddison & Maddison, 2005) to verify authentic mtDNA sequences and check for inappropriate codons. We deposited all sequences in GenBank (Table S1).

2.4 | Model and partition testing

We used Partitionfinder 2.1.1 (Lanfear, Frandsen, Wright, Senfeld, & Calcott, 2017) to assess the best-fit data

partitioning strategy and substitution models for conducting phylogenetic analyses on our mtDNA data set. The initial partitions examined were the codon positions and tRNA fragments associated with ND2 and ND4 for a total of eight initial starting partitions. We used the Bayesian Information Criterion (BIC) (Schwarz, 1978) to compare partitions and models because BIC enforces high penalties for models with more parameters. We ran Partitionfinder with the Greedy Algorithm (Lanfear, Calcott, Ho, & Guindon, 2012) with both PhyML (Guindon et al., 2010) and RAxML (Stamatakis, 2014). We used Partitionfinder to find the best-fit partitions and models for all of our phylogenetic analyses, limiting the program to assess only those models that downstream phylogenetic programs could implement.

2.5 | Phylogenetic analyses

To examine phylogenetic relationships within *E. coerulea*, we generated phylogenetic trees under both maximum-likelihood (ML) and Bayesian inference (BI) frameworks. We performed ML analyses with RAxML 8.0.24 (Stamatakis, 2014), using default settings. We used MrBayes 3.2.2 (Ronquist et al., 2012) to perform (BI) analyses, running 20,000,000 generations with one cold chain and three heated chains and sampling every 1,000 generations. We used Tracer 1.6 (Rambaut & Drummond, 2007) to assess convergence and discarded the first 25% of samples. We repeated BI analyses three times with different random number seeds in an effort to avoid the possibility that the Markov chain was trapped on a local optimum. We also performed BI analyses with a mixed model to assess the effect that model selection priors might have played on the analysis. We ran BI analyses on the CIPRES Science Gateway (Miller, Pfeiffer, & Schwartz, 2010).

2.6 | Molecular dating analyses

To estimate the timescale of lineage divergences in *E. coerulea*, as well as the appropriateness of historical niche modeling (see below), we performed a molecular dating analysis in BEAST 1.8.0 (Drummond, Suchard, Xie, & Rambaut, 2012). A primary goal of the divergence dating analysis was to determine if the major diversification events in *E. coerulea* fall within the timescale appropriate for niche modelling with Pleistocene climatic data. Although fossil *Elgaria* are known, they are all Pleistocene in occurrence (Holman, 1995) and not useful as time calibration points in molecular dating. Thus, we employed molecular rates of 0.007 and 0.006 changes per lineage per million years (after Macey et al., 1999), as well as the mean of 0.0065 changes per lineage per million years. We ran BEAST analyses for 10,000,000 generations, sampling every 1,000 generations and repeating analyses four times with different starting number seeds for each molecular rate

(0.006, 0.0065, 0.007). We constrained the major clades of interest to monophyly to record MRCA statistics.

2.7 | Population structure and diversity

We further examined population structure and assessed genetic variation within and between lineages of *E. coerulea*. First, we estimated the number of genetic (mtDNA) clusters in *E. coerulea*, as well as the most likely ancestral region of *E. coerulea*. We used a coalescent-based Bayesian clustering approach designed for use with haplotype trees (Manolopoulou & Emerson, 2012). We implemented these analyses in R 3.2.2, using the BPEC package with the following parameters: maxmig = 8, ds = 0, post-samples = 20 with 2 MCMC chains each with 500,000 iterations.

To further examine the genetic diversity within *E. coerulea*, we performed a series of Analyses of Molecular Variation (AMOVA) in Arlequin 3.5.1.3 (Excoffier & Lischer, 2010). We partitioned genetic diversity by (a) major phylogeographic groupings (see Results) recovered in our tree-based analyses, grouping the three clades in the Sierra Nevada mountains (clades 8–10), and the non-Sierran clades (1–7), (b) grouping clusters in accordance with the four subspecies designations, (c) grouping in accordance with the two pattern classes identified by Good (1985) and (d) grouping the clades in the same manner as recovered in our BPEC analyses. We carried out all AMOVA analyses with 10,000 permutations in Arlequin.

Finally, we calculated diversity and subdivision measures using Arlequin. We calculated the number of pairwise differences (π) within and between lineages, as well as pairwise comparisons of F_{ST} , Slatkin's linearized F_{ST} (Slatkin, 1995) and Nei's D (Nei, 1972) for each major lineage.

2.8 | Niche modelling

We estimated current and historic ecological niche models (ENMs) for *E. coerulea* to determine the role of past climate on lineage diversification and on the distribution of contemporary genetic diversity. We generated ENMs using maximum entropy as implemented in MaxEnt 3.3.3 (Phillips, Dudik, & Schapire, 2010) for all of *E. coerulea* samples, as well as for all museum samples that we could unambiguously assign to each of the major clades (based on location). We then projected these models onto the Last Glacial Maximum (LGM) scenario to estimate how distributions may have changed over time, and how populations may have fragmented. We obtained current climate data from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at a resolution of 1 arcmin, and LGM climate data were based on models developed through the Paleoclimate Modelling Intercomparison Project (PMIP2) at a resolution of 2.5

arcmin and the Miroc simulation (Braconnot et al., 2007). We used a Pearson correlation to check for strong correlations among variables, removed those that were highly correlated and retained ten climate variables for model building (Table S2). Because models built at the clade level contained a limited number of unique localities, we used 100 bootstrap replicates to ensure that the models were robust. We used Area Under the Curve (AUC) to assess model performance and interpreted models with AUC scores above 0.90 indicating excellent discriminatory power (after Swets, 1988). We estimated stable areas for the combined and clade-level models by applying the threshold that maximizes kappa to the estimated suitability surfaces, thereby classifying each grid cell into predicted presence or absence. We then summed the thresholded models together and determined stable areas as those areas with predicted presences during both time periods (Carnaval & Moritz, 2008; VanDerWal, Shoo, Williams, & Ladiges, 2009).

3 | RESULTS

3.1 | Alignment characteristics

Our final alignment of 181 ingroup samples and three outgroup samples was 1,665 bp in length, with 259 phylogenetically informative characters among ingroup samples, and 336 phylogenetically informative sites when including outgroups. The best-fit partitioning structure and models of evolution obtained using Partitionfinder are listed in Table S3.

3.2 | Phylogenetic analysis

The topologies produced by the ML and BI analyses were nearly identical and recovered ten geographically structured mtDNA clades (Figure 2). However, support for the deeper nodes in the tree was often weak and differed between analyses.

In the Sierra Nevada Range, we found three well-supported clades consisting of (a) a northern clade found from Lassen National Park south to, and including, the American River Watershed; (b) a central clade from the Yosemite Region south to, and including, the San Joaquin Drainage; and (c) a southern clade consisting of localities in the Kings and Kern River Drainages, including populations at the southern end of the range in the Greenhorn Mountains and Breckenridge Mountain. All three Sierra Nevada clades also contained well-supported substructure that appears to be defined by the major watersheds of the region. In the northern Sierra Nevada clade, subclades are associated with the Feather, Yuba and American Rivers; the central Sierra Nevada clade contained three subclades, one associated with the San Joaquin watershed, one in the Yosemite region and one extremely localized from essentially a single locality

along Tioga Pass (east of Yosemite); and the southern Sierra Nevada clade contained subclades associated with the King and Kern River watersheds. The Sierra Nevada clades do not appear to form a monophyletic group. A clade consisting of the northern and southern Sierra Nevada clades, excluding the Central Sierra Nevada, appears in both the ML and BI analyses, but received high levels of support only in the ML analysis.

We also recovered three clades along the north coast and Cascade Ranges of northern California and southern Oregon: (a) a Lower Cascades group localized in the southern Cascades, primarily in the Mount Lassen region on the north-eastern side of the GCV; (b) a localized clade in the Yolla Bolly Mountains on the north-west side of the GCV; and (c) a more widespread Northern California clade ranging from the Eel River watershed north into the Klamath Mountains in northern California and southern Oregon, including the disjunct "sky island" population from the Warner Mountains of north-eastern Nevada in the Great Basin Desert. We found additional western and eastern topological structure within this Northern California clade, though these groupings were not statistically robust. These three clades formed a well-supported grouping in all analyses, with the localized Yolla Bolly and Lower Cascades clades representing highly supported sister clades, to the exclusion of the widespread Northern California clade. It is unclear without further sampling if the two localized clades (Yolla Bolly and Lower Cascades) meet around the north end of the GCV or if they are intersected by members of the Northern California clade.

Finally, we uncovered a widespread lineage along the coast of California that spreads north through the Pacific Northwest into southern Canada. This widespread coastal/Pacific Northwest lineage contains four clades: (a) a Southern Coast Range clade, extending from Monterey Bay north to San Francisco Bay and terminating at the Golden Gate outlet; (b) a Northern Coast Range clade that extends north from the Golden Gate outlet and San Francisco Bay to the Russian River watershed; (c) an Interior Coast Range clade from the interior of the Coastal Ranges, starting at Lake County and extending north to the Yolla Bolly Mountains; and (d) a widespread Pacific Northwest clade that occurs from at least Coos Bay in Oregon to the species' northern range limits in British Columbia. The southernmost of these clades, the Southern Coast Range clade, contains some geographic substructure congruent with geographical features such as the Santa Cruz Mountains, San Francisco Peninsula, Monterey Bay and East Bay Hills, whereas a northernmost clade, the Pacific Northwest clade, lacks internal geographic structure. These four clades form a highly supported assemblage, with the Northern and Southern Coast Range clades forming a well-supported

group, sister to a geographically disjunct Interior Coast Range and Pacific Northwest clade.

Relationships among these three major regional clades (Northern California, Coast Ranges/Pacific Northwest and Sierra Nevada) remain somewhat ambiguous due to weak support in the analyses. The Northern California clades were placed sister to the Coastal/Pacific Northwest clades; however, this only received high support in the Bayesian analysis. The position of the Sierra Nevada clades relative to the rest of *E. coerulea* was also weakly supported in all analyses, as was the position of the Central Sierra Nevada clade to the other Sierra Nevada clades.

3.3 | Divergence dating

Both the fast and slow molecular rates place all divergences within *E. coerulea* approximately in the Pleistocene (Table S4). In general, divergences between and among the Sierra Nevada clades occurred earlier than was the case for other parts of the range. This rough molecular dating established *E. coerulea* as an appropriate candidate for Pleistocene niche modelling. Divergence of *E. coerulea* from the rest of *Elgaria* (outgroups) appears quite ancient, and we estimate this split occurred during the Miocene, with a mean date of ca. 12 million years ago.

3.4 | Population structure and diversity

The Bayesian clustering method identified six mtDNA clusters that correspond closely to those inferred from our tree-based analyses. The clustering analysis delimited the Pacific Northwest clade, the North and South Coast Range clades and the Northern Sierra Nevada clade as distinct clusters. However, it collapsed the Southern and Central Sierran clades into one cluster, and also collapsed the Northern California, Interior Coast Range, Yolla Bolly Mountains and Lower Cascades clades into a single cluster. According to this analysis, the most likely ancestral location for *E. coerulea* is in the Southern Sierra Nevada (Figure S1).

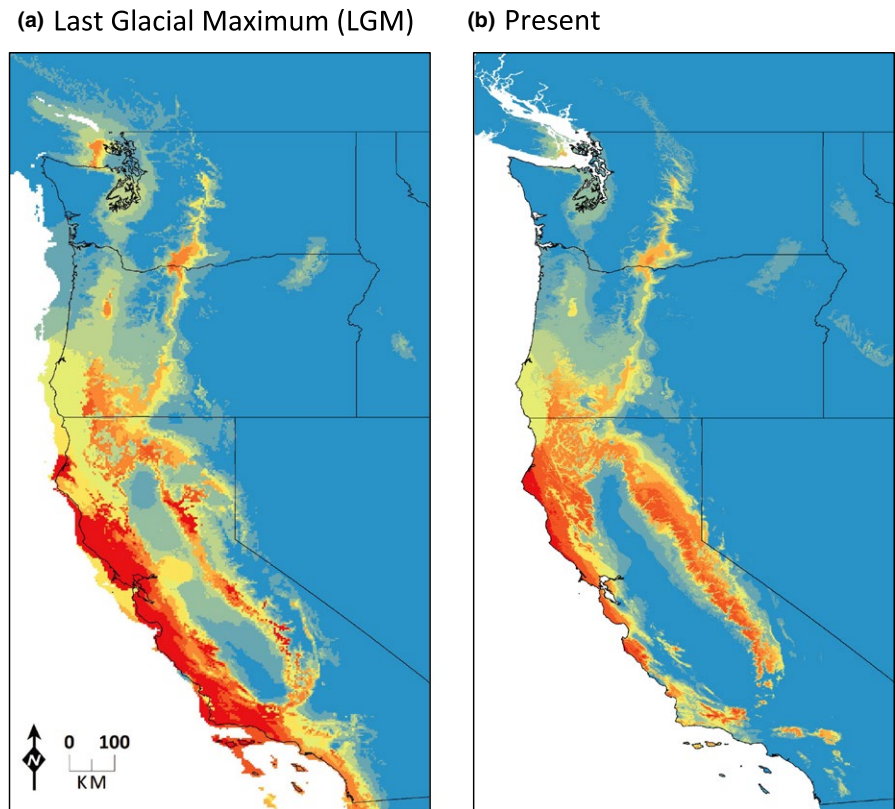
Results from the AMOVA revealed that the genetic variation within *E. coerulea* is best explained by the clade structure recovered in our tree-based analyses (Table 1). While some of the variance is also explained by higher level groupings such as pattern class, subspecies designation, population cluster or major phylogenetic group, these higher groupings only explained 16%–20% of the variance. The partitioning of genetic variance between populations in *E. coerulea* suggests that there is limited gene flow among the recovered clades.

Finally, diversity metrics (F_{ST} , Nei's distance and π) suggest that most lineages are well differentiated (Table S5).

TABLE 1 Results of AMOVA analyses on various grouping schemes of *Elgaria coerulea* populations, showing the proportion of the total genetic variation in mtDNA data explained by variance among groups, among populations and within populations

Grouping scheme	Variance among groups (%)	Variance among populations (%)	Variance within populations (%)
(a) Clade	16.11	60.94	22.95
(b) Subspecies	20.02	56.02	23.95
(c) Pattern class	18.72	58.62	22.66
(d) BPEC cluster	16.05	59.37	24.38

FIGURE 3 Ecological Niche Models of *Elgaria coerulea* based on museum records of specimens with unique localities. Warm colours (red and yellow) represent more highly suitable habitat, whereas cool colours (blue) represent more unsuitable habitat. (a) Projection of suitable habitat at the Last Glacial Maximum, which includes portions of the coastline no longer available as sea levels have risen over time. (b) Projection of contemporary suitable habitat. Note the dramatic shift in suitable habitat from along the coast to the Sierra Nevada. Also note that portions of central and southern California where *E. coerulea* does not occur are projected to contain highly suitable environmental conditions for this species



3.5 | Environmental niche models

Clade-level environmental niche models (not shown) generally predict the ranges occupied by other clades. In some instances, the single clade models predict a large proportion of the entire range of *E. coerulea*, suggesting that lineage differentiation is not accompanied by substantial divergence in abiotic requirements. Thus, we proceeded to build ENMs for *E. coerulea* under current and LGM climate models using all museum samples. Current niche models with the combined samples reveal high suitability along the outer Coast Ranges of Central and Northern California, and throughout the Sierra Nevada (Figure 3). Models projected onto LGM climate scenario actually suggest far more suitable habitat in the Coast Ranges of California in the past, with greater available habitat along the inner Coast Ranges, and suitable habitat extending deep into Southern California and the Transverse Ranges. On the other hand, LGM models suggest decreased suitability in the Sierra Nevada in the past.

4 | DISCUSSION

The Northern Alligator Lizard (*E. coerulea*) is a native of western North America, restricted to cooler forested habitats of the Sierra Nevada and Coastal Ranges from California through the Pacific Northwest. We reconstructed the phylogeography of *E. coerulea* to understand contemporary patterns of population structure, assess the biogeographic history of this taxon, and contrast spatial patterns of genetic variation with those of other co-occurring animals.

4.1 | Biogeographic origins

Our phylogeny and molecular dating analysis suggest that *E. coerulea* is a relatively old species, having diverged from other *Elgaria* species on the order of ca. 12 million years ago. Ancestral area reconstruction indicates that the

Southern Sierra Nevada is the most likely ancestral area for *E. coerulea*. Previous work on the taxon suggests that the species emerged out of the Southern Sierra Nevada and spread north into the Pacific Northwest and south into the Coastal Ranges (Peabody & Savage, 1958). Our results are consistent with this "Out of Sierra Nevada" biogeographical scenario. In addition, Good (1988) suggested that uplift in the Sierra Nevada Range (ca. 12 million years ago) was responsible for the initial divergence of *E. coerulea*, concordant with our molecular estimates of the divergence of *E. coerulea* from other *Elgaria* species. While the uplift of the Sierra Nevada seems a likely candidate for the original divergence of *E. coerulea*, we should be cautious about this interpretation because the age of the Sierra Nevada remains contentious, with some estimates placing the orogeny of the range far earlier in the Cenozoic (Hren, Pagani, Erwin, & Brandon, 2010; Mix, Ibarra, Mulch, Graham, & Page, 2016). All other major divergences among extant *E. coerulea* mtDNA lineages appear to have occurred during the late Pliocene or early Pleistocene. Phylogeographic relationships within *E. coerulea* hint at a more complicated scenario than a simple expansion out of the Southern Sierra Nevada and suggest that the Coast Ranges served as a dispersal corridor. Furthermore, the surprising amount of phyletic diversity (10 clades) and geographic structure within *E. coerulea* suggests that vicariant events, such as geographic barriers and range contractions, have been important in shaping spatial patterns of diversity.

4.2 | Ten clades and comparative biogeography

A surprising result of our phylogeographic analysis is the number of geographically defined lineages. We uncovered 10 clades within *E. coerulea*, and almost every one of these clades contained additional, localized substructure. Many of the boundaries between the ten clades that we recovered are concordant with those identified for other species, suggesting the existence of common geographic barriers among forest and woodland taxa. The phylogeographic analysis shows that *E. coerulea* in the Sierra Nevada is divided into three clades. The boundaries between them likely reflect two breaks that have been observed in other taxa; one creating a Southern Sierra Nevada lineage, and the other a mid-Sierra Nevada break.

The isolation of the Southern Sierra Nevada due to glaciation (Gillespie & Zehfuss, 2004; Moore & Moring, 2013) and uniqueness of the fauna of this area is demonstrated by the distinct lineages seen across multiple groups, such as ice-crawlers (*Grylloblatta* sp.; Schoville & Roderick, 2010), Alpine butterflies (*Colias behrii*; Schoville, Lam, & Roderick, 2012), *Greya* moths (*G. politella*; Rich, Thompson, & Fernandez, 2008), Yellow-legged Frogs (*Rana mucosa*; Vredenburg et

al., 2007), Slender Salamanders (*Batrachoseps* sp.; Jockusch, Yanev, & Wake, 2002), California Newts (*Taricha torosa*; Kuchta & Tan, 2006; Tan & Wake, 1995), Sharp-tailed Snakes (*Contia tenuis*; Feldman & Spicer, 2002, 2006; Feldman & Hoyer, 2010), Southern Alligator Lizards (*Elgaria multicarinata*; Feldman & Spicer, 2006), Mountain Kingsnakes (*Lampropeltis zonata*; Rodriguez-Robles, Denardo, & Staub, 1999) and Great Grey Owls (*Strix nebulosi*; Hull et al., 2010).

The central Sierra Nevada also experienced multiple glaciation events responsible for the formation of the many dramatic geological features in this area, such as Yosemite Valley, during glacial maxima (Gillespie & Zehfuss, 2004). These events are thought to have fractured and isolated formerly contiguous species, leading to shared patterns of genetic structure in many species that span the Sierra Nevada. Indeed, the mid-Sierra Nevada break in *E. coerulea* is roughly concordant with similar divergences seen in *Ensatina eschscholtzii* (Kuchta et al., 2009), shrews (*Sorex ornatus*; Maldonado, Vila, & Wayne, 2001) and woodrats of the *Neotoma fuscipes* complex (Matocq, 2002). In addition, both the Yosemite Toad (*Anaxyrus canorus*) and Long-toed Salamander (*Ambystoma macrodactylum*) appear to have been affected by a central Sierra Nevada barrier, with the former not occurring north of the central Sierra Nevada, and the latter reaching a Southern range limit in the central Sierra (Stebbins, 2003).

The northern limit for the Sierra Nevada clades occurs in the vicinity of Mount Lassen, a region where long-term volcanic activity as well as glaciation has occurred (Crandell, 1972). This region was likely unsuitable for forest and woodland taxa at some point in the past, because a number of other species display concordant genetic breaks in this area, including Rubber Boas (*Charina bottae*; Rodriguez-Robles, Stewart, & Papenfuss, 2001), *Ensatina* (*E. eschscholtzii*; Kuchta et al., 2009), Apollo butterflies (*Parnassius phoebus* complex; Todisco et al., 2012) and even pine martens (*Martes americana*; Slauson, Zielinski, & Stone, 2009).

Overall, the three clades of the Sierra Nevada match surprisingly well with our ecological niche model (EMN) projections of suitable areas during the Last Glacial Maximum (LGM). These models suggest there were three, potentially isolated areas of high niche suitability in the Sierra Nevada, and these areas correspond almost perfectly with contemporary patterns of genetic structure in the Sierra Nevada (compare Figures 1 and 3). Thus, climate, glaciation and volcanism appear to have fractured *E. coerulea* into three geographically confined clusters in the Sierra Nevada.

Along the Coast Ranges, *E. coerulea* is also partitioned into three clades. The North Coast clade is separated from more northern populations by a break at the North Coast Divide, an area where numerous taxa including forest amphibians have biogeographic boundaries, although they

are not necessarily precisely spatially concordant (Good, 1989; Rissler et al., 2006). Interestingly, *E. coerulea* is the only squamate reptile to display corresponding breaks with these co-occurring amphibians. The amphibians that exhibit breaks in this area are typically forest-dependent salamanders (Rissler et al., 2006), whereas the amphibians that do not exhibit genetic breaks in this region tend to be more habitat generalists that are tolerant of arid conditions, such as toads (*Anaxyrus* sp.) and chorus frogs (*Pseudacris* sp.). Thus, the North Coast Divide may represent a filter barrier to more mesic-adapted or forest-dependent taxa.

The second biogeographic break divides the North Coast Range clade from the South Coast Range clade at the Golden Gate. Numerous amphibian and reptile taxa share this biogeographical boundary (Feldman & Spicer, 2006; Kuchta et al., 2009; Martínez-Solano, Jockusch, & Wake, 2007; Reilly & Wake, 2015), which is not surprising given that the Golden Gate is currently the outlet of the several major river drainages that flow through the GCV. Finally, the coastal range of *E. coerulea* terminates near Monterey Bay, a third important biogeographic barrier along the Pacific Coast. Monterey Bay was both a former seaway and later the main outlet to the Pacific Ocean for the GCV until approximately 600,000 years ago, when the drainages of the Sierra Nevada and Central Valley switched to exiting through the Golden Gate (Hall, 2002; Sarna-Wojcicki et al., 1985). Not surprisingly, these outflows have been postulated as major barriers for numerous taxa (Feldman & Spicer, 2006; Kuchta et al., 2009; Myers et al., 2013; Rissler et al., 2006; Schierenbeck, 2014). The inability of *E. coerulea* to expand beyond Monterey Bay may reflect the importance of the Monterey embayment and historic Salinas River because our models suggest that suitable climatic habitat is nearly continuous south of Monterey Bay, and yet *E. coerulea* is absent from these remaining pockets of redwood habitat.

Many of the biogeographical patterns and apparent barriers we note in *E. coerulea* are shared with sympatric salamanders, but not with other squamate reptiles. This oddity may be explained by the physiological tolerances of *E. coerulea*. As in sympatric salamanders, the Northern Alligator Lizard may be more susceptible to heat stress at the higher temperatures and more arid conditions typically favoured by other squamate reptiles (Telemeco & Addis, 2014; Telemeco et al., 2017). One pattern that *E. coerulea* does share with many squamate reptiles is a signature of recent expansion into the Pacific Northwest (see Feldman & Spicer, 2006; Rodriguez-Robles et al., 2001), as exemplified by a lack of genetic substructure in the northern reaches of its distribution. *Elgaria coerulea* exhibits this pattern north of the Klamath Mountains. However, the Northern Alligator Lizard differs from other squamates in the region in that its range extends farther northward, and contains an exclusive lineage in the Pacific Northwest. The level of phylogeographic structure

in *E. coerulea* in the Northern part of the California Floristic Province is unusual for a squamate reptile and may be the only squamate that shows such a high degree of population genetic structure so far north. Unlike other squamates that have been hypothesized to have expanded northward with warmer interglacial climates, *E. coerulea*, with its preference for cooler mesic habitats, may have been present in this region earlier or persisted longer.

4.3 | The disjunct corridor

The phylogeography of *E. coerulea* provides an unusual case, where regional clades appear to be only distantly related to more geographically proximate surrounding clades. This example involves the Coastal Ranges and Pacific Northwest, where the North, South and Interior Coast Range clades form a well-supported monophyletic grouping with the Pacific Northwest clade (and, indeed, the Interior Coast Range clade is sister to the Pacific Northwest clade). Despite the monophyly of these populations, the Pacific Northwest clade is geographically separated from the closely related Coast Range clades by intervening populations representing the distantly related Yolla Bolly Mountains and Northern California clades (Figure 2).

One potential explanation for this observed disjunction may be extirpation of populations of one clade, followed by replacement with another. If niches are conserved among clades, as our niche modelling suggests, then replacement would simply involve the extirpation of the Coast Range/Pacific Northwest clades in northern California, with subsequent replacement by members of the Northern California clade. Indeed, our niche modelling indicates dramatic changes in habitat stability in the recent past, where portions the species range in North-western California may have contracted during the LGM and then subsequently expanded (Figure 3). A potential second example of a disjunction in *E. coerulea* may occur in the Sierra Nevada, as the Central Sierra Nevada Clade falls outside the adjacent northern and southern Sierra Nevada clades in BI analyses. Further work is needed to resolve relationships at the base of the *E. coerulea* tree and to determine ancestor-descendant relationships of populations in the Sierra Nevada.

4.4 | Southern range limits

The range of *E. coerulea* consists of a partial ring around the GCV in California as well as around the dryer Columbia Plateau region in the Pacific Northwest. In the north, the current range may represent a range retraction as Holocene warming dried portions of the north-west (Carstens, Brunsfeld, Demboski, Good, & Sullivan, 2005; Whitlock, 1992), leaving isolated populations *E. coerulea* in south-eastern Oregon, the Warner Mountains and other Great Basin sky islands. To

the south, the partial ring-like structure of *E. coerulea* around the GCV is of particular interest because this region is one of the few global topographic features around which ring species have been documented (Cacho & Baum, 2012; Kuchta & Wake, 2016; Monahan, Pereira, & Wake, 2012). However, it is unclear whether *E. coerulea* was formerly distributed entirely around the GCV and has suffered a range contraction, or whether *E. coerulea* has never completed the ring around the southern portion of the valley.

Discriminating between these two alternative biogeographical scenarios is difficult, particularly in the absence of fossil evidence. We favour the later hypothesis, that *E. coerulea* has simply been unable to colonize southern portions of the Coastal Ranges and Transverse Ranges to complete the ring. The Transverse Ranges linking the Coastal Ranges and Southern Sierra Nevada are not a single unit, but appear to comprise different biogeographical areas that may act as filter barriers for some taxa but not others (Chatzimanolis & Caterino, 2007). The current range limit of *E. coerulea* along the coast occurs just south of Monterey Bay. Monterey Bay has formed a long-standing barrier for terrestrial vertebrates (Feldman & Spicer, 2006; Rissler et al., 2006; Schierenbeck, 2014), due to previous embayments and because this bay was, until recently, the main outlet to the drainages of the GCV (Hall, 2002). If the Peabody and Savage (1958) “Out of the Sierra Nevada” scenario is correct, then *E. coerulea* dispersing south along the coast may have been halted by Pliocene marine embayments and historic rivers (Hall, 2002).

While geology and timing are likely major factors in shaping the southern range limits of *E. coerulea*, the presence of a second, wide-ranging alligator lizard species, *E. multicarinata*, may have also played a role. Although *E. coerulea* and *E. multicarinata* differ in their environmental tolerances (*E. coerulea* tolerating cooler temperatures and *E. multicarinata* warmer temperatures), they actually have similar physiological preferences (Telemeco & Addis, 2014; Telemeco et al., 2017) and would be expected to prefer the same thermal microclimates. However, *E. multicarinata* is much larger and more aggressive (Nussbaum et al., 1983; Stebbins, 2003) and thus may exclude the smaller *E. coerulea* from occupying portions of Central and Southern California that are physiologically preferable for both species.

4.5 | Cryptic variation, pattern classes and subspecies

The phylogeographic patterns observed in *E. coerulea* are consistent with some aspects of both the subspecies taxonomy proposed by Fitch (1938) and the Pattern Classes proposed by Good (1985). For example, the clades south and north of San Francisco Bay roughly approximate the range of *E. c. coerulea*, the Pacific Northwestern clade is largely congruent with the proposed range of *E. c. principis*, the clades of Northern

California approximate the range of *E. c. shastensis*, and the three clades in the Sierra Nevada approximate the distribution of *E. c. palmeri*. However, it is unclear how the Interior Coast Range clade would be treated under the current taxonomy, as this clade is sister to the Pacific Northwest, not the nearby Coast Range clades. Additionally, the clades of the Sierra Nevada may not actually form a monophyletic group, with the Central Sierra Nevada clade potentially representing the sister clade to the remaining *E. coerulea* lineages.

While we did not find genetic support for the pattern classes exactly as proposed by Good (1985), the Coast Range and Pacific Northwest clades form a monophyletic assemblage. Even Fitch (1938) noted that coastal examples belonging to *E. c. shastensis* have some of the pattern and morphology of the smaller Coast Range/Pacific Northwest animals that would form Good’s pattern class A. Good (1985) suggested that selection was likely maintaining these pattern classes. Our phylogeny showed no genetic break between coastal individuals and more interior individuals in the Coastal Ranges, with multiple clades cutting across the smaller Pattern Class A and larger Pattern Class B. Furthermore, our AMOVA showed that a small portion of the genetic structure in *E. coerulea* is explained by either the pattern class or subspecies. Thus, the morphological classes of Good (1985) and the subspecies designations (Fitch, 1938) appear to have a poor correspondence to underlying population genetic variation (at least as characterized in the mitochondrial genome). This discordance may not be surprising if the colour patterns and morphology are the result of patterns of selection, rather than deeper genetic structure driven largely by neutral or biogeographical processes. Future work might reexamine morphological variation in light of the underlying clade structure we have described, and with modern approaches to detecting morphological patterns (e.g., geometric morphometrics).

5 | CONCLUSIONS

The Northern Alligator Lizard provides another rich chapter in the dynamic biogeographic story of the California Floristic Province and Pacific Northwest. The taxon appears to have a Sierra Nevada origin and then moved both north and west to occupy its current distribution (as postulated 60 years ago), diversifying into a number of geographically confined clades along the way. The patterns of range limits and clade boundaries shared between *E. coerulea* and other codistributed forest and woodland species provides compelling evidence that a handful of major biogeographic barriers and historical events (e.g., San Francisco Bay and Monterey Bay outlets, Sierra Nevada glaciation) have been instrumental in shaping phylogeographic patterns and have likely influenced species range limits and even patterns of community assembly in the

California Floristic Province. Further, in depth, examination of *E. coerulea* and other species will continue to shed light on patterns of biodiversity in the California Floristic Province, and the mechanisms that have generated and now maintain that diversity.

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