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The integration of whole-genome resequencing and ecological niche modelling to conserve profiles of local adaptation

Jong Yoon Jeon[1] | **Yucheol Shin**[2] | **Andrew J. Mularo**[3] | **Xiao Feng**[4] | **J. Andrew DeWoody**[1,3]

[1]Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana, USA

[2]Department of Biological Sciences, Kangwon National University, Chuncheon, Korea

[3]Department of Biological Sciences, Purdue University, West Lafayette, Indiana, USA

[4]Department of Biology, University of North Carolina, Chapel Hill, North Carolina, USA

Correspondence
Jong Yoon Jeon, Department of Forestry and Natural Resources, Purdue University, 715 W State St, West Lafayette, IN 47907, USA.
Email: jeon96@purdue.edu

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Abstract

Background: Ecological and genomic attributes of populations can provide two orthologous perspectives on the biological profiles associated with local adaptation. The ability of organisms to track suitable habitats (ecological adaptability) and of populations to shift allele frequencies (adaptive potential) are prerequisite for population sustainability.

Aims: Many contemporary populations are threatened by habitat loss (ecological vulnerability) and a lack of adaptive potential (evolutionary vulnerability). Technical advances provide new opportunities to address these challenges in biological conservation: Future habitat shifts can be predicted by ecological niche modelling and adaptive genetic diversity can be discerned using genome sequence data. Together, these two approaches illuminate the local adaptation profile and help identify the environmental and genomic conditions that should maximize evolutionary fitness.

Materials and Methods: Here, we reviewed the primary literature to identify key studies that utilize both whole-genome resequencing (WGR) and ecological niche modelling (ENM) in an effort to envisage future research directions that may benefit conservation efforts.

Results: We identified ways to integrate different approaches, such as ENM-informed adaptive genomics and adaptive genomics-informed ENMs, that can be used to delineate and conserve local adaptation profiles.

Discussion: Integrative approaches can identify adaptive characteristics, vulnerable populations subject to environmental changes, and the patterns of local adaptation from geographic and genomic analyses. We discuss future research directions, limitations and their potential solutions with suggestions for collaborative workflows.

Conclusion: The integration of WGR and ENM is promising with their continuous advancement. An integrative approach can be used to evaluate eco-evolutionary attributes, at both organismal and molecular levels, that can be used to help conserve local adaptation profiles.

KEYWORDS
adaptive evolution, gene–environment interactions, habitat suitability modelling, landscape genomics, natural selection, species distribution modelling

1 | THE USE OF GENOMICS AND NICHE MODELLING TO CONSERVE PROFILES OF LOCAL ADAPTATION

The conservation of threatened and endangered species requires that viable populations maintain suitable habitat and genetic/genomic diversity in the face of environmental flux. Revealing the distribution of adaptive genomic variants across space and time (i.e., adaptation profile) is particularly critical for understanding population persistence in the face of environmental perturbations (e.g., emerging infectious diseases, climate change, habitat fragmentation, etc.). Adaptation profiles can form the scientific foundation for management efforts, such as prioritizing geographic regions to conserve or identifying the best source populations for assisted migration efforts. Furthermore, associations between genotype and environment can highlight both genomic and geographic regions that are worthy of further investigation as potential drivers of local adaptation (Lasky et al., 2023). Although it is much easier to demonstrate correlation than causation, the still-emerging fields of conservation genomics and niche modelling are now intersecting and have great synergistic potential to help provide a detailed roadmap for future mechanistic studies into adaptation profiles.

Technological advances over the last decade have resulted in the widespread adoption of population whole-genome resequencing (WGR) approaches, whereby the entire genomes of multiple individuals are sequenced for comparison to a representative reference sequence of the species and to each other. For economic reasons, WGR approaches are often conducted at low coverage in non-model species, and in this review, we refer primarily to such low-coverage WGR datasets. With the development of novel bioinformatics tools, falling prices for DNA sequencing, and enhanced computing infrastructure, large WGR projects are now feasible even in species with genomes >1 Gb (e.g., Andrews et al., 2023; Mathur, Mason, et al., 2023; Mathur, Tomeček, et al., 2023). Lou et al. (2021) showed that the sequencing price of low-coverage WGR projects is comparable with that of reduced representation sequencing studies (RRS; e.g., genotyping-by-sequencing and restriction size-associated DNA sequencing). The number of such WGR projects is growing rapidly relative to RRS for many reasons (Figure 1 and Appendix S1 for details; DeWoody et al., 2022).

When integrating genomic and environmental variation, we think WGR is the most desirable approach to characterize adaptive profiles. This is because of its ability to identify all manner of genomic variants, from single nucleotide polymorphisms (SNP; genetic variants at a single base position in the DNA sequence such as an adenosine, "A," or a thymine, "T") to structural variants. WGR can be used to detect large genomic variants and patterns of linkage disequilibrium (e.g., using Manta (Chen et al., 2016) and Delly (Rausch et al., 2012) for structural variants; ngsLD (Fox et al., 2019) and PLINK (Chang et al., 2015) for linkage; see also Liu et al., 2023). Often, such variants are associated with local adaptation (Akopyan et al., 2022; Mérot et al., 2023; Wilder et al., 2020). The increased statistical power associated with the vast number of WGR loci is another critical benefit for population genetic analyses (e.g., effective population sizes, selection signals and functional connectivity) as WGR leverages a dense array of markers spread across an entire genome whereas RRS typically surveys <5% of a genome (Davey & Blaxter, 2010). Although inexpensive, the sparse genomic coverage of RRS undermines its value, especially in selection scans since there is no direct way to capture signals of adaptation on particular

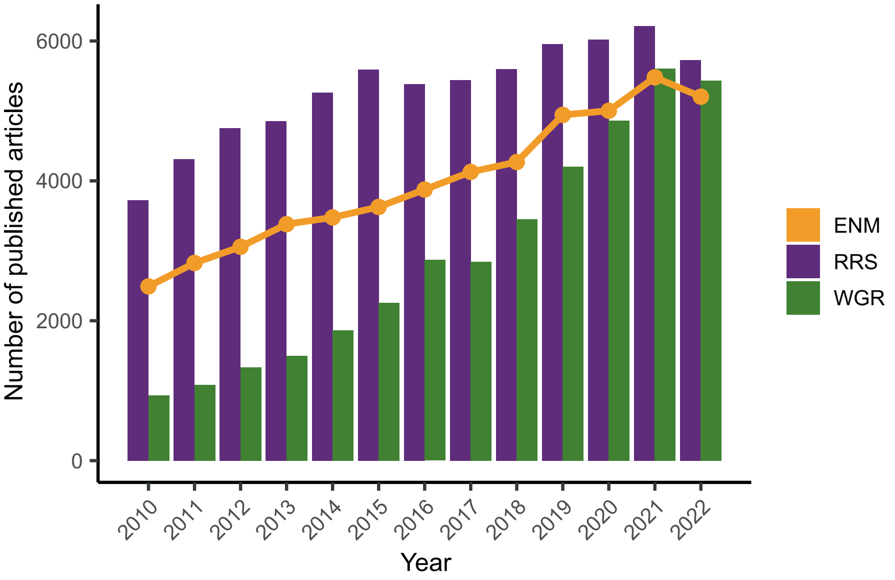

FIGURE 1 Trends in the number of published articles used Ecological Niche Modelling (ENM; yellow line), Reduced Representation Sequencing (RRS; purple bar), and whole-genome resequencing (WGR; green bar) from 2010 to 2022. ENM and WGR studies continue to increase at a similar rate, whereas RRS studies appear to be approaching a plateau.

genomic regions (Lou et al., 2021; Lowry et al., 2017). For example, Mathur, Mason, et al. (2023) and Mathur, Tomeček, et al. (2023) have used WGR data to quantify both genetic load (the burden of deleterious alleles) or genetic thrust (the benefit of adaptive alleles) by leveraging annotations of protein-coding genes and their biochemical properties to categorize alleles into function bins that can be compared across populations. Annotated reference genomes and WGR datasets can be leveraged to identify genomic regions containing elevated (or reduced) variation that are indicative of strong selection (Hohenlohe et al., 2021). WGR analyses can focus entirely on such genic regions to more accurately reflect the specific nucleotide substitutions that underlie adaptive variation, or focus on gene deserts (i.e., intergenic regions) that are more prone to stochastic genetic drift (and less to natural selection) as a product of population demography. Therefore, unlike RRS studies, WGR studies can reveal both the patterns and processes associated with the generation and maintenance of adaptive variation in wild organisms.

Ecological niche modelling (ENM), in the strictest sense, can be an umbrella term for techniques used to characterize ecological niches, suitable habitats, and either potential or actual distributions (Peterson & Soberón, 2012). ENM as an analytical technique is also termed as habitat suitability modelling or species distribution modelling, depending on the ultimate objective (Peterson & Soberón, 2012). Herein, we refer to ENM as a general term that can encompass both habitat suitability and species distribution modelling. ENM has been broadly used in ecology and evolutionary studies, and it is frequently used to provide a quantitative basis for conservation practices (Araújo et al., 2019; Franklin, 2010; Peterson et al., 2011). The ENM approach typically builds upon the known geographic range of a species and the associated environmental conditions to quantify habitat requirements. ENM is commonly used to identify the potential distribution of a species given spatial and temporal constraints. As we usually do not have reliable data on the absence of species (Gu & Swihart, 2004), ENM predictions are often based on pseudoabsence data and usually interpreted as the relative probability of a species' occurrence or the relative suitability of a particular habitat (Merow et al., 2013). Ecological niche modelling provides critical insights into habitat suitability over time (e.g., Mendoza-González et al., 2013) and these models can then be associated with studies of genetic/genomic diversity (GD) across the landscape (e.g., Duncan et al., 2015). For example, theory predicts that habitat that has long supported large populations will harbour more GD than geographically restricted or isolated habitats (e.g., islands) that can only support small populations (Reed, 2004).

The intersection of conservation genomics and habitat modelling has already provided important insights into adaptation profiles. For example, recent synergistic studies that combined ENM and WGR have yielded insights into the fluctuation of species' distribution over time compared to their historical demographic trajectories (e.g., Brüniche-Olsen et al., 2021), the ecological niches of genetic lineages (genomics-informed ENM; Hudson et al., 2021), and to infer habitat corridors for gene flow (Shryock et al., 2021). These three examples are all based on "neutral" genomic approaches, meaning that their inferences were based on genome-wide outcomes primarily determined by demographic events rather than natural selection. However, a significant advantage of combining ENM and WGR resides in the detection of locally adapted genes, species, or populations because the analyses complement each other. For example, many genomic methods such as Genotype-Environment Association (GEA; Lasky et al., 2023) and genomic offset (Rellstab et al., 2021) are dependent on statistical relationships (linear, logistic, or curvilinear, etc.) at the "gene" level to identify potential GEAs. In contrast, ENM is based on environmental associations at the "individual" or "population" level, regardless of the implicit complexity of them. Thus, "ENM-informed genomics" should be powerful in the context of adaptive genomics, just like "genomics-informed ENM" in the context of niche modelling.

Historically, ENM has been integrated with RRS data in studies of local adaptation (Razgour et al., 2018, 2019). RRS approaches have provided key insights and are especially valuable for species with gigantic genomes (e.g., salamanders and ferns). Here we exploit the rising number of WGR studies to demonstrate why and how WGR should be integrated with ENM with particular focus on the ability of WGR data to illuminate adaptive genetic characteristics. Efforts to integrate genomics and ENM are accelerating (e.g., the recent WIGGIS workshop, https://wiggis.eu/) as WGR becomes more affordable (Wetterstrand, 2021) and as ENM applications broaden (Peterson et al., 2022). Like others (e.g., Waldvogel et al., 2020), we think that comprehensive, integrative studies of individual genomes and their distributions in space and time have great potential to identify adaptation profiles and help guide conservation efforts. In this paper, we have reviewed recent studies that have utilized both ENM and adaptive/structural genetic variation to characterize local adaptation (a detailed description of our overall review process and the exact search terms we used are in Appendix S1). We aim to bridge the current gap between the analysis of WGR data and the application of ENM, with particular emphasis on the conservation of local adaptation profiles. Both fields are replete with technical terms, so we provide a brief glossary in Box 1. [Throughout this paper, we use the term "population" to refer to a group of entities (individuals of DNA samples, individuals with geocoordinates, or individuals in the wild, etc.) that share similar genetic, ecological, or geographic characteristics that make them suitable to analyse collectively. We use the term "cluster" to denote a collection of "populations" that are characterized by their ecological or genetic similarities, whereas we use the term "lineage" when a historical context is associated with a genetic cluster.] Our paper is both retrospective and prospective, as we highlight empirical examples from the recent literature and where we think future studies could prove fruitful.

2 | APPROACHES THAT INTEGRATE WGR AND ENM

Whole-genome resequencing data can be united with ecological niche modelling in many ways. The general workflows of WGR and

BOX 1 Glossary.

Adaptive Capacity: The general ability of a species or population to respond to environmental change by phenotypic plasticity, dispersal, or genetic diversity.

Adaptive Potential: The potential ability of species or population to adapt to selective forces through heritable changes.

Balancing Selection: A type of selection in which genetic variation is elevated and maintained longer than neutral expectation due to heterozygote advantage, frequency-dependent selection, spatiotemporally varying fitness, etc.

Ecological Adaptability: The potential ability of species or population to adapt by modifying their ecological characteristics such as distribution or behaviours.

Ecological Vulnerability: The decrease in future habitat suitability (for a given species or population) as estimated by ecological niche modelling.

Ensemble Modelling: A methodological framework whereby potential outcomes are predicted by many different models/algorithms or by many different datasets.

Evolutionary Rescue: A strategy or phenomenon where population growth is recovered, and extinction risks are mitigated by augmented genetic diversity, usually from translocated or dispersed individuals from genetically healthy populations to genetically depauperated populations.

Evolutionary Vulnerability: The decrease in adaptability often because of limited adaptive genetic diversity (genomic vulnerability).

Fundamental Niche: The set of abiotic conditions under which a species exists.

Genetic Load: The decrease in fitness of a population due to the accumulation and expression of deleterious mutations, most realized in inbred populations.

Genetic Thrust: The increase in fitness of a population due to the accumulation and expression of advantageous mutations.

Genomic Offset: The mismatch between the current and future adaptive genomic composition required due to environmental conditions, a measure of genomic vulnerability.

Genotype-Environment Interaction: Differential responses of various genotypes in various environments, often studied via common garden (i.e., transplant) experiments.

Genotype Likelihood: The probability of observing a particular genotype at a given nucleotide site (e.g., G/A heterozygote or GG homozygote), incorporates statistical uncertainty from diverse error sources, such as sequencing and mapping errors.

ENM Hindcasting/Forecasting: A practice in ENM that projects a calibrated ecological niche model to historic or future environmental conditions.

Incomplete Lineage Sorting: Persistence of ancestral trans-species polymorphisms due to random genealogical processes such that gene trees do not correspond to species trees, more likely observed in historically large populations than in historically small populations.

Introgressive Hybridization: Incorporation of alleles from one species into the gene pool of another species via hybridization and subsequent backcrossing.

Landscape Genetics: The scientific discipline that integrates population genetics, landscape ecology, and spatial statistics to identify and quantify landscape features that impede/facilitate gene flow or affect microevolutionary processes, can progress into landscape genomics with the use of genome-wide markers.

Linkage Disequilibrium: Often abbreviated LD, the non-random association between alleles at different loci; LD is often due to close physical proximity of genes, random genetic drift, or natural selection that favours a coadapted gene or allele complex.

Pangenome: The complete gene pool (i.e., collection of all genomic variants) of an entire species, population segment, or phylogenetic lineage.

Raster: Spatial data defined as an array of grid cells with attribute values.

Realized Niche: The subset of ecological conditions that permit a species to exist in the presence of biotic interactions and abiotic restrictions, a segment of the fundamental niche which represents the entire set of abiotic ecological conditions in which a species can persist.

BOX 1 (Continued)

Selective Sweep: An evolutionary process by which a beneficial allele increases its frequency while concomitantly reducing genetic variation of linked loci.

Spatial Extent: A geographic range defined by two-dimensional geocoordinates, onto which niche models are fitted and predicted.

Spatial Resolution: The dimension of the raster grid cells that determines the precision of spatial representation.

Standing Genetic Variation: Preexisting variation in a gene pool.

Structural Genetic Variation: Often called SVs for structural variants, these are large polymorphisms (often defined as ≥50 base pairs in length) that include insertions, deletions, inversions, translocations, and duplications, that may produce copy number variants.

Temporal Resolution: Temporal scales of species occurrence and environmental datasets.

ENM are each summarized in Figure S1. These two approaches can be merely combined (i.e., comparing independent findings of two approaches) or they can be unified (i.e., findings from one approach can provide a base for the other) as shown in Figure 2. Here we focus on the adaptive aspects of genomics that can be inferred only by WGR. For detailed explanations of the workflows and practical approaches, see Boxes S1, S2 and Tables S1–S3.

2.1 | Combining independent ENM and WGR results to identify local adaptation

Most simply, a species' adaptive genetic variation and ecological niche can be analysed independently in parallel and then combined for interpretation (Figure 2a). The two approaches of WGR and ENM are complementary as they assess both ecological and evolutionary facets of conservation which together contribute to a population's adaptive capacity for environmental change (Seaborn et al., 2021). Both ENM and WGR-based approaches assess environmental features as independent variables to identify important predictors that explain a species' eco-evolutionary characteristics (i.e., ecological requirements or adaptive loci). One can then interpret the results from the viewpoint of local adaptation at different scales or under different environmental conditions. For example, key environmental variables that explain the geographic distribution of distinct ginkgo tree lineages are associated with putative functions of positively selected genes (Zhao et al., 2019), illustrating that mechanistic insights into adaptive profiles can be inferred from combined analyses.

The future trajectory and adaptive capacity of populations under environmental change can also be inferred by combining ENM and WGR data. For example, Han et al. (2021) evaluated thermal adaptation of a marine fish, the Japanese whiting (*Sillago japonica*), in China and Japan. Comparing genomes of warm- and cold-adapted populations revealed temperature-driven parallel adaptation among isolated warm-temperature populations that shared adaptive genes and structural variants. At the macro scale, the adaptively diverse Chinese group exploited warmer temperatures and expanded their habitats under future climate ENMs, in contrast to the Japanese group. Similarly, Liu (2022) forecasted future interactions of black cottonwood (*Populus trichocarpa*) populations. Selective sweep scans for each population, ecological niche models under climate change, and genetic cluster distribution models (Jay et al., 2015) collectively predict that northward colonization will ransack the current spatial organization of cottonwoods and that the population

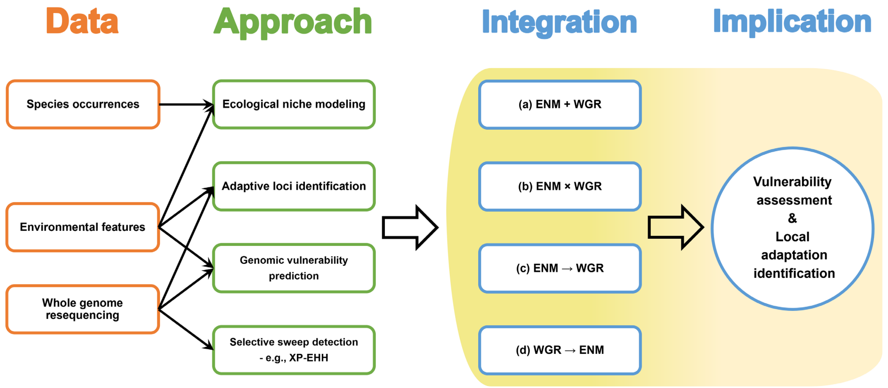

FIGURE 2 A general framework for integrating whole-genome resequencing (WGR) and ecological niche modelling (ENM). Section labels in the "Integration" column are referenced at corresponding places in the main text (e.g., Figure 2a). "+" indicates combination of the two at the interpretation step (i.e., after independent analyses), "×" indicates unification of the two during the analysis step, and "→" indicates the influence of the left factor on the right one.

with the greatest adaptive potential may be key to cope with future climate change. Thus, these studies highlight the importance of both adaptive potential and environmental conditions in conservation planning.

Independent analyses of ENM and WGR can be further developed to assess ecological vulnerability and evolutionary vulnerability, respectively, by ENM forecasting and analyses of genomic offset. Ecologically vulnerable populations and genomically vulnerable populations may not coincide geographically, as in DeSaix et al. (2022) and Tournebize et al. (2022), illustrating the need for both genomic and ecological vulnerability assessments. This is because evolutionary vulnerability evaluates the required adaptive potential for persistence at the organism level, whereas ecological vulnerability evaluates the availability of habitats to persist at the landscape level—both of which are obviously critical to population productivity.

2.2 | Indices that integrate WGR- and ENM-based results

A more sophisticated approach to characterizing profiles of local adaptation is to integrate WGR- and ENM-based results into an index for future persistence and adaptive capacity (Figure 2b). The integrative indices of genomic and ecological vulnerability should be most useful when there is a contrasting pattern between the two vulnerability assessments. Chen et al. (2021, 2022) implemented this approach and demonstrated its merit with two independent studies; one predicted a pest moth's rise or fall and the other assessed the conservation of two threatened birds. They calculated genomic offset using adaptive SNPs (identified by GEA) and modelled habitat suitability of the species. Results demonstrated that regions of higher genomic risk and regions of higher habitat reduction did not correspond, so they developed an “eco-genetic index” (or “genome-niche index”) that multiplied genomic offset and niche suitability change. Based on the index values, Chen et al. (2021) predicted that most moth populations should undergo low to moderate eco-genetic interruptions, which means that they are unfortunately likely to maintain their pest status for the foreseeable future. Chen et al. (2022), on the other hand, compared the index values among three locally adapted populations and the populations with the lowest genome-niche index value were regarded as potential donors for evolutionary rescue. Together, these two studies illustrate the potential power of integrating ENM and WGR to produce novel insights that are relevant to conservation efforts.

2.3 | Reinforcing evidence of local adaptation by unified analyses of ENMs and WGR

One approach to unite ENM with WGR is to unify micro-scale genomics results with macro-scale ENM results at the analysis step (Figure 2b). The analytical unification of ENMs and WGR may create a powerful synergy that reciprocally reinforces the evidence of local adaptation beyond a mere comparison of the two independent results at the interpretation step. One study by Hodel et al. (2018) evaluated the statistical correlation among allele frequencies of candidate genes, habitat suitability values, and individual environmental variables. Their results were unclear, perhaps due to small sample sizes, but we think their general approach has potential merit and should be explored further in future studies.

Many studies have directly unified WGR and ENM. For example, Tremble et al. (2023)'s comparative genomics study of the mushroom *Boletus edulis* demonstrated that a unification of WGR and ENMs can reveal introgression and local adaptations even in species with high dispersal capacity. Introgression and genomic divergence analyses among geographically structured lineages found that high levels of ancient genomic divergence were retained even in the face of considerable introgression, suggesting local adaptation. The authors modelled the ecological niche of each lineage, buttressing the genetic results, where strong geographic structure and differentiated local adaptation among lineages were validated by limited niche overlap.

In some cases, however, the unification of WGR and ENM reveals that introgression appears to have enhanced local adaptation (as in Morales-Cruz et al., 2021). Introgressive hybridization among distinct species could arrange adaptively advantageous combinations of alleles. Comparative genomics can then be applied to identify introgressed regions that are retained in multiple species, the underlying reasons, and the potential function of these regions with respect to local adaptation. To infer whether formerly sympatric pairs of species are sharing suspected genomic regions of adaptive introgression, species-specific ENMs for the present and the past can be modelled and compared. Similarly, unifying ENMs and WGR can identify complicated local adaptation derived from polyploidization-based introgression. Polyploidization creates new combinations of alleles that can unlock new ecological niches, but in return for adaptive fitness at the original, optimal niche. See Napier et al. (2022) for a discussion of this selective trade-off.

On the other hand, Luqman et al. (2023) introduced an interesting novel approach to trace the history of local adaptation—“hindcasting genomic offset,” or “glacial genomic offset.” It is different from the usual genomic offset (which is focused on the predicted future change in genomic composition) and can trace the historic change in genomic composition. With hindcasting ENMs, the hindcasting genomic offset can infer how range shifts shape clines of local adaptation. The concept is grounded on the expectation that populations in different environments harbour different genotypes and that heterogeneous landscapes effectively filter, or sieve, genotypes during range shifts. The process of hindcasting ENMs to a series of environmental conditions in the past can estimate the changes of potential habitat suitability and reconstruct the range shifts of each lineage from historical refugium to the present habitats. Hindcasting genomic offset can be calculated between the two locations. Higher hindcasting genomic offset implies the present habitats are more dissimilar from the ancestral environments whereas lower values indicate greater environmental similarity over time. Hindcasting genomic offset may be positively correlated with increased derived allele frequencies, which can further bolster inferences of range shift imprints and spatiotemporal selection. This process can help identify the strength and profile of local adaptation in the current range that is due to the historical range shift.

2.4 | ENM-informed adaptive genomics

Genomics can inform the ENM approach by discriminating among independent genetic entities, a procedure known as genomics-informed ENM (Ikeda et al., 2017; May et al., 2011). However, ENM can also inform genomic analyses (Figure 2c). For example, ENM can identify key environmental variables which can be used for adaptive genomic analyses or establish ecological clusters as informative priors for Bayesian analyses of spatial genetic structure. Alternatively, habitat suitability itself (based on a robust modelling process; see Box S2) can be incorporated as a variable to detect adaptive genes. Bellis et al. (2020) did so by using ENM habitat suitability score of a parasitic weed (*Striga hermonthica*) as a single predictor variable in a GEA of its host sorghum landraces. They found that structural variants (detectable only with WGR data) yielded practical insights into the spatiotemporal balancing selection that has shaped this weed, which devastates human food crops in sub-Saharan Africa.

Essential environmental variables identified from ENM may have shaped the local adaptation landscape, assuming long-term static environmental conditions drive selective pressure (Gienapp et al., 2014). Key environmental variables can be identified a priori (i.e., before genomic analyses) from ENMs specific to each geographic population that explain the environmental heterogeneity among them (Gheyas et al., 2021; Lu & Lee, 2020). Populations at each extreme environmental condition can be grouped and compared for each key variable in genomic analyses. Effect sizes of different genetic variants (i.e., standing variation or new mutations) can be examined and compared in the context of local adaptation (Gheyas et al., 2021). Several different analyses of selection can be further employed to detect putative genetic variants/sweeps, and their biological functions or association with environmental conditions. For example, gradient forest analysis (Ellis et al., 2012), which estimates the explanatory power of environmental gradients against allele frequency variation, indicates that both new mutations and populations subject to drastic precipitation shifts are especially vulnerable to climate change (Lu & Lee, 2020).

The delineation of ecology-driven genetic clusters among geographic populations has great advantages over ordinary neutral genetic clusters (e.g., those identified by a typical genetic ancestry admixture analyses) because they presumably reflect population structure shaped by local adaptation. ENM-based niche similarity can be used to cluster distinct ecotypes among geographic populations. These ENM-defined ecotypes can underpin downstream analyses to detect selective sweeps. A GEA to detect environment-associated SNPs of the sweep regions can identify major environmental variables. Using this approach, Vallejo-Trujillo et al. (2022) found that (1) SNPs associated with all major environment variables fell within sweep regions of most ENM-defined ecotypes and (2) some sweep regions included SNPs associated with several environmental variables, indicating that different environmental drivers (and their interactions) collectively contributed to each ecotype and some genomic regions. The use of ENM-defined ecotypes is desirable in the context of GEAs since ENM can detect resultant, convoluted genotype-environment interactions, in contrast to popular GEA methods that can only detect correlative, linear genotype-environment interactions (e.g., redundancy analysis; Capblancq & Forester, 2021).

2.5 | Adaptive genomics-informed ENMs

Genomic offset and GEA are effective at detecting loci strongly associated with environmental gradients, but loci under long-term balancing selection may be difficult to detect due to inherently higher levels of polymorphism (Charlesworth, 2006). However, subtle signals of balancing selection can be magnified with ENM-based approaches that consider the geographic distribution of adaptive alleles. This allows the ecological drivers of adaptive evolution to be inferred and associated with adaptive alleles (Figure 2d).

For example, Wu et al. (2017) detected incomplete lineage sorting, or trans-species polymorphism, using whole-genome scans of the weed *Arabidopsis thaliana* and its relative *Capsella rubella*. Their premises (which were ultimately validated) were that only adaptive polymorphism under balancing selection should have persisted over a protracted time scale and that trans-species orthologous genes maintained by balancing selection should exhibit loci that cluster by alleles, not species (unlike neutral polymorphisms). The authors divided samples into two genealogical groups for each selective loci, then modelled the ecological niche of each group and tested niche identity between the groups. All genes analysed exhibited statistical associations with specific environmental variables, strongly suggesting that they are causative loci responsible for local adaptations. As illustrated by Wu et al. (2017), we think ENM-based niche divergence of distinct adaptive clusters (i.e., genomics-informed ENM) has the potential to verify whether the adaptive genomic divergence between ecotypes has been phenotypically realized.

Ecological niche modelling can help delineate the geographic distribution not only of individuals, but of a given ecological attribute by associating the attribute with focal environmental variables. Combining multiple ENMs that use various types of information (e.g., phenotypic, genotypic, allelic) should be more powerful than a simple distribution of individuals (Figure 2d). Exposito-Alonso et al. (2018) modelled the distribution of phenotypic information (e.g., drought-survival index), genotypic information (e.g., genetic cluster membership), and allelic information (drought-adaptive SNPs) to collectively predict the adaptive potential of *Arabidopsis thaliana* under future droughts. Statistical associations between phenotypic, genotypic, and allelic information described the local adaptation regime, as well as the genomic background, based on the modelled geographic distribution. Exposito-Alonso et al. (2018) fit independent ENMs for each of 221 drought-adaptive SNPs under current and future climates, then overlapped these 221 models to represent the geographic density of the alleles and the most likely genotype at each location. They found that regions harbouring sufficient drought-adaptive SNPs should easily adapt to future climates with standing variation, but that other vulnerable geographic locales may need effective gene flow for future persistence. Their approach helps to compare the most likely genotypes of the present and anticipated adaptive genotypes of the future at a given location, which facilitates comparisons of the most likely genotypes between locations at a certain time point. The information can be used to identify the required gene flow over time under future conditions; to predict its feasibility based on the realistic dispersal ability of the focal species; and to choose donor populations for genetic rescue efforts.

2.6 | Synthesis and implications

The integration of WGR and ENM approaches can provide insights into adaptation profiles that are relevant to conservation and management by identifying evolutionary responses to both genomic and ecological adaptations. These two approaches allow the identification of (1) adaptive characteristics, in terms of either the genome or the niche, of a population or a species; (2) populations that may become vulnerable to predicted environmental changes; and (3) the overall geographic and genomic patterns of local adaptation. Local adaptation profiles could play a significant practical role, such as helping to accurately predict outbreeding depression when considering assisted migration or range shifts expected under climate change. From such insights, locally adapted populations and critical habitats that harbour high genetic or niche diversity can be more effectively prioritized in customized conservation plans.

ENMs can accommodate diverse information (phenotypic, genotypic, and allelic, etc.) to help conservationists understand the architecture of local adaptation both now and in the future (Exposito-Alonso et al., 2018). ENM forecasts should also be able to plot distributions and expected changes in distribution of adaptive alleles (including structural variants revealed by WGR), if they have geographic attributes and are assumed to be correlated with environmental variables in ENMs. Accordingly, one might be able to estimate genomic offset from ENMs (an "ENM-based genomic offset") by calculating the local density of adaptive alleles—and possibly weighting them by suitability values across the predicted habitats—and the change of allele densities over time. Other potential implications of successful WGR and ENM integration include the identification of geographic or genomic regions that reveal contradictory ecological and evolutionary vulnerability (allowing the quantification of net vulnerability), associating ecological characteristics with genetic variants, or explicitly testing local adaptation using both genetic and niche characteristics.

Our survey of the literature also revealed clear strengths of whole-genome resequencing as compared to reduced representation sequencing (with the notable exception being the absolute price differential, which is rapidly disappearing). Chromosome-scale WGR data now allow scans for selective sweeps or introgressed regions; both structural variants and SNPs can be queried in GEA. Focusing these analyses on known genic regions (based on annotation profiles) can explicitly associate these fitness-related genetic variants with environmental conditions. Soon, we think that studies of this kind will rapidly expand as both techniques become more accessible and innovative new integrative approaches are developed. We think that heretofore hidden local profiles of adaptation will be revealed on an ever-finer scale to aid conservation and management efforts.

3 | FUTURE DIRECTIONS

Here we consider some limitations of current approaches, then speculate on how WGR and ENM might be further integrated and applied in the future. We cheerfully admit that our crystal ball is a bit opaque, but we offer these ideas to stimulate further research.

There is much room for improvement in the application of ENMs by genomicists. Niche modelling has typically been limited to some common correlative ENMs, such as MaxEnt or an ensemble approach of several algorithms (e.g., Brüniche-Olsen et al., 2021). Additional biological realism is needed especially for conservation efforts. With only a few exceptions (e.g., Exposito-Alonso et al., 2018; Luqman et al., 2023), the incorporation of dispersal ability into the ENM has been limited by distance kernels, constraining latitude/longitude, or keeping the current population genetic structure, which are fine enough. However, ENM tools that can reflect the dispersal ability of a focal species have recently been developed, including packages megaSDM (Shipley et al., 2022) or RangeShifter (Bocedi et al., 2021). By attaching a species' dispersal rate internally in the ENM (Holloway et al., 2016; Seaborn et al., 2020), researchers can now compare ENMs with and without dispersal in a consistent fashion and generate more realized expansion/contraction of niche distribution (Shipley et al., 2022).

The role of biotic Interactions in determining a species' geographic distribution has long been recognized (Soberon & Peterson, 2005), but has only recently been explored in the literature. By considering biotic interactions, ENMs may be able to predict more realistic dynamics of local adaptation. In practice, a simple approach is to use the distribution (or probability of presence) of one species as a predictor of another species (Gherghel et al., 2018). More complex, and hopefully realistic, joint species distribution models (JSDM; Pollock et al., 2014) can infer the strength of biotic interactions based on the co-occurrence of multiple species (Pollock et al., 2014; Wilkinson et al., 2021). Phylogenetic niche modelling, on the other hand, can incorporate aspects of niche evolution through time and biotic interactions among niche-overlapping species from phylogenetic information (Guillory & Brown, 2021; McHugh et al., 2022; Yesson & Culham, 2006).

Other potential advances on the ENM side include trait-ENM that reflects variation of phenotypic trait, and associated fitness by including the trait information as predictors (Benito Garzón et al., 2019; Vesk et al., 2021). The trait-ENM then can test whether the species can persist in situ (i.e., without changes in its geographic range) under future environmental change (Benito Garzón et al., 2019). This approach depends on common-garden data or standardized sampling protocols to infer phenotypic plasticity and local adaptation (Benito Garzón et al., 2019; Vesk et al., 2021), but it could be an insightful way to include phenotypic information in ENMs that would further complement results from WGR studies.

From the WGR side, the function of candidate genes can be explored with gene ontology enrichment analysis, network analysis, or pathway analysis. While these analyses can provide locus-specific insights, the associated bioinformatic tools can produce false positives and this problem is exacerbated in non-model organisms (Fridrich et al., 2019). Thus, evidence based exclusively on nucleotide sequences should be corroborated with other datasets, such as phenotypic data or transcriptomic analyses of gene expression (Chen et al., 2021; Fridrich et al., 2019), ideally using a hypothesis testing framework as in Bellis et al. (2020).

In principle, one could also utilize patterns of gene expression (e.g., transcriptomic and/or regulatory sequences) to infer species adaptability/vulnerability owing to future environmental change. A "transcriptomic offset" or "exomic offset" might be useful to predict changes in gene expression patterns in various tissues due to environmental factors. Similarly, "regulatory offset" could be estimated based on regulatory sequence variation, which might help provide insights on adaptability across important genomic regulatory regions.

Genomic methods have been widely employed to assess dispersal capacity, especially for those species where tracing dispersal distances is challenging (e.g., Zou et al., 2023). Genomic analyses of pairwise relationships can estimate individual dispersal distances, and landscape genomics can compare gene flow patterns in different genomic regions (e.g., adaptive loci in comparison with neutral loci) while pinpointing the most important environmental constraints (e.g., Ledger et al., 2023). In the future, we expect that combining genomics-informed dispersal with an ENM specific to a focal adapted cluster will help reveal whether adaptive loci could flow into non-adapted clusters via suitable habitats.

Through their work in "community genetics," Whitham et al. (2003) and others (reviewed in Crutsinger, 2016) have shown that heritable genetic variation within a given species can have community and ecosystem consequences. Hand et al. (2015) have expanded this concept into "landscape community genomics," which evaluates interspecific genomic interactions across environmental conditions. For example, the molecular evolutionary networks underlying the expression of heat shock proteins could help explain the geographic distribution of desert fauna. Given the ongoing characterization of pangenomes (see Box 1: Glossary; Tettelin et al., 2005), we anticipate tremendous biological insights when the field of "landscape community pangenomics" ultimately emerges. For instance, a pangenomic approach could advance our understanding of adaptation by employing structural variants such as chromosomal inversions into GEA (Heraghty et al., 2022).

We think integrative analyses of environmental niche and genetic load or genetic thrust have the potential to provide key insights that could be important for conservation and management efforts. Bertorelle et al. (2022) provide a thorough review of genetic load, which varies among populations depending on their demographic histories and on selection regimes (e.g., purging or positive selection; Mathur & DeWoody, 2021; Mathur, Mason, et al., 2023; Mathur, Tomeček, et al., 2023). We think careful WGR evaluations of load (or thrust) in light of ENM-informed adaptive profiles have the potential to significantly improve assisted migration or genetic rescue efforts. On the whole, we believe that integrating more realistic ENMs (such as dispersal-attached ENMs) and advanced WGR-based approaches (such as pangenomics) will greatly enhance our understanding of local adaptation and community interactions.

3.1 | Potential limitations and solutions

Potential limitations applicable to the integration of ENM and WGR are discussed in Lovell et al. (2023), Miller et al. (2004), and Rellstab et al. (2021). We highlight two crucial limitations known as the "space-for-time substitution" and "extrapolation beyond the scope of space and time." The "space-for-time substitution" refers to substituting temporally varying conditions with spatially varying conditions, and the "extrapolation beyond the scope" refers to projecting biological trends outside of space or time parameters that were applied in the model training. These approaches can limit biological inferences in that the former ignores the possibility of different biotic responses over time compared to over space (Lovell et al., 2023), whereas the latter ignores the uncertainty of the model under the unobserved environment (Miller et al., 2004). For example, when we assess vulnerability of populations under future climate conditions, we assume that the identical set of putatively adapted loci identified across spatial variation is the same under temporal variation of environment, which may not be true (Therkildsen et al., 2013; but see Wogan & Wang, 2018). Furthermore, populations are assumed to be vulnerable under unobserved future climatic conditions, which might not follow predictions (Feng, Park, Liang, et al., 2019; Feng, Park, Walker, et al., 2019; Qiao et al., 2019) regardless of whether the predicted vulnerability is assessed by the contemporary adaptive loci or under the predicted future climate.

The key to dealing with these limitations is to identify the credible boundary for interpretation, such as quantifying the transferability of ENMs (Qiao et al., 2019). Analysing contemporary and ancient DNA for comparison (Rellstab et al., 2021) or simulating genomes over time under changing future environments (e.g., inputting environment rasters at time intervals in SLiM simulations; Haller & Messer, 2023) may help to determine how the genomes change with environments.

Both niche modelling and population genomics have grown too large to be fully understood and properly conducted by most novices. Inappropriate analyses can and do occur when genomicists try to utilize ENMs or ecologists try to incorporate genomics results without fully appreciating the limitations of each dataset. We have seen published examples where there were substantive mismatches between the temporal scales of collected sample and environmental data (e.g., DNA data from ancient or historical samples used with contemporary climate data), mismatches between spatial scales of species' ecology and environmental data, questionable or unvalidated locality data associated with museum samples, and a lack of consideration for sampling biases.

We strongly recommend active cross-talk between WGR genomicists and ENM ecologists to foster collaboration. (Figures 3 and 4; see also Hodel et al., 2018; Chen et al., 2022; and DeSaix et al., 2022). Figure 3 shows an example of prospective workflows (based on Gheyas et al., 2021 and Vallejo-Trujillo et al., 2022) which unify WGR and ENM to cope with future threats. In this ENM-informed adaptive genomics workflow, an ENM is fitted for each population and the populations are then grouped according to their niche similarity. Clusters that share similar niche characteristics are then analysed for their adaptive genomic characteristics to identify regions associated with local adaptation. In contrast, Figure 4 (based on Luqman et al., 2023) represents a retrospective workflow to infer historical local adaptation. Serial hindcasting ENMs and neutral genomic inferences are conducted independently to infer and cross-check population histories. Historical genomic offset could then be computed between present-day populations and their historical refugia and characterized using key environmental variables. Sophisticated new software packages can further assist the workflows by simulating characteristics of both genome-scale data and niche prediction, such as SLiM (Haller & Messer, 2023), Geonomics (Terasaki Hart et al., 2021), and RangeShifter (Bocedi et al., 2021).

The harmonious integration of niche modelling and population genomic data will typically require collaboration. It will also require practitioners to reexamine pervasive misconceptions (e.g., population genomics is completely unaffordable or too convoluted, or that meaningful ENMs can be generated in one "click") (Bilodeau et al., 2019; Breed et al., 2019; Feng, Park, Liang, et al., 2019; Feng, Park, Walker, et al., 2019). We expect that collaborations will be most productive and insightful when partnerships are developed between experienced population genomicists and niche modellers who recognize the strengths and weaknesses of their own fields. Their united efforts will produce more accurate insights regarding local adaptation and its reliable conservation.

4 | CONCLUSIONS

We have summarized recent efforts to integrate ecological niche modelling and whole-genome resequencing to characterize local adaptation profiles. We have also suggested additional avenues whereby WGR-ENM integration could be pursued in the future. The novel merits of integrating the two stem from the fact that WGR as a type of data and ENM as a method of analyses can assess two different eco-evolutionary aspects (organismal and molecular) at two different scales (macro and micro). We think the orthogonal aspects of WGR-ENM integration can and should be carefully exploited for the benefit of conservation and management efforts around the world.

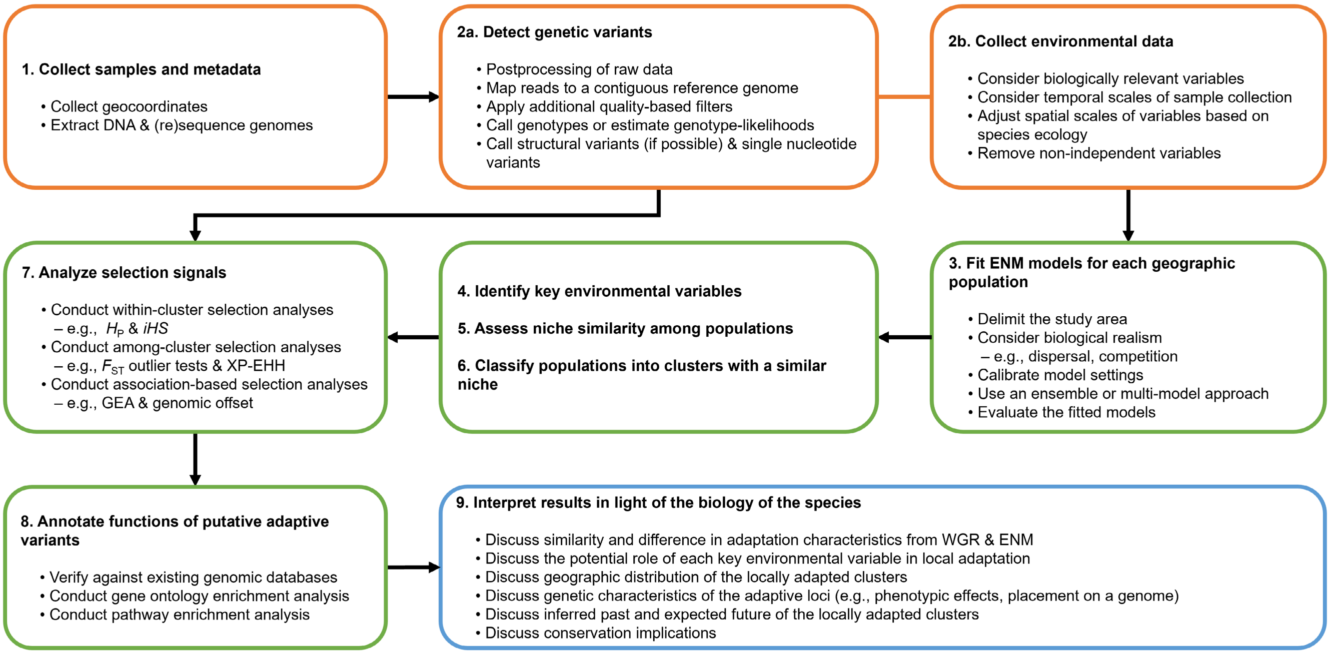

FIGURE 3 A prospective workflow for identifying and conserving local adaptation, based on Gheyas et al. (2021) and Vallejo-Trujillo et al. (2022). This workflow of ENM-informed adaptive genomics unifies whole-genome resequencing (WGR) and ecological niche modelling (ENM) to discriminate clusters of different niche characteristics and to characterize adaptive genetic variants in each of them. The colour scheme of the outline follows Figure 2.

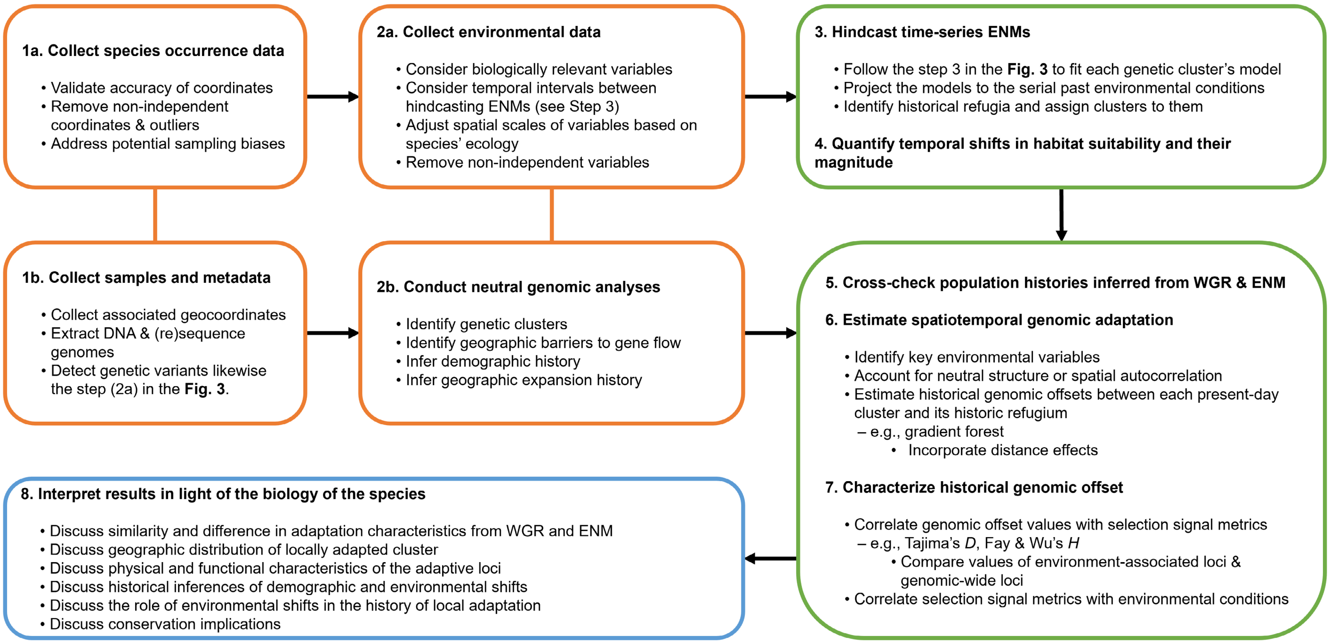

FIGURE 4 A retrospective workflow for identifying local adaptation and inferring its historical causes, based on Luqman et al. (2023). This workflow of historical genomic offset combines whole-genome resequencing (WGR) and ecological niche modelling (ENM) to hindcast serial ecological niches and infer the history of local adaptation developing from glacial refugia to their present-day genetic clusters. The colour scheme of the outline follows Figure 2.

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The authors declare no competing interests.

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ORCID

Jong Yoon Jeon https://orcid.org/0000-0002-2840-8425
Yucheol Shin https://orcid.org/0000-0002-4606-2907

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BIOSKETCHES

Jong Yoon Jeon is a PhD candidate at Purdue University interested in conservation genomics of local adaptation. His current research uses whole-genome resequencing data to help determine conservation status and to identify signals of local adaptation.

Xiao Feng Lab at University of North Carolina studies biogeography and biodiversity. The lab uses statistical and computational approaches to answer macroecological questions to ultimately address conservation management issues under global change.

J. Andrew DeWoody Lab at Purdue University uses genomic approaches to answer questions in conservation and evolutionary biology. The lab group studies various wild vertebrates and cooperates with private, state, and federal agencies to help resolve conservation and management issues.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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