Received: 31 January 2022 | Revised: 16 December 2022 | Accepted: 4 January 2023

DOI: 10.1111/ddi.13676

RESEARCH ARTICLE

Diversity and Distributions WILEY

Staying in situ or shifting range under ongoing climate change: A case of an endemic herb in the Himalaya-Hengduan Mountains across elevational gradients

Nan Lin[1,2] | Qun Liu[3] | Jacob B. Landis[4,5] | Hum Kala Rana[1] | Zhimin Li[3] | Hengchang Wang[6] | Hang Sun[1,7] | Tao Deng[1,7]

[1]CAS Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, China

[2]College of Life Science, Henan Agricultural University, Zhengzhou, China

[3]School of Life Sciences, Yunnan Normal University, Kunming, China

[4]School of Integrative Plant Science, Section of Plant Biology and the L.H. Bailey Hortorium, Cornell University, Ithaca, New York, USA

[5]BTI Computational Biology Center, Boyce Thompson Institute, Ithaca, New York, USA

[6]CAS Key Laboratory of Plant Germplasm Enhancement and Specialty Agriculture, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, China

[7]Yunnan International Joint Laboratory for Biodiversity of Central Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, China

Correspondence
Hengchang Wang, CAS Key Laboratory of Plant Germplasm Enhancement and Specialty Agriculture, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, China.
Email: hcwang@wbgcas.cn

Hang Sun and Tao Deng, CAS Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, China.
Email: sunhang@mail.kib.ac.cn and dengtao@mail.kib.ac.cn

Funding information
the Key Projects of the Joint Fund of the National Natural Science Foundation of China, Grant/Award Number: U1802232; the Chinese Academy of Sciences "Light of West China" Program; the International Partnership Program of Chinese Academy of Sciences, Grant/Award Number: 151853KYSB20180009; the Major Program for Basic Research Project of Yunnan Province, Grant/Award Number: 202101BC070002; the Second Tibetan Plateau Scientific Expedition and Research (STEP) program, Grant/Award Number: 2019QZKK0502; the Strategic Priority Research Program of

Abstract

Aim: How species respond to ongoing climate change has been a hot research topic, especially with the controversy in shifting range (movement) or persisting in local habitat (in situ) as the primary response. Assessing the relative roles of range shifts, phenotypic plasticity and genetic adaptation helps us predict the evolutionary fate of species. We aim to explore the evolutionary strategies of plants under climate change from a keystone herb in alpine ecosystems, *Mirabilis himalaica*, along its elevational gradient.

Location: Himalaya-Hengduan Mountains, China.

Methods: We combined evidence from population genomics and ecological data in both space and time to investigate the state of "staying" or "moving". We identified migration events by assessing historical and contemporary gene flow and changes in species distribution. Morphological variation was compared by measuring five traits using specimen data. Moreover, we explored climate-driven genetic variation and local selection regimes acting on populations in the alpine landscape along an elevational gradient.

Results: Our results argue that staying in situ by morphological variation and local genetic evolution rather than range shifting plays an important role in *M. himalaica* response to climate change. We first found trace evidence of upward or climatic-driven shifting along an elevational gradient, although asymmetric gene flow was restricted

Nan Lin and Qun Liu contributed equally to this work.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2023 The Authors. *Diversity and Distributions* published by John Wiley & Sons Ltd.

Chinese Academy of Sciences, Grant/Award Number: XDA20050203; the Young Academic and Technical Leader Raising Foundation of Yunnan Province, Grant/Award Number: 2019HB039; the Youth Innovation Promotion Association of Chinese Academy of Sciences, Grant/Award Number: 2019382; the Yunnan Young & Elite Talents Project, Grant/Award Number: YNWR-QNBJ-2019-033

Editor: Noé U. de la Sancha

within microenvironments of mid-elevational populations. Furthermore, morphological variation comparisons revealed clinal variation, as resource allocation showed a declining pattern in vegetative growth but increased reproductive growth with increasing elevation. Outlier tests and environment association analyses indicated adaptative loci primarily related to thermal-driven selection and continuous adaptations to high elevation in the Himalaya-Hengduan Mountains.

Main Conclusions: Our findings show *M. himalaica* may persist in local habitats rather than shifting range under climate change, exhibiting a low risk of genomic vulnerability in current habitats. This study has important implications in improving our understanding of the evolutionary response in alpine plants to climate change.

KEYWORDS
adaptive evolution, elevational gradients, global climate change, migration, morphological variation, RADseq

1 | INTRODUCTION

As a unique ecosystem, alpine ecosystems are distinguished by their spatially heterogeneous landscapes, high climate diversity and low disturbance by human activities. This makes them the most important refuge of biodiversity (Körner, 2003, 2004). Climatic changes in alpine areas are of particular interest in that temperature, precipitation and solar radiation differ drastically among closely adjacent areas, providing a natural laboratory for studying climate change and its effects on species distribution (Zu & Wang, 2022). In addition, alpine ecosystems harbour a high rate of endemism, in which species face major and recurrent challenges to changes in temperature and precipitation patterns under climate shifts (Parmesan, 2006; Perrigo et al., 2020). Accordingly, global climate change has been affecting alpine biodiversity and altering ecosystem functions, with a greater vulnerability than ever before with over 20% species facing extinction (Losapio et al., 2021; Mantyka-Pringle et al., 2015). There is increasing accumulation of evidence for many plants exploring alpine species range shifts across elevational landscapes in response to climate change (e.g., Platts et al., 2019; Rumpf et al., 2018; Usinowicz & Levine, 2021). The inverse situation is that plants persist in situ in the face of environmental change, which may facilitate the persistence of species (e.g., phenology, physiology, resource allocation and behaviour for broad environmental tolerances) (Alberto et al., 2013; Hobbs et al., 2018; Valladares et al., 2014; Waterhouse et al., 2018). Whether plants stay in situ or shift their distribution along elevational gradients under ongoing climate change is still not clear, thus more studies are essential to explore the evolutionary mechanisms of alpine plants responding to global change and further contribute to management of conservation.

Alpine plants are highly sensitive to rapid climatic change and respond with three main strategies: (1) range shift to track ecological niche (Chen et al., 2011; Lenoir et al., 2008), (2) phenotypic plasticity to tolerate extreme environmental change and (3) genetic evolution to adapt to new local conditions (Charmantier et al., 2008; Hoffmann & Sgrò, 2011; Jump & Peñuelas, 2005). Moving to a suitable ecological niche is the fastest way for plants to cope with climate change (Alberto et al., 2013). The rate of species extinction is closely related to dispersal ability to changing biotic and abiotic conditions, and implicit in the view that plants with high dispersal ability usually shift their distribution range tracking ecological niche along the climate gradient (Aitken et al., 2008; Hannah et al., 2014; Platts et al., 2019; Waterhouse et al., 2018). Investigations utilizing surveys and species distribution modelling are most commonly used for such studies, and research findings in southern California, the Alps and Qinghai-Tibetan Plateau (QTP) demonstrate many tree species shift upslope by over 50 m to higher elevations driven by thermal and drought stresses (He et al., 2019; Kelly & Goulden, 2008; Liang et al., 2018; Rumpf et al., 2018). In contrast to an upward shift tracking their ecological niche, phenotypic plasticity and adaptation to climatic change can maintain stability and sustainability for populations in local conditions (Alberto et al., 2013; Gonzalo-Turpin & Hazard, 2009). Faced with sudden climate changes, species with expansive plasticity may persist in new or stressful environments across different conditions (Bakhtiari et al., 2019). Plants at higher elevations usually allocate resources by trading off vegetative and reproductive growth; transplanting and physiological experiments along the elevations are mainly employed to explore the magnitude of phenotypic plasticity (Gentili et al., 2021). Remarkable variation has been observed in plant size, leaf area, flower/seed size and sexual selection responding to precipitation or temperature change in alpine plants (Aubin-Horth & Renn, 2009; de Villemereuil & Gaggiotti, 2015; Lopez-Goldar & Agrawal, 2021). However, under the circumstances of consistently directional selection and long-term physiological costs, genetic adaptation is proposed to be the most persistent response to climate change (Visser, 2008). Several studies have identified signatures of selection and important candidate genes involved in climate adaptation of non-model species (Benestan et al., 2016; Coop et al., 2010; Franks & Hoffmann, 2012; Waldvogel et al., 2020). Genome scanning based on humans, animals and crops in alpine environments has tested whether climate change can trigger extensive

reshaping of genomes expressed as local adaptive selection involved in thermal and hypoxia responses across elevational gradients (e.g., Geng et al., 2021; Hao et al., 2019; Peng et al., 2020; Rasica et al., 2021; Sun et al., 2018; Zhang, Qiao, et al., 2019; Zhang, Suren, et al., 2019). Traditional studies for monitoring species' response to climate change mostly rely on a variety of observations of populations across distribution ranges, experimental approaches and time–space points, such as catching, marking and tracking a large number of individuals, as well as occurrence and absence data (Waldvogel et al., 2020). Genomic data combined with ecological data can provide novel insights to investigate underlying space–time dispersal, climate-driven morphological variation and adaptive evolution under a changing climate (Aubin-Horth & Renn, 2009; Broquet & Petit, 2009; Rellstab et al., 2016).

Exploring how species respond to climate change is urgent for conservation of biodiversity (Brown et al., 2016; Fitzpatrick & Keller, 2015; Pecl et al., 2017; Urban et al., 2016). Currently, evidence for plant range shifts along elevations mostly come from field observations, while gene flow is a key evolutionary parameter reflecting species dispersal (Broquet & Petit, 2009). Gene flow among populations inhabiting different environmental gradients can be a potential strategy to predict the alpine's range shift to climate change (Broquet & Petit, 2009; Waldvogel et al., 2020). Within alpine plant communities, the extent and magnitude of gene flow is determined by a variety of pollen and seed dispersal mechanisms, which can be quantified by population genomics analyses as historical or contemporary gene flow (Cortés et al., 2014; Fan et al., 2019). Historical gene flow considers all migration events between populations from the current generation back to the most recent common ancestor, while contemporary gene flow refers to the current generation back to the past few generations on a smaller timescale (DeSilva & Dodd, 2020). Studies have suggested that gene flow occurs over large distances and more frequently than expected in alpine landscapes, and the dynamics of gene movement in heterogeneous alpine landscapes can be estimated by contemporary gene flow (Buehler et al., 2012). Meanwhile, species distribution modelling and distribution change based on collected specimens can also provide an important reference to forecast plant movement dynamics, and recent genomic vulnerability assessment can accurately predict plant evolution by combining allele turnover with environmental data (Dauphin et al., 2020; Ruegg et al., 2018). Furthermore, integrating analyses of herbarium specimen data in the past century supplements time–space morphological data for exploring morphological variation along elevational gradients (Willis et al., 2017). Using genotype–environment association (GEA) analyses and the strength of population structure among loci (F_{ST} outliers) to detect signatures of selection and patterns of local adaptation is likely to provide the best inferences for rejecting possible false positive loci (Vernesi et al., 2016). Thus, incorporating landscape genomics with geographic location, environmental gradient and specimen data from populations can be useful to depict how alpine species evolve in response to climate changes in situ or movement (Chen et al., 2011; Piao et al., 2019; Usinowicz & Levine, 2021).

The Himalaya-Hengduan Mountains (HHM-HDMs; hereafter HDMs refers to the Hengduan Mountains and HHM refers to the Himalayas) region is considered one of the most important biodiversity hotspots in the world, in which the elevation ranges from 1000 m on valley floors to >6000 m on mountain peaks with the mean elevation exceeding 4000 m (Xu et al., 2014). The area is therefore an ideal region for the study of species distribution responding to climate change. Empirical genomic studies have demonstrated the QTP uplift and Quaternary glaciation influenced genetic structure of plants in the HHM-HDMs (see introduction in Wu et al., 2021), as well as genetic adaption of species from high elevations above 3500 m (e.g., Guo et al., 2020; Wang et al., 2021; Zhang et al., 2016). However, these studies rarely directly relate population dynamics in elevational gradients, and how alpine plants evolve to cope with climate change along elevational gradients remains unclear. Predicting the roles of range shift, morphological variation and local adaption under rapid climate change has been challenging, due to the requirement of target plants with established populations along a continuous range of elevations and divergent habitats. *M. himalaica* Edgew (Nyctaginaceae) represents an ideal system given the species is endemic and continuously distributed in mountainous areas throughout the HHM-HDMs ranging from 1400 to 4000 m and having evolved in highly heterogeneous ecological conditions including thickets, hillsides, grasslands and dry-hot valley (Wang et al., 2019). Recent phylogeographic studies of *M. himalaica* examined mountain uplift and Pleistocene climatic change as major contributors to genetic structure, but less is known about how the species responds to climate change and whether the three response strategies coexist or complement each other within populations along the elevation gradient (Rana et al., 2020). In the present study, we focus on *M. himalaica* as a representative alpine plant and describe relative roles of range shift, morphological variation and local adaption in the face of rapid environmental changes for plants in the HHM-HDMs. We address questions by sampling *M. himalaica* populations along different elevation gradients across its range and implementing population genomics, specimen data and landscape genomics. The specific objectives include (1) identifying evidence of upward movement by quantifying the historical and contemporary gene flow between populations along elevation gradients; (2) evaluating how *M. himalaica* populations survive in situ by comparing the morphological variation associated with environmental changes and (3) identifying and annotating the potentially climate-associated loci responding to ongoing global change and assessing genomic vulnerability under future climate change.

2 | METHODS

2.1 | Sample collection and morphological variation

We sampled a total of 176 individuals from 23 populations spanning most of the distribution range and elevational gradients observed in *M. himalaica* (Rana et al., 2020). At each population, fresh leaves of 4–14 individuals spaced at least 50 m apart were collected and dried in silica gel (Figure 1a; Table S1). According to previous studies and field investigations, a total of morphological traits [i.e.,

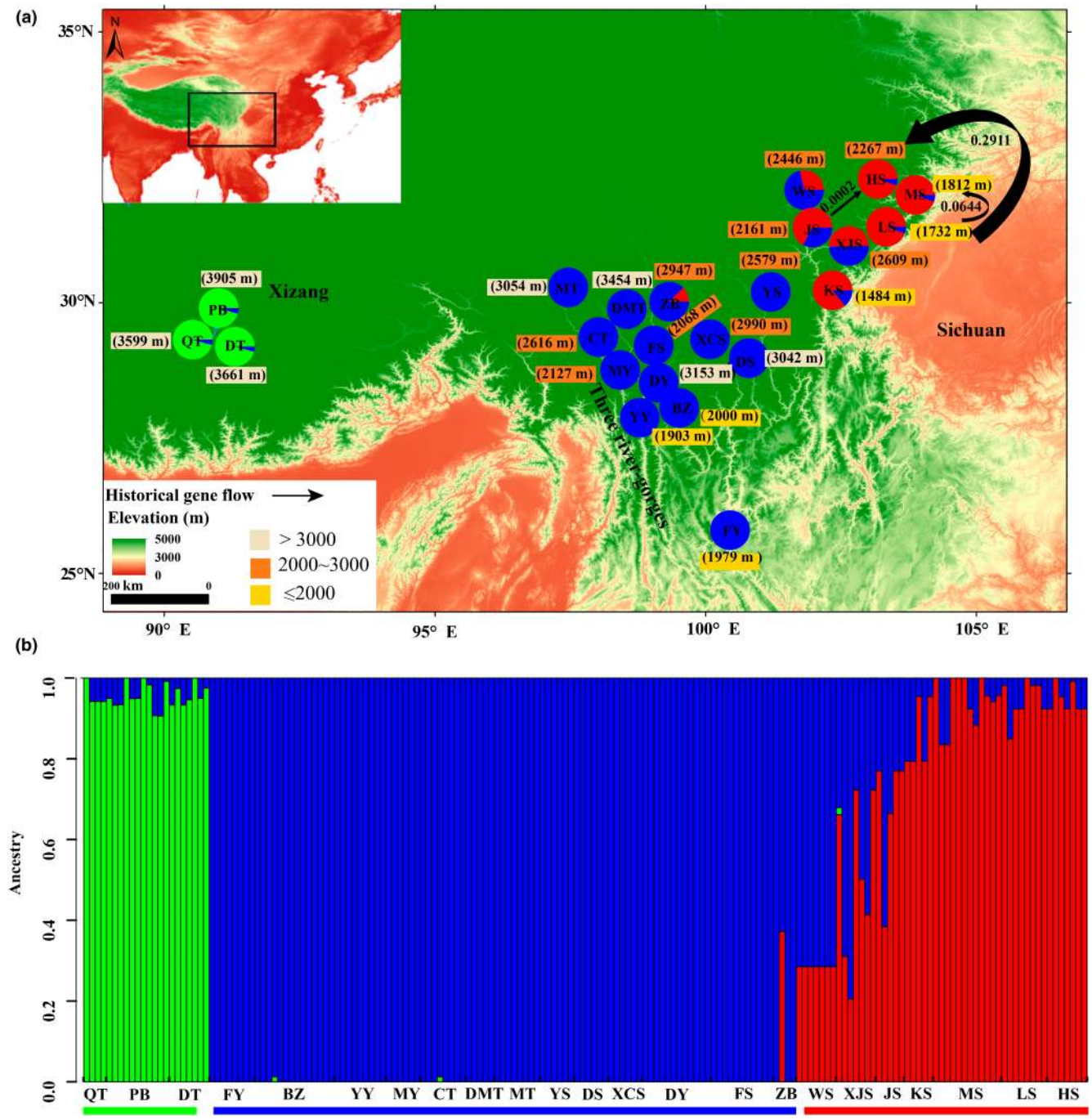


FIGURE 1 Geographic distribution, elevations and mapping of the genetic clusters of *Mirabilis himalaica*. (a) Three main clusters are indicated by green (Cluster I), red (Cluster III) and blue (Cluster II) based on ADMIXTURE analysis of neutral SNPs from 23 populations. The directional arrows referred to the historical gene flow from TreeMix analysis based on all 23 populations, and the thickness of the line corresponds to the gene flow level. Rectangles with numerical value indicated elevation for populations, and rectangles with the same colour were assigned to identical elevational groups for the following analyses. (b) Histogram of the ADMIXTURE analysis for *Mirabilis himalaica* with $K = 3$. Each vertical bar represents one individual.

average plant internode length (cm), leaf area (cm^2), ratio of leaf length and leaf width, petiolule length (cm) and number of inflorescence branch of leaf axil (n)] were measured for morphological estimation from representative herbarium specimens collected during the flowering time period for *M. himalaica*. These specimens were composed of 23 specimens within the same locations as each genetically sampled population and 15 well-preserved specimens in the Herbarium of Kunming Institute of Botany. All traits were measured of healthy, mature leaves from the same position with a vernier calliper and Digimizer v4.1 (Salvarzi et al., 2018). Outlier values were eliminated to avoid possible biases, and the following statistics and visualization were conducted with stats v3.5.1 package and ggplot2 v3.3.6 package in the R environment (R Core Team, 2021).

2.2 | Geography and environmental data

Studies have shown that distance-based Moran's eigenvector map (dbMEMs) are independent vectors to summarize the geographical variables among sites (Borcard & Legendre, 2002). For dbMEMs, GPS coordinates (longitude and latitude in degrees) based on WGS84 system were first converted to Cartesian coordinates with the geoXY function in the SoDa v1.0-6.1 package of R (Chambers, 2008; R Core Team, 2021), and a Euclidian distance matrix was computed using the dist function in vegan v2.6-2 package of R (Oksanen et al., 2013; R Core Team, 2021). Then the PCNM function was performed on the matrix using the PCNM v2.1-2 package transforming the spatial distances to rectangular data which has been suggested for better constrained ordination (permutations = 1000, Borcard & Legendre, 2002; R Core Team, 2021). Then the first three eigenvectors were created (dbMEMs1, dbMEMs2 and dbMEMs3) for geographical variable. The 19 bioclimatic current conditions (1960–1990) and future predictions (2070) were extracted from WorldClim v.1.4 raster layers at 30 s (~1 km^2) resolution (http://www.worldclim.org; Hijmans et al., 2005). Previous studies have shown distinct changes in clay content of the soil (clay), organic carbon density of soil (OCDm) and pH of soil (PH_H2O) along elevational gradients and revealed significant correlations between these soil variables and species distribution in the Himalaya-Hengduan Mountains (e.g., Li et al., 2014; Wang et al., 2022; Wang, Kou, et al., 2017; Wang, Li, et al., 2017; Zhao et al., 2022). Thus, these three soil variables were further extracted from the Harmonized World Soil Database version 1.21 at 30 s (~1 km^2) resolution (https://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en; Nachtergaele et al., 2012). To avoid multicollinearity, both variance inflation factor (VIF > 10) and Pearson correlation coefficient ($r > |.75|$) were employed to remove highly correlated climate variables in R (R Core Team, 2021). The variance inflation factor (VIF) is primarily used to measure how much the variance of a regression coefficient is inflated due to multicollinearity in the model and a VIF value over 10 empirically indicates a problematic amount of collinearity (James et al., 2014). Ultimately, eight climatic variables were retained: five climatic variables (temperature isothermality (bio3), temperature annual range (bio7), mean temperature of wettest quarter (bio8), precipitation seasonality (bio15), precipitation of warmest quarter (bio18)), and three soil variables (clay content of the soil (clay), organic carbon density of soil (OCDm), pH of soil (PH_H_2O)) (Tables S1 and S2; Figure S1). These environmental variables, together with the geographic location of the population decomposed by dbMEMs (dbMEMs1, dbMEMs2 and dbMEMs3), were used in subsequent analyses.

2.3 | DNA extraction and RAD sequencing

Total genomic DNA was exacted from dry leaf tissue using a modified cetyltrimethylammonium bromide (CTAB) method (Doyle, 1991). Restriction site associated DNA (RAD) libraries were prepared according to a previously published protocol (Baird et al., 2008). In brief, each sample was digested with EcoRI (restriction site 5′GAATTC3′), and a P1 adapter containing 4–8 bp individual-specific nucleotide barcodes was ligated to the fragments. The ligation products were subsequently pooled and randomly sheared. A second adapter was then ligated to the DNA (P2, a divergent "Y" adapter), and DNA fragments with a length of 350–550 bp were were collected for library construction. Finally, libraries were enriched by PCR amplification and RADs for each individual were sequenced (4 individuals per sequencing lane) on an Illumina Hiseq2500 platform at Beijing Genomics Institute (BGI, Wuhan, China) with 150 bp paired-end reads. After inspecting an overview of the sequenced data with FastQC v0.11.9 (Andrews, 2010; http://www.bioinformatics.babraham.ac.uk/projects/ fastqc/), raw reads by the removal of uncalled bases (-c) and low-quality scores (-q, a Phred score of 10) and demultiplexed using the process_radtags program in Stacks v2.0 (Catchen et al., 2011, 2017). All 176 samples were processed for SNP calling using the denovo_map.pl wrapper in Stacks v2.0, with a maximum of two nucleotide mismatches ($M = 2$) and a minimum stack depth of four ($m = 4$) according to Ilut et al. (2014), and reads were aligned de novo with each other to create catalogue of consensus loci containing all the individuals, and finally compared each individual genotype against the merged catalogue (Catchen et al., 2011, 2017). To obtain a high quality and number of SNPs, we first retained RAD tags with a minimum depth (m) of 10 to a maximum depth of 100 avoiding SNPs with very low coverage or highly overrepresented sites due to repeats. We then set a gradient test for a minimum genotype call rate of individuals from each population ($r = .5–1$) in at least 20 populations (minimum number of populations a locus, $p = 20$). We further filtered SNPs with a minor allele frequency (MAF) higher than 0.05 to avoid bias in the estimation of the baseline differentiation, sequencing and PCR error and SNPs with observed heterozygosity higher than 0.5 were filtered to exclude potential paralogs (Hohenlohe et al., 2011). Only the first SNP per locus was used to avoid linkage bias, and PGDSPIDER v2.1.1.5 and vcftools v0.1.16 were used to convert format for downstream analyses (Danecek et al., 2011; Lischer & Excoffier, 2012).

2.4 | Signature of local adaptation from F_{ST} and GEA outlier methods

Combined population differentiation (F_{ST} outlier) and genome–environment association (GEA outlier) methods were used to detect SNPs under selection. First, BAYESCAN v2.1 and ARLEQUIN v3.5 were used to find genetically differentiated loci that deviate from neutral selection (Excoffier & Lischer, 2010; Foll & Gaggiotti, 2008). BAYESCAN, a Bayesian method based on a logistic regression model, directly estimates the posterior probability for each locus potentially under selection using the following parameters: 100,000 iterations; 10 thinning intervals; 100 pilot runs of length 5000; 50,000 burn-in and a prior odd of 30 for neutral model and a strict filtered threshold value were set by setting the false discovery rate (FDR) below 0.05

to reduce the false positives loci (Foll & Gaggiotti, 2008). We also identified F_{ST} outlier SNPs using ARLEQUIN, which is based on the infinite island model that integrates heterozygosity and simulates a distribution for neutrally distributed loci. We ran 20,000 simulations and 100 demes per population, with the FDR set at 0.05 (Excoffier & Lischer, 2010). Based on the above two analyses of F_{ST} outlier methods, we divided our data set in two matrices, outlier SNPs (an outlier identified from both F_{ST} outlier methods) and putatively neutral SNPs (remaining SNPs without outliers SNPs) for downstream analyses.

We also integrated two GEA approaches to identify outlier loci under local adaptation associated with environmental. We first employed BAYESCENV to identify selective loci associated with environmental factors using Bayes factor (BF) representing the ratio of correlation probabilities under generalized linear mixed models (de Villemereuil & Gaggiotti, 2015). For BAYESCENV, 10 independent runs of 10^5 MCMC cycles were produced for each SNP, and SNPs with log10 (BF) >1 were identified with strong support for associations between allele frequencies and environmental gradient (Coop et al., 2010; Jeffreys, 1998). We then performed Pearson test via the 'cor.test' function included in R to identify allele frequencies for SNPs significantly associated with ($p < .001$ and $r > |.85|$) for at least one of the environmental variables.

2.5 | Loci annotation

To detect putative outliers associated with adaptation, we further identified candidate genes in genomic regions (within 2 kb) surrounding our RAD-Tags. We annotated outlier loci that were identified from at least one GEA method to obtain the putative adaptive loci associated with environmental factors. As no reference genome is available for *M. himalaica*, we aligned all the candidate consensus sequence to the closely related available genome of *Beta vulgaris* (https://phytozome-next.jgi.doe.gov/info/ Bvulgaris_EL10_1_0) using BLASTN with *e*-value threshold of 1×10^{-5} (McGrath et al., 2020).

2.6 | Population genetic structure, diversity and relationship between genetic variation and environmental gradient

We used putatively neutral SNPs to determine genetic structure and admixture of populations. We implemented ADMIXTURE v1.3.0 to estimate individual ancestries with a maximum likelihood method from $K = 2$–24 and optimal partitioning of the population was achieved at the lowest cross-validation error (Alexander et al., 2009). A maximum likelihood (ML) tree using the ascertainment bias correction (−m ASC_GTRGAMMA, −asc-corr = lewis) with 1000 bootstrap replicates was inferred using RAxML v8.2.10 (Stamatakis, 2014) to study population evolutionary history, while principal component analysis (PCA) was performed from the genome-wide complex trait analysis (GCTA) to assess overall distribution of genetic variation (Yang et al., 2013). Although genetic clusters partially correspond to elevational differentiation among populations (see Section 3), we reclassified the 23 populations into three elevational groups for further analysis (Figure 1; Table S1; Low group: <2000 m, Mid group: 2000–3000 m and High group: >3000 m). This clustering better represents how populations respond across environmental gradients and avoids uneven elevation distribution within genetic clusters. Genetic diversity including mean frequency of observed heterozygosity (H_O), expected heterozygosity (H_E), fixation index (F_{IS}) and nucleotide diversity (π) for all populations and elevational groups were calculated using Stacks v2.0 (Catchen et al., 2011, 2017) with the populations module.

Redundancy analyses (RDA) and partial redundancy analyses (pRDAs) were conducted to investigate the relative contribution of geography and environmental data to both neutral and putatively adaptive genetic structure using vegan v2.6-2 package in R (Oksanen et al., 2013). We first ran the RDA to explore the global significance of all variables using an initial model via a permutations test with an *n* of 1000, and further performed the ordistep function to select variables of the optimal model avoiding collinearity issues to determine the independently effect of each variable for RDA and partial RDA. We tested the significance of each individual variable from ordistep results by a RDA marginal effect permutation test with 1000 permutations removing each term one by one. In the case of the partial RDAs, the effect of the single considered variable RDA axis after conditioning all other variables was compared with that obtained for conditioned RDA estimating the specific effect of other variables. To further explore the effects of environmental factors on morphological traits, redundancy analysis (RDA) was performed to investigate the relationship between traits, geography and environmental data using vegan v2.6-2 package in R (Oksanen et al., 2013), as well as to identify the relative importance of the effect of each environmental variable separately.

2.7 | Estimates of historical and contemporary migration events

To examine migration dynamics of *M. himalaica* under climate change along an elevational gradient, we estimated recent and historical gene flow across populations. BayesAss3-SNPs based on putatively neutral SNPs was used to estimate rates and direction of recent migration events for the past few generations between each population based on a MCMC sampling method (Mussmann et al., 2019; Wilson & Rannala, 2003). A preliminary run of 1,000,000 steps was first conducted to investigate the acceptance rates of the mixing parameters for allele frequencies and inbreeding coefficients, then 10 longer runs were performed for 20,000,000 iterations with a burn-in of 1,000,000 and sampling every 1000 steps. Additionally, a maximum likelihood method in TreeMix v1.13 was performed to estimate historical gene flow based on putatively neutral SNPs, performing a population-level phylogeny on the basis of allele frequencies with migrant events ranging from 1 to 23 with 10 replicates (Pickrell

& Pritchard, 2012). Meanwhile, the optimal number of migration events was determined with the OptM v0.1.6 package in R with the linear method (Fitak, 2021).

2.8 | Species distribution modelling and prediction of genomic vulnerability under future climate change

To find distribution shifts across elevation, we divided the 81 available specimens with elevational records into two periods (pre-1980 and 1980-present) reflecting a temperature shift point in the HHM-HDMs (IPCC, 2013; Shrestha et al., 2012). Shifts in mean elevation and significance were analysed using the Mann–Whitney *U* Test function in R (R Core Team, 2021). The occurrence points from specimens and eight variables were further used for species distribution modelling under current (1960–1990) and future (2070; Representative Concentration Pathways, RCP 85) layers from the Model for Interdisciplinary Research on Climate (MIROC) forecasting species distribution change. All models were run in MaxEnt 3.2 with 10 replicates calibrated using 25% of the data to evaluate the quality of the models (Phillips et al., 2006). We further reclassified distribution changes in the future conditions compared to current suitability (60% probability) into stable, expanded and contracted areas. Genomic vulnerability was also tested in our study which combined the population allele frequencies and future environment to predict the adaptive potential of species (Rellstab et al., 2016). Mean difference between current and future expected allele frequencies across contemporary climate gradients was used as a baseline to predict the future genomic vulnerability. A gradient forest (GF) analysis was performed using the R package gradientForest v0.1-32 for the analysis of genomic vulnerability. We first modelled the associations of climate variables with population allele frequencies from the SNPs and extracted current bioclimatic variables for each population (parameter settings: 500 regression trees per SNP; maxLevel = $\log_2(0.368n)/2$; variable correlation threshold: 0.5) (Fitzpatrick & Keller, 2015). We then used the predict function to explore the allelic turnover across the whole landscape using our fitted model (gf) and the climate values to predict genomes under current and future climate scenarios across the distribution range of the *M. himalaica*.

3 | RESULTS

3.1 | Morphological variation along elevation gradient

Morphological variation of the five traits were found among the three elevational groups (Figure 2; Figure S2). Based on testing for the mean difference between elevational groups, we detected significant differences in leaf area and inflorescence branch (Figure 2). Correlation analysis uncovered that internode length, leaf area and petiole length decrease with elevation, but an increasing in ratio of leaf length and width ($p > .05$; Figure S2). Compared to low elevation, we found a significant increase in inflorescence branches at high elevation ($p < .0001$; Figure S2).

3.2 | Composition of data sets: Outlier SNPs and putatively neutral SNPs

After quality filtering, the number of reads per sample averaged 27.23×10^6 (minimum: 3.25×10^6; maximum: 78.74×10^6) with an average read depth of 23.87 (range: 5.58–54.25) (Figures S3 and S4). After site filtering, we used 42,220 SNPs ($r = .85$ and $p = 20$) retaining SNPs that were present in at least 50% of almost all individuals, of which 28,500, 30,688 and 26,967 SNPs were found in

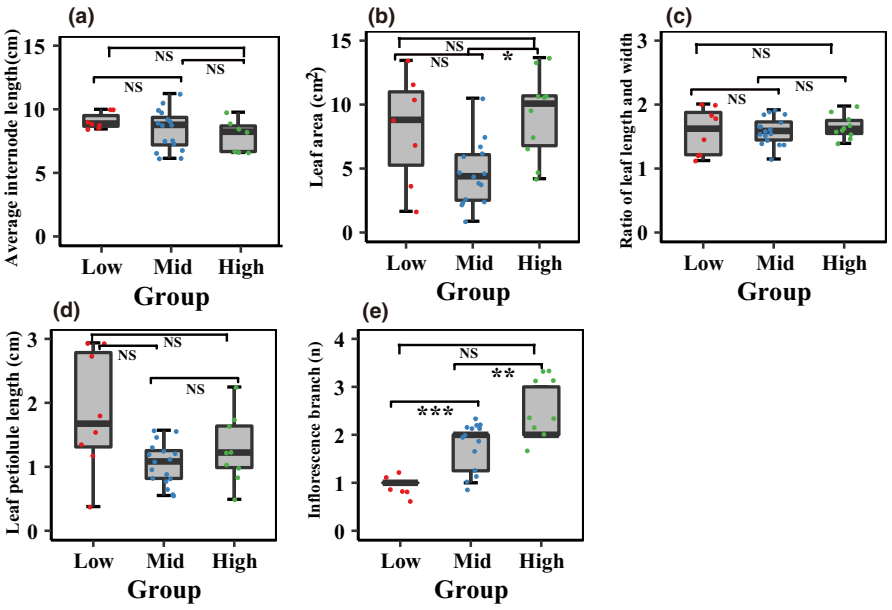


FIGURE 2 Phenotypic comparisons among three elevational groups from specimens along an elevational gradient. Representative phenotypes include (a) Average internode length, (b) leaf area, (c) ratio of leaf length and width, (d) leaf petiolule length, (e) inflorence branch. Boxes indicate first quartile, median and third quartile, and the whiskers represent the upper and lower bound. NS represents not significant, $^*p < .05$; $^{**}p < .01$; $^{***}p < .001$.

the High, Mid and Low groups, respectively (Figure S5). Based on the BAYESCAN results, we detected 22, 37 and one positive F_{ST} outlier SNPs in the High, Mid and Low groups (Figure 3; Figure S6). ARLEQUIN identified 2858, 1677, 156 F_{ST} outlier SNPs in the High, Mid and Low groups, respectively (Figure 3). At the same significance level ($p < .05$), 22, 18, and one F_{ST} outlier SNPs in the High, Mid and Low elevational groups were overlapping in the BAYESCAN and ARLEQUIN results for outlier SNPs and were included in downstream analyses of adaptive genetic structure (Figure 3). We thus used the 28,478, 30,670 and 26,966 putatively neutral SNPs for downstream analyses of neutral genetic structure across three elevational groups.

3.3 | Screening for loci associated with climatic-driven adaptation

For the High elevation group, BAYESCENV identified 185 SNPs potentially linked to geographical variable (Figure S7), while correlation tests revealed a set of 6602 SNPs showing significant associations with at least one of the 11 predictors (Figure 3). We identified four overlapping SNPs between the two GEA analyses, two of which were also detected by ARLEQUIN (Figure 3). For the Mid group, BAYESCENV identified 43 SNPs potentially linked to a soil variable (clay) and geography (dbMEM-1 and dbMEM-3; Figure S7), while correlation tests revealed a set of 367 SNPs showing significant

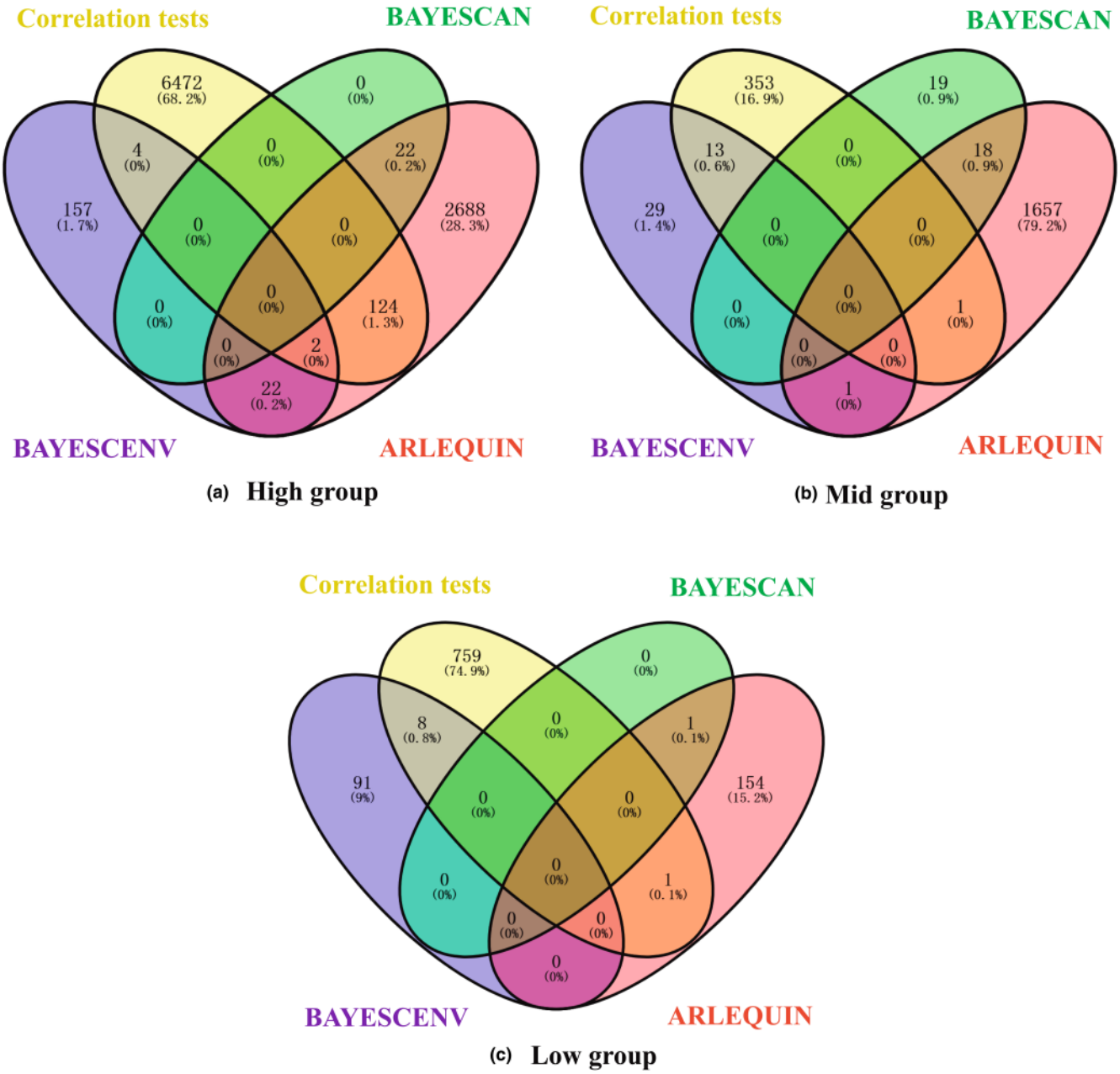


FIGURE 3 Venn diagrams showing the number of SNPs identified as putatively under selection from two F_{ST} methods (BAYESCAN and ARLEQUIN for F_{ST} outlier SNPs) and two GEA methods (BAYESCENV and correlation tests for GEA outlier SNPs) for three elevational groups.

associations with at least one of the 11 the predictors, and a total of 13 SNPs shared in two GEA methods. For the Low group, 99 SNPs were identified by BAYESCENV linked to geographical variable (Figure S7), while correlation tests revealed a set of 768 SNPs showing significant associations with at least one of the 11 the predictors with eight SNPs shared in two GEA methods (Figure 3).

We further aligned candidate consensus sequences of outliers to a reference genome to explore their putative gene function. A total of 150 candidate SNPs defined as potentially under divergent selection in the High elevation group, and 55 of them were successfully aligned to the *B. vulgaris* genome using BLASTN, and a total of 24 hits with an *E*-value smaller than 10^{-5} (Table S3). Specifically, most of the divergent loci were involved in stress responses to high-altitude and climatic-driven stress, such as the BAG family molecular chaperone regulator 3, probable inactive purple acid phosphatase 1, WRKY transcription factor 22, NAD(P)H-quinone oxidoreductase subunit 5. Within the Mid group, 15 candidate SNPs were identified as potentially under divergent selection and 12 of them were successfully annotated, and only four of them had an *E*-value smaller than 10^{-5} (Table S3). From these four successfully annotated genes, most are related to high-altitude adaptation, such as DEAD-box ATP-dependent RNA helicase 38 and 2,3-bi sphosphoglycerate-independent phosphoglycerate mutase. Within the Low group, we successfully annotated five of the nine candidate SNPs and two of them with an *E*-value smaller than 10^{-5}, including NAD(P)H-quinone oxidoreductase subunit I and protoporphyrinogen oxidase 2.

3.4 | Populations genetic structure and diversity

Genetic structure analysis in ADMIXTURE provided support for a three-cluster model (Figure 1; Figure S8). Within *M. himalaica* when $K = 3$, three populations (QT, PB, DT) located in the southeastern Himalayas were assigned to cluster I (median altitude = 3661 m), 13 populations located in the southwestern parts of the Hengduan Mountains were assigned to cluster II (median altitude = 2616 m), and seven populations located in the northeastern parts of the HDMs were assigned to cluster III (median altitude = 2161 m). Phylogeny and PCA results generated identical clustering with a clear divergence among the 23 populations (Figure S9). To better explore genetic variations along elevational gradients, we defined three elevational groups (Low group: <2000 m, Mid group: 2000–3000 m and High group: >3000 m) for following analyses making it more representative of the environmental gradients. Comparative analyses found that populations in the Mid group have a higher nucleotide diversity (Mid group: $P_i = 0.0215$) than populations in high and low elevation (Low group: $P_i = 0.0144$; High group: $P_i = 0.0142$). Similar patterns for all other estimated genetic variables (i.e., H_o, H_e and F_{is}) were observed (Table S4).

3.5 | Association between geography, environmental factors and genetic variation

Our results found the first 10 PCs were meaningful and accounted for over 80% of the 28,478, 30,670 and 26,966 putatively neutral SNPs of the three elevational groups (Table S5). Furthermore, our RDA analyses and pRDA based on the putatively neutral genetic variation and adaptive genetic variation is significantly explained by geography, climatic and soil variables for all elevational groups (Table 1). For neutral genetic variation in the High group, the RDA was globally significant with an adjusted coefficient of determination of 0.769 ($p < .001$). When we controlled for the effect of two of the three set of variables (i.e., geography, climatic and soil variables) in a partial RDA model, the geography, climatic and soil variables was significantly explained 17%, 7.7% and 5.5% of the genetic variation, respectively ($p < .001$, Table 1). For putatively neutral genetic variation in the Mid group, the RDA was globally significant with an adjusted coefficient of determination of 0.711 ($p < .001$). In the partial RDA models conditioned on geography and soil variables, climatic factors explained the highest proportion of 20.4% SNP variation ($p < .001$). Regarded as putatively neutral genetic variation in the Low group, geography and climatic factors explained 21.1% and 16.5% SNP variance, respectively, when controlled the effect of another one in a partial RDA ($p < .001$).

For the analyses based on SNPs putatively under divergent selection within the three elevational groups, the first 10 PCs accounted for 89%, 97.7% and 100% of the putatively adaptive genetic variation of the 22, 18 and one SNPs, correspondingly (Table S5). For adaptive genetic variation in the High group, the RDA was globally significant with an adjusted coefficient of determination of 0.535 ($p < .001$, Table 1). The different partial RDAs identified that 5.3% of the explained variance was associated with geography, 7.7% was due to climatic variation, 6.1% was due to soil variation. For putatively adaptive genetic variation in the Mid group, our partial RDA models showed geography explained 6.8% genetic variation, while climatic and soil variables explained 22.2% and 8.2% SNP variation ($p < .001$), respectively. Regarded as putatively adaptive genetic variation in the Low group, 46% genetic variation was explained by climatic and soil variables when constraining geography and soil variables ($p < .001$). Furthermore, RDA was globally significant with an adjusted coefficient of determination of 0.524, 0.980 and 0.650 in High, Mid and Low group separately for morphological variation in the groups (Table 1; $p < .001$). For the High group, the different partial RDAs identified that 7.6% of the morphological variance was associated with geography, 4.2% was due to climatic variation, 14.1% was due to soil variation (Table S6). For the variation in the Mid group, our partial RDA models showed climatic variables explained 54% of morphological variation ($p < .001$). Regarded as putatively adaptive genetic variation in the Low group, climatic variables also explained the highest of 53.9% morphological variation when constraining geography and soil variables.

3.6 | Pattern of contemporary and historical gene flow

Recent migration rates (i.e., the proportion of migrant individuals per population per generation for the past few generations) yielded results that migration rates were lower of ~0.01 in all cases (Table S7).

TABLE 1 Summary and partitioning of the genetic variance associated with geography and environmental variables for potentially neutral and adaptive genetic variation from the three elevational groups.

	Neutral SNPs		Outliers SNPs	
Groups	Explanatory variables (ordistep function)	Adjusted R^2	Explanatory variables (ordistep function)	Adjusted R^2
High group	**Global RDA**	**.769*****	**Global RDA**	**.535*****
	Geography	**.181*****/.170*****	**Geography**	**.053*****/.051*****
	dbMEM-1	.181***/.170***	dbMEM-1	.053***/.051***
	Climate	**.077*****/.077*****	**Climate**	**.077*****/.078*****
	bio3	.033***/.033***	bio7	.009***/.008***
	bio15	.032***/.031***	bio15	.058***/.057***
	Soil	**.055*****/.055*****	**Soil**	**.061*****/.061*****
	clay	.021***/.021***	clay	.014***/.014***
	PH_H2O	.037***/.036***	OCDm	.011***/.011***
Mid group	**Global RDA**	**.711*****	**Global RDA**	**.577****
	Geography	**.177*****/.177*****	**Geography**	**.068*****/.068*****
	dbMEM-1	.054***/.054***	dbMEM-2	.029***/.033***
	dbMEM-2	.054***/.054***	dbMEM-3	.029***/.033***
	dbMEM-3	.055***/.054***		
	Climate	**.204*****/.204*****	**Climate**	**.222*****/.189*****
	Bio3	.050***/.051***	Bio3	.043***/.047***
	Bio8	.033***/.033***	Bio7	.039***/.043***
	Bio15	.027***/.027***	Bio15	.040***/.041***
	Bio18	.043***/.043***	Bio18	.023***/.034***
	Soil	**.084*****/.084*****	**Soil**	**.082*****/.082*****
	clay	.044***/.043***	clay	.044***/.058***
	PH_H2O	.030***/.031***	PH_H2O	.013***/.026***
Low group	**Global RDA**	**.648*****	**Global RDA**	**1** ^{NS}
	Geography	**.166*****/.165*****	**Geography**	**.056*****/.056*****
	dbMEM-2	.079***/.079***	dbMEM-2	.056***/.056***
	dbMEM-3	.029***/.028***		
	Climate	**.212*****/.212*****	**Climate**	**.460*****/.460*****
	Bio8	.049***/.049***	Bio8	.420***/.420***
	Bio15	.054***/.054***	Bio15	.007***/.007***
	Bio18	.080***/.080***		
			Soil	**.005*****/.005*****
			clay	.005***/.005***

Note: The influences of each set of variables (geography, climatic and soil variables) have been tested separately and together based on redundancy analysis (RDA) and partial RDA (pRDA). The values for each variable on the left and right sides of the slash represent the RDA and pRDA results, respectively. Only variables from ordistep function were retained here and significant explanatory variables are indicated with the following symbols: $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$.

The bold value mean the influences of each set of variables (geography, climatic and soil variables) separately.

Three historical gene flow events across populations were detected by TreeMix (Figure 1). Notably, the three gene flow events were concentrated at low to mid altitudes of the northern HDMs [i.e., 0.2911 from LS (1732 m) to HS (2267 m), 0.0644 from LS (1732 m) to MS (1812 m), 0.0002 from JS (2161 m) to HS (2267 m)] with the direction from low to high elevation. Since this might lead to an underestimation of historical gene flow, we further explored gene flow within microhabitats of northern HDMs, southern HDMs and the Himalaya region, independently. According to our results, asymmetric gene flow was found between populations within northern HDMs or southern HDMs, but not found in the Himalaya regions (Figure S10). For example, we found the obvious upward gene flow in

the southern HDMs [e.g., 0.3768 from YS (2579 m) to XCS (2990 m), 0.0988 from MT (3054) to DY (3153 m)], as well as in the northern HDMs [e.g., 0.2609 from WS (2446 m) to XJS (2609 m)]. Whereas we identified clear migration events from high to low elevation, such as 0.3096 from WS (2446 m) to JS (2161 m) and 0.1350 from DMT (3454 m) to XCS (2990 m).

3.7 | Prediction of species distribution and genomic vulnerability to future climate change

The projected current distribution of *M. himalaica* is highly consistent with known occurrences. Moreover, the predicted future distributions suggest that there will be shifts in suitable climate to higher elevations and latitudes (Figure 4a). Regarding the area of suitable climate, *M. himalaica* is predicted to experience a clear loss south of the Three River-Gorges subregion, and expansion to the northwest of the HDMs compared to the present distribution (Figure 4a). Under a model of future climate conditions, genomic vulnerability for *M. himalaica* was low across the its range, with the highest value predicted in the southern and eastern part of the Himalaya edges (Figure 4b), corresponding to the range of the marginal range of the species' current distribution. Meanwhile, genomic vulnerability for *M. himalaica* was low across the entire range.

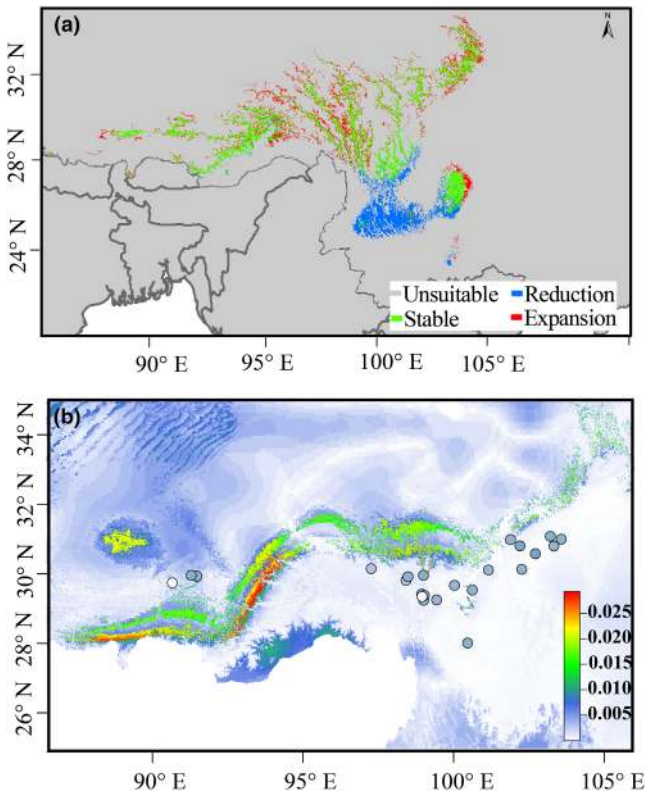


FIGURE 4 Maps of the potential distribution and genomic vulnerability across *Mirabilis himalaica* distribution in the future (2070). (a) Maps of the potential species distribution of reduced (blue), stable (green) and expansion (red) areas compared between current versus future (based on the output of MIROC, RCP8.5). (b) Map of genomic vulnerability across *Mirabilis himalaica* distribution in the future (2070). Red = high genomic vulnerability; blue = low genomic vulnerability. The population locations are represented by coloured dots corresponding to the genomic vulnerability value.

4 | DISCUSSION

An increasing number of studies have implied that alpine plants respond to climate change by upward ecological niche expansion to track their climatic niches ("move") or remain in situ and tolerate the new conditions by phenotypic change, cooperating with substantial local adaptive evolution (Hamala & Savolainen, 2019; Lopez-Goldar & Agrawal, 2021; Waldvogel et al., 2020). Unlike animals, plants are sessile and the ability of movement depends on dispersal characteristics that are differentiated between species (Hobbs et al., 2018). In contrast, phenotypic plasticity to tolerate various environmental and local adaptation to changing conditions might be persistent and effective approaches to future climate change (Chu et al., 2021; Zhang, Qiao, et al., 2019; Zhang, Suren, et al., 2019). In the current study, we devised genome-wide and ecological data sets of a keystone species in alpine ecosystems, *M. himalaica*. Our results indicate that even though the signals of three evolutionary mechanisms were detected simultaneously, morphological variation and local adaptation are prominent among *M. himalaica* populations across different elevations. We first found low levels of asymmetric gene flow among mid-elevation populations within microhabitats (Figure 1; Figure S10). Furthermore, morphological variation and genomic evidence demonstrated that *M. himalaica* populations present a continuous high-altitude and climate-driven adaptation to heterogeneous environments along different elevations (Figures 2 and 3). Taken together, these results mostly support *M. himalaica* remaining in situ to tolerate new environmental condition across alpine landscapes, providing the innovative surviving strategies of alpine plants responding to climate change.

4.1 | Morphological variation in relation to increasing elevation

Alpine plants usually face rapidly changing environmental conditions in terms of solar radiation, atmospheric pressure, temperature and showing regional morphological variation patterns (Aubin-Horth & Renn, 2009). Plants cope with resource deficit by allocating biomass between vegetative growth and reproductive growth along increasing elevation to adapt to stressful environments (Gentili et al., 2021). Consistent with previous studies, our study revealed considerable morphological variation in terms of plant height, leaf shape and flower number in *M. himalaica*. Overall, *M. himalaica* reduced its size of vegetative traits (plant internodes leaf area and petiolule length) along the elevational gradient, but this contrasts with patterns of reproductive traits (inflorescence branch) (Figure S2). Our results showed a trend towards smaller plants at higher elevation based on average internode length although this

was not significant between groups (Figure 2; Figure S2), suggesting low elevation conditions are likely to be more favourable for optimum plant growth. The declining plant size at higher elevation can reduce the exposure to extreme environments and reduce the damage caused by low temperature and drought, especially when approaching the range edge at high elevations (Körner, 2003; Zhao et al., 2006). Alternatively, a smaller plant size can form a warm environment for flowers to attract more insects for seed transfer (Yang et al., 2008). Additionally, leaf area was found to decrease and leaf shape lengthened, which conforms to previous studies (e.g., *Saussurea*, *Roscoea* and *Epilobium*) reflecting the leaf adaptation to increased environmental stress (Paudel et al., 2019; Stöcklin et al., 2009; Wang & Yue, 2014). Smaller leaf size is driven by low temperatures, high solar irradiation and wind exposure typical of high elevation environments, and the decreasing leaf size enables reduction of transpiration and ability to maintain efficient utilization of water (Guerin et al., 2012; Royer et al., 2008; Wang & Gao, 2004). In contrast, inflorescence branching significantly increased with elevation in *M. himalaica*, similar to resource allocation schemes in other alpine plants (Takahashi & Matsuki, 2017). With increasing elevation, the increase in reproductive investment may be in response to lower mean individual size (Körner, 2003; Wang, Kou, et al., 2017; Wang, Li, et al., 2017). We also found the density leaf "hairs" of the upper and lower surface leaves gradually increased with the increase of altitude in the fields, which can reduce the impact of strong airflow on stomata, decreasing evaporation and preventing direct light damage to the plant (Takahashi & Matsuki, 2017). Our results partly revealed that *M. himalaica* undergoes local adaptation by modifying plant height, leaf area and shape and inflorescence in response to the varying detrimental effects associated with the elevational climate change. However, our limited samples might have influences on the final results, and extensive sample size is needed for further observation and verification.

4.2 | Continuous genetic adaptation in situ under climate change

Evidence is accumulating that alpine species have the capacity to adjust to environmental change in situ via adaptive evolution (Waterhouse et al., 2018). The alpine landscape, characterized by steep valleys and high mountain ridges, makes assessing genetic variations patterns and drivers across populations difficult. In agreement with previous studies, our partitioned redundancy analysis (pRDA) results found geography as the important factor explaining the genomic variation in neutral SNPs among different elevational groups (Table 1; Borcard & Legendre, 2002). However, we still identified environmental factors that are correlated with changes in genetic variation for both putatively neutral and adaptive SNPs in our study. In particular, our results suggest that precipitation seasonality (bio15) has a significant impact on neutral genetic variation among three elevational groups (Table 1). Moreover, all the identified putatively adaptive SNPs were significantly related to the climatic variables, and climatic variables have explained the highest genetic variation in partial RDA model of the three elevational groups (Table 1). This result suggests that environmental factors have contributed to the genetic composition and inferred potential adaptation across elevational gradients. Therefore, these associations between genomic variation and environmental change can allow the further detection of ecological effects of natural selection on populations and the prerequisites to explore loci under selection. In this study, we combined population differentiation (F_{ST}) and environmental association (GEA) approaches to detect candidate loci of alpine adaptation, which reduced false-positive discoveries and maximize chances of detecting potential signals of selection (Benestan et al., 2016; Francois et al., 2016). In total, we found that GEA analyses identified more candidate markers than F_{ST} analyses in our three groups, which is in agreement with previous studies (Villemereuil et al., 2014). To further find candidate genes under local adaptation, we defined a number of candidate SNPs potentially under divergent selection, and only one-third of candidate SNPs aligned to the *B. vulgaris* coding regions with a high-quality *E*-value due to the absence of the *M. himalaica* reference genome (Table S3). Nonetheless, we discovered accumulation of candidate genes of climate-driven adaptation at increasing elevations rather than the evolution at specific elevations. Previous studies have shown that high elevation populations of the HHM-HDMs present genomic signals of selection related to reproduction, DNA damage repair, and cold tolerance (e.g., Chen et al., 2019; Wang et al., 2021; Zhang, Qiao, et al., 2019; Zhang, Suren, et al., 2019). However, these studies uniformly focused on high elevational species, how plants adapt to alpine environments starting from low elevations under climate change is unclear. Our evidence from *M. himalaica* along an elevational gradient disentangled continuously genetic adaptation in situ from low to high altitude. Within the low group, two high-quality annotated candidate loci were located in *NDH1* and *PPO2*, which may play key roles creating an ionic motive force used to generate ATP and driving chlorophyll synthesis pathway processes (Liu et al., 2019; Zhang et al., 2016). Studies have tested photosynthetic rate and have shown that photosynthetic efficiency increases significantly with increasing temperature, thus the genes related to adaptive evolution in low elevation might be thermal responses in situ to global warming (Ren et al., 2014). Within the Mid group, high-quality annotated candidate loci were located in *ACR4*, *CaMRLK*, *iPGAM*, and *RH38*, and all the genes are associated with high-altitude adaptation and thermal stress. *iPGAM* is primarily involved in vegetative growth and stomatal movement, and *ACR4* plays important roles in cell division and differentiation, both of which are involving in plant growth (Zhao et al., 2017). *RH38* is a member of the DEAD-box family primarily involved in abiotic stress, and a study found *RH38* having upregulated expression under cold stress but more sensitive to thermal stress in *Arabidopsis thaliana* (Chen & Peng, 2016). *CaMRLK* plays vital roles in protein phosphorylation in eukaryotes, related to high temperature, cold and drought stress in plants (Ding et al., 2021). In addition, we found more complex adaptation in

high elevations (>3000 m) including five kinds of genes responsible for the regulation of alpine evolution (Table S3). Most of these genes are involved in photosynthetic repair (e.g., *RanBP2*, *rpl2*, *psbB* and *NDH5*), which is consistent with previous studies (Chen et al., 2019; Wang et al., 2021; Zhang, Qiao, et al., 2019; Zhang, Suren, et al., 2019). Furthermore, we identified cold and drought-related genes including *BAG3*, *CAMTA* and *SHMT6*, which show upregulation after stress treatment in *A. thaliana*, *Zea mays* and *Triticum aestivum* (Hu et al., 2022; Wang et al., 2018; Xiao et al., 2021). We also found genes involved in soil stress and defence response (e.g., *WRKY22*, *CBL1* and *PAP1*) (Jiang et al., 2017; Wu et al., 2018). Notably, we detected genes involved in plant development and embryo progress (*CHD3* and *UGT1*), although a few studies have reported a direct function in chromatin remodelling and morphological variation (Ma et al., 2015). Meanwhile, the related genes of *M. himalaica* indicate that divergent selection might contribute to the observed morphological alterations in populations at different elevations (such as *iPGAM*, *ACR4* and UGT1). For instance, several of the adaptive leaf phenotypes among populations possibly evolving independently under the functional constrains of their common ancestral populations, but detecting a direct regulatory mechanism is hard unless physiological experiment and transcriptome evidence is utilized in future experiments. On the other hand, we found most of the SNPs were synonymous polymorphisms that are not acting on encoded proteins. Given the RAD-seq method, the list of loci represents only a very small portion of the genome potentially under divergent selection, and many other targets under selection may have been missed. In summary, our current analyses provide further empirical evidence for how alpine herbs survive in situ responding to environmental changes, as all the annotated adaptive genes among the three groups are closely related to the physiological stresses produced by cold, drought and/or thermal stress. As indicated in our results, we found the high-altitude adaption is not unique for extreme high-altitude populations, which could be detected from a relatively low altitude of 1500–2000 m, suggesting plants at low altitudes have already evolved molecular adaptations to reduced oxygen content, increased UV radiation and cold stress (Sun et al., 2018) across elevational gradient. Taken together, both morphological variation and genetic evidence support the high-altitude adaptation and play an important role to maintain population stability in situ and consistently response to climate change in alpine region. However, current studies relying on RAD sequencing approaches likely miss many signals of local adaptation and further study based on genome or transcriptome data are essential to explore the genetic adaptations in plants found at increasing altitudes.

4.3 | Asymmetric gene flow limited to mid-elevation populations within microhabitats

Climate-driven range shifts of alpine plants have been well documented in previous studies, and one commonly held hypothesis is that plants respond to rising temperatures by shifting their ranges upslope to higher elevations (Hadly et al., 2009; Rahmstorf & Coumou, 2011; Shiono et al., 2018). However, these hypotheses are rarely tested especially using genomic data for sensitive herb plants in the HHM-HDMs (He et al., 2019; Liang et al., 2016, 2018). We assessed migration events among populations in two ways: (1) evidence of mixed ancestry, as inferred from admixture proportions estimated by ADMIXTURE and (2) estimations of long term and recent rates of migration using TreeMix and BayesAss, respectively. We detected low values of contemporary gene flow (<0.1) suggesting a migration rate in which two populations are not exchanging sufficient migrants to influence each other's dynamics (Table S7). As an alpine herb, this may be caused by complex topography in the HHM-HDMs region and the limited dispersal capacity during past generations of *M. himalaica* (Zu & Wang, 2022). Nevertheless, we further found historical gene flow among populations along elevational gradients, most of which is restricted to mid-elevation populations (Figure 1; Figure S10). This gene flow among populations was broadly supported by estimates of admixture proportions (Figure 1). Like many other studies, our results demonstrate that low populations are sources and high populations are sinks of migrants among *M. himalaica* populations in alpine landscapes, as we identified three upward migration events across all 23 populations based on TreeMix (Figure 1). In particular, the three gene flow events were located in the northern HDMs and only concentrated on mid-elevation sites from 1732 to 2267 m, suggesting gene flow was strongly biased towards microhabitats and mid-elevation populations. Given that valley rivers and mountains can be physical barriers blocking gene flow between populations (e.g., Gao et al., 2007; Liu et al., 2013; Meng et al., 2015), we further tested gene flow between populations at a small scale (Figure S10; northern HDMs, southern HDMs and HHM, separately). Similarly, we found upward gene flow between mid-elevation populations within the northern HDMs and southern HDMs (such as from YS to XCS and from WS to XJS) and rarely between extreme low-elevation and high-elevation populations (Figure S10). If the strategy of range shifts play a major role for alpine plants responding to climate change, we inferred that thermal tolerance in low elevation and range limits combining with biotic interactions in high elevation might cause the only occurrence of restricted gene flow in mid-elevation populations (Colwell et al., 2008; Rumpf et al., 2018). However, our results still found highly asymmetric gene flow, not predominantly from downslope to upslope (Figure S10; e.g., DMT to XCS and WS to JS). To explore whether this asymmetric gene flow is influenced by rising temperatures or changing precipitation patterns under climate change, we further compared the trend of temperatures and precipitation among the direction of migration events. As a result, we found no evidence where gene flow is moving to regions of lower temperatures or more abundant precipitation (Table S1, Figure 1). In addition, we also could not find significant elevational shifts upward in mean elevation between the two time periods of pre-1980 and 1980-current from specimen records (Table S8). Meanwhile, the fragmentation of the range of *M. himalaica* likely dates to the last glacial maximum with most current populations

diverging from 100 ka to 9 Ka, thus subsequent spatial shifts in populations may have occurred over a relatively short time inferring recent climate-driven distribution change instead of historical expansions or contractions (Rana et al., 2020). Thus, these current asymmetric gene flow patterns and species distribution changes across the elevation gradient demonstrates that moving to a high elevation is not the counter measure for *M. himalaica* responding to climate warming. Similar gene flow patterns have also been detected in other alpine species, such as *Sequoiadendron giganteum*, *Arabis alpina* and *Arabidopsis lyrata* inferring the randomness of gene flow (DeSilva & Dodd, 2020; Hamala & Savolainen, 2019; Waterhouse et al., 2018). For alpine herbs, we speculate that limited dispersal capacity and finite scope for upward movement may be a fundamental reason for plants to stay in local conditions rather than moving. Furthermore, the species shifting in range may encounter new biotic and abiotic pressures to which the species could be maladapted, thus reducing fitness (Graae et al., 2018; Hobbs et al., 2018). Overall, evidence for current results along continuous elevational gradient suggest that, in the face of climate change, *M. himalaica* may have to rely on local adaptations or morphological variation in order to survive the predicted magnitudes of environmental change.

4.4 | Genomic vulnerability and species distribution under future climate change

According to the predicted potential distribution in 2070, *M. himalaica* may lose its potential suitability in the southern HDMs region at lower elevations (Figure 4). Meanwhile, *M. himalaica* will extend upstream of Three River-Gorges subregion with higher elevation and northwestern regions. The rate of warming in the HHM-HDMs regions is approximately 1.5°C each year (Shrestha et al., 2012). According to physiological stress experiments of most plants, high temperature stress over 10°C can lead to abnormalities in germination, blooms and fertilization (Yao et al., 2014; Yu et al., 2022). Thus, when the rate of climate change is much greater than the rate of adaptive evolution and the limits of physiological plasticity, species will be forced to move to higher altitudes for surviving. By using climate projections for 2070, our metric of "genomic vulnerability" predicts that most populations of *M. himalaica* are at a low risk of climate-induced extinction. However, the marginal distribution regions in the Himalayas present a higher risk of genomic vulnerability, suggesting high extinction risk in these high elevation regions. Comparative results from species distribution modelling and genomic vulnerability suggest paying attention to the monitoring of high-altitude areas in the Himalayas for *M. himalaica*.

5 | CONCLUSION

In this study, we assessed potential shift dynamics, local adaptation and morphological variation in a representative herb, *M. himalaica*, by identifying SNPs from genome-wide data. Our findings complement the current hot topic of how species respond to global climate change and the specific strategies using population genomics rather than field observations or common garden experiments. We identified asymmetric gene flow mainly occurring at mid altitudes, even though this is not the main reason for population stability. Additionally, we identified molecular adaptation and morphological variation maintaining populations in situ rather than moving by increasing altitudes in response to climate change. This study provides new insights into the evolutionary mechanisms for plateau endemic herbs responding to future climate changes, and continued research is essential to quantify the intensity of adaptations and morphological variation along altitudes gradient under climate changes.

ACKNOWLEDGMENTS

We thank X.H. Huang, Y. Z. Zhang, S. K. Rana and D. G. Zhang for help with the sample collection. We also thank F. Liu for help with diagrams' revision.

FUNDING INFORMATION

This study was supported by the Second Tibetan Plateau Scientific Expedition and Research (STEP) program (2019QZKK0502), the Strategic Priority Research Program of Chinese Academy of Sciences (XDA20050203), the Key Projects of the Joint Fund of the National Natural Science Foundation of China (U1802232), the Youth Innovation Promotion Association of Chinese Academy of Sciences (2019382), the Yunnan Young & Elite Talents Project (YNWR-QNBJ-2019-033), the International Partnership Program of Chinese Academy of Sciences (151853KYSB20180009), the Major Program for Basic Research Project of Yunnan Province (202101 BC070002), the Young Academic and Technical Leader Raising Foundation of Yunnan Province (2019HB039) and the Chinese Academy of Sciences "Light of West China" Program.

CONFLICT OF INTEREST STATEMENT

The authors declare they have no competing interest.

DATA AVAILABILITY STATEMENT

The raw reads used for this article are available in the NCBI Short Read Archive (SRA) (Bioproject No. PRJNA806355). The SNP data have been deposited in Dryad (https://doi.org/10.5061/dryad.m63xsj469).

ORCID

Tao Deng https://orcid.org/0000-0003-4163-3368

REFERENCES

Aitken, S. N., Yeaman, S., Holliday, J. A., Wang, T. L., & McLane, S. C. (2008). Adaptation, migration or extirpation: Climate change outcomes for tree populations. *Evolutionary Applications*, *1*, 95–11. https://doi.org/10.1111/j.1752-4571.2007.00013.x

Alberto, F. J., Aitken, S. N., Alía, R., González-Martínez, S. C., Hänninen, H., Kremer, A., Lefèvre, F., Lenormand, T., Yeaman, S., Whetten, R., & Savolainen, O. (2013). Potential for evolutionary responses

to climate change – Evidence from tree populations. *Global Change Biology*, *19*(6), 1645–1661. https://doi.org/10.1111/gcb.12181

Alexander, D. H., Novembre, J., & Lange, K. (2009). Fast model-based estimation of ancestry in unrelated individuals. *Genome Research*, *19*, 1655–1664. https://doi.org/10.1101/gr.094052.109

Andrews, S. (2010). *FastQC: A quality control tool for high throughput sequence data*. http://www.bioinformatics.babraham.ac.uk/projects/fastqc/

Aubin-Horth, N., & Renn, S. C. (2009). Genomic reaction norms: Using integrative biology to understand molecular mechanisms of phenotypic plasticity. *Molecular Ecology*, *18*(18), 3763–3780. https://doi.org/10.1111/j.1365-294X.2009.04313.x

Baird, N. A., Etter, P. D., Atwood, T. S., Currey, M. C., Shiver, A. L., Lewis, Z. A., Selker, E. U., Cresko, W. A., & Johnson, E. A. (2008). Rapid SNP discovery and genetic mapping using sequenced RAD markers. *PLoS One*, *3*, e3376. https://doi.org/10.1371/journal.pone.0003376

Bakhtiari, M., Formenti, L., Caggìa, V., Glauser, G., & Rasmann, S. (2019). Variable effects on growth and defense traits for plant ecotypic differentiation and phenotypic plasticity along elevation gradient. *Ecology and Evolution*, *9*, 3740–3755. https://doi.org/10.1002/ece3.4999

Benestan, L., Quinn, B. K., Maaroufi, H., Laporte, M., Clark, F. K., Greenwood, S. J., Rochette, R., & Bernatchez, L. (2016). Seascape genomics provides evidence for thermal adaptation and current-mediated population structure in American lobster (*Homarus americanus*). *Molecular Ecology*, *25*(20), 5073–5092. https://doi.org/10.1111/mec.13811

Borcard, D., & Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, *153*, 51–68. https://doi.org/10.1016/S0304-3800(01)00501-4

Broquet, T., & Petit, E. J. (2009). Molecular estimation of dispersal for ecology and population genetics. *Annual Review of Ecology and Systematics*, *40*, 193–216. https://doi.org/10.1146/annurev.ecolsys.110308.120324

Brown, C. J., O'Connor, M. I., Poloczanska, E. S., Schoeman, D. S., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Pandolfi, J. M., Parmesan, C., & Richardson, A. J. (2016). Ecological and methodological drivers of species' distribution and phenology responses to climate change. *Global Change Biology*, *22*, 1548–1560. https://doi.org/10.1111/gcb.13184

Buehler, D., Graf, R., Holderegger, R., & Gugerli, F. (2012). Contemporary gene flow and mating system of *Arabis alpina* in a central European alpine landscape. *Annals of Botany*, *109*, 1359–1367. https://doi.org/10.1093/aob/mcs066

Catchen, J. M., Amores, A., Hohenlohe, P., Cresko, W., & Postlethwait, J. H. (2011). Stacks: Building and genotyping loci de novo from short-read sequences. *G3: Genes Genomes, Genetics*, *1*, 171–182. https://doi.org/10.1534/g3.111.000240

Catchen, J. M., Hohenlohe, P. A., Bernatchez, L., Funk, W. C., Andrews, K. R., & Allendorf, F. W. (2017). Unbroken: RADseq remains a powerful tool for understanding the genetics of adaptation in natural populations. *Molecular Ecology Resources*, *17*, 362–365. https://doi.org/10.1111/1755-0998.12669

Chambers, J. M. (2008). *Software for data analysis: Programming with R*. Springer.

Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E., & Sheldon, B. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, *320*, 800–803. https://doi.org/10.1126/science.1157174

Chen, D., & Peng, X. B. (2016). DEAD-box: Function on growth and development in *Arabidopsis thaliana*. *Plant Science Journal*, *34*, 941–948.

Chen, I. C., Hill, J. K., Ohlemuller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*(6045), 1024–1026. https://doi.org/10.1126/science.1206432

Chen, J. H., Huang, Y., Brachi, B., Yun, Q. Z., Zhang, W., Lu, W., Li, H. N., Li, W. Q., Sun, X. D., Wang, G. Y., He, J., Zhou, Z., Chen, K. Y., Ji, Y. H., Shi, M. M., Sun, W. G., Yang, Y. P., Zhang, R. G., Abbott, R. J., & Sun, H. (2019). Genome-wide analysis of Cushion willow provides insights into alpine plant divergence in a biodiversity hotspot. *Nature Communications*, *10*(1), 5230. https://doi.org/10.1038/s41467-019-13128-y

Chu, X., Gugger, P. F., Li, L., Zhao, J. L., Li, Q. J., & Sun, J. (2021). Responses of an endemic species (*Roscoea humeana*) in the Hengduan Mountains to climate change. *Diversity and Distributions*, *27*(11), 2231–2244. https://doi.org/10.1111/ddi.13397

Colwell, R. K., Brehm, G., Cardelus, C. L., Gilman, A. C., & Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, *322*, 258–261. https://doi.org/10.1126/science.1162547

Coop, G., Witonsky, D., Di Rienzo, A., & Pritchard, J. K. (2010). Using environmental correlations to identify loci underlying local adaptation. *Genetics*, *185*, 1411–1423. https://doi.org/10.1534/genetics.110.114819

Cortés, A. J., Waeber, S., Lexer, C., Sedlacek, J., Wheeler, J. A., van Kleunen, M., Bossdorf, O., Hoch, G., Rixen, C., Wipf, S., & Karrenberg, S. (2014). Small-scale patterns in snowmelt timing affect gene flow and the distribution of genetic diversity in the alpine dwarf shrub *Salix herbacea*. *Heredity*, *113*(3), 233–239. https://doi.org/10.1038/hdy.2014.19

Danecek, P., Auton, A., Abecasis, C., Albers, C. A., Banks, E., DePristo, M. A., Handsaker, R. E., Lunter, G., Marth, G. T., Sherry, S. T., McVean, G., Durbin, R., & 1000 Genomes Project Analysis Group. (2011). The variant call format and VCFtools. *Bioinformatics*, *27*, 2156–2158. https://doi.org/10.1093/bioinformatics/btr330

Dauphin, B., Rellstab, C., Schmid, M., Zoller, S., Karger, D. N., Brodbeck, S., & Gugerli, F. (2020). Genomic vulnerability to rapid climate warming in a tree species with a long generation time. *Global Change Biology*, *27*, 1181–1195. https://doi.org/10.1111/gcb.15469

de Villemereuil, P., & Gaggiotti, O. E. (2015). A new FST-based method to uncover local adaptation using environmental variables. *Methods in Ecology and Evolution*, *6*, 1248–1258. https://doi.org/10.1111/2041-210x.12418

DeSilva, R., & Dodd, R. S. (2020). Fragmented and isolated: Limited gene flow coupled with weak isolation by environment in the paleoendemic giant sequoia (*Sequoiadendron giganteum*). *American Journal of Botany*, *107*(1), 45–55. https://doi.org/10.1002/ajb2.1406

Ding, H., Qian, Y., Fang, Y., Ji, Y., Sheng, J., & Ge, C. (2021). Characteristics of SlCML39, a tomato calmodulin-like gene, and its negative role in high temperature tolerance of *Arabidopsis thaliana* during germination and seedling growth. *International Journal of Molecular Sciences*, *22*, 11479. https://doi.org/10.3390/ijms222111479

Doyle, J. (1991). DNA protocols for plants-CTAB total DNA isolation. In *Molecular techniques in taxonomy* (pp 283–293). Springer.

Excoffier, L., & Lischer, H. E. (2010). Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, *10*, 564–567. https://doi.org/10.1111/j.1755-0998.2010.02847.x

Fan, X. R., Njeri, H. K., Li, W., & Chen, Y. Y. (2019). Abundant historical gene flow within and among river systems for populations of *Ottelia acuminata* var. *jingxiensis*, an endangered macrophyte from southwest China. *Aquatic Botany*, *157*, 1–9. https://doi.org/10.1016/j.aquabot.2019.05.002

Fitak, R. R. (2021). OptM: Estimating the optimal number of migration edges on population trees using Treemix. *Biology Methods and Protocols*, *6*, bpab017. https://doi.org/10.1093/biomethods/bpab017

Fitzpatrick, M. C., & Keller, S. R. (2015). Ecological genomics meets community-level modelling of biodiversity: Mapping the genomic landscape of current and future environmental adaptation. *Ecology Letters*, *18*, 1–16. https://doi.org/10.1111/ele.12388

Foll, M., & Gaggiotti, O. (2008). A genome-scanmethod to identify selected loci appropriate for both dominant and codominant markers: A Bayesian perspective. *Genetics*, *180*, 977–993. https://doi.org/10.1534/genetics.108.092221

Francois, O., Martins, H., Caye, K., & Schoville, S. D. (2016). Controlling false discoveries in genome scans for selection. *Molecular Ecology*, *25*, 454–469. https://doi.org/10.1111/mec.13513

Franks, S. J., & Hoffmann, A. A. (2012). Genetics of climate change adaptation. *Annual Review of Genetics*, *46*, 185–208. https://doi.org/10.1146/annurev-genet-110711-155511

Gao, L. M., Möller, M., Zhang, X. M., Hollingsworth, M. L., Liu, J., Mill, R. R., Gibby, M., & Li, D. Z. (2007). High variation and strong phylogeographic pattern among cpDNA haplotypes in *Taxus wallichiana* (Taxaceae) in China and North Vietnam. *Molecular Ecology*, *16*(22), 4684–4698. https://doi.org/10.1111/j.1365-294X.2007.03537.x

Geng, Y., Guan, Y., Qiong, L., Lu, S., An, M., Crabbe, M. J. C., Qi, J., Zhao, F., Qiao, Q., & Zhang, T. (2021). Genomic analysis of field pennycress (*Thlaspi arvense*) provides insights into mechanisms of adaptation to high elevation. *BMC Biology*, *19*(1), 143. https://doi.org/10.1186/s12915-021-01079-0

Gentili, R., Ambrosini, R., Augustinus, B. A., Caronni, S., Cardarelli, E., Montagnani, C., Müller-Schärer, H., Schaffner, U., & Citterio, S. (2021). High phenotypic plasticity in a prominent plant invader along altitudinal and temperature gradient. *Plants (Basel)*, *10*(10), 2144. https://doi.org/10.3390/plants10102144

Gonzalo-Turpin, H., & Hazard, L. (2009). Local adaptation occurs along altitudinal gradient despite the existence of gene flow in the alpine plant species *Festuca eskia*. *Journal of Ecology*, *97*(4), 742–751. https://doi.org/10.1111/j.1365-2745.2009.01509.x

Graae, B. J., Vandvik, V., Armbruster, W. S., Eiserhardt, W. L., Svenning, J.-C., Hylander, K., Ehrlén, J., Speed, J. D., Klanderud, K., Brathen, K. A., Milbau, A., Opedal, Ø. H., Alsos, I. G., Ejrnæs, R., Bruun, H. H., Birks, H. J., Westergaard, K. B., Birks, H. H., & Lenoir, J. (2018). Stay or go – How topographic complexity influences alpine plant population and community responses to climate change. *Perspectives in Plant Ecology, Evolution and Systematics*, *30*, 41–50. https://doi.org/10.1016/j.ppees.2017.09.008

Guerin, G. R., Wen, H., & Lowe, A. J. (2012). Leaf morphology shift linked to climate change. *Biology Letters*, *8*, 882–886. https://doi.org/10.1098/rsbl.2012.0659

Guo, W., Xin, M., Wang, Z., Yao, Y., Hu, Z., Song, W., Yu, K., Chen, Y., Wang, X., Guan, P., Appels, R., Peng, H., Ni, Z., & Sun, Q. (2020). Origin and adaptation to high altitude of Tibetan semi-wild wheat. *Nature Communications*, *11*(1), 5085. https://doi.org/10.1038/s41467-020-18738-5

Hadly, E. A., Spaeth, P. A., & Li, C. (2009). Niche conservatism above the species level. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 19707–19714. https://doi.org/10.1073/pnas.0901648106

Hamala, T., & Savolainen, O. (2019). Genomic patterns of local adaptation under gene flow in *Arabidopsis lyrata*. *Molecular Biology and Evolution*, *32*, 2557–2257. https://doi.org/10.1093/molbev/msz149

Hannah, L., Flint, L., Syphard, A. D., Moritz, M. A., Buckley, L. B., & McCullough, I. M. (2014). Fine-grain modeling of species' response to climate change: Holdouts, stepping-stones, and microrefugia. *Trends in Ecology and Evolution*, *29*, 390–397. https://doi.org/10.1016/j.tree.2014.04.006

Hao, Y., Xiong, Y., Cheng, Y. L., Song, G., Jia, C. X., Qu, Y. H., & Li, F. M. (2019). Comparative transcriptomics of 3 high-altitude passerine birds and their low-altitude relatives. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(43), 21949. https://doi.org/10.1073/pnas.1916622116

He, X., Burgess, K. S., Yang, X. F., Ahrends, A., Gao, L. M., & Li, D. Z. (2019). Upward elevation and northwest range shifts for alpine Meconopsis species in the Himalaya-Hengduan Mountains region. *Ecology and Evolution*, *9*(7), 4055–4064. https://doi.org/10.1002/ece3.5034

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*(15), 1965–1978. https://doi.org/10.1002/joc.1276

Hobbs, R. J., Valentine, L. E., Standish, R. J., & Jackson, S. T. (2018). Movers and stayers: Novel assemblages in changing environments. *Trends in Ecology and Evolution*, *33*, 116–128. https://doi.org/10.1016/j.tree.2017.11.001

Hoffmann, A., & Sgrò, C. (2011). Climate change and evolutionary adaptation. *Nature*, *470*, 479–485. https://doi.org/10.1038/nature09670

Hohenlohe, P. A., Amish, S. J., Catchen, J. M., Allendorf, F. W., & Luikart, G. (2011). Next-generation RAD sequencing identifies thousands of SNPs for assessing hybridization between rainbow and west-slope cutthroat trout. *Molecular Ecology Resources*, *11*, 117–122. https://doi.org/10.1111/j.1755-0998.2010.02967.x

Hu, P., Song, P., Xu, J., Wei, Q., Tao, Y., Ren, Y., Yu, Y., Li, D., Hu, H., & Li, C. (2022). Genome-wide analysis of serine hydroxymethyl transferase genes in *Triticeae* species reveals that TaSHMT3A-1 regulates fusarium head blight resistance in wheat. *Frontiers in Plant Science*, *13*, 847087. https://doi.org/10.3389/fpls.2022.847087

Ilut, D. C., Nydam, M. L., & Hare, M. P. (2014). Defining loci in restriction-based reduced representation genomic data from nonmodel species: Sources of bias and diagnostics for optimal clustering. *BioMed Research International*, *2014*, 675158. https://doi.org/10.1155/2014/675158

IPCC. (2013). *Climate change 2013: The physical science basis*. (contribution of working group I to the fifth assessment. Report of the intergovernmental panel on climate change). Cambridge University Press, 1535.

James, G., Witten, D., Hastie, T., & Tibshirani, R. (2014). An introduction to statistical learning: With applications in R Springer Publishing Company. *Incorporated*, https://doi.org/10.1007/978-1-4614-7138-7

Jeffreys, H. (1998). *The theory of probability*. Oxford University Press.

Jiang, J., Ma, S., Ye, N., Jiang, M., Cao, J., & Zhang, J. (2017). WRKY transcription factors in plant responses to stresses. *Journal of Integrative Plant Biology*, *59*(2), 86–101. https://doi.org/10.1111/jipb.12513

Jump, A. S., & Peñuelas, J. (2005). Running to stand still: Adaptation and the response of plants to rapid climate change. *Ecology Letters*, *8*, 1010–1120.

Körner, C. (2003). *Alpine plant life: Functional plant ecology of high mountain ecosystems*. Springer.

Körner, C. (2004). Mountain biodiversity, its causes and function. *Ambio: A Journal of the Human Environment*, *13*, 11–17. https://doi.org/10.1007/0044-7447-33.sp13.11

Kelly, A. E., & Goulden, M. L. (2008). Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 11823–11826. https://doi.org/10.1073/pnas.0802891105

Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P., & Brisse, H. (2008). A significant upwardshift in plant species optimum elevation during the 20th century. *Science*, *320*, 1768–1771. https://doi.org/10.1126/science.1156831

Li, Y. Y., Dong, S. K., Liu, S. L., Wang, X. X., Wen, L., & Wu, Y. (2014). The interaction between poisonous plants and soil quality in response to grassland degradation in the alpine region of the Qinghai-Tibetan Plateau. *Plant Ecology*, *215*(8), 809–819. https://doi.org/10.1007/s11258-014-0333-z

Liang, E., Wang, Y., Piao, S., Lu, X., Camarero, J. J., Zhu, H., Zhu, L., Ellison, A. M., Ciais, P., & Peñuelas, J. (2016). Species interactions slow warming-induced upward shifts of treelineson the Tibetan Plateau.

Proceedings of the National Academy of Sciences of the United States of America, *113*, 4380–4385. https://doi.org/10.1073/pnas.1520582113

Liang, Q. L., Xu, X. T., Mao, K. S., Wang, M. C., Wang, K., & Xi, Z. X. (2018). Shifts in plant distributions in response to climate warming in a biodiversity hotspot, the Hengduan Mountains. *Journal of Biogeography*, *45*(9), 1334–1344. https://doi.org/10.1111/jbi.13229

Lischer, H. E. L., & Excoffier, L. (2012). PGDSpider: An automated data conversion tool for connecting population genetics and genomics programs. *Bioinformatics*, *28*, 298–299. https://doi.org/10.1093/bioinformatics/btr642

Liu, J., Moller, M., Provan, J., Gao, L. M., Poudel, R. M., & Li, D. Z. (2013). Geological and ecological factors drive cryptic speciation of yews in a biodiversity hotspot. *New Phytologist*, *199*(1), 1093–1108. https://doi.org/10.1111/nph.12336

Liu, Y. F., Wang, Z. Q., Lu, J. Z., Zhang, Y. F., Liu, H. L., Wang, F., Qi, M. F., & Li, T. L. (2019). Regulation of chloroplast NAD(P)H dehydrogenase complex in photosynthesis. *Plant Physiology Journal*, *55*, 932–940.

Lopez-Goldar, X., & Agrawal, A. A. (2021). Ecological interactions, environmental gradient, and gene flow in local adaptation. *Trends in Plant Science*, *26*(8), 796–809. https://doi.org/10.1016/j.tplants.2021.03.006

Losapio, G., Cerabolini, B. E., Maffioletti, C., Tampucci, D., Gobbi, M., & Caccianiga, M. (2021). The consequences of glacier retreat are uneven between plant species. *Frontiers in Ecology and Evolution*, *8*, 616562. https://doi.org/10.3389/fevo.2020.616562

Ma, X., Ma, J., Zhai, H., Xin, P., Chu, J., Qiao, Y., & Han, L. (2015). CHR729 is a CHD3 protein that controls seedling development in rice. *PLoS One*, *10*(9), e0138934. https://doi.org/10.1371/journal.pone.0138934

Mantyka-Pringle, C. S., Visconti, P., Di Marco, M., Martin, T. G., Rondinini, C., & Rhodes, J. R. (2015). Climate change modifies risk of global biodiversity loss due to land-cover change. *Biological Conservation*, *187*, 103–111. https://doi.org/10.1016/j.biocon.2015.04.016

McGrath, J. M., Funk, A., Galewski, P., Ou, S., Townsend, B., Davenport, K., Daligault, H., Johnson, S., Lee, J., Hastie, A., Darracq, A., Willems, G., Barnes, S., Liachko, I., Sullivan, S., Koren, S., Phillippy, A., Wang, J., Liu, T., … Dorn, K. (2020). A contiguous de novo genome assembly of sugar beet EL10 (*Beta vulgaris* L.). *bioRxiv*. https://doi.org/10.12172/202101140001

Meng, L., Chen, G., Li, Z., Yang, Y., Wang, Z., & Wang, L. (2015). Refugial isolation and range expansions drive the genetic structure of *Oxyria sinensis* (Polygonaceae) in the Himalaya-Hengduan Mountains. *Scientific Reports*, *5*, 10396. https://doi.org/10.1038/srep10396

Mussmann, S. M., Douglas, M. R., Chafin, T. K., & Douglas, M. E. (2019). BA3-SNPs: Contemporary migration reconfigured in BayesAss for next-generation sequence data. *Methods in Ecology and Evolution*, *10*, 1808–1813. https://doi.org/10.1111/2041-210x.13252

Nachtergaele, F., van Velthuizen, H., vanEngelen, V., Fischer, G., Jones, A., Montanarella, L., Petri, M., Prieler, S., Teixeira, E., & Shi, X. (2012). *Harmonized World Soil Database (version 1.2)* (pp. 1–50). ORNL.DAAC, Oak Ridge, TN, USA.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H., Szoecs, E., & Wagner, H. (2013). *Package 'vegan,'*. http://cran.rproject.org/web/packages/vegan/index.html

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, *37*(7), 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.1

Paudel, B. R., Dyer, A. G., Garcia, J. E., & Shrestha, M. (2019). The effect of elevational gradient on alpine gingers (*Roscoea alpina* and *R. purpurea*) in the Himalayas. *PeerJ*, *7*, e7503. https://doi.org/10.7717/peerj.7503

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., & Clark, T. D. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*, 6332. https://doi.org/10.1126/science.aai9214

Peng, C. J., Ren, J. L., Deng, C., Jiang, D. D., Wang, J. C., Qu, J. Y., Chang, J., Yan, C., Jiang, K., Murphy, R. W., Wu, D. D., & Li, J. T. (2020). The genome of shaw's sea snake (*Hydrophis curtus*) reveals secondary adaptation to its marine environment. *Molecular Biology and Evolution*, *37*, 1744–1760. https://doi.org/10.1093/molbev/msaa043

Perrigo, A., Hoorn, C., & Antonelli, A. (2020). Why mountains matter for biodiversity. *Jounal of Biogeography*, *47*, 315–325. https://doi.org/10.1111/jbi.13731

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M., & Zhu, X. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, *25*(6), 1922–1940. https://doi.org/10.1111/gcb.14619

Pickrell, J. K., & Pritchard, J. K. (2012). Inference of population splits and mixtures from genome-wide allele frequency data. *PLoS Genetics*, *8*, e1002967. https://doi.org/10.1038/npre.2012.6956.1

Platts, P. J., Mason, S. C., Palmer, G., Hill, J. K., Oliver, T. H., Powney, G. D., Fox, R., & Thomas, C. D. (2019). Habitat availability explains variation in climate-driven range shifts across multiple taxonomic groups. *Scientific Reports*, *9*, 15039. https://doi.org/10.1038/s41598-019-51582-2

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rahmstorf, S., & Coumou, D. (2011). Increase of extreme events in a warming world. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 17905–17909. https://doi.org/10.1073/pnas.1101766108

Rana, H. K., Luo, D., Rana, S. K., & Sun, H. (2020). Geological and climatic factors affect the population genetic connectivity in *Mirabilis himalaica* (Nyctaginaceae): Insight from phylogeography and dispersal corridors in the Himalaya-Hengduan biodiversity hotspot. *Frontiers in Plant Science*, *10*, 1721. https://doi.org/10.3389/fpls.2019.01721

Rasica, L., Porcelli, S., Limper, U., Mrakic-Sposta, S., Mazzolari, R., Gelmini, F., Beretta, G., & Marzorati, M. (2021). Beet on Alps: Time-course changes of plasma nitrate and nitrite concentrations during acclimatization to high-altitude. *Nitric Oxide*, *107*, 66–72. https://doi.org/10.1016/j.niox.2020.12.004

Rellstab, C., Zoller, S., Walthert, L., Lesur, I., Pluess, A. R., Graf, R., Bodénès, C., Sperisen, C., Kremer, A., & Gugerli, F. (2016). Signatures of local adaptation in candidate genes of oaks (*Quercus* spp.) with respect to present and future climatic conditions. *Molecular Ecology*, *25*, 5907–5924. https://doi.org/10.1111/mec.13889

Ren, J., Wang, H. M., Wang, W. J., Qu, D., Wang, Q., & Zhan, Z. L. (2014). Responses of photosynthesis, chlorophyll fluorescence of poplar leaf and bark chlorenchyma to elevated temperature. *Bulletin of Botanical Research*, *34*, 758–764.

Royer, D. L., McElwain, J. C., Adams, J. M., & Wilf, P. (2008). Sensitivity of leaf size and shape to climate within *Acer rubrum* and *Quercus kelloggii*. *New Phytologist*, *179*, 808–817. https://doi.org/10.1111/j.1469-8137.2008.02496.x

Ruegg, K., Bay, R. A., Anderson, E. C., Saracco, J. F., Harrigan, R. J., Whitfield, M., Paxton, E. H., & Smith, T. B. (2018). Ecological genomics predicts climate vulnerability in an endangered southwestern songbird. *Ecology Letters*, *21*(7), 1085–1096. https://doi.org/10.1111/ele.12977

Rumpf, S. B., Hülber, K., Klonner, G., Moser, D., Schütz, M., Wessely, J., Willner, W., Zimmermann, N. E., & Dullinger, S. (2018). Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 1848–1853. https://doi.org/10.1073/pnas.1713936115

Salvarzi, E., Choobineh, A., Jahangiri, M., & Keshavarzi, S. (2018). Facial anthropometric measurements in Iranian male workers using Digimizer version 4.1. 1.0 image analysis software: A pilot study. *International Journal of Occupational Safety and Ergon*, *24*(3), 570–576. https://doi.org/10.1080/10803548.2018.1433578

Shiono, T., Kusumoto, B., Yasuhara, M., & Kubota, Y. (2018). Roles of climate niche conservatism and range dynamics in woody plant diversity patterns through the Cenozoic. *Global Ecology and Biogeography*, *27*, 865–874. https://doi.org/10.1111/geb.12755

Shrestha, U. B., Gautam, S., & Bawa, K. S. (2012). Widespread climate change in the Himalayas and associated changes in local ecosystems. *PLoS One*, *7*, e36741. https://doi.org/10.1371/journal.pone.0036741

Stöcklin, J., Kuss, P., & Pluess, A. R. (2009). Genetic diversity, phenotypic variation and local adaptation in the alpine landscape: Case studies with alpine plant species. *Botanica Helvetica*, *119*(2), 125–133. https://doi.org/10.1007/s00035-009-0065-1

Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, *30*, 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Sun, Y. B., Fu, T. T., Jin, J. Q., Murphya, R. W., Hillisd, D. M., Zhang, Y. P., & Che, J. (2018). Species groups distributed across elevational gradient reveal convergent and continuous genetic adaptation to high elevations. *Proceedings. National Academy of Sciences. United States of America*, *115*(45), E10634–E10641. https://doi.org/10.1073/pnas.1813593115

Takahashi, K., & Matsuki, S. (2017). Morphological variations of the *Solidago virgaurea* L. complex along an elevational gradient on Mt Norikura, Central Japan. *Plant Species Biology*, *32*, 238–246. https://doi.org/10.1111/1442-1984.12148

Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J. B., Pe'er, G., Singer, A., Bridle, J. R., Crozier, L. G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C., Pantel, J. H., … Travis, J. M. (2016). Improving the forecast for biodiversity under climate change. *Science*, *353*(6304), eaad846. https://doi.org/10.1126/science.aad8466

Usinowicz, J., & Levine, J. M. (2021). Climate-driven range shifts reduce persistence of competitors in a perennial plant community. *Global Change Biology*, *27*(9), 1890–1903. https://doi.org/10.1111/gcb.15517

Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M. B., Balaguer, L., Benito-Garzón, M., Cornwell, W., Gianoli, E., van Kleunen, M., Naya, D. E., Nicotra, A. B., Poorter, H., & Zavala, M. A. (2014). The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters*, *17*(11), 1351–1364. https://doi.org/10.1111/ele.12348

Vernesi, C., Hoban, S. M., Pecchioli, E., Crestanello, B., Bertorelle, G., Rosà, R., & Hauffe, H. C. (2016). Ecology, environment and evolutionary history influence genetic structure in five mammal species from the Italian Alps. *Biological Journal of the Linnean Society*, *117*, 428–446. https://doi.org/10.1111/bij.12651

Villemereuil, P., Frichot, E., Bazin, E., Francois, O., & Gaggiotti, O. E. (2014). Genome scan methods against more complex models: When and how much should we trust them? *Molecular Ecology*, *23*, 2006–2019. https://doi.org/10.1111/mec.12705

Visser, M. E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 649–659. https://doi.org/10.1098/rspb.2007.0997

Waldvogel, A. M., Feldmeyer, B., Rolshausen, G., Exposito-Alonso, M., Rellstab, C., Kofler, R., Mock, T., Schmid, K., Schmitt, I., Bataillon, T., Savolainen, O., Bergland, A., Flatt, T., Guillaume, F., & Pfenninger, M. (2020). Evolutionary genomics can improve prediction of species' responses to climate change. *Evolution Letters*, *4*(1), 4–18. https://doi.org/10.1002/evl3.154

Wang, Q., Wu, X., Liu, B., Wan, J., Jin, H., Tao, K., & Hou, T. P. (2022). Deciphering environmental factors driving soil microbial elevational distribution in the southeastern Qinghai-Tibetan Plateau. *European Journal of Soil Biology*, *113*, 103444. https://doi.org/10.1016/j.ejsobi.2022.103444

Wang, R., & Gao, Q. (2004). Morphological responses of *Leymus chinensis* (Poaceae) to the large-scale climatic gradient along the North-East China Transect (NECT). *Diversity and Distributions*, *10*, 65–73. https://doi.org/10.1111/j.1472-4642.2004.00056.x

Wang, S. L., Li, L., Ci, X. Q., Conran, J. G., & Li, J. (2019). Taxonomic status and distribution of *Mirabilis himalaica* (Nyctaginaceae). *Journal of Systematics and Evolution*, *57*(5), 431–439. https://doi.org/10.1111/jse.12466

Wang, X., Liu, S., Zuo, H., Zheng, W., Zhang, S., Huang, Y., Pingcuo, G., Ying, H., Zhao, F., Li, Y., Liu, J., Yi, T. S., Zan, Y., Larkin, R. M., Deng, X., Zeng, X., & Xu, Q. (2021). Genomic basis of high-altitude adaptation in Tibetan *Prunus* fruit trees. *Current Biology*, *31*(17), 3848–3860.e8. https://doi.org/10.1016/j.cub.2021.06.062

Wang, Y. F., Kou, J., Wang, W. J., Ma, Y. X., & Li, Y. Y. (2017). Allometic variation of fruiting resource allocation along elevations in Saussurea Kansuensis. *Journal of Northwest Normal University*, *53*, 87–97.

Wang, Y. F., & Yue, Y. C. (2014). Effects of resource allocation and floral traits on the number and mass of *Saussurea undulata* seeds from different elevations in eastern Qinghai-Xizang Plateau. *Chinese Journal of Plant Ecology*, *38*, 366–374.

Wang, Y. S., Li, C. N., Kou, Y. P., Wang, J. J., Tu, B., Li, H., Li, X. Z., Wang, C. T., & Yao, M. J. (2017). Soil pH is a major driver of soil diazotrophic community assembly in Qinghai-Tibet alpine meadows. *Soil Biology and Biochemistry*, *115*, 547–555. https://doi.org/10.1016/j.soilbio.2017.09.024

Wang, Z. N., Li, L. H., Ren, M. J., & Xu, R. H. (2018). Research progress of BAG family proteins in plants. *Journal of Agricultural Biotechnology*, *26*, 176–182.

Waterhouse, M. D., Erb, L. P., Beever, E. A., & Russello, M. A. (2018). Adaptive population divergence and directional gene flow across steep elevational gradient in a climate-sensitive mammal. *Molecular Ecology*, *27*, 2512–2528. https://doi.org/10.1111/mec.14701

Willis, C. G., Ellwood, E. R., Primack, R. B., Davis, C. C., Pearson, K. D., Gallinat, A. S., Yost, J. M., Nelson, G., Mazer, S. J., Rossington, N. L., Sparks, T. H., & Soltis, P. S. (2017). Old plants, new tricks: Phenological research using herbarium specimens. *Trends in Ecology and Evolution*, *32*, 531–546. https://doi.org/10.1016/j.tree.2017.03.015

Wilson, G. A., & Rannala, B. (2003). Bayesian inference of recent migration rates using multilocus genotypes. *Genetics*, *163*, 1177–1191. https://doi.org/10.1093/genetics/163.3.1177

Wu, S. D., Wang, Y., Wang, Z. F., Shrestha, N., & Liu, J. Q. (2021). Species divergence with gene flow and hybrid speciation on the Qinghai-Tibet Plateau. *New Phytologist*, *234*, 392–404. https://doi.org/10.1111/nph.17956

Wu, W., Lin, Y., Liu, P., Chen, Q., Tian, J., & Liang, C. (2018). Association of extracellular dNTP utilization with a GmPAP1-like protein identified in cell wall proteomic analysis of soybean roots. *Journal of Experimental Botany*, *69*(3), 603–617. https://doi.org/10.1093/jxb/erx441

Xiao, P., Feng, J. W., Zhu, X. T., & Gao, J. (2021). Evolution analyses of CAMTA transcription factor in plants and its enhancing effect on cold-tolerance. *Frontiers in Plant Science*, *12*, 758187. https://doi.org/10.3389/fpls.2021.758187

Xu, B., Li, Z. M., & Sun, H. (2014). *Seed plants of alpine subnival in Hengduan Mountains*. Science Press.

Yang, J., Lee, S. H., Goddard, M. E., & Visscher, P. M. (2013). Genome-wide complex trait analysis (GCTA): Methods, data analyses, and interpretations. *Methods in Molecular Biology*, *1019*, 215–236. https://doi.org/10.1007/978-1-62703-447-09

Yang, Y., Körner, C., & Sun, H. (2008). The ecological significance of pubescence in *Saussurea medusa*, a high-elevation Himalayan "woolly plant". *Arctic, Antarctic, and Alpine Research*, *40*, 250–255. https://doi.org/10.1657/1523-0430(07-009)

Yao, Y., Li, X. X., Pan, X. W., Liu, W. Q., & Li, Y. C. (2014). Research advances on mechanism of spikelet sterility under heat stress and flowering characteristics of heat tolerant lines in rice. *Hybrid Rice*, *29*, 1–6.

Yu, C. H., Chen, D., Yang, Q. X., Yang, C. L., He, L. Y., & Liang, Y. L. (2022). Research progress on the opening and closing of plant flowers in response to temperatures. *Hunan Agricultural Sciences*, *4*, 96–100.

Zhang, J., Tian, Y., Yan, L., Zhang, G., Wang, X., Zeng, Y., Zhang, J., Ma, X., Tan, Y., Long, N., Wang, Y., Ma, Y., He, Y., Xue, Y., Hao, S., Yang, S., Wang, W., Zhang, L., Dong, Y., … Sheng, J. (2016). Genome of plant Maca (*Lepidium meyenii*) illuminates genomic basis for high-altitude adaptation in the central Andes. *Molecular Plant*, *9*(7), 1066–1077. https://doi.org/10.1016/j.molp.2016.04.016

Zhang, M., Suren, H., & Holliday, J. A. (2019). Phenotypic and genomic local adaptation across latitude and altitude in *Populus trichocarpa*. *Genome Biology and Evolution*, *11*(8), 2256–2272. https://doi.org/10.1093/gbe/evz151

Zhang, T., Qiao, Q., Novikova, P. Y., Wang, Q., Yue, J., Guan, Y., Ming, S., Liu, T., de, J., Liu, Y., al-Shehbaz, I. A., Sun, H., van Montagu, M., Huang, J., van de Peer, Y., & Qiong, L. (2019). Genome of *Crucihimalaya himalaica*, a close relative of *Arabidopsis*, shows ecological adaptation to high altitude. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(14), 7137–7146. https://doi.org/10.1073/pnas.1817580116

Zhao, Y., Liu, X., Xu, Z., Yang, H., & Li, J. (2017). Characterization and enzymatic properties of protein kinase ACR4 from *Arabidopsis thaliana*. *Biochemical and Biophysical Research Communications*, *489*(2), 270–274. https://doi.org/10.1016/j.bbrc.2017.05.163

Zhao, Y. F., Wang, X., Jiang, S. L., Xiao, J. J., Li, J., Zhou, X. H., Liu, H. Y., Hao, Z. G., & Wang, K. C. (2022). Soil development mediates precipitation control on plant productivity and diversity in alpine grasslands. *Geoderma*, *412*, 115721. https://doi.org/10.1016/j.geoderma.2022.115721

Zhao, Z. G., Du, G. Z., Zhou, X. H., Wang, M. T., & Ren, Q. J. (2006). Variations with altitude in reproductive traits and resource allocation of three Tibetan species of Ranunculaceae. *Australian Journal of Botany*, *54*, 691–700. https://doi.org/10.1071/bt05015

Zu, K. L., & Wang, Z. H. (2022). Research progress on the elevational distributions of mountain species in response to climate change. *Biodiversity Science*, *30*, 21451. https://doi.org/10.17520/biods.2021451

BIOSKETCH

Nan Lin is an assistant professor at College of Life Science, Henan Agricultural University. Her research group members main interests are in the origin, diversification and evolution of the flora of the Qinghai Tibetan Plateau-Hengduan Mountains.

Author contributions: H.C.W., H.S. and T.D. conceived and designed this study; H.K.R., Z.M.L. and Q.L. aided in field collections and lab work; N.L. and Q.L. analysed the data; N.L. wrote the manuscript and J.B.L. edited and revised the manuscript. All authors read and approved the final manuscript.

SUPPORTING INFORMATION

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

How to cite this article: Lin, N., Liu, Q., Landis, J. B., Rana, H. K., Li, Z., Wang, H., Sun, H., & Deng, T. (2023). Staying in situ or shifting range under ongoing climate change: A case of an endemic herb in the Himalaya-Hengduan Mountains across elevational gradients. *Diversity and Distributions*, *29*, 524–542. https://doi.org/10.1111/ddi.13676