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Evolutionary and ecological drivers of local adaptation and speciation in a North American avian species complex

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Abstract

Throughout the speciation process, genomic divergence can be differentially impacted by selective pressures, as well as gene flow and genetic drift. Disentangling the effects of these evolutionary mechanisms remains challenging, especially for nonmodel organisms. Accounting for complex evolutionary histories and contemporary population structure often requires sufficient sample sizes, for which the expense of full genomes remains prohibitive. Here, we demonstrate the utility of partial-genome sequence data for range-wide samples to shed light into the divergence process of two closely related ducks, the Mexican duck (*Anas diazi*) and mallard (*A. platyrhynchos*). We determine the role of selective and neutral processes during speciation of Mexican ducks by integrating evolutionary and demographic modelling with genotype–environment and genotype–phenotype association testing. First, evolutionary models and demographic analyses support the hypothesis that Mexican ducks originally diverged ~300,000 years ago in climate refugia arising during a glacial period in southwest North America, and that subsequent environmental selective pressures played a key role in divergence. Mexican ducks then showed cyclical demographic patterns that probably reflected repeated range expansions and contractions, along with bouts of gene flow with mallards during glacial cycles. Finally, we provide evidence that sexual selection acted on several phenotypic traits as a co-evolutionary process, facilitating the development of reproductive barriers that initially arose due to strong ecological selection. More broadly, this work reveals that the genomic and phenotypic patterns observed across species complexes are the result of myriad factors that contribute in dynamic ways to the evolutionary trajectories of a lineage.

KEYWORDS
adaption, *Anas*, ddRAD-seq, evolution, mallard, Mexican duck, speciation

1 | INTRODUCTION

During the earliest stages of speciation, the various mechanisms of evolution (i.e., selection and gene flow) can differentially impact genomes among populations in response to changing environmental conditions (Byers et al., 2017; Harvey et al., 2019; Tobias et al., 2020). While such heterogeneous pressures can often cause local adaption (Lenormand, 2012; Meier et al., 2018; Rundle & Nosil, 2005), whether these adaptive differences result in speciation depends largely on the balance between selection and other factors such as effective population size and gene flow (Martin & Pfennig, 2009; Payne et al., 2020; Savolainen et al., 2013). Given that prezygotic reproductive barriers are slow to develop during the earliest stages of divergence (Kautt et al., 2020; Price & Bouvier, 2002), pervasive gene flow can act to homogenize the genome and swamp out locally adaptive alleles (Kautt et al., 2020; Tigano & Friesen, 2016). In addition, demographic processes (e.g., population bottlenecks) can stochastically decrease the frequency of adaptive traits due to

the differential impacts of drift (Allendorf, 1986; Chen et al., 2019). Recent species radiations—particularly those adapted to more extreme habitats (e.g., deserts)—provide unique opportunities to assess how strong, yet varied evolutionary pressures influence the speciation process (Nevo, 2011; Tobler et al., 2018). Landscape-level population sampling in conjunction with genomic data is often required to uncouple the influence of these varied evolutionary forces on the species divergence process (Ellegren, 2014).

Here, we integrate evolutionary and demographic modelling with genotype–environment and genotype–phenotype association testing to determine the role of selective (e.g., environmental and sexual) versus neutral (e.g., demographic) processes in driving divergence between mallards (*Anas platyrhynchos*) and their closely related sister species, the Mexican duck (*Anas diazi*). Mexican ducks are hypothesized to have diverged from mallards within the last 500,000 years as they became isolated in a glacial refugium and adapted to the arid habitats of southwest North America (Kulikova et al., 2005; Lavretsky, Hernández-Baños, et al., 2014; Lavretsky et al., 2015). However, incomplete lineage sorting and the potential for hybridization has made it challenging to reconstruct their true evolutionary history (Lavretsky, Hernández-Baños, et al., 2014; Lavretsky, McCracken, et al., 2014). In fact, a high prevalence of mallard-like morphological traits found in some Mexican duck populations once resulted in the inference of pervasive hybridization with mallards (Hubbard, 1977); however, recent genomic work found this to be incorrect, and rather determined that the retention of such traits in Mexican ducks was due to ancestry (Lavretsky et al., 2015). Additionally, Lavretsky et al. (2015) found that while a significant proportion of the genome was shared between these taxa, several locations were under divergent selection in either the mallard (i.e., Z-sex chromosome and autosomal chromosomes 1–4) or Mexican duck (Chromosome 14), which suggests that these regions may be associated with traits responsible for maintaining reproductive barriers. Overall, the rapid divergence of these two species caused by extreme environmental conditions provides an excellent study system for disentangling the effects that different evolutionary mechanisms have on the process of speciation.

Though speciation research has often focused on how genomic barriers develop (Cruickshank & Hahn, 2014; Feder et al., 2012; Turner et al., 2005; Wolf & Ellegren, 2017), relating these barriers to nongenic (e.g., environment and phenotype) variables is an essential next step in truly understanding the speciation process (Huang et al., 2017; Seehausen et al., 2014; Wang et al., 2020). Whereas ecological niche models have traditionally been used to approximate a species' relationship with environmental variables (Sillero, 2011), these methods fail to consider the underlying intraspecific genomic variation and local adaptation driving these connections (Layton et al., 2021; Razgour et al., 2019). Instead, using genotype–environment associations (GEAs) to model genetic niche space has been shown to improve forecasting (Capblancq et al., 2020; Rhoné et al., 2020), as these methods allow for the exploration of how genomic diversity is influenced by the environment (Razgour et al., 2019; Smith et al., 2019; Wang et al., 2010). Additionally, by estimating "genomic offset" or "genomic vulnerability"—the degree of mismatch between genomic variation modelled under current vs. past or future climate conditions—GEA approaches are being applied to approximate species' historical and future genetic niche spaces (Bay et al., 2018; Fitzpatrick & Keller, 2015; Ruegg et al., 2018). In particular, understanding how contemporary genetic variation is related to historical climate conditions can shed light on the origins of intraspecific adaptation and fine-scale population structure (Bemmels et al., 2016; Theodoridis et al., 2020; Yannic et al., 2014).

In this study, we demonstrate how environmental selection, gene flow and demographic patterns acted both individually and jointly through time to initiate divergence between these two species, and that secondarily, sexual selection has proceeded to reinforce reproductive barriers. First, we test among evolutionary scenarios, and estimate divergence time, rates of gene flow and effective population size between Mexican ducks and mallards. We also estimate time-series demographic models for both species to understand the influence of North American glacial cycles on fluctuations in demographic history. Next, we implement a multivariate machine-learning program, gradient forest (GF), to model the relationship between allele frequency changes and environmental variables. In addition to reconstructing the contemporary adaptive landscape for each of the species, we identify unique genetic niche space using a model that combines genomic information from each species. We then hindcasted the model of genotype turnover for Mexican ducks across historical climate conditions, to identify the circumstances under which Mexican ducks may have speciated. Next, given that sexual selection often acts secondarily on phenotypic differences arising from environmental selection, we use redundancy analysis (RDA) to measure the effects of genetic diversity on phenotypic variation found across Mexican ducks and mallards. We use this as a proxy for measuring whether sexual selection has been an important aspect of assortative mating and has played a significant role in maintaining species boundaries since divergence. Finally, we estimated the adaptive potential of Mexican ducks by projecting their GF model across future climate conditions, identifying areas where they are vulnerable to future climate change.

2 | METHODS

2.1 | Sampling, DNA extraction and ddRAD-seq library preparation

A total of 208 and 64 samples representing the North American ranges of Mexican ducks and mallards, respectively, were included in analyses (Table S1). In addition to previously published raw ddRAD (double digest restriction-site associated DNA) sequences of Mexican ducks (N = 95; BioProject PRJNA516035, Lavretsky et al., 2015, 2021; Lavretsky, Janzen, et al., 2019) we filled in geographical gaps by sampling tissue or blood from individuals collected from the southwest USA (N = 30); Chihuahua, Mexico (N = 65); and the western coast of Mexico (i.e., Sinaloa and

Sonora; $N = 18$) (Table S1; BioProject PRJNA800412). In addition to the ddRAD-seq data previously published for North American wild mallards ($N = 35$; BioProject PRJNA516035, Lavretsky et al., 2015, 2021; Lavretsky, Janzen, et al., 2019), we collected blood and tissue from 29 wild mallards from the southwest USA (Table S1; BioProject PRJNA800412).

For a total of 142 new samples, genomic DNA was extracted from blood or tissue using a DNeasy Blood & Tissue kit following the manufacturer's protocols (Qiagen). DNA quality was visually assessed on a 1% agarose gel to ensure high molecular weight bands, and quantified using a Qubit 3 Fluorometer (Invitrogen) to ensure a minimum concentration of 20 ng μl^{-1}. ddRAD-seq library preparation followed protocols outlined in DaCosta and Sorenson (2014; also see Lavretsky et al., 2015). In short, genomic DNA was enzymatically fragmented using *Sbf*I and *Eco*RI restriction enzymes, and Illumina TruSeq compatible barcodes ligated for future demultiplexing. Libraries were quantified, pooled in equimolar amounts, and the multiplexed library sent to the University of Oregon Core Genomics Facility for 150-bp, single-end chemistry sequencing on an Illumina HiSeq 4000 (detailed methods can be found in Document S1).

Raw Illumina reads were demultiplexed and processed using the computational pipeline described by DaCosta and Sorenson (2014; Python scripts available at http://github.com/BU-RAD-seq/ddRAD-seq-Pipeline; also see Lavretsky et al., 2015). Briefly, sequences were parsed into individual sample reads based on barcode sequences. Low-quality reads were then filtered, and identical reads were concatenated and clustered using USEARCH version 5 (Edgar, 2010) with an identity threshold of 0.85. Reads that had a quality score below 20 and do not cluster with other reads from the same individual at a 90% threshold were removed. Loci were parsed into chromosomes by using BLASTN version 2 (Altschul et al., 1990) and mapped to a mallard reference genome (Accession nos SS263068950—SS263191362; Huang et al., 2013; Kraus et al., 2011). The aligned sequences were then genotyped using custom python scripts (Dacosta & Sorenson, 2014). Homozygous genotypes were scored if >93% of reads were consistent with a single haplotype. Heterozygotes were scored if a second haplotype was represented by at least 29% of sequence reads. Samples with a secondary haplotype in 7%–20% of reads, and putative heterozygote samples with a third haplotype in more than 10% of reads were flagged as ambiguous. To further limit the effect of sequencing error, we required a minimum sequencing depth of five reads to score an allele, such that a minimum of 10 reads was required to score a locus as homozygous or heterozygous. Loci with <15% missing genotypes were retained for downstream analyses, and final output files. More detailed bioinformatics methods can be found in Document S1.

To limit the effects of recent introgression with mallards on GEA and demographic analyses, only Mexican ducks of pure ancestry were included (Bay et al., 2018; Fitzpatrick & Keller, 2015). In addition, only wild mallards collected from their North American breeding grounds were used.

2.2 | Gene flow at an evolutionary scale

First, we used the diffusion approximation program ∂a∂i (Gutenkunst et al., 2010) to test empirical data against specified evolutionary models of divergence between Mexican ducks and mallards. Briefly, ∂a∂i uses a forward in time diffusion approximation modelling approach to create a model site-frequency spectrum (SFS) based on a specified evolutionary scenario to test against an empirical SFS. We calculated the best fit model for comparisons between mallards and all Mexican ducks. We converted Nexus-formatted concatenated sequencing data into a folded two-dimensional SFS for each species (Gutenkunst et al., 2009, 2010; Hernández et al., 2021). To account for missing data and a lack of shared variants, we projected down the number of alleles for each data set by averaging across all possible resamplings of the full sample size—Mexican ducks ($N = 325$ alleles) and mallards ($N = 100$ alleles). We tested empirical data against five different evolutionary models including Isolation-with-Migration, Isolation-without-Migration, Split-Migration (i.e., secondary contact), Split-without-Migration and Neutral-No-Divergence. We determine the best-fit model based on the best log-likelihood of the optimal parameters across five replicates of each model. We then performed 50 independent parameter optimization runs and used the geometric mean of these results as the final optimal parameters, as well as to calculate uncertainty metrics (i.e., standard deviation; Coffman et al., 2016; Gutenkunst et al., 2009). Evolutionary models in ∂a∂i simultaneously estimate time since divergence ($t = T \times 2N_{ANC}$; t = time since divergence in generations), contemporary ($N_i = v_i \times N_{ANC}$) and ancestral ($\theta = 4N_{ANC} \times \mu$; N_{ANC} = ancestral effective population size) effective population sizes, and migration rates ($m_{i \leftarrow j} = M_{i \leftarrow} j/(2N_{ANC})$; $m_{i \leftarrow j}$ = proportion of migrants per generation in population i from population j) using a scaling factor θ (Gutenkunst et al., 2009).

To convert parameter estimates from ∂a∂i demographic models into biologically informative values, we estimated generation time (G) and overall mutation rates (μ). First, generation time (G) is calculated as $G = \alpha + (s/(1 - s))$, where α is the age of maturity and s is the expected adult survival rate (Sæther et al., 2005). For both Mexican ducks and mallards, we used an age of maturity (α) of 1 (Baldassarre, 2014). Additionally, given that data on Mexican duck survival are lacking, we used the adult survival (s) as estimated in mallards ($s = 0.574$; Reynolds et al., 1995). Finally, to obtain a scaled mutation rate for autosomal markers, we started with a mutation rate of 1.2×10^{-9} substitutions per site per year, which is considered to be the mean nuclear mutation rate for various mallard complex species (Peters et al., 2012, 2014). While variation in the rate of substitutions across the genome can influence ∂a∂i parameter conversions, this best estimate is based on the mean overall rate as calculated across 22 noncoding loci, with each locus being located on a different chromosome (Peters et al., 2012). This mutation rate was then scaled to the generation time for each species ($G = 2.35$) before being multiplied by the total number of base pairs ($N = 270{,}895$) to get a final mutation rate scaled to substitutions per site per generation (s/s/g).

2.3 | Modelling demographic history through time

Long-term demographic histories for Mexican ducks and mallards were estimated following the approach of Hernández et al. (2021), which uses ∂a∂i to model changes in effective population size through time. Briefly, we used custom python scripts (scripts available at https://github.com/jibrown17/Dove_dadi.demographics; Hernández et al., 2021) to calculate a one-dimensional SFS from Nexus-formatted concatenated sequencing data. Each species' SFS was folded and masked (Gutenkunst et al., 2009, 2010; Hernández et al., 2021) before being projected down by averaging across a resampling of the larger data set (N_{MEDU} = 400 alleles, N_{MALL} = 140 alleles). Next, based on a custom demographic model (Hernández et al., 2021; https://github.com/jibrown17/Dove_dadi.demographics) that uses 100 iterations of the single population integration function ("*Integration.one_pop*" in ∂a∂i), ∂a∂i creates a model SFS which is used to estimate the optimum parameters of effective population ($N_n = v_n \times N_{ANC}$, N_n = effective population size at the *n*th time interval) and time intervals ($t_n = T_n \times 2 \times N_{ANC} \times G$, t_n = total years before present at the *n*th time interval and G = generation time) for each integration step. These optimum parameters are then scaled to the empirical data using θ ($\theta = 4N_{ANC} \times \mu$; N_{ANC} = ancestral effective population size), which is then used to calculate the actual effective population size through time (for detailed methods on custom demographic models see Hernández et al., 2021). We then used the geometric mean calculated across 50 replicates of parameter optimization for each model and estimated the goodness of fit for each model by calculating the log-likelihood of the model given the empirical data. Finally, we estimated confidence intervals (CIs) using parameter uncertainty metrics included in ∂a∂i (Coffman et al., 2016; Gutenkunst et al., 2009). Uncertainty metrics were calculated across a range of step sizes ($\varepsilon = 10^{-2}$ to 10^{-7}) to maximize the number of parameters for which ∂a∂i is able to return a true estimate of uncertainty (Blischak et al., 2020; Coffman et al., 2016; for detailed methods on uncertainty metrics see Hernández et al. (2021). We converted each ∂a∂i parameter into biologically informative values as described above.

2.4 | GEA modelling with GF

For GEA testing, we obtained contemporary environmental data that are available at a high resolution from several public databases. We chose a total of 27 environmental variables that are thought to have impacts on bird physiology and ecology, and that might be strong drivers of adaptation (Table S3; Bay et al., 2018).

We downloaded and used as predictors a suite of 19 climate variables from the WORLDCLIM version 1.4 database (https://www.worldclim.org/version1, 30 arc-second [~1 km] resolution; Hijmans et al., 2005); Landsat Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI) and Net Primary Productivity data from the USGS AppEEARS database (https://lpdaacsvc.cr.usgs.gov/appeears); and elevation data from the Global Land Cover Facility (http://www.landcover.org). In order to differentiate the effects of annual versus seasonal vegetation processes, we calculated an average annual, summer (June) and winter (December) value for NDVI and EVI based on data collected from 2000 to 2019.

Following the approach of Bay et al. (2018; also see Fitzpatrick & Keller, 2015), we used a GF analysis as implemented by the R package GRADIENTFOREST (Ellis et al., 2012) to test which environmental predictor variables most strongly explain patterns of allele frequency turnover in Mexican ducks and mallards. GF analysis was originally created to detect the effects of environmental predictor variables on species turnover across a landscape (Ellis et al., 2012), but has since been adapted for measuring allele frequency turnover (Bay et al., 2018; Fitzpatrick & Keller, 2015). Briefly, GF uses a machine learning regression tree-based algorithm (i.e., random forests) to detect shifts in allele frequency across an environmental gradient, where a function is built for each individual single nucleotide polymorphism (SNP; the response) before an aggregate function is created for all SNPs across each independent predictor variable (Fitzpatrick & Keller, 2015).

For use in GF, we converted independent bi-allelic SNPs into minor allele frequencies using the package POPGENOME (Pfeifer et al., 2014) in the program R and subsequently filtered any SNP that was polymorphic in fewer than five total sampling sites (Fitzpatrick & Keller, 2015). Using a large number of trees (N = 5000), GF produced an R^2 ranked list of weighted importance for all environmental variables. To assess the performance of actual GF models for both species, and to rule out the chance that results were influenced by spurious correlations, the environmental predictor data were randomized in relation to sampling sites. We then compared the performance of 100 models created with randomly generated data to our observed model. To visualize the GF model for each species across North America, we extracted values for the top five environmental variables from random points generated across their home range. We then used a principal components analysis (PCA) to summarize the transformed values from the top five predictor variables (based on R^2 weighted importance) for each point. Finally, we transformed the top three principal components to create a RGB colour scale that was used to visualize different patterns of adaptive genetic diversity across the landscape. In the end, colours reflect associations between allele frequencies and the environmental predictor variables that allow us to draw conclusions about how the environment has affected genetic diversity and putatively driven adaptation.

Finally, in a novel use of GF analysis, we combined independent species' models of allele frequency turnover to test for partitioning of genetic niche space between species. Briefly, the *combinedGradientForest* function in R acts to standardize independent models to one another by calculating a combined function of cumulative importance, which represents the overall relationship in both species between allele frequency turnover and the environmental predictor variables. Additionally, during standardization, cumulative importance functions for each variable are weighted based on the total R^2 value of the combined GF. As previously described, we visualized the combined model by predicting the GF object across geographical

space before converting the PCA into a standardized RGB colour scale.

2.5 | Modelling past and future patterns of diversity

To estimate the potential threat of climate change to Mexican ducks, we used GF to model GEA across future climate conditions and subsequently measure the genetic offset (i.e., Euclidean distance between contemporary and future GF models) from current GEA space (Bay et al., 2018; Fitzpatrick & Keller, 2015). Additionally, we extended this method to measure the offset between contemporary and historical patterns of genetic diversity to better understand the evolution and adaptation of Mexican ducks through time. Future and past bioclimatic variables from Global Climate Models (GCMs) were downloaded at the highest available resolution: Last Interglacial (LIG; ~130,000 years before present [BP]; 30 arc-second resolution; Otto-Bliesner et al., 2006); Last Glacial Maximum (LGM; ~22,000 years BP; CCSM4 at 2.5 arc-minute resolution; Hijmans et al., 2005); Mid-Holocene (~6000 years BP; CCSM4 at 30 arc-second resolution; Hijmans et al., 2005); and two future (2070) scenarios of climate change (rcp2.6 and rcp8.5; CCSM4 at 30 arc-second resolution; Hijmans et al., 2005).

2.6 | RDA phenotype–genotype association testing

Using a subset of individuals ($N_{MEDU} = 165$; $N_{MALL} = 6$; Table S1) for which phenotypic data were available, we used RDA to test for associations between genotypes and phenotypic traits that could be important for assortative mating. The traits used here were previously identified to differentiate pure Mexican ducks from mallards and their hybrids (Table S2). We compared all samples and each sex separately using a concatenated Autosomal + Z-sex chromosome data set. Additionally, we also tested for significant associations within the Z-sex chromosome only as this region was predicted to be linked to phenotypic traits between these two species (Lavretsky et al., 2015).

Following the procedure of Talbot et al. (2017), we used a PCA to summarize genotypic variability from bi-allelic SNP loci and reduce the number of predictor variables to be included in RDA. Briefly, bi-allelic SNPs were filtered for linkage-disequilibrium in PLINK version 1.07 (Purcell et al., 2007) and reformatted as a STRUCTURE file. We then performed a PCA in the R package *ADEGENET* (Jombart, 2008) with the "*dudi.pca*" function; we kept the top 50 PCs (hereafter referred to as genotypic PCs) for association testing with RDA. For each of the data sets described, we tested the effect of genotypic PCs on phenotypic variability using the "*rda*" function in the R package *VEGAN* (Dixon, 2003; Legendre & Gallagher, 2001). To account for bias created by population structure, we assigned each individual sample a value of 1–5 that corresponded to previously identified genetic clusters (Lavretsky et al., 2015), and used this variable as a confounding factor. Here, RDA was used to account for multiple response variables and provided an estimate of the effect of genotypic variation on the phenotypic traits as a whole (Talbot et al., 2017). Additionally, we identified individual traits within the tails of the distribution for RDA loadings ($\alpha = 0.1$), as well as the genotypic PCs most strongly associated with them. We then returned to the initial genetic PCA to count the number of SNPs found in the tails of the distribution of significant genotypic PCs ($\alpha = 0.05$). Finally, we used the "*envfit*" function from the R package *VEGAN* (Dixon, 2003) to test if these individual genotypic PCs identified by RDA significantly explain the response variables.

3 | RESULTS

3.1 | ∂a∂i evolutionary models

∂a∂i analyses of autosomal SNPs supported an optimum evolutionary model of split-with-migration (Table S4). Parameters were converted into biologically informative values using an average mutation rate of 7.63×10^{-4} s/s/g. First, ancestral N_e for Mexican ducks and mallards ($N_{e\ ANC} = 451{,}092$; 95% CI = ±11,032) was lower than contemporary estimates (Table S4). Contemporary effective population size of mallards ($N_e = 1{,}372{,}661$; 95% CI = ±97,899) is ~2 times larger than Mexican ducks ($N_e = 608{,}035$; 95% CI = ±21,590). Divergence time between Mexican ducks and mallards was 995,227 years BP (95% CI = ±25,796), which was nearly three times those estimated from ∂a∂i demographic models as well as previous studies (Lavretsky et al., 2015; Lavretsky, DaCosta, et al., 2019). We note that the discrepancy in time since divergence estimates is probably the result of the constraints within and the simplicity of premade ∂a∂i evolutionary models used here; additionally, when using these simplistic models of speciation, ∂a∂i has been shown to dramatically overestimate divergence in cases of complex cyclical population change (Momigliano et al., 2021). Finally, with bidirectional gene flow assumed in the split-with-migration model and in terms of chromosomes per generation, we scaled these values to the N_e of each population to get the number of migrants per generation. Migration was significant in both directions, but with estimates of migration from mallards into Mexican ducks ($m_{MALL\text{-}MEDU} = 20$; 95% CI = ±0.60) being ~2 times higher than from Mexican ducks into mallards ($m_{MEDU\text{-}MALL} = 9$; 95% CI = ±0.27).

3.2 | ∂a∂i demographic modelling

Models of demographic history estimated N_e up to at least 500,000 years BP (Figure S1), and demarcated distinct demographic histories for mallards and Mexican ducks. First, we find that mallards retained an N_e of ~1.6 million individuals (95% CI = ~1,500,000 to ~1,900,000) until ~500,000 years BP and have since experienced an exponential increase to a contemporary N_e of ~3.3 million individuals (Figure 1). For Mexican ducks,

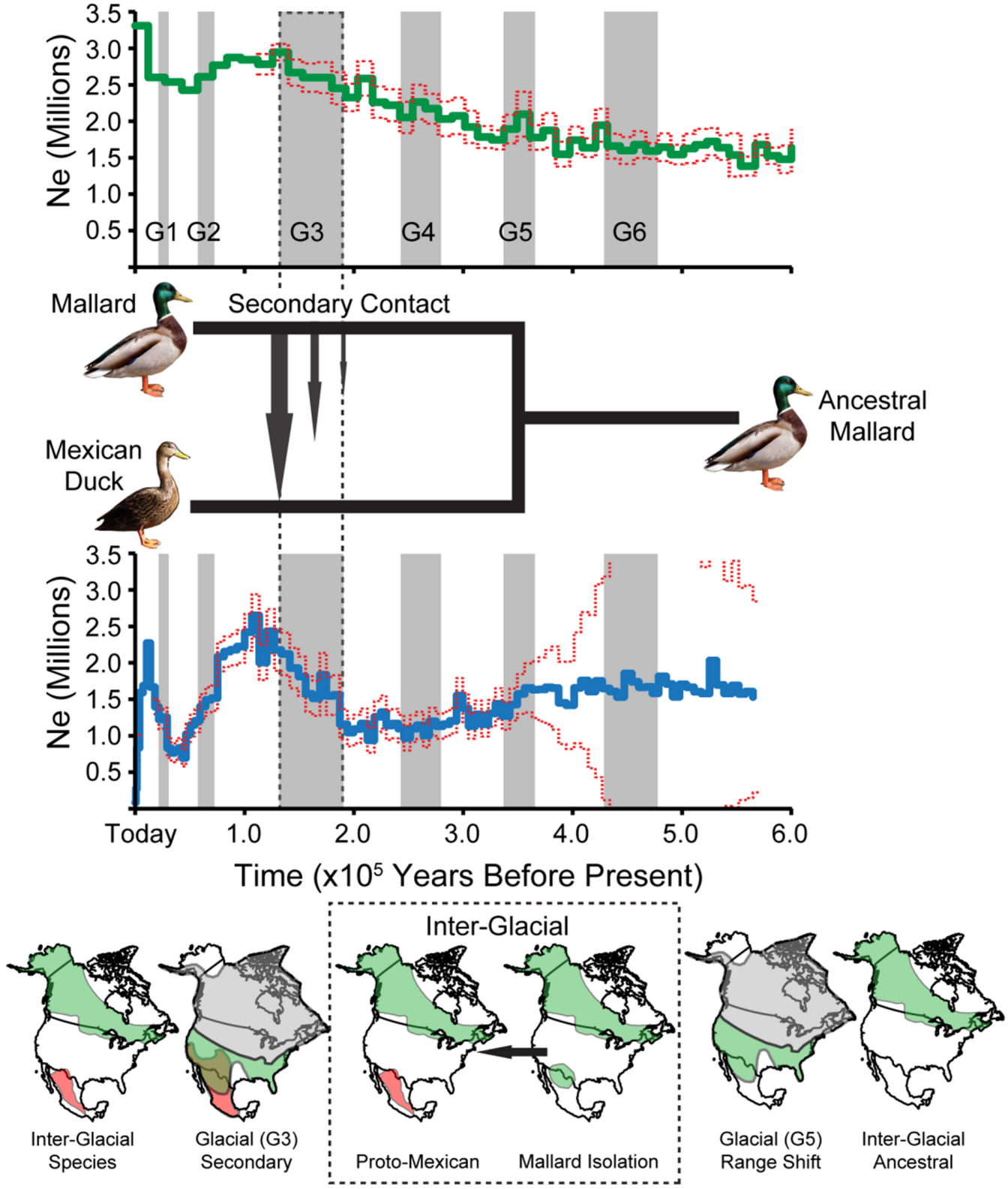

FIGURE 1 Time-series ∂a∂i demographic models for Mexican ducks and mallards. Dotted red lines indicate 95% confidence intervals. Glacial and interglacial periods are denoted in grey and white bars, respectively, with glacial advancements also identified (Batchelor et al., 2019). An evolutionary model of the divergence process between Mexican ducks and mallards is overlaid, including how glacial cycles impacted this process

we recovered cyclical trends in their N_e. Specifically, Mexican ducks retained a consistent N_e of ~1.6 million individuals (95% CI = 0 to ~2,000,000) that broadly overlapped mallards until ~350,000 years BP. At this time, Mexican ducks diverged in N_e by declining slightly until ~200,000 years BP, followed by a gradual rise to ~2.5 million individuals; this was nearly identical to the N_e

of mallards at that time point (Figure 1; see Section 4). Finally, this increase was followed by two distinct bottleneck events that occurred within the last 100,000 years, with the most recent one providing a contemporary estimate of ~130,000 Mexican ducks (Figure 1).

3.3 | GEA modelling

The GF model for Mexican ducks found associations between genotype and environment in 1005 out of 9158 SNPs (11.0% of SNPs had a positive R^2 value), while the mallard model recovered 410 out of 4386 SNPs (9.3% of SNPs had a positive R^2 value). The number of SNPs with positive R^2 values ($N = 1005$) and the mean R^2 value ($N = 0.134$) for the Mexican duck data set was consistently greater than the upper 95% quartile of values from randomized data sets (Figure S2). GF analysis for only mallards was not significant compared to randomized models (SNPs with positive R^2 value: $N = 410$; mean R^2 value: $N = 0.114$). Finally, the combined Mexican duck × mallard GF model did have more SNPs with positive R^2 values ($N = 1450$) and a mean R^2 value ($N = 0.125$) higher than that of the combined randomized data sets.

Of the top five environmental predictors identified by GF for Mexican ducks, three were related to seasonal changes (Bio15, NDVI-winter, Bio11), while the second most predictive variable was elevation (Figure 2). Variables related to precipitation, geography, vegetation and temperature were all found to be important, suggesting that a variety of environmental factors play a role in driving Mexican duck allele frequencies across their range (Figure S3). While GF models for mallards did not perform better than the randomized models, three of the top five variables were similarly related to seasonal changes (Bio10, Bio5, EVI-winter), although temperature and vegetation growth played a more important role in driving genotype frequencies than precipitation (Figure S3).

Graphing principal components of GF outputs for Mexican ducks showed a signal of local adaptation, with different environmental predictors having the strongest effects in different populations (e.g., allele frequencies in west coast samples are more strongly affected by the temperature variable Bio11; Figure S4). We then generated a map of environmentally associated allelic turnover across North America based on the PCAs for Mexican duck, mallard and combined GF models (Figure 2). In Mexican ducks, GF showed the most significant genomic turnover outside of its native range (i.e., the Rocky Mountain region, the central Canadian prairies, and the eastern USA). More subtle differences that correspond to population structure occurred within its range in the central highlands of Mexico (i.e., southwestern USA and Chihuahua, Mexico) and along the western coast of Mexico (i.e., Sinaloa and Sonora). Alternatively, mallards show minimal genotype turnover across their primary breeding grounds in central Canada, which is reflected by the tighter clustering of samples in GF PCA results (Figure S4). Finally, the combined GF model showed significant genotype turnover concordant with the native range of Mexican ducks in southwestern North America, and with the combined PCA clearly partitioning GEA space between the two species. Together, this suggests that environmental selective pressures are differentially driving divergence in allele frequencies between Mexican ducks and mallards.

3.4 | Genotype–phenotype association testing

RDA showed a significant effect of genotypic PCs on phenotypic traits for the full data set as well as in the male-only data sets; there were no significant effects found in females (Table 1). All associations were significant when accounting for population structure (Table 1). All of the concatenated Autosomal/Z-sex chromosome data sets as well as the Z-sex chromosome male-only data set had a similar percentage of genetic markers identified as being significantly associated with phenotypic variation (12.6%–13.6%), which was ~3 times the percentage identified within female Z-sex chromosome markers (4.7%). Phenotypic traits identified as significant varied across data sets, with male variation generally being associated with wing characteristics and females being characterized by a mix of traits on the wing, head and belly (Table S5; Figure S7). Finally, strong partitioning between Mexican duck and mallard samples plotted along RDA axes showed that genetic variation within these species can explain at least a portion of their phenotypic variation (Figure S8).

3.5 | Genomic offset from past and future climate conditions

Using only the top five temperature and precipitation variables (Bio4, Bio8, Bio11, Bio15, Bio18) we subtracted GF-modelled allele frequencies under contemporary climate from differing historical and future climate conditions, to get a measure of genomic offset (the difference between genomic variation as related to environment through time) in Mexican ducks (Figure 3 and Figure S5). Models of genotype turnover for Mid-Holocene (~6000 years BP) climate conditions resembled contemporary models, with the only noticeable offset being predicted along the western coast of Mexico (Figure S6). Next, there is significant offset from the LGM (~22,000 years BP) and the LIG (~130,000 years BP) periods. During the LGM, genetic offset identified a significant increase in the Mexican duck's southwestern US range where their genetic diversity is associated with favourable environmental conditions. In contrast, LIG climate conditions probably caused a restriction in adaptive niche space for Mexican ducks in the northern and eastern parts of its contemporary range, leaving their core adaptive range restricted to deep interior Mexico. Finally, genetic offset from future climate (2070 rcp2.6 and rcp8.5) identified severe habitat loss under the most severe climate change conditions only (rcp 8.5), with habitats along the western coast of Mexico and in the central Mexican highlands of Chihuahua to be most impacted (Figures 3, S5 and S6).

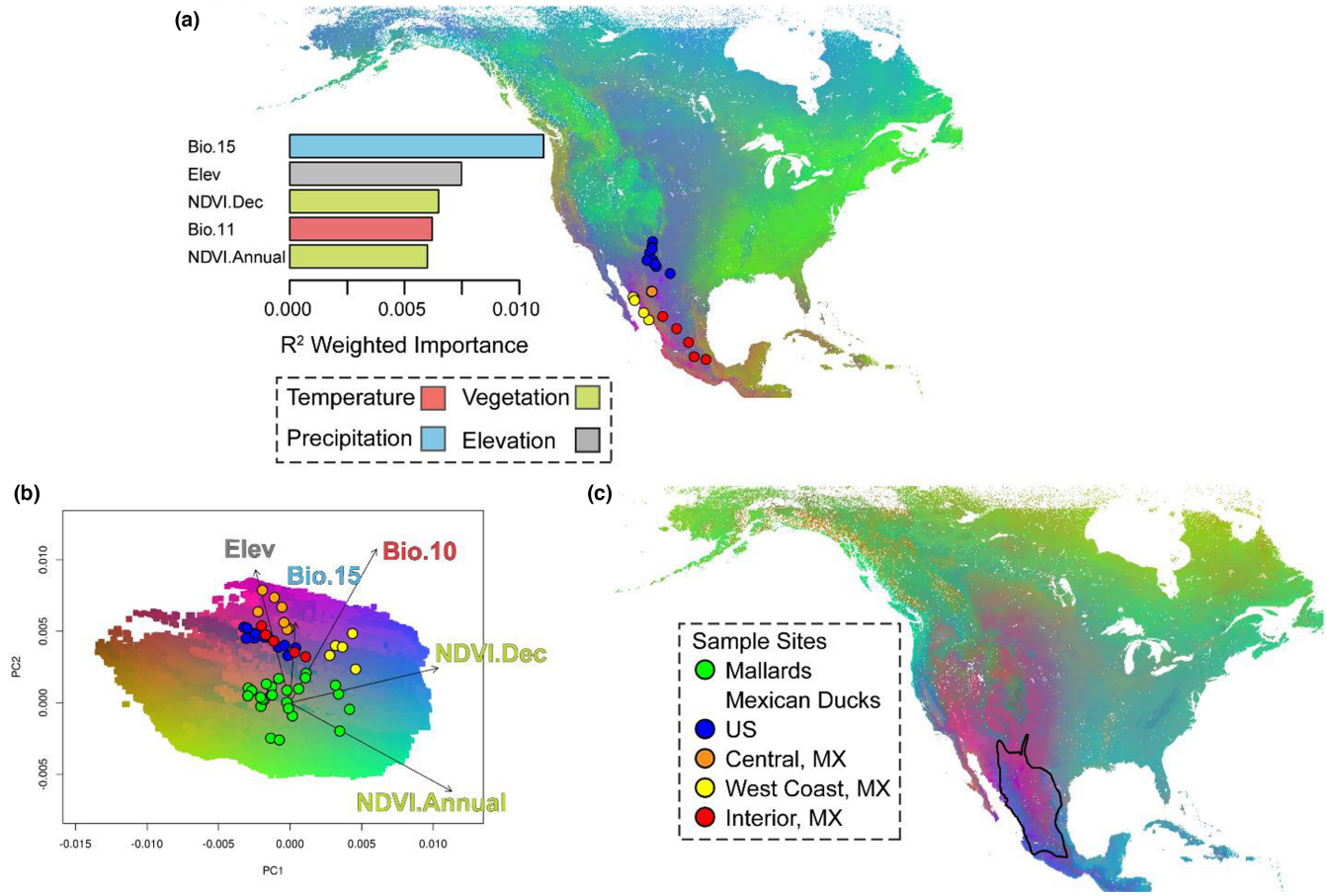

FIGURE 2 Genotype–environment association models from gradientForest (GF) mapped across North America for (a) Mexican ducks. Sample sites are categorized (i.e., US, Central, etc.) according to genetic populations identified by Lavretsky et al. (2015). Inset: the top five most predictive environmental variables based on cumulative R^2 weighted importance. The combined Mexican duck and mallard GF model (b) PCA and (c) map. The black outline represents the current Mexican duck range as adapted from *Birds of the World* (Drilling et al., 2020)

TABLE 1 Significance and R^2 of RDA testing for phenotype–genotype associations

	Aut & Z chromosomes	Aut & Z chromosomes males	Aut & Z chromosomes female	Z chromosome males	Z chromosome females
p	**.005**	**.015**	.843	**.039**	.185
Conditional[a] R^2	.1282	.1463	.20445	.1463	.205
Constrained[b] R^2	.3492	.4585	.769	.433	.791
No. of predictive SNPs	1178 (12.6%)	1247 (13.2%)	1082 (13.0%)	30 (13.6%)	11 (4.7%)

Note: Bold values indicate a model where genetic markers explain a significant proportion of the phenotypic variation ($p \leq .05$).

[a]Proportion of the variation explained by conditional variables (i.e., population structure).

[b]Proportion of the variation explained by constrained axes.

4 | DISCUSSION

4.1 | Glacial cycles induce divergence, secondary contact and range shifts between two closely related species of ducks

While vicariance resulting from glacial advancement has been directly responsible for the diversification of many North American avian taxa (Johnson & Cicero, 2004; Licciardi et al., 2004; Weir & Schluter, 2004), arid habitats of the Southwest were indirectly impacted by heterogeneous climate conditions across the landscape (Hewitt, 1996, 2000). This kind of environmental heterogeneity would result in habitat fragmentation, subsequently giving rise to isolated "climate refugia" (Gavin et al., 2014; Jaeger et al., 2005). Taxa with wide distributions and high adaptive potential (e.g., mallards) are more likely to use these fragmented climate refugia during glacial periods (Douglas et al., 2006; Stewart et al., 2010), which can often result in rapid divergence in isolation (Hewitt, 2000; Stewart et al.,

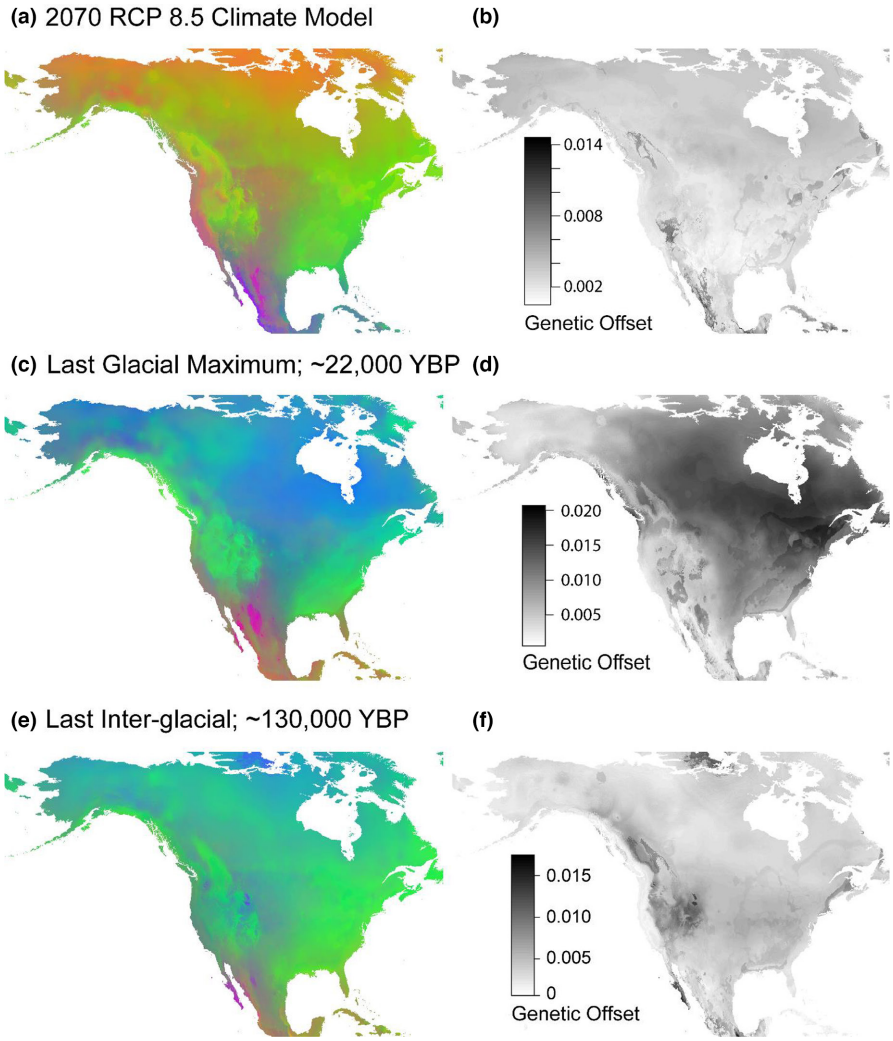

FIGURE 3 Mexican duck genotype–environment association models from gradientForest (GF) based on only the top five most predictive temperature and precipitation variables. Associations are modelled across historical and future environmental data for (a) 2070 under the most extreme (rcp8.5) projections of climate change, (c) the Last Glacial Maximum (~22,000 years BP) and (e) the Last Interglacial (~130,000 years BP). (b, d, f) Genomic offset calculated from the Euclidean distance between models based on contemporary and historical climate conditions mapped across North America

2010). First, our study further supports the importance of these climate refugia in southwestern North American species divergence. In doing so, we provide concordant evidence for the hypothesis that Mexican ducks originated when strong selective pressures allowed a subset of isolated mallards to persist within a southwestern climate refugium (Figure 1). In particular, mapping combined genetic niche space across North America not only recapitulated current breeding ranges of both species, but also demarcated significant genotypic turnover in transition zones of their distributions (Figure 2). Such partitioning in genetic niche space probably indicates that ecologically driven divergent selection could be an important evolutionary force that differentially impacted the genetic diversity of Mexican ducks and mallards.

In reconstructing the evolutionary history of the Mexican duck, all analyses support a scenario in which Mexican ducks and mallards have only recently diverged and have come into secondary contact one or more times since. Such an evolutionary scenario is supported by both species' comparative (Table S4) and species-specific demographic (Figure 1) models. Specifically, effective population sizes remained identical until ~350,000 years BP (Figure 1), a time of divergence that is identical to earlier estimates (Lavretsky, Hernández-Baños, et al., 2014), suggesting that this time-period was when a proto-Mexican duck population first began to diverge from an ancestral mallard population. The advancing Laurentide ice sheet probably initiated species divergence by creating isolated pocket(s) of mallards in known southwestern North American glacial refugia (Figure 1; Hernández et al., 2021; Sarabia et al., 2020). Based on models of the LGM (~22,000 years BP; Berger et al., 2016) there is high genomic offset for Mexican ducks throughout much of northern and eastern North America, indicating that southwestern North America was probably a climate refugium (Figure 3; Batchelor et al., 2019).

While the expansion and contraction of the Laurentide ice sheet during the G5 glaciation created a more hospitable niche space that allowed Mexican ducks to initially diverge from mallards, subsequent glacial periods continued to cause fluctuations in range that would probably bring about cycles of isolation and secondary contact. Following the initial divergence in demographic history ~350,000 years BP, these two species continued on independent trajectories until Mexican ducks began increasing ~200,000 years BP, reaching an effective population size nearly identical to that of mallards (N_e = ~2,000,000; Figure 1). Although it is possible that Mexican duck numbers naturally increased over this 50,000-year period, estimates of effective population size are unlikely to reflect this type

of sudden increase, as they often lag behind increasing census sizes (Gasca-Pineda et al., 2013; Lonsinger et al., 2018; Miller & Waits, 2003). Instead, these patterns are more consistent with the effects of gene flow, which can artificially increase estimates of diversity (Sato et al., 2020); thus, the convergence of effective population suggests that a major gene flow event occurred during the G3 glacial period ~150,000 to ~200,000 years ago (Figure 1). Note that this G3 glacial period is the longest of those occurring since Mexican ducks diverged from mallards, and thus provided mallards the greatest opportunity for secondary contact with recently diverged Mexican ducks (Figure 1). Pervasive gene flow occurring during this major period of secondary contact is therefore likely to be responsible for the unbalanced number of migrants moving from mallards into Mexican ducks as detected by our evolutionary models (Table S4). Moreover, models of GEA and genomic offset confirm that glacial periods were more conducive to a northern expansion, as suitable genetic niche space for Mexican ducks during the LGM was more expansive throughout the Southwest and intermountain regions of North America (Figure 3). Alternatively, interglacial periods showed a more fragmented and limited range of stable niche space restricted deep in western interior Mexico; significant turnover across the northern parts of this range also indicates strong barriers to expansion during interglacial periods. Together, we hypothesize that a simultaneous northern expansion of Mexican ducks and southern push of the mallard's range during glacial periods results in increased range overlap, while warm interglacial periods result in phases of isolation and limited gene flow (Figure 1; Moodley et al., 2020; Yamasaki et al., 2020).

Since this major secondary contact event, we find that mallards and Mexican ducks have maintained divergent effective population sizes. Specifically, mallard populations continued growing while Mexican ducks fluctuated (Figures 1 and 3). Given that Mexican ducks currently maintain low levels of hybridization despite the capacity to interbreed with mallards (i.e., ~0%–5%; Lavretsky et al., 2015), as well as show significant divergence from mallards in genetic diversity associated with ecologically (Figure 2) and sexually selected traits (Tables 1 and S5), we posit that the major gene flow event occurring early in the divergence process probably acted to facilitate the development of strong reproductive barriers (Butlin & Smadja, 2018; Feder et al., 2012). In general, here we provide support for the role of glacial cycles in facilitating local adaptation and subsequent species divergence, as well as demonstrate how glaciers may significantly influence genomic diversity and adaptation throughout the entire speciation process. Moreover, our study further demonstrates that when working with landscape-level species sampling, partial genome sequencing data are effective in modelling complex evolutionary histories, estimating fine-scale demographic changes, and identifying associations between genotypes and phenotypes or the environment.

4.2 | Environmental drivers of adaptive divergence

GF models indicate that not only did glacial events provide the strong ecological selection necessary to induce divergence of proto-Mexican duck populations from mallards, but that their partitioned niche space continues to have differing selective impacts on contemporary genomic diversity. First, unlike mallards, for which GF found that allele frequencies are minimally impacted by the environment, genetic diversity among sampled Mexican ducks showed a significant association with various environmental factors (Figures 2 and S3). Specifically, precipitation seasonality (Bio15) was identified as the most important environmental variable affecting Mexican ducks (Figure 2), which was expected given that water availability is limited across its range (Lecomte et al., 2009; Perez-Arteaga et al., 2002; Scott & Reynolds, 1984). Additionally, we found that variables related to geography (i.e., elevation), seasonal vegetation and seasonal temperature changes are also important, suggesting that allele frequencies are responding to changes in seasonal weather patterns (excluding elevation) as opposed to annual precipitation and temperature. This kind of response to seasonal weather shifts is consistent with other desert-adapted waterfowl, such as grey teal (*A. gracilis*) and Pacific black ducks (*A. superciliosa rogersi*) in Australia (McEvoy et al., 2017; Roshier et al., 2006), which generally breed year-round when habitat and climate conditions become ideal (Cumming & Ndlovu, 2015).

Next, whereas temperate species often experience increased habitat suitability and population growth during interglacial periods (Hewitt, 1999; Provan & Bennett, 2008), our GF models provide further evidence supporting the claim that species in more arid habitats respond in a contradictory manner (Stewart et al., 2010). In concordance with patterns seen in other avian taxa from more arid habitats, for example white-throated butcherbirds (*Cracticus subgenus Bulestes*; Kearns et al., 2014), we show that increased Mexican duck habitat suitability occurs during glacial periods when temperate vegetation is more abundant across the Southwest, while contracting during interglacial periods when this range becomes arid (Metcalfe et al., 2002). Specifically, in a pattern that was probably repeated throughout the Pleistocene (Lockwood, 2001), southwestern habitats of the LGM were dominated by continuous woodlands of pinyon pine and juniper, which became fragmented by expanding desert vegetation under the extreme drought conditions that began during the current interglacial period (~13,000 years ago; Betancourt, 2004; Thompson & Anderson, 2000). Therefore, reduced habitat connectivity during interglacial periods probably limits dispersal across environmental gradients, facilitating strong intraspecific genetic structure and local adaption. In fact, this fragmentation is most evident in our contemporary interglacial model for Mexican ducks, where the central highlands of Chihuahua are acting as montane habitat "islands" surrounded by mountainous regions (i.e., the Sierra Madre Occidental to the west and the Sierra Madre Oriental in the east) and which are represented by areas of high genomic turnover (Figure 2). Overall, these results demonstrate not only the inverse responses of southern and northern latitude taxa to glacial cycles, but the potential impact these cycles have on future intraspecific genetic diversity and local adaption of southern latitude groups.

4.3 | Sexual selection as a post-divergence co-evolutionary mechanism

Sexual selection often acts as a co-evolutionary process that promotes divergence on top of other evolutionary mechanisms (Rundle & Rowe, 2018). This secondary process occurs as selection arising from ecological differences accentuates variance in plumage characteristics that simultaneously act as species recognition cues (Price, 1998). For Mexican ducks, it is now evident that the loss of dichromatic mallard-like traits occurred as proto-Mexican duck populations diverged and eventually became monochromatic. This phenomenon is common in southerly species facing harsh habitat conditions (i.e., deserts; Hill, 1994), as sexual selection is often relaxed where natural selection is strongest (Lavretsky et al., 2020; Omland, 1997; Stuart-Fox & Ord, 2004). However, the partitioning between Mexican ducks and mallards in genetic diversity that is significantly associated with phenotypic characters related to female mate choice suggests that sexual selection has secondarily acted to promote assortative mating (Figure S8; Marchetti, 1993; Seddon et al., 2013). Among traits, those associated with wings were the most significant across analyses (Table S5, Figures S7 and S8), with the speculum being particularly important. Given that wing markings and speculum colour are known cues for waterfowl mate pairing (Eliason & Shawkey, 2012; Omland, 1996), this suggests that the drab plumage coloration originally arising due to strong environmental selection on proto-Mexican duck populations has since become an important species recognition cue that acts as a prezygotic reproductive barrier (Seddon et al., 2013). Moreover, sexual selection working in concert with environmental selection can reduce the propensity for lineage fusion during secondary contact events (Cooney et al., 2017). Future work to understand the role of sexual selection in the speciation process would benefit from mate-pair studies to determine how female mate choice occurs in Mexican ducks and mallards. Additionally, ddRAD-seq loci used here are noncoding and are therefore unlikely to be under the direct influence of selection (DaCosta & Sorenson, 2014; Lavretsky et al., 2015); thus, whole genome sequencing will be necessary for a more fine-scale investigation of potential linkage between sexually and environmentally selected traits.

4.4 | Vulnerability to future climate conditions

Understanding the genetic basis for adaptation has become a major component of evaluating the vulnerability of natural populations under future climate change scenarios (Razgour et al., 2019). Incorporating adaptive potential allows us to better predict areas where contemporary diversity may harbour alleles that remain adaptive under future climate conditions, as well as identify migratory pathways to suitable habitat that becomes newly available (Gougherty et al., 2021; Meester et al., 2018). While GEA modelling under the mildest estimate of climate change (rcp2.6) shows very little offset from contemporary conditions (Figure S6), the more extreme model (rcp8.5) suggests that Mexican ducks may be vulnerable to future maladaptation throughout the core of their range in central Chihuahua as well as along the western coast of Mexico (Figure 3). In fact, the extreme offset in central Chihuahua is consistent with past interglacial periods where intense drought conditions throughout the region have caused large bodies of water to be reduced or lost altogether (Castiglia & Fawcett, 2006). Moreover, wetland loss will probably be exacerbated by land-use changes, which cannot be accounted for in GF modelling, as wetlands throughout the central highlands of Mexico are being drained at a rapid pace for agricultural purposes (Perez-Arteaga et al., 2002). This has already led to a serious decline in local waterbird populations throughout the region as critical breeding habitat is lost (Mellink et al., 2018; Perez-Arteaga et al., 2002). Along the western coast of Mexico, increasing surface temperatures in the Pacific Ocean are affecting sea-levels and regular climate oscillations (Lim et al., 2019). Specifically, sea-level rise is associated with saline intrusion along coastal wetlands, which can subsequently lead to habitat loss through native plant mortality and invasive plant encroachment (Saintilan et al., 2019). Additionally, El Niño events have become weaker as the region warms, which has been shown to negatively affect breeding and moulting phenology in local populations (Mellink, 2000; Wingfield et al., 1999). While incorporating genomic diversity allows us to more effectively model how adaptive potential can mitigate the effects of habitat loss in the future, we cannot predict how these negative trends may act to exacerbate the effects of the bottlenecks Mexican ducks have experienced over the last 13,000 years, as the loss of genetic diversity often limits a species' adaptive potential (Willi et al., 2006). However, we note that without more explicit data on movement and migratory patterns of Mexican ducks, we cannot rule out the possibility of newly suitable habitat being colonized as they abandon deteriorating habitat conditions.

4.5 | Advancements and conclusions

Identifying the relationship between genomic divergence and the myriad evolutionary mechanisms that underly these patterns is the critical next step in understanding the speciation process. However, recognizing such relationships can be especially challenging when the effects of selection, drift and gene flow are working together in a way that creates only subtle signals of divergence in the observed, contemporary genome. Here, we overcome this by using an extensive range-wide sample set of Mexican ducks to model GEAs and genotype–phenotype associations occurring throughout the genome, and find that GF models identified a significant subset of SNPs in Mexican ducks that are strongly associated with environmental variables. While standard outlier methods based on relative differentiation (i.e., F_{ST}) have alternatively been used to identify islands of differentiation (Irwin et al., 2018; Turner et al., 2005), these methods depend on the strength of selection and background divergence. In particular, loci putatively under selection can be missed in cases of local adaptation not linked to reproductive barriers, as relative divergence often remains low when selection is acting on many alleles of small effect (Le Corre & Kremer, 2012; Yeaman, 2015). For example, while Lavretsky

et al. (2015, 2019) were able to use F_{ST} outlier methods (e.g., Bayescan) to identify a few genomic regions under strong divergent selection in either Mexican ducks or mallards, our GEA analysis finds evidence of selection acting throughout the genome. Overall, we contend that when full genome sequencing data are unavailable, a landscape-level GEA analysis of reduced-representation sequencing data can be more effective at detecting evidence of selection acting on alleles of small effect than traditional F_{ST} outlier methods.

Finally, our study provides insight into broad spatiotemporal responses to changing selective pressures in a uniquely desert-adapted species of waterfowl, demonstrating the role of climate refugia and glacial cycles in driving intra- and interspecific divergence. Looking at models of evolutionary and demographic histories, GEAs and phenotype–genotype associations demonstrates that a complex relationship between the environment, selection and adaptation exists throughout the speciation process. Additionally, we report that GEA methods could be effective at demonstrating ecologically based divergent selection between closely related species, as well as at visualizing how past climatic conditions act to structure contemporary genetic diversity on the landscape. Specifically, we find that Mexican ducks probably diverged within a climate refugium arising during a glacial period, and that cyclical population expansions and contractions in response to these glacial cycles subsequently facilitated intraspecific population structure (Figure 1). More broadly, our work reveals that the evolutionary mechanisms driving speciation are not singular, and that the complex associations between many different factors play a role in this process. Additionally, we demonstrate the importance of incorporating adaptive potential when predicting vulnerability to future climate conditions, as these types of landscape-level data sets can help to identify areas where conservation efforts will be most critical. Finally, we demonstrate that reduced-representation molecular data for landscape-level sample sets remain useful and powerful in providing insight into the evolutionary history of nonmodel systems. Nevertheless, future work would benefit from whole genome sequencing, which would allow for a more nuanced look at the effects of neutral vs. selective processes on genomic architecture.

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CONFLICT OF INTEREST

All authors declare that they have no conflicts of interest.

AUTHOR CONTRIBUTIONS

J.I.B. and P.L. conceptualized the project. P.L. supported data acquisition. J.I.B., R.H. and P.L. collected and analysed molecular data and equally contributed to the writing of the manuscript.

DATA AVAILABILITY STATEMENT

DNA sequences: BioProject PRJNA800412, GenBank accessions SAMN25245926–SAMN25247720.

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