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# Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections

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**Local adaptations can determine the potential of populations to respond to environmental changes, yet adaptive genetic variation is commonly ignored in models forecasting species vulnerability and biogeographical shifts under future climate change. Here we integrate genomic and ecological modeling approaches to identify genetic adaptations associated with climate in two cryptic forest bats. We then incorporate this information directly into forecasts of range changes under future climate change and assessment of population persistence through the spread of climate-adaptive genetic variation (evolutionary rescue potential). Considering climate-adaptive potential reduced range loss projections, suggesting that failure to account for intraspecific variability can result in overestimation of future losses. On the other hand, range overlap between species was projected to increase, indicating that interspecific competition is likely to play an important role in limiting species' future ranges. We show that although evolutionary rescue is possible, it depends on a population's adaptive capacity and connectivity. Hence, we stress the importance of incorporating genomic data and landscape connectivity in climate change vulnerability assessments and conservation management.**

global climate change | genetic adaptations | ecological niche models | conservation genomics | evolutionary rescue

Climate change is predicted to result in widespread population and species extinctions (1), and climate-related local extinctions have already been observed in hundreds of species (2). However, an equivalent number of species did not experience local extinctions at their warm range edge (2), indicating that either phenotypic plasticity or genetic adaptations may enable some populations to persist under warmer conditions. This highlights the importance of incorporating intraspecific adaptations into climate change vulnerability assessments (3, 4). However, methodologies to adequately incorporate genomic data into projections of species responses to current and changing climatic conditions (5) and into conservation management strategies (6) are still missing.

Vulnerability to climate change is most commonly assessed based on forecasted distributional changes using ecological niche modeling approaches (also known as species distribution models), which project future changes in the distribution of suitable climatic conditions that characterize species' current ranges (7). A major limitation of these approaches, which can lead to erroneous predictions and misplaced conservation efforts, is the disregard of intraspecific climatic adaptations and the consequent differences in population responses to climate change (8). Evidence of contrasting patterns of physiological variation in thermal tolerance among and within species highlights the importance of incorporating intraspecific variation in climatic adaptations into ecological niche models (ENMs) (9). However, such model improvements are limited by the

paucity of observational and experimental studies of local climatic adaptations (10).

To date, studies attempting to incorporate genetic variation into ENMs primarily use neutral markers to identify phylogeographic structure and generate separate models for each genetically distinct population. These have resulted in more pessimistic forecasts than traditional ENMs, predicting increased threats from climate change due to range losses in vulnerable populations (11), but have not affected projections of range size changes at the species level (12). These attempts are limited in scope because neutral markers provide information on the species' evolutionary history and barriers to gene flow but not on the ability of individuals to adapt and survive under changing conditions. Moreover, range shifts under future climate change are predicted to result in genetic homogenization across species ranges and loss of historic and current population subdivisions (13). More recent studies integrated genomic adaptations with ENM projections to identify vulnerable populations that will need to adapt to survive under future climate change (14, 15).

## Significance

**Forecasts of species vulnerability and extinction risk under future climate change commonly ignore local adaptations despite their importance for determining the potential of populations to respond to future changes. We present an approach to assess the impacts of global climate change on biodiversity that takes into account adaptive genetic variation and evolutionary potential. We show that considering local climatic adaptations reduces range loss projections but increases the potential for competition between species. Our findings suggest that failure to account for within-species variability can result in overestimation of future biodiversity losses. Therefore, it is important to identify the climate-adaptive potential of populations and to increase landscape connectivity between populations to enable the spread of adaptive genetic variation.**

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The authors declare no conflict of interest.

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Data deposition: The raw sequence data from this study have been deposited at the European Nucleotide Archive (ENA), <https://www.ebi.ac.uk/ena> (accession no. PRJEB29086).

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Table 1. Results of the ecological niche models, including percentage of Iberia predicted to be climatically suitable under present and future (2070, RCP 8.5) conditions and percentage range changes within Iberia

Taxon	<i>n</i>	AUC ROC	TSS <sup>a</sup>	AUC-test	Percentage suitable, present	Percentage suitable, future	Percentage range change
<i>Myotis escaleraei</i> , all	313	0.941	0.781	0.850	38.40	20.38	−46.94
<i>M. escaleraei</i> , hot–dry	19	0.914	0.727	0.876	46.82	49.50	+5.72
<i>M. escaleraei</i> , cold–wet	41	0.946	0.806	0.841	29.27	12.08	−58.73
<i>Myotis crypticus</i> , all	168	0.926	0.729	0.896	20.51	2.61	−87.28
<i>M. crypticus</i> , hot–dry	25	0.908	0.752	0.836	14.34	7.54	−47.42
<i>M. crypticus</i> , cold–wet	18	0.940	0.798	0.896	4.89	<0.01	−99.96

See [SI Appendix, Table S2](#), for range change projections across the study area and for the RCP 4.5 scenario. AUC ROC, area under the receiver operating characteristic curve for ensemble models; AUC-test, AUC cross-validation scores for Maxent models;  $n$ , sample size. Bold denoted projected range increases.

<sup>a</sup>For ensemble models.

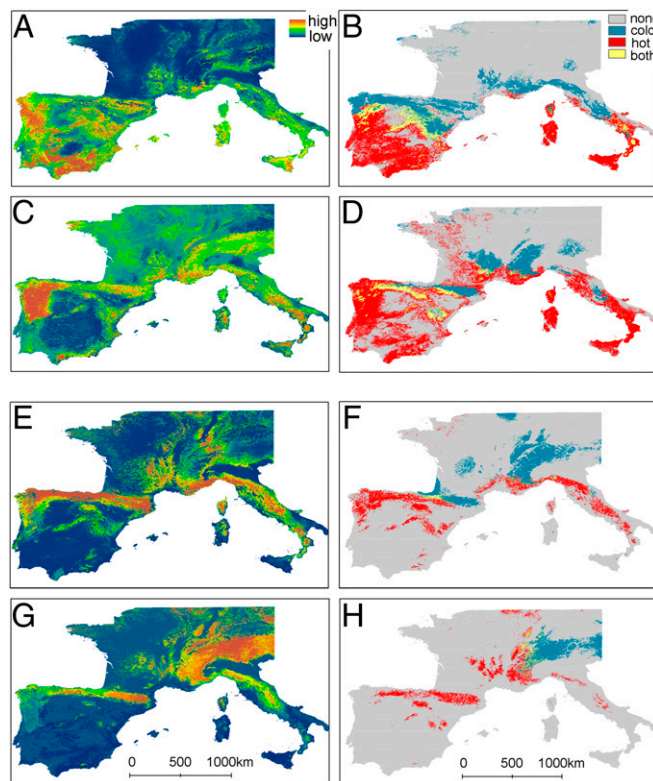
different GCMs is 38–53%) of its Iberian range by the end of this century but only 19% (range of 13–25%) based on the combined ranges of hot-dry- and cold-wet-adapted individuals, resulting in up to 60% reduction in projected Iberian range losses (16% based on the moderate scenario RCP 4.5 W/m<sup>2</sup>). Similarly, *M. crypticus* is projected to lose 87% (range of 75–94%) of its Iberian range based on the full dataset but only 58% (range of 44–68%) based on the combined adaptive ranges (33% reduction in projected losses with RCP 8.5 versus 40% reduction with RCP 4.5; Fig. 2 and [SI Appendix, Fig. S3](#) for RCP 4.5; Table 1; [SI Appendix, Table S2](#)). There is a mismatch between the low extinction rates observed during Pleistocene climatic changes and the high rates forecasted by traditional future ENMs (25). Our findings suggest that incorporating adaptive intraspecific genetic variation is essential for realistic projections of species range losses under climate change and for preventing overestimation of future biodiversity losses.

Hot-dry-adapted *M. escalerai* individuals are the only group predicted to have substantial increases in climatic suitability across Europe (+34%) under future climate change. However, increases are projected mainly outside Iberia (Fig. 2 B and D), where the species is not currently found [except in the Pyrénées-Orientales in France (26)] and where it is likely to encounter interspecific competition with two cryptic congeners, *M. crypticus* and *Myotis nattereri sensu stricto* (19). However, more modest range gains (+5.7%) are also projected within Iberia. *M. escalerai* is restricted to its glacial refugia, likely due to range expansion limitations imposed by interspecific competition (20). The life history traits, habitat specialization, and restricted distribution of *M. escalerai* suggest it is particularly vulnerable to climate change (7). However, our study predicts that *M. escalerai* will be able to survive in situ across much of its currently occupied range as a result of its adaptive capacity.

Overall, hot-dry genotypes are predicted to expand their range at the expense of cold-wet genotypes. However, survival at the trailing (equatorward) edge of species ranges depends on the maximum thermal tolerance of the species. Species living in warm environments may be unable to physiologically adapt to increased heat because their niches are close to their upper thermal limits, which were shown to be phylogenetically conserved and therefore less likely to evolve (27). On the other hand, at least for ectotherms, the equatorward range limit does not reflect maximum warm temperature tolerance, and therefore, species may be able to physiologically tolerate higher thermal stress at their warm range limits under future climate change (28). Genomic data support the genetic basis of greater thermal tolerance in individuals living in warmer microclimates under higher heat stress (29). In contrast, individuals adapted to cold-wet conditions will experience the most severe range losses. Cold-wet *M. escalerae* genotypes are projected to lose more than half of their Iberian range and retract to mountain ranges (Fig. 2D), while cold-wet *M. crypticus* genotypes are projected to entirely

disappear from Iberia and Italy with the exception of the Alps (Fig. 2H and Table 1). Bay et al. (4) show that populations exhibiting a strong mismatch between current local genetic adaptations and future climatic conditions have a higher likelihood of declining.

Considering adaptive variation increased the predicted potential for interspecific competition, through increased range overlap. Range overlap between species in Iberia was predicted to decrease under future conditions (84% reduction, from 10.5 to 1.7% of Iberia), but estimations of future range overlap were more than 4 times higher when the ranges of hot-dry and cold-wet individuals were combined (7.1%; *SI Appendix, Fig. S3*). Changing species interactions have already been implicated in



**Fig. 2.** The effect of integrating intraspecific climatic adaptations into ecological niche model projections. Ecological niche modeling outputs for *M. escalerae* (A–D) and *M. crypticus* (E–H), including the full dataset (A, C, E, and G) and overlap between separate models for individuals adapted to hot–dry (red) and cold–wet (blue) conditions (B, D, F, and H) under present (A, B, E, and F) and future (2070, RCP 8.5) (C, D, G, and H) climatic conditions. Relative probability of occurrence ranges from low in blue to high in orange.

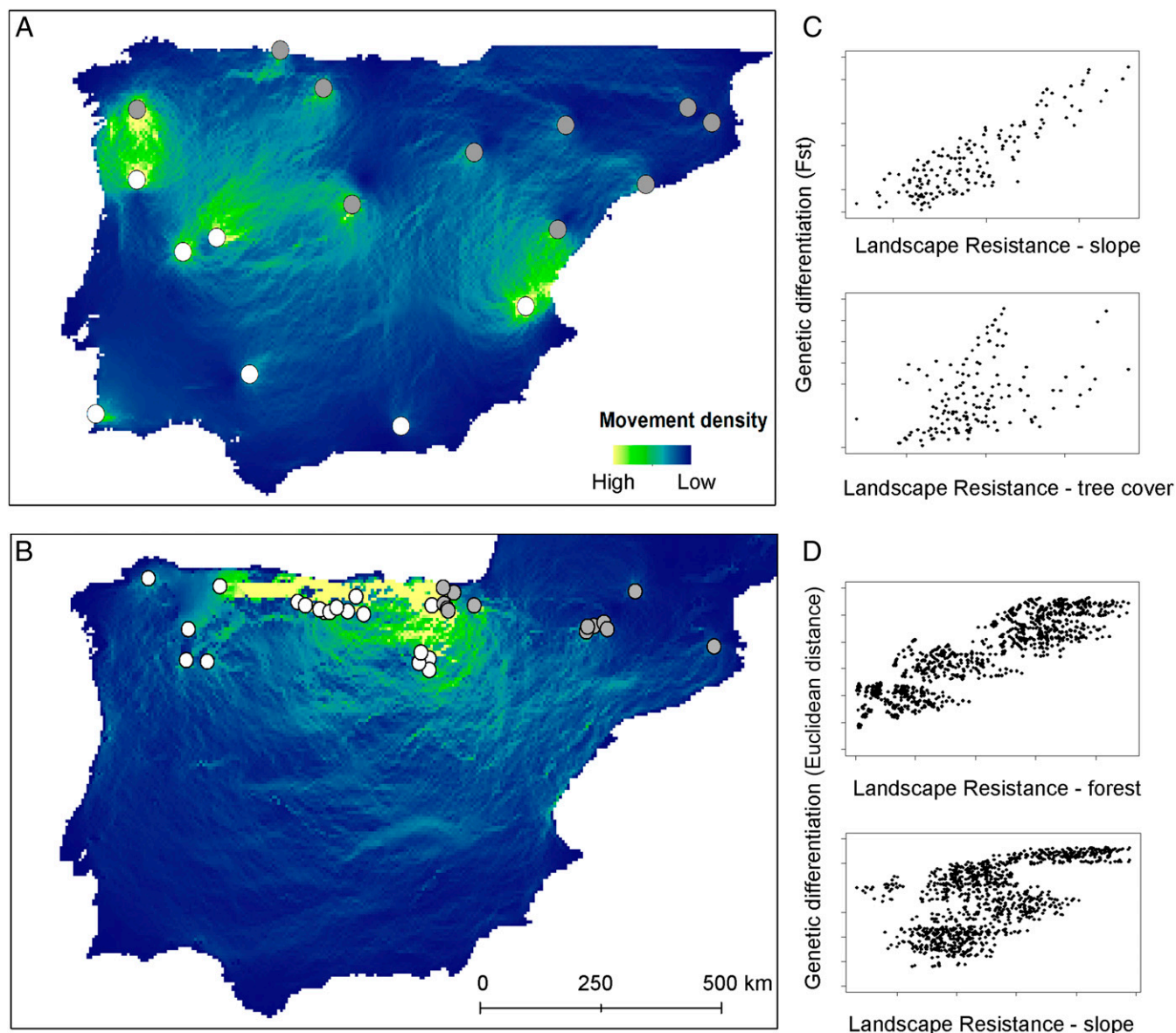
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**Fig. 3.** Modeling evolutionary rescue potential under future climate change in (A) *M. escaleraei* and (B) *M. crypticus*, depicted as the predicted density of movement (yellow is high and blue is low) from populations or individuals adapted to hot-dry conditions (white circles) to those adapted to cold-wet conditions (gray circles) based on the effect of slope and tree cover (A) or slope and forest cover (B) on movement. The relationship between landscape resistance and genetic differentiation in *M. escaleraei* (C) and *M. crypticus* (D).  $F_{st}$  is Wright's fixation index measure of population differentiation resulting from genetic structure.

**Identifying Climate-Adaptive Genotypes and Individuals.** We carried out a GEA analysis to identify a signature of climate-driven genetic variation based on associations between allele frequencies and local conditions. We focused on two ecologically relevant climatic variables, maximum temperatures of the warmest month and precipitation of the warmest quarter (Bio5 and Bio18, downloaded from WorldClim, [www.worldclim.org](http://www.worldclim.org)). GEA analysis was performed with the latent factor mixed model approach (42) and a redundancy analysis (RDA) (43) (see *SI Appendix* for running procedures). We used a conservative approach (21), whereby only SNPs that were identified as being under climate-driven selection for either climatic variable by both GEA methods were classified as climate-adaptive SNPs. RDA was used to plot the spread of individuals in the ordination space based on their climate-adaptive SNPs relative to the maximum temperature and summer rainfall axes (*SI Appendix*).

**Modeling Range Losses Under Future Climate Change.** ENMs were run using the ensemble modeling approach in the R package biomod2 version 3.3-7 (44). Models were replicated 10 times (five for models with low sample sizes,  $n < 50$ ) using the cross-validation approach. Model performance was evaluated based on total ensemble model area under the receiver operator

curve scores, TSS, and comparison with null models (see *SI Appendix* for ENM running procedures).

The study extent was set as around 500 km north of the known range limit of *M. crypticus* (the species with the larger range size) to include areas within the theoretical dispersal ability of the species by the end of the century (45). Cell size was set at 30 arc s (~1 km). Models included bioclimatic variables (downloaded from WorldClim), a static topographic variable that is independent of temperature changes (slope, generated from the Shuttle Radar Topography Mission (SRTM) altitude map, <https://www2.jpl.nasa.gov/srtm/>), and distance to karsts (Karst Regions of the World) (46) because *M. escaleraei* primarily roosts in caves and mines. We removed autocorrelated variables ( $R > 0.75$ ) and variables that did not contribute to model gain (see *SI Appendix, Table S2* for final model variables). Models were projected to the future (2070) using three general circulation models [Hadley Centre Global Environment Model version 2 Earth Systems model (HadGEM2\_ES), Institut Pierre-Simon Laplace Coupled Model 5th Assessment Low Resolution (IPSL-CM5A-LR), and Max Planck Institute for Meteorology Earth System Model Low Resolution (MPI-ESM-LR)] and two RCP scenarios (47), the worst-case scenario, RCP +8.5 W/m<sup>2</sup>, and the more moderate RCP +4.5 W/m<sup>2</sup> scenario.

For each species or group we ran separate models for each GCM, producing an ensemble of 30–60 models for each RCP scenario that were merged together into a single layer.

ENMs included 313 and 168 genetically confirmed records of *M. escalerae* and *M. crypticus*, respectively (the full datasets), obtained from this study and previous studies of the species (19, 20, 26). We also ran separate models for individuals within each species identified as adapted to hot-dry (*M. escalerae*,  $n = 19$ ; *M. crypticus*,  $n = 25$ ) and cold-wet ( $n = 41$ , 18, respectively) conditions based on our genomic dataset to determine whether their climatic niche is different and whether they will be affected differently by future climate change. We calculated extent of overlap in geographic and ecological space (range and niche overlap; *SI Appendix*).

**Landscape Genetics and Evolutionary Rescue Analyses.** The landscape genetics analysis for *M. escalerae* was carried out at the population level (18 populations,  $n = 162$ ), while for *M. crypticus* it was carried out at the individual level, retaining a single sample (the first sample) from each location ( $n = 47$ ). The extent of the analysis was set as the respective species' ranges. Landscape variables (including habitat suitability, forest cover, land cover, topographic, and climatic variables) were converted to resistance cost surfaces in ArcGIS and assigned costs ranging from 1 (no resistance to movement) to 100 (strong barrier to movement) (*SI Appendix, Table S8*). Circuitscape version 4.0.5 (48) was used to calculate resistance distance matrices between populations or individuals and estimate potential movement pathways across

the landscape based on the cumulative cost of movement due to landscape resistance. Although bats are capable of flight, the studied species have relatively limited dispersal ability (49) and therefore are more likely to have a landscape-mediated population structure (50). Potential for evolutionary rescue was determined according to the potential for gene flow from hot-dry-adapted to cold-wet-adapted populations and individuals based on the effect of the landscape on current patterns of genetic differentiation (*SI Appendix*).

**Data Availability.** The raw sequence data from this study have been deposited at the European Nucleotide Archive (ENA), accession no. PRJEB29086 (41). Final SNP datasets for the two species in Genepop format are given in *Datasets S2* and *S3*.

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