



# Phylogenomics of arboreal alligator lizards shed light on the geographical diversification of cloud forest-adapted biotas

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## Abstract

**Aim:** The proximate ecological and evolutionary processes underlying the high biodiversity of neotropical montane cloud forests are still very poorly understood. Climatic oscillations may have contributed to vicariance and cladogenesis, but also promoted secondary contact and erosion of genetic divergence. Here we tested whether geographical diversification – or its lack thereof – in a complex of arboreal alligator lizards is explained by range shifts during Quaternary climatic oscillations.

**Location:** Pine–oak and cloud forests, central Mexico.

**Taxon:** *Abronia taeniata–graminea* species complex (Squamata: Anguillidae: Gerrhonotinae).

**Methods:** We generated genomic data (ddRADseq) to infer patterns of geographical diversification in the complex, reconstruct its demographic history, estimate the timing of lineage split, and test for the presence of contemporary and/or historical hybridization. We evaluated whether the tempo and mode of diversification (i.e. strict isolation vs. secondary contact with introgression) are explained by the contemporary distribution of suitable habitats and/or range shifts experienced by the complex since the Last Glacial Maximum (LGM), as inferred from environmental niche modelling (ENM).

**Results:** Genomic data supported a marked genetic structure within the complex, and phylogenomic and dating analyses revealed cryptic lineage diversification starting at the onset of the Pleistocene followed by secondary contact with limited introgression. ENM pointed to considerable range expansions of the complex during the LGM and a marked fragmentation and scarce connectivity among contemporary populations, which was supported by genomic-based demographic reconstructions.

**Main Conclusions:** The geographical diversification of the complex has been moulded by vicariant events promoted by Pleistocene geologic and climatic changes impacting the distribution of their pine–oak and cloud forest habitats. Our data supported a model of divergence with introgression, indicating that pulses of population

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fragmentation and expansion during the Quaternary have led to multiple opportunities for both allopatric isolation and secondary contact.

#### KEYWORDS

hybridization, introgression, Mesoamerica, Reptilia, Squamata

## 1 | INTRODUCTION

Neotropical montane oak forests extend from central Mexico to Andean Colombia in northern South America (Kappelle, 2006). A particular type of montane oak forests are cloud forests, which are characterized by the persistent presence of clouds and mists. These forests have a remarkable vascular plant diversity, accompanied by an extraordinary richness of non-plant species (Espejo-Serna, 2014), such as gall-forming insects (Oyama et al., 2006), bats (Sánchez-Cordero, 2001), amphibians (Gual-Díaz & Goyenechea Mayer-Goyenechea, 2014; Wake, 1987) and reptiles (Goyenechea Mayer-Goyenechea & Gual-Díaz, 2014; Wilson et al., 2010), among many other taxa. The geographical distribution of these cloud forests has been conditioned by the geological and climatic history of the American continent and the evolution of its flora (Kappelle et al., 1992). Cloud forests present a highly fragmented distribution forming a 'sky-island archipelago' (Flantua et al., 2020), which makes them well-suited for vicariance modelling and analysing the geological and climatic drivers of diversification (Gutiérrez-Rodríguez et al., 2011; Luna-Vega et al., 2004). The remarkable high biodiversity associated with cloud forests has been hypothesized to be promoted by the volcanic activity and climate changes occurring during the late Pliocene and Pleistocene (Ferrusquía-Villafranca, 1993; Ornelas et al., 2013; Rzedowski, 1993). Environmental changes promoted the fragmentation and expansion of these habitats during Quaternary climatic oscillations, being of particular importance to some species associated with the cloud forest ecosystem (Jaramillo-Correa et al., 2009; Ramírez-Barahona & Eguiarte, 2013). The distributions of these species likely contracted and fragmented during interglacial periods and expanded into the lowlands during glacial cycles (Colinvaux et al., 2000), which is expected to have led to the progressive isolation of populations, shaped its spatial patterns of genetic variation and contributed to processes of species diversification.

The major centre of oak species diversity is located in the highlands of central and eastern Mexico (Nixon, 1993) and overlaps in distribution with the centre of diversification of *Abronia* Gray, 1838 (Anguidae: Gerrhonotinae), a genus of alligator lizards endemic to Mesoamerica. The genus *Abronia* currently contains 40 recognized taxa that form multiple independent clades of arboreal and terrestrial species distributed from northeastern Mexico to southern Honduras (Clause et al., 2020; Gutiérrez-Rodríguez et al., 2021; Solano-Zavaleta & Nieto-Montes de Oca, 2018). Most species of arboreal *Abronia* have allopatric distributions and usually occur in montane habitats with cloud and seasonally dry pine-oak forests

(Campbell & Frost, 1993). Here we focus on the *Abronia taeniata-graminea* species complex, which currently comprises two closely related species surrounded by considerable taxonomic uncertainty: *Abronia taeniata* (Wiegmann, 1828) and *A. graminea* (Cope, 1864). Phylogenetic analyses indicate that *A. graminea* is paraphyletic with respect to *A. taeniata* (Gutiérrez-Rodríguez et al., 2021) and recent studies have also suggested that the two taxa might be sympatric and potentially interbreed in contact zones (Clause et al., 2018; Woolrich-Piña et al., 2017).

The geographical distribution of the *A. taeniata-graminea* species complex is of considerable biogeographical interest because it lies at the confluence of three physiographic provinces (Ferrusquía-Villafranca, 1993): Sierra Madre Oriental (SMO), Trans-Mexican Volcanic Belt (TMVB) and Sierra Madre del Sur (SMS). Few studies have focused on the analysis of diversification processes of arboreal taxa inhabiting this region, being mainly restricted to small mammals and other organisms (Almendra et al., 2014; León-Paniagua et al., 2007; Ornelas et al., 2010; Rocha-Méndez et al., 2019; Vallejo & González-Cózatl, 2012). Most of these studies have shown that diversification among currently extant species occurred during the Pliocene–Pleistocene and phylogenetic inferences point to a colonization from the SMS to the SMO through the eastern end of the TMVB. Mexican physiographic provinces have a complex geological history. The SMO and SMS provinces mainly originated after deformation of Mesozoic rocks that were raised during the Laramide orogeny 40 to 20 million years ago (Ma) (De Antuñano et al., 2000; Nieto-Samaniego et al., 2006), and its current geomorphological configuration was not completed until the early Holocene (Brouillet & Whetstone, 1993; Maldonado-Koerdell, 1964). On the other hand, the TMVB has a relatively more recent origin dating from the Neogene (Ferrusquía-Villafranca, 1993; Ferrusquía-Villafranca et al., 2005). The intricate confluence of the above three physiographic provinces makes of this region one of the most important montane biodiversity hotspots in Mexico, especially for oak-pine cloud forests (Rzedowski, 2006).

In this study, we integrated genomic data and environmental niche modelling (ENM) to shed light on the historical processes shaping geographical diversification in the *A. taeniata-graminea* species complex. Specifically, we tested whether the tempo and mode of diversification (strict isolation vs. secondary contact with introgression) are explained by the contemporary distribution of suitable habitats and/or range shifts experienced by the complex linked to Pleistocene glacial–interglacial cycles. To this end, we first characterized the genetic structure of populations across the geographical distribution of the complex and employed diverse phylogenomic



approaches to reconstruct the relationships among main recovered lineages and assess the support for current taxonomic classification. In the second step, we used Bayesian clustering analyses to infer contemporary hybridization (or its lack thereof) among lineages in putative contact zones and performed phylogenetic network tests to evaluate alternative scenarios of post-divergence gene flow that might explain uncertain phylogenetic relationships and distinguish incomplete lineage sorting from introgression events. Third, we employed the multispecies coalescent model to estimate the timing of lineage split and determine whether the onset of diversification within the complex could be explained by geological and climatic changes during the Quaternary or if, alternatively, divergences largely predate the Pliocene–Pleistocene boundary. Finally, we used ENM and reconstructed changes in effective population size through time to evaluate whether shifting distributions and the demographic history experienced by the species complex explain geographical diversification and are compatible with processes of historical and/or contemporary gene flow inferred from genomic data.

## 2 | MATERIALS AND METHODS

### 2.1 | Taxon sampling

We generated ddRADseq data for a total of 38 specimens of *A. taeniata* and *A. graminea*. We used two specimens of *A. fuscolabialis* (Tihen, 1944) as an outgroup for phylogenomic analyses. This species was recovered as sister to *A. taeniata*+*A. graminea* in a recent study carried out for the genus *Abronia* (Gutiérrez-Rodríguez et al., 2021). Tissue samples of *A. graminea* and *A. taeniata* were collected across most of their respective geographical distributions, including specimens sampled near the respective type localities of the two taxa (Table S1; Figure 1a). We also sampled populations from the putative contact zone in the states of Puebla and Veracruz proposed by Clause et al. (2018) to test whether there has been gene flow between the two species. Specimens were identified following the morphological key to species in Clause et al. (2018) and Campbell and Frost (1993). We followed the classification of Mexican physiographic provinces proposed by Ferrusquía-Villafranca (1993).

### 2.2 | ddRADseq libraries

Genomic DNA was extracted using the EZ-10 Spin Column Genomic DNA Miniprep kit (BIO BASIC) and purified using 1.5× Sera-Mag Magnetic Speed-beads (Thermo Fisher®). We assessed DNA quality by means of agarose gel electrophoresis and quantified DNA using a Qubit Fluorometer (Thermo Fisher Scientific®).

We followed the ddRADseq protocol described by Peterson et al. (2012). In brief, genomic DNA from each sample was digested with the restriction enzymes *SbfI* (restriction site 5'-CCTGCAGG-3') and *MspI* (restriction site 5'-CCGG-3'). These fragments were purified with 1.5× Sera-Mag Magnetic Speed-beads. Subsequently,

specific adapters for the enzymes *SbfI* and *MspI* were ligated to the DNA fragments. DNA ligands were purified with 1.5× Sera-Mag Magnetic Speed-beads before amplification of the libraries. An enrichment PCR of each sample was performed using a KAPA Long Range DNA Polymerase (Kapa Biosystems) and specific adapters for the Illumina sequencer. We purified the ddRADseq libraries using 1.5× Sera-Mag Magnetic Speed-beads and performed DNA size selection at  $500 \pm 50$  bp using a Pippin Prep automated size selector (Sage Science®). Libraries were sequenced on an Illumina HiSeq 2500 platform (single-read, 150 bp) at the University of Georgia (USA).

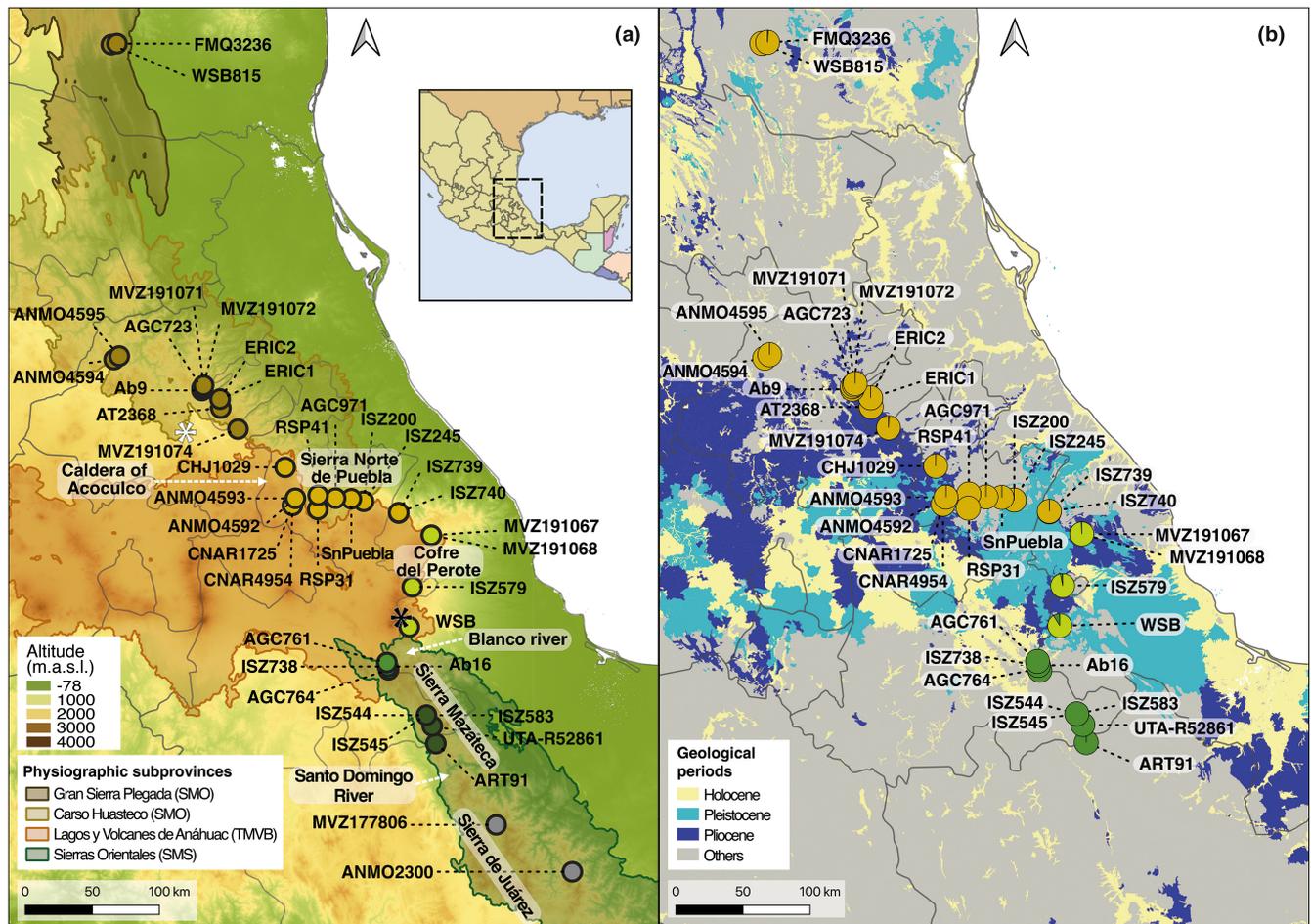
### 2.3 | ddRADseq bioinformatic processing

Quality of raw Illumina reads was assessed using the software program FASTQC 0.11.5 (Andrews, 2010). ddRADseq datasets were subsequently processed using the pipeline *ipyRAD* 0.7.19 (Eaton & Overcast, 2016). Reads were filtered using the default phred Q score offset for quality of 33, and sequences with more than 10 ambiguous (N) sites were discarded. We used the trimming option for removing all Illumina adapters. A de novo clustering was performed using *VSEARCH* 1.1.3 (Rognes et al., 2016), and the resulting clusters were aligned with *MUSCLE* 3.8.31 (Edgar, 2004). The level of sequence similarity was selected following Ilut et al. (2014) to avoid the use of an arbitrary clustering threshold and to minimize false homozygosity and heterozygosity. To this end, we ran custom scripts developed by Ilut et al. (2014) for each sample at different thresholds (from 0.80 to 0.99). The optimal clustering threshold (the inflection point of the linear plateau) was selected using the R package 'easynls' 5.0 (Arnhold, 2017). We generated nine different sequence alignment matrices with increments of ~10% in minimum number of samples with data per locus (Table S2). Analyses of these matrices allowed us to explore the effect that different percentages of missing data have on the robustness of phylogenetic analyses. We estimated the percentage of missing data in each matrix with the program *vcftools* 0.1.14 (Danecek et al., 2011).

### 2.4 | Phylogenetic analyses

We reconstructed the phylogenetic relationships among main lineages within the complex using two methods: the Maximum Likelihood (ML) method based on concatenated data implemented in *RAXML* 8.0 (Stamatakis, 2014) and the coalescent-based species-tree approach implemented in *ASTRAL-III* 5.6.3 (Zhang et al., 2018).

We performed ML phylogenetic analyses in *RAXML* using the nine matrices at different minimum percentages of samples with data for a locus to be included in the alignment (i.e. different proportions of missing data; Table S2). The matrices included all concatenated loci with single nucleotide polymorphisms (SNPs) and invariant sites to improve branch length and topological accuracy in phylogenetic reconstructions (Leaché et al., 2015). All analyses were run on the



**FIGURE 1** (a) Geographical distribution of the samples of arboreal alligator lizards of the *Abronia taeniata-graminea* species complex from central Mexico included in this study. Dot colours represent the five lineages recovered in phylogenomic analyses using RAXML and ASTRAL-III. Background shows the main physiographic subprovinces within the physiographic provinces of Sierra Madre Oriental (SMO), Trans-Mexican Volcanic Belt (TMVB) and Sierra Madre del Sur (SMS), following Ferrusquía-Villafranca (1993). White (*A. taeniata*) and black (*A. graminea*) asterisks indicate the type locality of each species. (b) Results of Bayesian clustering analyses in STRUCTURE. Pie charts show the probability of assignment of individuals to each genetic cluster for  $K = 3$ . Background shows main geological periods. Specimen codes as described in Table S1 and maps in Plate Carrée projection.

CIPRES Science Gateway 3.3 (Miller et al., 2010). We carried out a simultaneous search to obtain the best-scoring ML tree. Rapid bootstrap analyses were also conducted with the GTR-GAMMA model, using 1000 bootstrap replicates starting from random seeds.

We used the software ASTRAL-III and the most informative genomic dataset (matrix F96m80; see Table S2 and Section 3) to reconstruct a coalescent-based species tree. First, ML gene trees were estimated for each locus with the pipeline MAGNET 0.1.9 (Bagley, 2019a, 2019b) using the software RAXML. Rapid bootstrap analyses were also conducted with the GTR-GAMMA model and using 100 bootstrap replicates starting from random seeds. We collapsed branches with considerably low support (below 10% bootstrap support) in each gene tree using NEWICK 1.6 (Junier & Zdobnov, 2010), which can improve accuracy of species trees by reducing noise (Zhang et al., 2018). The species tree was then inferred in ASTRAL-III using as input 1404 ML gene trees. Phylogenetic trees were edited using the software FIGTREE 1.4.4 (Rambaut, 2018) and ADOBE ILLUSTRATOR CS5.

## 2.5 | Phylogenetic network analyses

We used PHYLONETWORKS 0.12.0 (Solís-Lemus et al., 2017) to assess whether a strictly bifurcating phylogenetic tree (i.e. no hybridization) or a phylogenetic network (i.e. one or more introgression events) better explains the evolutionary history of the *A. taeniata-graminea* species complex. First, we obtained quartet concordance factors for within-species four-taxon sets from previously obtained RAXML gene trees (as detailed above for species tree analyses). The species tree reconstructed in ASTRAL-III (see above) was used as the starting tree and the SNAQ method (Species Networks Applying Quartets; Solís-Lemus & Ané, 2016) was used to infer the best phylogenetic network testing a varying number of reticulation events ( $h$  from 0 to 5), each optimized with 15 independent runs. The optimal number of reticulation events was chosen using a heuristic approach by plotting negative pseudolikelihood scores against  $h$ -values, as recommended by Solís-Lemus et al. (2017).



## 2.6 | Divergence times

We estimated divergence times among the main lineages (i.e. species tree) using analyses A00 in software BPP 4.3.8 (Flouri et al., 2018). The .loci file from *ipyrad* was edited, converted into a BPP input file and filtered using custom R scripts (J-P. Huang, <https://github.com/airbugs/>; for details, see Huang et al., 2020). Since the examined sequences differ in length due to insertion–deletion polymorphisms (indels) at some loci, we trimmed them to 142bp and excluded those that were not represented in at least one individual per lineage (i.e. loci with missing taxa/lineages were removed). The resulting input file contained 1000 loci. We performed two A00 analyses in BPP. The first analysis was performed under the multispecies coalescent (MSC) model (Rannala & Yang, 2003), using as fixed topology the species trees obtained with ASTRAL-III. Because PHYLONETWORKS analyses inferred an introgression event from *A. graminea* into *Abronia* sp. nov. L1 (see Section 3), we also ran a second analysis under the multispecies-coalescent-with-introgression (MSCi) model (Flouri et al., 2020). We applied an automatic adjustment of fine-tune parameters and used the ‘diploid’ option to indicate that the input sequences are unphased (Flouri et al., 2018). To ensure the convergence of the analyses (effective sample size >200), we ran two independent replicates for 1,000,000 generations each, sampling every two generations, after a burn-in of 200,000 generations. We estimated divergence times using the equation  $\tau = 2\mu t$ , where  $\tau$  is the divergence in substitutions per site estimated by BPP,  $\mu$  is the per site mutation rate per generation, and  $t$  is the absolute divergence time in years (Walsh, 2001). We considered a mutation rate per site per year of  $5.60 \times 10^{-10}$ , which was previously estimated for glass lizards (Anguidae *Ophisaurus*; Perry et al., 2018).

## 2.7 | Analyses of genetic structure and admixture

We used STRUCTURE 2.3.4 (Pritchard et al., 2000) to investigate the genetic structure and admixture among samples of *A. taeniata* and *A. graminea*. We ran these analyses using a dataset of 1644 unlinked SNPs generated for the 38 specimens of the *A. taeniata*–*graminea* species complex (i.e. excluding the outgroup *A. fuscolabialis*). We ran STRUCTURE under the admixture model, with 200,000 iterations and discarding the first 100,000 as burn-in. We evaluated  $K$  genetic clusters (from  $K = 1$  to  $K = 10$ ), with 15 independent replicates for each value of  $K$ . We used the  $\Delta K$  statistic to interpret the number of genetic clusters ( $K$ ) that best describes our data (Evanno et al., 2005). We used the ‘greedy’ algorithm in CLUMPP 1.1.2 (Jakobsson & Rosenberg, 2007) to align multiple runs for the same  $K$  value and visualized the results using STRUCTURLY 0.1.0 (Criscuolo & Angelini, 2020).

## 2.8 | Historical demography

We assessed historical changes in effective population size ( $N_e$ ) through time for each lineage using STAIRWAY PLOT 2 (Liu & Fu, 2020),

a method based on the site frequency spectrum (SFS) that does not require whole-genome sequence data or reference genome information (Liu & Fu, 2015). To calculate the SFS for each lineage, remove all missing data, minimize errors with allele frequency estimates and maximize the number of variable SNPs retained, we downsampled each population group (lineage) to 75% of individuals using the *easySFS.py* script (I. Overcast, <https://github.com/isaacovercast/easySFS>). Final site frequency spectra contained between 1863 (*A. taeniata* L1) and 3014 (*Abronia* sp. nov. L1) variable SNPs. In analyses, we considered a 3-year generation time (Clause et al., 2016), assumed a mutation rate per site per year of  $5.60 \times 10^{-10}$  (Perry et al., 2018) and performed 200 bootstrap replicates to estimate 95% confidence intervals (Liu & Fu, 2015).

## 2.9 | Environmental niche modelling

Occurrence records of *A. taeniata* and *A. graminea* were obtained from voucher specimens deposited in natural history museums (Clause et al., 2018; García-Vázquez et al., 2022) and collected during the course of this study. To reduce the effects of sampling biases across geographical space, we ran our dataset using the ‘spThin’ package 0.2.0 in R (Aiello-Lammens et al., 2015) with 100 iterations and 10 km between localities (Boria et al., 2014; Merow et al., 2013). We obtained a final thinned dataset with 30 retained localities. To build the ENM, we used the 19 bioclimatic variables based on modified versions of the CHELSA dataset 1.2 (available at <https://chelsa-climate.org/>; Karger et al., 2017) available at Paleoclim ([www.paleoclim.org](http://www.paleoclim.org); Brown et al., 2018) with a resolution of 30 arcsec (ca. 1 km) (Table S3). Models were calibrated applying a buffer of 0.5° of radius around the thinned localities, thus likely including every area within the species’ dispersal capabilities. We built the models using WALLACE 1.1.0 (Kass et al., 2018) with the presence-background algorithm MAXENT 3.4.1 (Phillips et al., 2006, 2017), which allows to select specific model settings approximating optimal levels of complexity using the ‘ENMeval’ 2.0.0 R package (Muscarella et al., 2014). We tested different combinations of feature classes (FC: Linear; Quadratic; Linear and Quadratic; Hinge; Linear, Quadratic, and Hinge) and regularization multipliers (RM: 1.0–5.0, with 0.5 intervals). The optimal model was selected based on the Akaike information criterion corrected for small sample sizes (AICc; Warren & Seifert, 2011). Complementary to this, we evaluated the performance of the models using the ‘block’ method for data partitioning into training and testing datasets (Muscarella et al., 2014). Specifically, we calculated the area under the receiver-operating characteristic plot on the testing data ( $AUC_{TEST}$ ) and the minimum training presence omission rate ( $OR_{MTP}$ ). An  $AUC_{TEST}$  value >0.9 suggests a high discriminatory ability of the model (Peterson et al., 2011), whereas an  $OR_{MTP}$  close to zero is indicative of a low degree of model overfitting (Radosavljevic & Anderson, 2014). The ENM was projected to the present and the Last Glacial Maximum (LGM) climate conditions using the R package ‘dismo’ (Hijmans et al., 2011). Projection to the LGM (ca. 21 ka) was based on layers derived from the implementation of the CHELSA

algorithm on PMIP3 data (CHELSA; Karger et al., 2017) and available with a resolution of 30 arcsec at Paleoclim.

## 2.10 | Comparison of climatic niches

We compared the climatic niches between species pairs using the occurrence records previously applied to estimate the ENM for the species complex. We assigned species membership based on the genetic distribution of the three delineated species (*A. graminea*, *A. taeniata* and *Abronia* sp. nov.; see below) and discarding occurrences located close to the borders between them. We used the same four bioclimatic variables retained for ENM to calculate niche overlap and perform niche equivalency and niche similarity tests based on a principal component analysis (PCA-env, described in Broennimann et al., 2012; Warren et al., 2008) with the R package 'ecospat' 3.2.1 (Di Cola et al., 2017). We quantified niche overlap between each pair of species using occurrence density grids and the metric Schoener's D (Schoener, 1968). Finally, we performed niche equivalency and niche similarity tests between all pairs of species (Broennimann et al., 2012; Warren et al., 2008). We used the option 'alternative' to test for niche conservatism (alternative = 'higher'; i.e. the niche overlap is more equivalent/similar than random) or for niche divergence (alternative = 'lower'; i.e. the niche overlap is less equivalent/similar than random). We performed 1000 permutations to test each hypothesis.

## 3 | RESULTS

### 3.1 | Genomic dataset

We obtained a total of 55,710,569 single-end sequence reads from our 40 genotyped specimens, with an average of 1,392,764 reads per sample (range = 197,331–3,100,078; SD = 847,955; Table S1). The levels of homozygosity and heterozygosity at different clustering thresholds (from 0.80 to 0.99) are shown in Figure S1. The homozygosity and heterozygosity levels increased and decreased, respectively, when the clustering threshold increased. The percentage of candidate paralogous loci (i.e. with more than two alleles) decreased with higher clustering thresholds (Figure S1). The optimal clustering threshold estimated with 'easynls' was 0.96. The optimal minimum taxon coverage for the dataset was selected based on the number of loci retained, percentage of missing data and phylogenetic signal obtained in ML phylogenetic analyses in RAXML. The most informative matrix was the one in which each locus had data for a minimum of 80% of the samples in the alignments (hereafter, F96m80 dataset; Table S2). A total of 644,836 clusters were obtained for the F96m80 dataset using 10 or more reads for majority rule base calling. The number of parsimony-informative characters and unlinked SNPs for the dataset were 5087 and 1373, respectively (Table S2). The *ipy-rad* analyses estimated a mean heterozygosity of 0.0057 and a mean error rate of 0.0021.

### 3.2 | Phylogenetic analyses

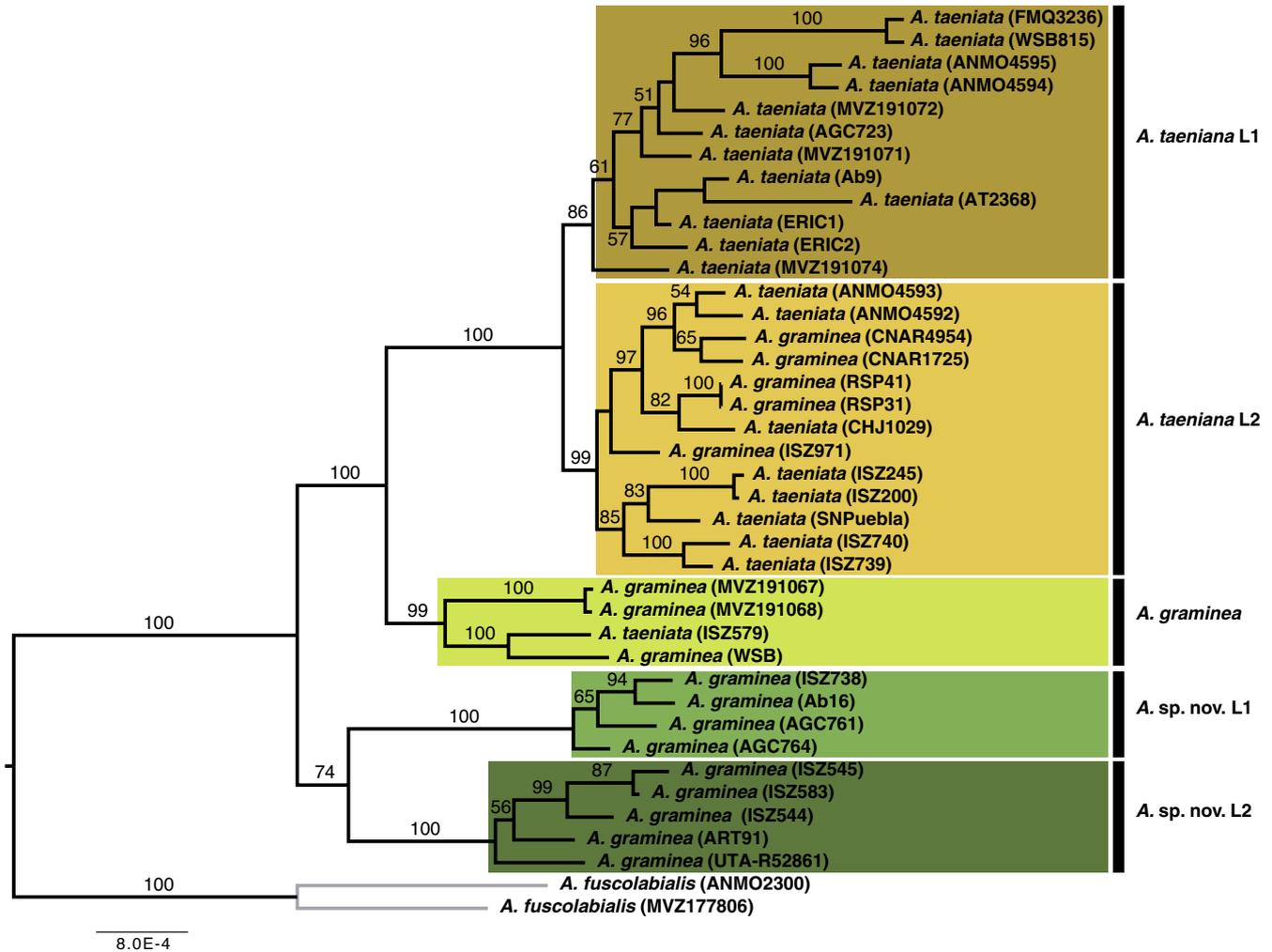
Concatenated RAXML analyses that employed different minimum taxon coverage values had virtually identical topologies (Figure 2), with the exception of the analyses based on the matrix in which each locus had data for a minimum of 70% of the samples (hereafter, F96m70 dataset; Figure S2). *Abronia graminea* and *A. taeniata* were not recovered as reciprocally monophyletic in any analysis. The topology recovered by most analyses comprises five main clades with a clear geographical pattern. Of these main clades, two exclusively contained specimens of *A. graminea* and *A. taeniata*, respectively, whereas the remaining clades included intermingled samples assigned to the two taxa (Figure 2). Of the five main clades, one contains specimens from the northernmost distribution of *A. taeniata* in the Gran Sierra Plegada and Carso Huasteco subprovinces of the SMO (hereafter, *A. taeniata* L1). This clade is sister to a clade with intermingled specimens of *A. taeniata* and *A. graminea* from central Veracruz and northern Puebla in the Carso Huasteco subprovince (hereafter, *A. taeniata* L2). These two main clades are sister to a clade composed of specimens of *A. graminea* from central Veracruz and a specimen of *A. taeniata* from Quimixtlán in central Puebla (hereafter, *A. graminea* lineage), both in the TMVB. The above three main clades are sister to two clades composed by specimens from localities in the northern portion of the SMS, one with samples exclusively assigned to *A. graminea* and restricted to Puerto del Aire in Veracruz (hereafter, *Abronia* sp. nov. L1) and a second with specimens assigned to *A. graminea* from southern Puebla and northern Oaxaca (hereafter, *Abronia* sp. nov. L2). Coalescent-based gene tree analyses in ASTRAL-III recovered the same five main clades that were obtained in the concatenated ML analysis with the F96m80 matrix (Figure 2), although with higher branch support values (Figure S3).

### 3.3 | Phylogenetic network analyses

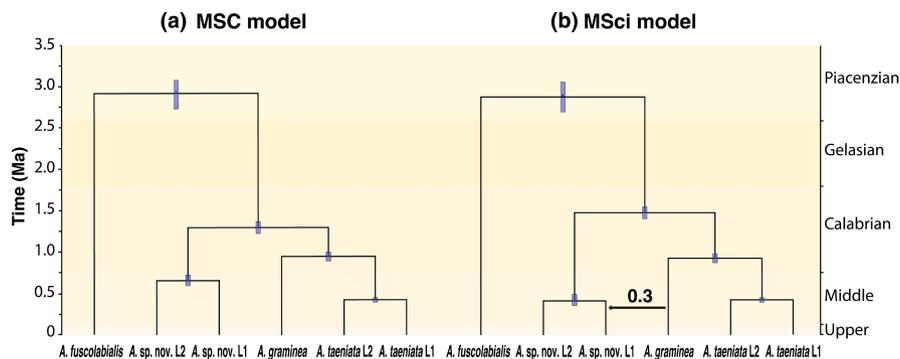
PHYLONETWORKS analyses showed a marked increase in the pseudolikelihood score from  $h = 0$  to  $h = 1$  (−13.375 vs. −9.931; Figure S4a), supporting one hybridization event as the scenario best fitting the genomic data. The hybridization event involved the introgression from *A. graminea* into *Abronia* sp. nov. L1, with ca. 24% of the genome of this lineage ( $\gamma = 0.244$ ) originated from *A. graminea* (Figure S4b).

### 3.4 | Divergence times

Time-calibrated species trees under the MSC and MSci models are shown in Figure 3. The analysis under the MSci model estimated that the split between *A. fuscolabialis* and the *A. taeniata-graminea* species complex occurred 2.82 Ma (95% highest posterior densities [HPD]: 2.64–3.00 Ma; Figure 3b). The divergence between *Abronia* sp. nov. and the most recent common ancestor of *A. taeniata* and *A. graminea* took place 1.46 Ma (95% HPD: 1.36–1.56 Ma; Figure 3b) and the divergence between *A. taeniata* and *A. graminea* dates back



**FIGURE 2** Maximum likelihood consensus tree based on RAXML analyses of arboreal alligator lizards of the *Abronia taeniata*–*graminea* species complex from central Mexico. Analyses are based on the F96m80 matrix, that is, minimum number of samples with data for a locus to be included in the alignment = 80%. Bootstrapping support values are indicated next to their respective branches. Individual codes as described in Table S1.



**FIGURE 3** Time-calibrated species trees of *Abronia taeniata*–*graminea* complex from central Mexico estimated using BPP under (a) the multispecies coalescent (MSC) model and (b) the multispecies coalescent model with introgression (MSCi). Bars on nodes indicate 95% highest posterior densities (HPD) for divergence time estimates. Geologic ages within the Pliocene (Piacenzian) and Quaternary (Gelasian, Calabrian, Middle and Upper) periods are indicated in the right y-axis.

914 ka (95% HPD: 846–983 ka; Figure 3b). The introgression from *A. graminea* into *Abronia* sp. nov. L1 occurred 367 ka (95% HPD: 304–429 ka; Figure 3b), slightly later than the separation of the two lineages of *Abronia* sp. nov. (416 ka; 95% HPD: 344–492 ka; Figure 3b).

The introgression probability ( $\phi$ ) estimated by BPP for the introgression event from *A. graminea* into *Abronia* sp. nov. L1 was 0.302 (Figure 3b), which is similar to the inheritance parameter estimated by PHYLONETWORKS ( $\gamma = 0.244$ ; Figure S4b). The split between the two lineages of

*A. taeniata* took place 429 ka (95% HPD: 401–461 ka; Figure 3b). As expected, the divergence time between the two lineages of *Abronia* sp. nov. was considerably overestimated (median = 667 ka; 95% HPD: 606–737 ka; Figure 3a) under the MSC model without considering the introgression event.

### 3.5 | Analyses of genetic structure and admixture

Bayesian clustering analyses performed with STRUCTURE supported an optimal clustering solution for  $K = 2$  according to the  $\Delta K$  criterion. At  $K = 2$ , one cluster included the specimens of the *A. taeniata* L1 and L2, and the second cluster grouped populations of *Abronia* sp. nov. L1 and L2 (Figure S5). Specimens from Pico de Orizaba in central Veracruz and from central Puebla (*A. graminea*) were identified to have an admixed ancestry. STRUCTURE analyses for  $K = 3$  detected an additional hierarchical level of genetic structuring, showing that the admixed individuals of *A. graminea* detected at  $K = 2$  form a new genetic cluster (Figure 1b; Figure S5).

### 3.6 | Historical demography

STAIRWAY PLOT 2 analyses revealed declines of effective population size ( $N_e$ ) from the LGM to present for each analysed lineage of the *A. taeniata-graminea* species complex (Figure 4). In the case of *A. taeniata* L1 and *A. taeniata* L2,  $N_e$  peaked around the LGM

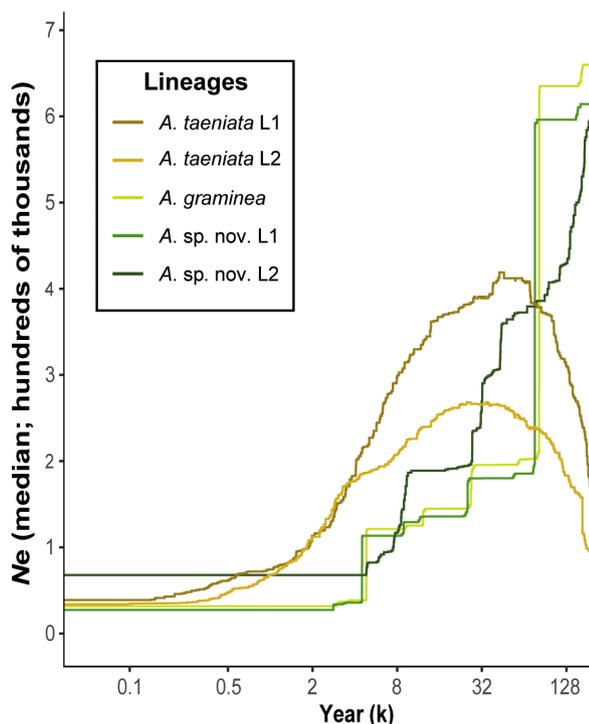


FIGURE 4 Demographic history of each lineage of *Abronia taeniata-graminea* species complex from central Mexico estimated using STAIRWAY PLOT 2. Panels show median effective population sizes ( $N_e$ ) over time (x-axis in a logarithmic scale).

followed by an abrupt demographic decline from the LGM to present (Figure 4). Analyses for the rest of the lineages (*A. graminea*, *Abronia* sp. nov. L1, and *Abronia* sp. nov. L2) suggested a continuous decline of  $N_e$  from the onset of the last glacial period to present, but they must be interpreted with extreme caution due to small sample sizes ( $n = 4$ –5 genotyped specimens per lineage; Figure 2).

### 3.7 | Environmental niche modelling

The optimal ENM according to the AICc was that with the settings LQH 4.5 (FC = Linear, Quadratic and Hinge; beta multiplier = 2.5; Figure S6). The high  $AUC_{TEST}$  ( $AUC_{TEST} = 0.887$ ) and low  $OR_{MTP}$  ( $OR_{MTP} = 0.05$ ) estimates for the model with the highest support indicate that it has high discriminatory power and a low degree of overfitting, respectively. The full summary of model comparisons is presented in Table S4. The four variables with the highest permutation importance retained in the model were precipitation of driest quarter (BIO16: 62.6%), minimum temperature of coldest month (BIO05: 31.0%), temperature annual range (BIO6: 5.7%) and mean temperature of wettest quarter (BIO07: 0.7%). The predicted potential distribution of the *A. taeniata-graminea* species complex was largely congruent with its distribution based on available records (Figure 5a). The model predicted that the distribution of the complex is almost continuous from the southern portion of the SMO (Carso Huasteco subprovince) to the SMS, with a small disjunct suitable area in the northern portion of the SMO (Gran Sierra Plegada subprovince) (Figure 5a). The projection of the ENM to LGM bioclimatic conditions predicted an expanded distribution for the complex during glacial periods in comparison to its current potential distribution, with a large area of continuous suitable habitat from SMO to SMS (Figure 5b).

### 3.8 | Comparison of climatic niches

The first two principal components of the environmental analysis explained 92.18% of the variation (54.06% and 32.43%, respectively). The niche equivalency test rejected the null hypothesis of niche identity for all pairwise comparisons ( $p < 0.05$ ; Table S5). However, no pairwise comparison showed significant niche divergence based on similarity tests (Table S5), indicating that the environmental niches of the species are not more different than expected by chance.

## 4 | DISCUSSION

Mesoamerican cloud forests are a centre of endemism for a large number of organisms (Harris et al., 2000; Rocha-Méndez et al., 2019). We have focused here on the confluence of the SMO, TMVB and SMS provinces from Central Mexico, a region with a complex

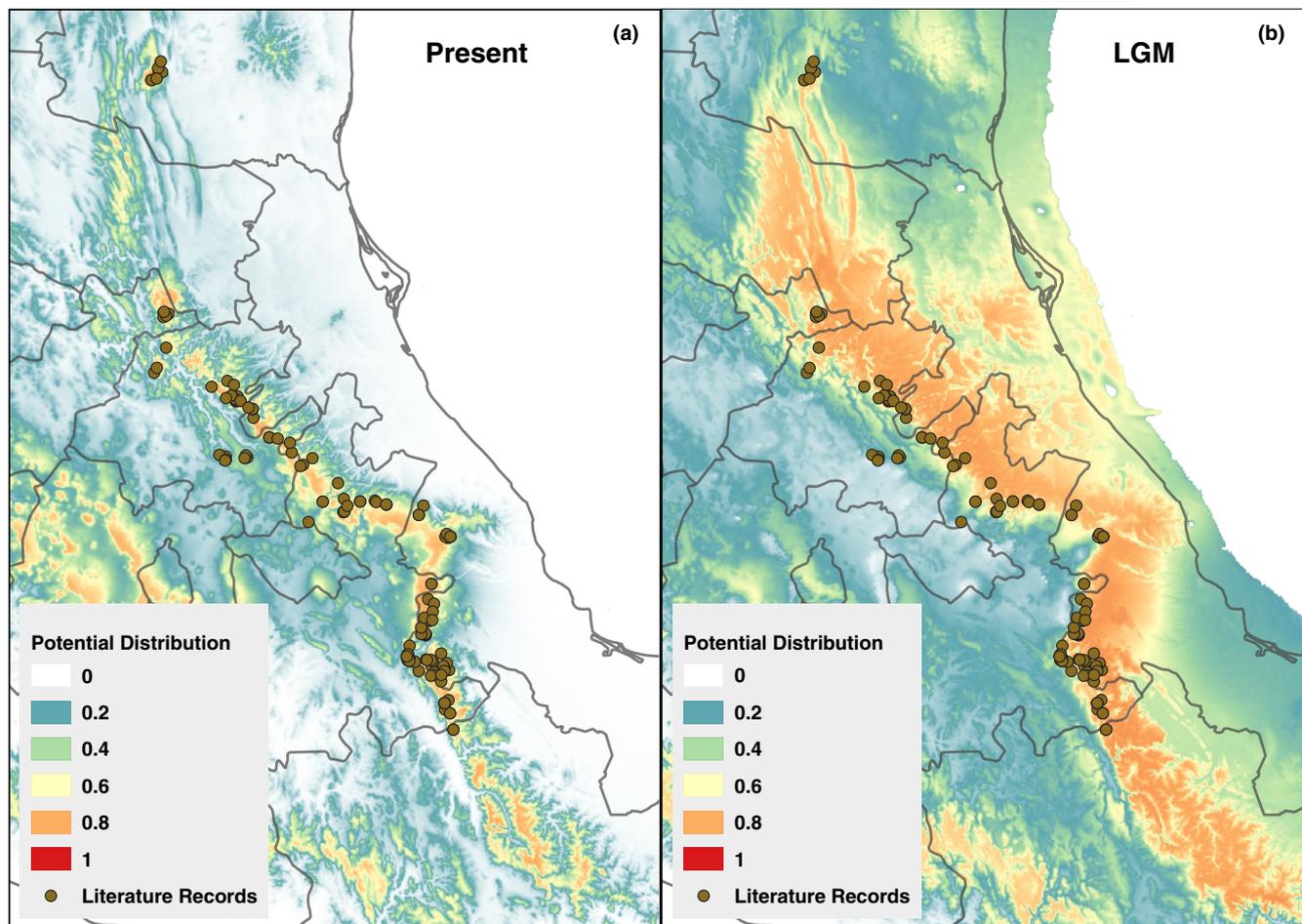


FIGURE 5 Present (a) and LGM (b) projections of the environmental niche model (ENM) in MAXENT for arboreal alligator lizards of the *Abronia taeniata-graminea* species complex from central Mexico. Dots represent all known localities of specimens deposited in herpetological collections. Maps in Plate Carrée projection. LGM, Last Glacial Maximum.

geological, geographical and climatic history (Caballero et al., 2019; De Cserna, 1989; Morrone, 2010; Sosa et al., 2016). Our results consistently supported the existence of three main genetic lineages within the *A. taeniata-graminea* complex, with a hierarchical north-to-south distribution linked to the physiographic provinces that they occupy and no evidence of sympatry between them (Figure 1). Pleistocene geologic and climatic changes have conditioned the naturally fragmented pine-oak and cloud forests inhabited by arboreal *Abronia*, which has probably limited population connectivity through extended periods of time and resulted in vicariant events within this species complex.

#### 4.1 | Diversification associated with geological events during the Pliocene–Pleistocene

Neotropical cloud forests have experienced an archipelago-like fragmentation process, making them highly suitable for studying geographical diversification and allopatric speciation processes (Luna-Vega et al., 2006). Our analyses indicated that the origin and diversification of the *A. taeniata-graminea* species complex has

been most likely shaped by the complex geologic history of the region and distributional changes of the pine-oak forests that they inhabit. Other groups of organisms inhabiting these cloud forests share similar cladogenesis patterns, including rodents (Ávila-Valle et al., 2012; Hardy et al., 2013; León-Paniagua et al., 2007), amphibians (Caviedes-Solis & Leaché, 2018; García-Castillo et al., 2018; Parra-Olea et al., 2020), lizards (Bryson et al., 2012) and birds (Mota-Vargas et al., 2017).

Palaeogeographical events associated with the formation of the low-elevation valley of the Santo Domingo River in the Papaloapan basin likely explain the split of the ancestor of the *A. taeniata-graminea* complex from *A. fuscolabialis* in the late Pliocene (2.82 Ma; 95% HPD: 2.64–3.00 Ma; Figure 3b). The age of this divergence is concordant with the radiation of arboreal mice species of the genus *Habromys*, where a vicariant speciation event was proposed to take place in this region ca. 3.92 Ma (León-Paniagua et al., 2007). Previous biogeographical studies have documented that the Papaloapan basin has played an important role promoting allopatric speciation in highland organisms with low vagility, such as small mammals (Carleton et al., 2002; Guevara & Sánchez-Cordero, 2018; Rogers et al., 2007; Sullivan et al., 1997; Vallejo & González-Cózatl, 2012), lizards (*A. antaues*

and *A. juarezi*; Solano-Zavaleta et al., 2017; *Xenosaurus grandis* and *X. manipulus*; Nieto-Montes de Oca et al., 2022), pine-oak forest birds (Mota-Vargas et al., 2017) and troglobiotic scorpions (Santibáñez-López et al., 2014). In the same line, our results suggest that climatically unfavourable areas across these low-elevation areas during both the LGM and present (Figure 5) limited and continue to limit secondary contact between populations at both sides of the valley of the Santo Domingo River (Sierra Mazateca and Sierra de Juárez).

Our dating analyses indicate that the diversification within the *A. taeniata-graminea* complex took place during the Pleistocene. The split between *Abronia* sp. nov. and *A. taeniata*+*A. graminea* occurred ca. 1.46 Ma (95% HPD: 1.36–1.56 Ma; Figure 3b), probably associated with the climatic conditions and orogenic processes of the TMVB. The topographic evolution of the TMVB began in the early- to mid-Miocene and finished in the late Pliocene and Pleistocene, changing considerably the region over the last 3 Ma (Mastretta-Yanes et al., 2015). At the end of the Pliocene, and because of a higher temperature, the geographical distribution of the *A. taeniata-graminea* complex was probably more restricted than today (Salzmann et al., 2011). At the same time, the volcanic activity of the Cofre de Perote-Citlaltépetl Volcanic Range (eastern TMVB) began in the Pliocene and continued during the Holocene, shifting southwards more recently (Negendank et al., 1985; Schaaf & Carrasco-Núñez, 2010) and promoting phylogenetic breaks in other taxa between the Sierra Mazateca and southern SMO associated with the Blanco River basin (Parra-Olea et al., 2020; Streicher et al., 2014). In this context, alternative biogeographical hypotheses have been proposed for the Oaxacan highlands. Based on vascular plants from cloud forests, the Sierra Mazateca could be a mixture between the SMO and the Sierra de Juárez (SMS; Luna-Vega et al., 1999). Alternatively, based on distributional patterns of vertebrate taxa, the Sierra Mazateca could be more closely related to the SMO than to the Sierra de Juárez (SMS) (León-Paniagua & Morrone, 2009). Our analyses support a biogeographical scenario in line with León-Paniagua and Morrone (2009)'s hypothesis.

Regarding the divergence event between *A. graminea* and *A. taeniata*, it was estimated to date back to ca. 914 ka (95% HPD: 846–983 ka; Figure 3b). According to geological records, the formation of basal structure of Cofre de Perote volcano began around 1.3–0.51 Ma (Carrasco-Núñez et al., 2010), probably limiting gene flow between populations of the common ancestor of *A. graminea*+*A. taeniata*. This biogeographical break is shared with species of anguid lizards of the genus *Celestus*. *Celestus enneagrammus* has a similar distribution than *A. graminea*, occurring in Xalapa and Orizaba in the state of Veracruz, whereas its sister species, *C. legnotus*, is distributed in the SMO of Puebla (Campbell & Camarillo, 1994; Werler & Campbell, 2004).

Finally, within *A. taeniata*, the split between the lineages *A. taeniata* L1 and *A. taeniata* L2 probably took place around Middle Pleistocene, ca. 429 ka (95% HPD: 401–461 ka; Figure 3b). Over the last 600 ka, fragmentation of species distributions was intensely favoured by climatic oscillations every ~100 ka between warm interglacial and cold glacial periods (Huybers, 2007). Besides, in the confluence zone between both lineages, situated in the Acoculco

caldera (between Hidalgo and Puebla states), the volcanic activity had an explosive event around 600 ka (Avellán et al., 2020), coinciding with the divergence between both lineages.

## 4.2 | Pleistocene climatic oscillations as an engine of speciation

Although it is clear that the high biodiversity in Mesoamerican highlands has been fuelled by a series of geological and climatic events occurred during the Pleistocene (Ferrusquia-Villafranca, 1993; Graham, 1999; Rzedowski, 1993), antagonistic hypotheses have been proposed to explain it. One hypothesis proposes that montane taxa associated with cloud forests were isolated in high-elevation refugia during Pleistocene glacial periods (Haffer, 1969; Toledo, 1982; Wendt, 1987). However, another hypothesis suggested a relict distribution of highland taxa during interglacial periods, with expansions to the lowlands during the coldest stages of the Pleistocene (Bush & Colinvaux, 1990; Colinvaux et al., 2000). In the case of the *A. taeniata-graminea* species complex, past climate model projections fit the second hypothesis. The confinement of contemporary populations to high elevations and their limited connectivity based on the projection of the distribution model to current bioclimatic conditions indicates that the species complex has probably experienced range contractions during interglacial periods. In contrast, ENM projections to the LGM inferred an increase in suitable habitats towards lowlands during the cooler stages of the Pleistocene (Figure 5). Inferences from ENM were supported by genomic-based reconstructions of the past demographic history of the complex, which showed a decrease in effective population size ( $N_e$ ) from LGM to present in all lineages (Figure 4). These results agree with genetic diversification of *Moussonia deppeana* (Gesneriaceae), a cloud forest shrub co-distributed with the *A. taeniata-graminea* species complex (Ornelas & González, 2014). During interglacial periods, warm climate would have led to the contraction and fragmentation of the cloud forest shrub populations and their displacement to higher elevations. In contrast, during the glacial periods with colder and wetter climates, populations of *M. deppeana* expanded downhill likely contributing to increased connectivity of associated arboreal lizard populations (Ornelas & González, 2014).

## 4.3 | Limited historical hybridization

Our genome-wide sequence data consistently showed no evidence for contemporary hybridization among the main lineages that integrate the *A. taeniata-graminea* species complex, which rejects the hypothesis of ongoing or recent hybridization between *A. graminea* and *A. taeniata* in a putative contact zone in the Sierra Norte de Puebla (Clause et al., 2018). The current habitat fragmentation and low connectivity among populations and the allopatric distribution of the different lineages (Figure 1a) are expected to have considerably limited the opportunity for contemporary hybridization.



However, phylogenetic network analyses revealed the existence of an introgression event (ca. 367 ka) from *A. graminea* into *Abronia* sp. nov. L1, with ca. 24% of the genome of the introgressed lineage originated from *A. graminea* (Figure 3b; Figure S4). In the same locality, a potential contact zone was described between two subspecies of the Sumichrast's harvest mouse (*Reithrodontomys sumichrasti sumichrasti* and *R. s. luteolus*; Hardy et al., 2013). Although the projection of the ENM to LGM bioclimatic conditions supported range expansions, considerable connectivity among populations, and likely secondary contact during the coldest stages of the Pleistocene, our results indicate that historical hybridization was limited to an ancient introgression event only involving two lineages with parapatric distributions. Different factors could explain limited evidence for historical gene flow. First, secondary contact between cloud forest-adapted lineages could have been limited by volcanic activity during glacial periods. This activity in the highlands from the eastern TMVB fragmented cloud forest habitats (Ferrari et al., 2012), which could have facilitated sky-island dynamics and promoted and maintained lineage divergence through the Pleistocene. Second, diverging lineages might have evolved reproductive isolation mechanisms preventing hybridization during periods of secondary contact, which might be particularly relevant considering the limited environmental niche divergence among the different species (i.e. lack of evidence for niche divergence; Table S5). Accordingly, the estimated timing of the introgression event suggests that the two lineages have not experienced gene flow during the last ca. 350 ka, despite several glacial–interglacial cycles have likely promoted shifting distributions since then and provided opportunity for secondary contact and gene flow. Thus, these two lineages could have developed reproductive isolation in allopatry or via reinforcement (i.e. selection against hybrids) during secondary contact (e.g. Tonzo et al., 2020).

The full-fledged species status of the three lineages is strengthened by the absence of contemporary gene flow between them and limited evidence for historical hybridization. In case of the existence of interbreeding between these taxa, it must be very limited geographically. The findings obtained in this study indicate the existence of three taxa that are genetically well differentiated and whose divergence dates back to >914 ka (Figure 3). The morphological characters used so far for species identification within this group, that is, adult dorsal coloration and the number of transverse dorsal and longitudinal nuchal scale rows (Clause et al., 2018), must therefore be reviewed based on our genomic-based inferences.

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## CONFLICTS OF INTEREST

The authors have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

Raw Illumina reads have been deposited at the NCBI Sequence Read Archive (SRA) under BioProject PRJNA825505. Input files for all analyses are available for download on Dryad (<https://doi.org/10.5061/dryad.6m905qg28>).

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**BIOSKETCH**

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