Population genetics under the Massenerhebung effect: The influence of topography on the demography of *Acer morrisonense*

Jui-Tse Chang | Min-Xin Luo | Hsin-Pei Lu | Yi-Ting Tseng | Pei-Chun Liao

**Abstract**

**Aim:** The Massenerhebung effect (Mass elevation effect) refers to heat- or wind-driven altitudinal distribution patterns of temperature-dependent parameters among massifs with narrower range and lower elevation around peripheral and isolated mountains compared to core and continuous ones. Although common in ecology, this effect is rarely discussed in population genetics. Here, we use genetic markers to reveal population genetic patterns and also test the mountain- and sky-barrier hypotheses relevant to the Massenerhebung distribution pattern of *Acer morrisonense* in Taiwan's rugged topography and varied local climates.

**Location:** The alpine and cloud forest of Taiwan.

**Taxon:** *Acer morrisonense* Hayata.

**Methods:** Two chloroplast DNA (cpDNA) fragments and 17 expressed sequence tag-simple sequence repeat (EST-SSR) loci, respectively, from 200 to 286 individuals were used to elucidate the phylogeographic pattern of pollen and seed dispersal of *A. morrisonense*. These data were combined with ecological niche modeling (ENM) to infer distribution range shifts and refugia. We also correlated the genetic-divergence indices with spatial factors to clarify latitudinal and altitudinal effects on genetic diversity.

**Results:** The incongruent phylogeographic patterns of genetic distributions between nuclear and cpDNA markers indicate unhindered pollen flow but spatially constrained seed dispersal. Taken together with ENM, the genetic pattern further reflects historical colonization from central-mountain refugia to edges since the Holocene. The Massenerhebung reduces the gene flow by the surrounding mountains and also causes lower genetic diversity compared to central alpine populations.

**Main conclusions:** This study is the first to reveal the influence of Massenerhebung effect on cpDNA genetic structure of montane trees and reflect the spatial trends of seed dispersal. This population genetic pattern can also be attributed to the demography-related range shifts with paleoclimate fluctuations under complex mountain topography, supporting the mountain-barrier hypothesis. The results have important implications for conserving the genetic diversity of species with a wide altitudinal distribution range.
1 INTRODUCTION

The influence of environmental dynamics across space and time on species dispersal, extinction, and evolution is a core issue in biogeography (Lomolino et al., 2010; Whittaker & Fernández-Palacios, 2007). Taiwan is the continental island with rugged topography and varied climates which harbor high species diversity evolved or colonized from the nearby Eurasian mainland, the Philippines, and Japan. For example, Macrotheca taiwanensis (Su et al., 2016) and species of Fatsia in Taiwan (Chiang et al., 2014) originated from Japan, Pachyrhynchus colonized from the Philippines via the Kuroshio Current (Tseng et al., 2018), and mammal fauna mainly originated from the Eurasian mainland (Kawamura et al., 2016). Taiwan emerged from the Pliocene orogeny, resulting in a rugged topography with high elevations up to 4000 m. Combined with its tropical to subtropical climate, the diverse environment of Taiwan provides plentiful choices of habitats and facilitates microevolutionary processes (e.g., Chiang and Schaal, 2006; Li et al., 2019).

As altitude and latitude decrease, the average temperature increases and species composition changes. However, the temperature lapse rate is much steeper with altitude (−6°C km−1 altitude) than with latitude (−6.9°C 1000 km−1 latitude) (Colwell et al., 2008; Freeman & Class Freeman, 2014). Temperature changes that occur more quickly than the physiogeological response of plants will significantly shift species ranges. Therefore, the species geographic distribution is supposed to be more susceptible to altitude than latitude, especially in the tropics and subtropics under climate change (Colwell et al., 2008). Two phenomena, the north-descending (Hsieh et al., 1996) and Massenerhebung modes (Su, 1984), are commonly used to explain the altitudinal distribution of vegetation in Taiwan.

The north-descending phenomenon describes the influence of the interactions between the Central Mountain Range (CMR) and winter monsoons on lower vegetation distribution in northeast Taiwan (Gansert, 2004). The north-south stretches of the CMR plus the northeast winter monsoon create leeward and windward sides in the southwest and northeast regions, respectively. This difference contributes to a steeper temperature lapse rate and a colder and more humid climate (−5.97°C km−1 and >4500 mm mean annual precipitation) in the northeastern portion of the CMR and Snow Mountain Range (SMR) compared to the southwest side (−4.51°C km−1 and <1500 mm annual precipitation) (Chang et al., 2018; Chiu et al., 2014). Consequently, the vegetation in the northeast area is north descending. Chiu et al., (2010) concluded that the north-descending effect of winter monsoons dominates the vegetation altitudinal distribution in Taiwan.

The Massenerhebung effect has also been reported in Taiwan, especially in montane cloud forests (Schulz et al., 2017; Zhang et al., 2013). The Massenerhebung effect is demonstrated in a higher and broader altitudinal distribution of temperature-dependent variables in core and connected mountain areas compared to the peripheral and isolated ones. This tendency was first found in the Alps, describing the broader and higher treeline in the central Alps than its fringes (de Quervain, 1904). Further studies focused mostly on tropical and subtropical regions or large mountain landmasses. The Massenerhebung effect was found in different spatial scales and biota (e.g., regional to global treelines Han et al., 2012; He et al., 2016; Irl et al., 2016; Wang et al., 2017; Zhang & Yao, 2016; Zhao et al., 2015) and montane cloud forest (Kumaran et al., 2011; Pouteau et al., 2018; Schulz et al., 2017). These studies summarized a variety of mechanisms of the Massenerhebung effect, including altitudinal differences in soil conditions (Grubb, 1971), heat retention (Holtmeier, 2009), the temperature lapse rate (Forster, 1982), ultraviolet radiation (Flenley, 1995), and different diurnal/annual temperature amplitudes (Leuschner, 1996). In addition to mechanisms, most research focused on ecology dimensions about its spatial distribution (Han et al., 2018) and influences species or environment distribution (Han et al., 2012; Naniwadekar & Vasudevan, 2006; Palin et al., 2011).

The Massenerhebung and north-descending effect will affect not only the altitudinal variation of the vegetation belt but also the genetic composition and species divergence. In contrast to the abundant studies of monsoon effects on micro- and macroevolutionary processes (Deng et al., 2018; Shih et al., 2018; Wu et al., 2013), the effect of Massenerhebung on species evolution is rarely discussed but should be considered (Schmidt et al., 2017). Here, we propose two contrasting eco-evolutionary hypotheses about the Massenerhebung effect on mountain species. The first is the sky-barrier hypothesis. Distance is a widely accepted mechanism of isolation. Mountain peaks are insulated by the spacious “sky barrier” and form sky islands that interrupt migration. Under this scenario, within the Massenerhebung-like vegetation belt, the higher alitudinal populations are more fragmented than lower altitude. Consequently, obvious population structure and lower genetic diversity are anticipated for higher-elevation populations. The edge populations in higher altitudes will resemble this genetic diversity pattern, but the genetic diversity in peaks of both low and high mountains will be similarly low. The alternative hypothesis is the mountain-barrier hypothesis. Mountain ridges function as barriers to pollen, spore, and seed dispersal (Garcia-Mozo et al., 2004; Li et al., 2019) and thus confine gene flow and colonization. Therefore, exposure to the atmosphere will be greater for populations at high elevations that are surrounded by lower mountain ridges. Under these conditions, long-distance gene flow and colonization will be more likely, particularly for wind-dispersed species. Accordingly, within the Massenerhebung-like vegetation belt, the higher alitudinal populations will be more connected by long-distance gene flow than lower-altitude populations. The pronounced genetic admixture and higher genetic diversity are expected among populations at higher altitudes.

Acer L. are diversified out of Asia and influenced by climate change (Gao et al., 2020). The wide distribution in Northern Hemisphere
indicates the diverse habitats of Acer. In Taiwan, the environment is heterogeneous, with 200 high mountains above 3000 meters above sea level (a.s.l.). There are six endemic Acer species with various distribution from low- to high-altitudinal environments, suggesting the climate influence on their distribution (Li et al., 2015; Li & Lo, 1993). Acer morrisonense Hayata is widely distributed at middle-to-high elevations in the montane cloud forest (Li et al., 2013). Although the north-descending effect would influence the species distribution, the hump-shaped distribution with condensed and lower elevation at north and south ends of Taiwan reveals the dominance of the Massenerhebung effect on A. morrisonense altitudinal distribution (Figure 1). This species is a sister to the temperate species A. morifolium Koidzumi or A. komarovi Pojarkova as inferred by nuclear DNA (nDNA) or chloroplast DNA (cpDNA), respectively (Zhang et al., 2010). These phylogenetic relationships imply speciation from temperate areas to the subtropics and tropics. Acer morrisonense is therefore suggested to be a temperate relict of the paleoclimate in the mountains of the subtropical island of Taiwan. The survival of temperate origin species in the subtropical area is sensitive to climate change, such as temperature (Friedl et al., 2014). Together with the Massenerhebung effect of the distribution pattern, A. morrisonense is particularly suitable for exploring the interplay of topography, climate, and evolutionary trajectories during colonization and gene flow.

In this study, we aim to (1) unveil the historical biogeography of A. morrisonense, (2) clarify the effects of latitude and altitude on genetic diversity and gene flow, and (3) test the two contrasting hypotheses of the Massenerhebung effect on seed and pollen flows based on population genetic structure. If the A. morrisonense populations in the core mountains are genetically structured and with lower diversity than peripheral ones, the sky-barrier hypothesis will be supported. Conversely, the mountain-barrier hypothesis predicts genetic homogeneity and comparatively higher diversity of A. morrisonense in the core mountain populations compared to the peripheral ones. Our work is the first to reveal the population genetic patterns putatively influenced by the Massenerhebung effect. Our results provide insights not only for understanding the influence of suboptimal habitats on the evolutionary trends of relict plants but also for predicting the genetic interactions of topography with anemophilous species.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling

The sampling range mainly focused on CMR following Chiou et al., (2010), and the SMR was also considered for its second-largest mountain range in Taiwan. Thirteen populations with 286 individuals (Table 1) and 12 populations with 200 individuals of A. morrisonense (Table 2) surrounding the SMR and CMR in Taiwan were sampled for nuclear SSR genotyping and cpDNA sequencing, respectively (Figure 2). The spacing between sampled individuals was at least 20 m. The altitudes of the sampling sites ranged from 1280 m to 2700 m a.s.l. Based on the altitudinal distribution pattern of A. morrisonense (Figure 1), the populations SKR, LLS, and TPS in the north and JBS, LD, and STC in the south were, respectively, defined as northern and southern peripheral populations compared to the rest of the core populations (Figure 2). Fresh leaves of each individual were collected and dried immediately in silica gel to prevent DNA degradation. Voucher specimens of each sample were deposited at National Taiwan Normal University.

FIGURE 1 The geographic distribution of A. morrisonense in Taiwan. The left and right panels indicate the horizontal and vertical distributions, respectively. The localities were from the GBIF and the exact sampling sites, and the map was created by distrmap_tw.qgis (https://github.com/mutolisp/distrmap_tw.qgis).
2.2 Molecular techniques

Total genomic DNA was extracted from dried leaf tissue following a modified cetyltrimethylammonium bromide (CTAB) method (Doyle & Doyle, 1987). The extracted DNA was dissolved in 1× TE buffer and stored at −20°C. The expressed sequence tag-simple sequence repeats (EST-SSRs) used for genotyping for the genetic diversity analyses were developed from transcriptomic assemblies of Acer saccharum Marshall (Accession: Acer saccharum 010515,Hardwood Genomics Project, http://www.hardwoodgenomics.org/) and Acer negundo L. (Accession: VFFP. One Thousand Plants (1KP) Consortium, https://sites.google.com/a/ualberta.ca/onekp/).

A total of 17 polymorphic EST-SSR loci were developed and used in this study (Table S1). For genotyping, the PCR products were analyzed by capillary electrophoresis on an Applied Biosystems 3730 DNA Analyzer (Applied Biosystem, USA). The fragment size was analyzed by Peak Scanner version 1.0 (Applied Biosystem, USA) at the National Center for Genome Medicine, Academia Sinica, Taiwan, and determined by reference to size standard ABI GSS500 LIZ (Applied Biosystems, USA). For peak picking and noise reduction, a minimum peak height of 100 was adopted for allelic calling. Those peaks with sizes falling into the expected range were manually checked and adjusted.

Additionally, two cpDNA fragments, the rpl16 intron and tmh-psbA spacer, were amplified and sequenced with the primer sets 5'-GCTATGCTTAGTGACTCGTGG-3' and 5'-CTTCTCTATGTTGACG-3' for the rpl16 intron and 5'-GTTATGCATGAACGTAATGCTC-3' and 5'-CGCCGATGGTTGATTCACAACTG-3' for the tmh-psbA spacer. DNA sequencing was conducted using an ABI PRISM® 3730XL DNA Sequencer (Perkin-Elmer, Foster City, CA, USA) with ExoSAP-IT (Thermo Fisher Scientific Inc., Waltham, MA, USA) and the ABI BigDye 3.1 Terminator Cycle Sequencing Kit (Applied Biosystem, Foster City, CA, USA). The cpDNA sequences were aligned and checked using BioEdit (Hall, 1999) for further analyses. The obtained sequences were deposited in GenBank (www.ncbi.nlm.nih.gov/genbank) under accession numbers MK258201-MK258681.

2.4 Calculation of the pollen-to-seed migration ratio

The AMOVA shows stronger population divergence in cpDNA, indicating small seed flow among populations of A. morrisonense. Therefore, based on the pairwise FST estimated from nuclear EST-SSR loci and cpDNA, the pollen-to-seed migration ratio (R) of the population was estimated using equation (5), [(1/(1 − FST(m))) − 2/ (1 − FST(m))] × (1 − FST(m)), in Ennos’s (1994) method. Both the pairwise FST and R were then correlated with the geographic and environmental distances using a generalized additive model (GAM) with the gam function of package “mgcv” in R 3.5.3. The environmental distance was calculated by 19 bioclim variables using the Euclidean distance.

2.5 Contemporary inbreeding and pairwise migration rate

Aside from the long-term pollen-to-seed migration ratio, current population pairwise migration rates and inbreeding coefficients were estimated by BayesAss version 3.0.4 (Wilson & Rannala, 2003) using multilocus genotypes in nEST-SSR. The two cpDNA were not considered due to a lack of representations of genome-wide migration. Before the Bayesian MCMC run, the mixing parameters (i.e., inbreeding coefficient, migration rate, and allele frequency) were fine-tuned to m = 0.8, a = f = 1 to adjust the acceptance rate between 20% and 60%. Each Bayesian MCMC run was set at 100 million iterations with 10 million burn-in and sampling every 5000 iterations. Ten independent Bayesian MCMC runs with different seeds were performed, and the convergence was qualified by Tracer version 1.7 (Rambaut et al., 2018). The median migration rates among 10 runs between high- to low- and low- to high-altitude populations were statistically compared by wilcox.test in R package “STATS”. Ten runs of population inbreeding coefficient (Fis), immigration (Im), and emigration (Em) rates were associated with latitude by loess method in R package “STATS”.

2.3 Genetic diversity estimation

The average number of alleles per locus (Na), effective number of alleles per locus (Ne), observed (Ho) and expected heterozygosity (He), and the inbreeding coefficient (FIS) of the EST-SSRs were calculated in GenALEX version 6.5 (Peakall & Smouse, 2012). For cpDNA, we estimated the number of haplotypes (H), segregating sites (S), haplotype diversity (Hd), and nucleotide diversity (a) for the combined sequences of the rpl16 intron and tmh-psbA spacer. The statistics Tajima’s D and Fu’s F were used to evaluate the excess of rare alleles and singletons, respectively, and to evaluate demographic change using Arlequin version 3.5.1.3 (Excoffier & Lischer, 2010). The minimum spanning network for the haplotype relationships was computed by the pairwise distance of haplotypes using Arlequin version 3.5.1.3 (Excoffier & Lischer, 2010).

2.6 Population genetic structure

We used Bayesian clustering analysis, a population model-based approach based on Hardy-Weinberg and linkage equilibria (Falush et al., 2003) to estimate the cluster membership coefficient (i.e., the Q matrix) of individuals (indQ) and populations (popQ) and to discriminate genetic clusters in the EST-SSR data with STRUCTURE version 2.3.4 (Hubisz et al., 2009). We estimated the posterior probability of the grouping number (K = 1-14) by 10 independent runs using 106 steps of Markov chain Monte Carlo (MCMC) replicates after 10% burn-in for each run to evaluate consistency. The best grouping number was evaluated by ΔK (Evanno et al., 2005) in STRUCTURE HARVESTER version 0.6.94 (Earl & Vonholdt, 2012). Analysis of molecular variance (AMOVA) with hierarchical groupings, including between and within populations, was performed.
### Table 1: Geographic information of sampling sites and genetic diversity estimated by EST-SSRs

<table>
<thead>
<tr>
<th>Population</th>
<th>Sample size</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Altitude (m)</th>
<th>N</th>
<th>Na Mean</th>
<th>Na SE</th>
<th>Ne Mean</th>
<th>Ne SE</th>
<th>Ho Mean</th>
<th>Ho SE</th>
<th>He Mean</th>
<th>He SE</th>
<th>F&lt;sub&gt;IS&lt;/sub&gt; Mean</th>
<th>F&lt;sub&gt;IS&lt;/sub&gt; SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALS</td>
<td>30</td>
<td>23°28'N</td>
<td>120°51'E</td>
<td>2299–2540</td>
<td>29</td>
<td>2.412</td>
<td>0.403</td>
<td>1.536</td>
<td>0.168</td>
<td>0.174</td>
<td>0.064</td>
<td>0.244</td>
<td>0.063</td>
<td>0.297</td>
<td>0.122</td>
</tr>
<tr>
<td>DD</td>
<td>6</td>
<td>23°46'N</td>
<td>121°10'E</td>
<td>2236–2455</td>
<td>6</td>
<td>1.882</td>
<td>0.241</td>
<td>1.461</td>
<td>0.127</td>
<td>0.196</td>
<td>0.069</td>
<td>0.234</td>
<td>0.059</td>
<td>0.267</td>
<td>0.131</td>
</tr>
<tr>
<td>DXS</td>
<td>30</td>
<td>24°14'N</td>
<td>120°58'E</td>
<td>1855-2034</td>
<td>28</td>
<td>2.235</td>
<td>0.315</td>
<td>1.466</td>
<td>0.141</td>
<td>0.17</td>
<td>0.056</td>
<td>0.228</td>
<td>0.06</td>
<td>0.295</td>
<td>0.103</td>
</tr>
<tr>
<td>JBS</td>
<td>2</td>
<td>22°43'N</td>
<td>120°45'E</td>
<td>1280–1306</td>
<td>2</td>
<td>1.294</td>
<td>0.143</td>
<td>1.204</td>
<td>0.108</td>
<td>0.147</td>
<td>0.071</td>
<td>0.103</td>
<td>0.048</td>
<td>-0.4</td>
<td>0.032</td>
</tr>
<tr>
<td>LD</td>
<td>36</td>
<td>23°14'N</td>
<td>120°59'E</td>
<td>1939–2309</td>
<td>36</td>
<td>3.647</td>
<td>0.658</td>
<td>1.584</td>
<td>0.153</td>
<td>0.191</td>
<td>0.051</td>
<td>0.282</td>
<td>0.059</td>
<td>0.37</td>
<td>0.086</td>
</tr>
<tr>
<td>LLS</td>
<td>19</td>
<td>24°41'N</td>
<td>121°24'E</td>
<td>2085–1577</td>
<td>17</td>
<td>3</td>
<td>0.47</td>
<td>1.615</td>
<td>0.174</td>
<td>0.166</td>
<td>0.052</td>
<td>0.281</td>
<td>0.06</td>
<td>0.429</td>
<td>0.124</td>
</tr>
<tr>
<td>MF</td>
<td>31</td>
<td>24°05'N</td>
<td>121°10'E</td>
<td>2087–2321</td>
<td>28</td>
<td>2.118</td>
<td>0.331</td>
<td>1.394</td>
<td>0.142</td>
<td>0.193</td>
<td>0.06</td>
<td>0.196</td>
<td>0.056</td>
<td>0.142</td>
<td>0.101</td>
</tr>
<tr>
<td>SKR</td>
<td>18</td>
<td>24°33'N</td>
<td>121°08'E</td>
<td>1933–2021</td>
<td>18</td>
<td>2.118</td>
<td>0.225</td>
<td>1.369</td>
<td>0.105</td>
<td>0.186</td>
<td>0.055</td>
<td>0.208</td>
<td>0.051</td>
<td>0.224</td>
<td>0.119</td>
</tr>
<tr>
<td>STC</td>
<td>10</td>
<td>23°16'N</td>
<td>120°55'E</td>
<td>2324</td>
<td>10</td>
<td>1.824</td>
<td>0.3</td>
<td>1.407</td>
<td>0.149</td>
<td>0.241</td>
<td>0.083</td>
<td>0.186</td>
<td>0.062</td>
<td>-0.256</td>
<td>0.044</td>
</tr>
<tr>
<td>SY</td>
<td>25</td>
<td>24°20'N</td>
<td>121°19'E</td>
<td>1796–2039</td>
<td>24</td>
<td>2.471</td>
<td>0.298</td>
<td>1.483</td>
<td>0.168</td>
<td>0.154</td>
<td>0.05</td>
<td>0.219</td>
<td>0.061</td>
<td>0.234</td>
<td>0.077</td>
</tr>
<tr>
<td>TPS</td>
<td>26</td>
<td>24°31'N</td>
<td>121°31'E</td>
<td>1471–1824</td>
<td>26</td>
<td>2.471</td>
<td>0.394</td>
<td>1.423</td>
<td>0.173</td>
<td>0.124</td>
<td>0.043</td>
<td>0.185</td>
<td>0.06</td>
<td>0.302</td>
<td>0.081</td>
</tr>
<tr>
<td>TRK</td>
<td>32</td>
<td>24°11'N</td>
<td>121°20'E</td>
<td>2336–2700</td>
<td>32</td>
<td>3.059</td>
<td>0.449</td>
<td>1.601</td>
<td>0.204</td>
<td>0.177</td>
<td>0.057</td>
<td>0.254</td>
<td>0.063</td>
<td>0.38</td>
<td>0.101</td>
</tr>
<tr>
<td>TTC</td>
<td>31</td>
<td>23°31'N</td>
<td>120°54'E</td>
<td>1648–2350</td>
<td>30</td>
<td>2.353</td>
<td>0.296</td>
<td>1.471</td>
<td>0.147</td>
<td>0.224</td>
<td>0.068</td>
<td>0.229</td>
<td>0.059</td>
<td>0.18</td>
<td>0.111</td>
</tr>
<tr>
<td>Total</td>
<td>296</td>
<td></td>
<td></td>
<td></td>
<td>286</td>
<td>6.235</td>
<td>1.13</td>
<td>1.578</td>
<td>0.175</td>
<td>0.18</td>
<td>0.05</td>
<td>0.261</td>
<td>0.062</td>
<td>0.398</td>
<td>0.088</td>
</tr>
</tbody>
</table>

N, sample size used for EST-SSRs; Na, number of alleles per locus; Ne, effective number of alleles per locus; Ho, observed heterozygosity; He, expected heterozygosity; F<sub>IS</sub>, inbreeding coefficient.
to assess population structure for both the cpDNA and EST-SSR datasets in Arlequin version 3.5.1.3 (Excoffier & Lischer, 2010).

### 2.7 Demographic change inferred from cpDNA

The coalescence-based extended Bayesian skyline plot (eBSP) was drawn using BEAST 1.8.4 (Drummond & Rambaut, 2007). The best substitution model of each locus was evaluated with AIC and BIC. Multiple times MCMC simulations were run to obtain better prior, and operator settings, and then 100 million MCMC simulations were performed with sampling every 10,000 generations. The first 25% of samplings were discarded as burn-in. Due to the absence of fossil records, we used the strict clock model to estimate the coalescence time with a constant evolutionary rate of $1.01 \times 10^{-9}$ substitutions per site per year for cpDNA (Wolfe et al., 1987).

### 2.8 Model test for latitudinal and altitudinal effects on genetic diversity

To explore whether altitude or/and latitude truly influence the differences in genetic diversity among populations, the GAM was

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### TABLE 2 Genetic diversity estimated by cpDNA

<table>
<thead>
<tr>
<th>Population</th>
<th>N</th>
<th>H</th>
<th>S</th>
<th>$Hd$ (std)</th>
<th>$1000 \times \pi$ (std)</th>
<th>Tajima’s $D$ (P)</th>
<th>Fu’s $Fs$ (P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MF</td>
<td>28</td>
<td>4</td>
<td>0</td>
<td>0.743 (0.039)</td>
<td>6.841 (3.320)</td>
<td>0 (N.A.)</td>
<td>9.413 (0.996)</td>
</tr>
<tr>
<td>TRK</td>
<td>20</td>
<td>4</td>
<td>0</td>
<td>0.700 (0.062)</td>
<td>9.568 (4.581)</td>
<td>0 (N.A.)</td>
<td>10.073 (0.999)</td>
</tr>
<tr>
<td>SY</td>
<td>18</td>
<td>3</td>
<td>2</td>
<td>0.569 (0.071)</td>
<td>4.405 (2.280)</td>
<td>−1.508 (0.054)</td>
<td>6.533 (0.991)</td>
</tr>
<tr>
<td>TPS</td>
<td>13</td>
<td>5</td>
<td>1</td>
<td>0.628 (0.143)</td>
<td>7.179 (3.600)</td>
<td>−1.149 (0.151)</td>
<td>3.787 (0.959)</td>
</tr>
<tr>
<td>DXS</td>
<td>10</td>
<td>2</td>
<td>0</td>
<td>0.556 (0.075)</td>
<td>4.444 (2.393)</td>
<td>0 (N.A.)</td>
<td>7.045 (0.995)</td>
</tr>
<tr>
<td>TTC</td>
<td>26</td>
<td>2</td>
<td>0</td>
<td>0.520 (0.028)</td>
<td>4.160 (2.137)</td>
<td>0 (N.A.)</td>
<td>10.374 (0.998)</td>
</tr>
<tr>
<td>ALS</td>
<td>23</td>
<td>3</td>
<td>0</td>
<td>0.423 (0.104)</td>
<td>11.312 (5.328)</td>
<td>0 (N.A.)</td>
<td>15.657 (1.000)</td>
</tr>
<tr>
<td>LD</td>
<td>30</td>
<td>2</td>
<td>15</td>
<td>0.067 (0.061)</td>
<td>8.733 (4.146)</td>
<td>−2.479 (&lt;0.001)</td>
<td>18.533 (1.999)</td>
</tr>
<tr>
<td>LLS</td>
<td>7</td>
<td>1</td>
<td>0</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (N.A.)</td>
<td>0 (N.A.)</td>
</tr>
<tr>
<td>STC</td>
<td>9</td>
<td>2</td>
<td>1</td>
<td>0.389 (0.164)</td>
<td>9.333 (4.738)</td>
<td>0.156 (0.753)</td>
<td>10.300 (1)</td>
</tr>
<tr>
<td>SKR</td>
<td>13</td>
<td>2</td>
<td>0</td>
<td>0.462 (0.110)</td>
<td>2.769 (1.566)</td>
<td>0 (N.A.)</td>
<td>5.769 (0.989)</td>
</tr>
<tr>
<td>DD</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>0.667 (0.314)</td>
<td>15.333 (9.515)</td>
<td>0 (N.A.)</td>
<td>4.946 (0.943)</td>
</tr>
<tr>
<td>Total</td>
<td>200</td>
<td>14</td>
<td>18</td>
<td>0.805 (0.016)</td>
<td>19.84 (8.810)</td>
<td>−2.459 (&lt;0.001)</td>
<td>29.283 (0.996)</td>
</tr>
</tbody>
</table>

$N$, sample size; $H$, number of haplotype; $S$, number of segregating sites (excluding indels); $Hd$, haplotype diversity; N.A., not allowed.

The haplotype variation in these populations was attributed to indels rather than substitutions.

---

**FIGURE 2** Genetic-composition distribution and haplotype network of _A. morrisonense_. (a) Genetic components of EST-SSRs inferred by STRUCTURE; (b) haplotype distribution of cpDNA; (c) proportions of genetic components of each sample inferred by STRUCTURE; and (d) haplotype network of cpDNA inferred by the parsimonious approach, in which the circle size roughly represents the relative abundance of haplotypes and is not plotted in proportion. SMR and CMR refer to Snow and Central Mountain Range.
estimated by the REML method in the R 3.5.3 package “mgcv”. The nucleotide diversity (\(\pi\)) and haplotype diversity (\(H_d\)) of cpDNA and expected heterozygosity (\(H_e\)) and inbreeding coefficients (\(F_{IS}\)) of the nuclear EST-SSRs were used as dependent factors to test the empty model (\(-1\)), latitude model (\(-\text{lat}\)), altitude model (\(-\text{alt}\)), and additive effect model (\(-\text{lat+alt}\)) by AIC. A smaller AIC value indicated a better model.

2.9 | Species distribution modeling

Ecological niche modeling (ENM) was further used to predict the potential distributions of A. morrisonense. We collected 70 current environmental factors, including 19 bioclimatic variables (Bioclim), average temperature, maximum monthly temperature, minimum monthly temperature, and monthly precipitation from the WorldClim website (http://www.worldclim.org/bioclim) with a resolution of 30 arc-sec (approximately 1 × 1 km), and the mean annual actual evapotranspiration, potential evapotranspiration, and annual aridity from the Consortium for Spatial Information (CGIAR-CSI, https://cgiarcsi.community/). We also collected paleoclimate data of the Last Glacial Maximum (LGM, 21 kya) and the Middle Holocene (6 kya) from the WorldClim website (http://www.worldclim.org/bioclim). Variables with high variance inflation factors (VIFs > 10) were removed to reduce multicollinearity. The remaining environmental variables were used to model the distribution ranges. To predict the potential habitats, species distribution models were built under the maximum entropy model implemented in MaxEnt 3.3.3 (Phillips & Dudik, 2008) and the R package “dismo” (Hijmans et al., 2013). The occurrence data of A. morrisonense were obtained from our sampling sites, herbarium data, and the Global Biodiversity Information Facility (GBIF, http://www.gbif.org). Unclear records and incorrect identifications were excluded. A maximum of 2000 iterations were conducted, and species occurrence data were randomly divided (10%) to train the model. One regularization multiplier and 10,000 background points were set for creating models. The logistic output consisting of a grid map with a suitability value range from 0 to 1 was generated and visualized with the R package "maptools" (Lewin-Koh et al., 2011).

3 | RESULTS

3.1 | Genetic diversity of EST-SSRs

The average observed (\(H_o\)) and expected heterozygosity (\(H_e\)) of the total population estimated from the 17 EST-SSR loci were 0.180 ± 0.050 (mean ± standard deviation) and 0.261 ± 0.062 for a total of 286 sampled individuals. In most populations, \(H_o\) and \(H_e\) did not differ significantly, resulting in a nonsignificant deviation from 0 of the inbreeding coefficient (\(F_{IS}\)), which ranged from 0.103 (JBS population) to 0.282 (LD population). Populations STC and JBS were the only exceptions, with significantly negative \(F_{IS}\) values (\(-0.256\) and \(-0.400\), \(p = 0.044\) and 0.032, respectively), suggesting a tendency of outcrossing in the mating system in these two populations (Table 1). The detailed genetic diversity indices estimated by EST-SSR loci are listed in Table 1.

3.2 | Genetic diversity of cpDNA

In total, 14 haplotypes were obtained from 200 individuals (12 populations). The haplotype diversity (\(H_d\)) varied among populations, ranging from 0 (LLS population) to 0.743 ± 0.039 (MF population), and the total \(H_d\) of A. morrisonense was 0.805 ± 0.016. The nucleotide diversity (\(\pi\)) also ranged from 0 (LLS population) to 0.0153 ± 0.0095 (DD population), and the total \(\pi\) was 0.0198 ± 0.0081. In general, the genetic diversity of A. morrisonense was high in the total population but varied among locations in Taiwan. Tajima's D and Fu's Fs were also estimated to infer recent demographic change. The total population was characterized by negative D (\(-2.459, \ p < 0.001\)) but a nonsignificant deviation of Fs from 0 (29.283, \(p = 0.996\)), indicating no or very few private singletons in the total population. These results indicate that the increase in rare alleles by demographic expansion was not very recent and/or was uneven among localities. This inference was supported by testing D and Fs for every population singly. Only the SY and LD populations had marginal and significant negative values of Tajima's D (\(D = -1.508\) and \(-2.479, \ p = 0.054\) and < 0.001, respectively) and positive but nonsignificant Fu's Fs in every population (Table 2). Detailed genetic diversity indices estimated by cpDNA are listed in Table 2.

3.3 | Analysis of molecular variance

AMOVA revealed significant population genetic differentiation according to both EST-SSRs (\(F_{ST} = 0.101, \ p < 0.00001\)) and cpDNA (\(F_{ST} = 0.762, \ p < 0.00001\)). However, the genetic variation of the EST-SSRs was mostly attributed to within-population variation (89.86%), while the genetic variation of cpDNA was mostly attributed to interpopulation variation (67.19%) (Table 3).

3.4 | Bayesian clustering analysis for EST-SSRs

Bayesian clustering analysis suggested that the best grouping number (K) of genetic components of A. morrisonense was two according to ΔK, which indicates the rate of change in the log probability of data in successive K values (Figure S2). However, these two genetic clusters were not geographically associated (Figure 2a) and could not separate the sampled populations into different groups (Figure 2c).
3.5 | cpDNA haplotype distribution

Fourteen haplotypes were identified from the two chloroplast fragments. Although all of the haplotypes except one in the LD population were closely connected in the parsimonious network, the north and south genotypes could be clearly distinguished (Figure 2d). The northern populations (i.e., north of DD populations) were mainly composed of multiple haplotypes, while the southern populations (i.e., south of TTC populations) were mostly derived from a common major haplotype (Figure 2d). With AMOVA results that genetic variations were primarily contributed by between populations in cpDNA, the population structure was stronger in maternal than by biparental inheritance markers, suggesting more frequent pollen flow than seed dispersability.

3.6 | Stable demographics inferred by the extended Bayesian skyline plot

The coalescence process traced the evolutionary history of A. morrisonense back to roughly 1.75 Mya (Figure S1) during the early Pleistocene (i.e., Calabrian stage) (Ogg et al., 2016). During this period, the effective population size was estimated at roughly one million individuals and did not change severely (Figure S1).

3.7 | Contrasting effects of geographic and environmental distances on the pollen-to-seed migration ratio

The average pairwise F$_{ST}$ estimated by cpDNA ($F_{ST} = 0.501 ± 0.269$) was higher than that estimated by nuclear EST-SSRs ($F_{ST} = 0.051 ± 0.017$), consistent with more inter-population variations of cpDNA than EST-SSRs by AMOVA (Table 3). The pollen-to-seed migration ratio (R) was $38.03 ± 45.15$, roughly twice the reported median value of $R$ of seed plants (Petit et al., 2004), indicating a predominance of gene flow by pollen in A. morrisonense. However, the high variance of $R$ showed that pollen flow (or/and seed dispersal) had an inhomogeneous effect on gene flow among populations.

We further tested whether the population genetic differentiation ($F_{ST}$) and pollen-to-seed migration ratio (R) were related to geographic and environmental (climatic) distances. GAM revealed significant but contrasting effects of both geographic and environmental distances on $F_{ST}$ of cpDNA: a positive trend of $F_{ST}$ with geographic distance ($F = 45.75, p < 2 × 10^{-16}$, Figure 3c) but a negative trend with environmental distance ($F = 16.70, p = 5 × 10^{-3}$, Figure 3d). However, the pattern of isolation by distance (IBD) in nuclear EST-SSRs was only detected at short ranges of geographic distance ($F = 2.958, p = 0.024$, Figure 3e), and the effect of environmental distance was nonsignificant ($F = 2.976, p = 0.051$, Figure 3f). In addition, positive and negative trends of the pollen-to-seed migration ratio (R) with geographic ($F = 18.891, p = 2 × 10^{-9}$, Figure 3a) and environmental distances ($F = 6.643, p = 0.001$, Figure 3b) were detected, respectively, suggesting that seed dispersal is more limited in space but occurs more easily to different habitats; by contrast, pollen may not spread effectively from the source to populations in different environments but is unhindered by geographic distance. The table of maternal and biparental pairwise $F_{st}$ was in supplementary (Table S2).

3.8 | High current inbreeding with consistently low population migration rate along latitude and altitude

Compared to long-term estimates of Fis by GenALEX (Table 1), recent inbreeding was high (Fis = 0.67–0.88) and migration was low in all populations (Figure S3c). Migration rates from high and low altitude were marginally significant ($W = 2540, p = 0.07$), exhibiting slightly stronger migration from high- to low-altitude (median = 0.0116 vs. 0.0107) populations (Figure S3d). Along the latitude, both the Im and Em were low (m = 0.0067–0.23) and not significantly different (Figure S3a and b).

3.9 | Latitudinal and altitudinal effects on the genetic diversity of cpDNA

The model selection revealed differences in latitudinal and altitudinal effects on genetic diversity between cpDNA and nuclear EST-SSRs. For cpDNA, altitude and latitude best-predicted nucleotide diversity ($\pi$) and haplotype diversity ($Hd$), respectively, according to the AIC values (Table S3). $\pi$ showed an increasing trend with elevation ($F = 6.201, p = 0.016$, Figure 4a), whereas $Hd$ was higher at middle latitudes but dropped in both north and south Taiwan ($F = 7.561, p = 0.015$, Figure 4b). This pattern indicates that the space constraint may affect the genetic diversity of seeds.

### TABLE 3 Summary results of AMOVA inferred by EST-SSRs and cpDNA

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>EST-SSRs</th>
<th>cpDNA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>SS</td>
</tr>
<tr>
<td>Among populations</td>
<td>12</td>
<td>144.499</td>
</tr>
<tr>
<td>Within populations</td>
<td>273</td>
<td>1145.664</td>
</tr>
<tr>
<td>Total</td>
<td>285</td>
<td>1290.163</td>
</tr>
</tbody>
</table>

*p < 0.00001.
However, latitudinal and altitudinal effects on genetic diversity were not detected for the EST-SSRs. Although altitude and latitude best predicted the heterozygosity ($H_e$) and inbreeding coefficients ($F_{IS}$), respectively, the predictive power of these two factors was not significant ($F = 3.552$, $p = 0.129$ for altitude on $H_e$, Figure 4c; $F = 2.340$, $p = 0.157$ for latitude on $F_{IS}$, Figure 4d).

### 3.10 Current and past potential distributions inferred by ecological niche modeling

After removing factors due to multicollinearity, nine environmental factors remained to predict the current distribution: four soil variables (BDTICM_M_250 m, CECSOL_M_sl5_250 m, CLYPPT_M_sl5_250 m, and PHIKCL_M_sl5_250 m), two bioclimatic variables (bio7 and bio9), and three monthly precipitation variables (prec3, prec8, and prec10). The current species distribution predicted under regularization multiplier 1 displayed a high match to the sparse specimen distribution around the mountains of Taiwan (Figure 5). However, this distribution pattern differed from the postdistribution at the last glacial maximum (LGM, 21 kya) and the Middle Holocene (Holocene Thermal Optimum, HTO, 6 kya) based on climate data (bio7, bio9, prec3, prec8, and prec10). At the LGM, the distribution was concentrated in the northern and southern mountains, where the northern parts were further divided into the northern CMR and the SMR (Figure 5). During the warmer Middle Holocene, the distribution range was severely restricted to tiny areas (refugia) of alpines (Figure 5). These results imply that *A. morrisonense* experienced a “spatial bottleneck” event with subsequent range expansion in the recent past.

### 4 Discussion

#### 4.1 Gene flow through different timescales suggest infrequent but persisting long-distance dispersal

The chlorotype variation of *A. morrisonense* showed apparent altitudinal and latitudinal effects, but these effects were not reflected in the nuclear EST-SSRs (Figure 4c and d). Pollen contains only paternal genetic material, which is reflected only in nuclear markers and
not cpDNA. Therefore, the low Fis and high pollen-to-seed migration ratio can explain the spatial-free structure of pollen flow. Studies of pollination ecology on *A. morrisonense* are lacking, but the phenology and morphology of reproductive organs in this species indicated both wind and insect pollination (i.e., ambophily). The small (21–33 μm × 16–25 μm) (Huang, 1972) and airborne nature of the pollen (Yang & Chen, 1998) and flowering before or during the unfolding of leaves (de Jong, 1976) facilitated wind dispersal. The nectar glands on male flower implicated insect pollinations. Accordingly, the contrasting pattern of high differentiation in cpDNA versus low differentiation in nDNA (Table 3) reflected high pollen-to-seed migration ratios promoted by wind and insects. Recurring gene flow may counteract the decreasing genetic diversity of the postglacial founder effect (Shi & Chen, 2012). In addition, due to the rapid evolution of SSRs, bygones can be easily obscured by more recent biogeographic events. Therefore, after the latest post-HTO expansion from refugia
(Figure 5), long-term effects of altitude and latitude on genetic variations were both difficult to detect in nDNA (Figure 4c and d).

In more recent timescale, nDNA exhibited low inter-population migrations with stronger inbreeding (Figure S3). This contrasting result to long-term migration patterns indicated infrequent but persistent long-distance pollen dispersal. The spring rainfall in Taiwan was consistent with the flowering time of A. morrisonense during March and April (Wang et al., 1994). The precipitation was stronger around the CMR, and interannual variation has become larger recently (Chen & Chen, 2003; Chen et al., 2003; Jiang et al., 2003). The heavier rainfall has been reported to precipitate the pollens and, therefore, may probably confine the long-distance dispersal of A. morrisonense (Markgraf, 1980; Silva Palacios et al., 2007). Therefore, despite the capability for long-distance pollen dispersal of A. morrisonense, the frequency was low and will be influenced by climate change (e.g., ENSO) (Jiang et al., 2003; Kuo et al., 2016). The pollination syndrome is a possible driver for Acer evolution (Gao et al., 2020). Future studies on the relative roles of biotic (e.g., insects) and abiotic factors (e.g., wind) in Acer evolution will be crucial.

4.2 Postglacial climate change influenced range shifts and genetic distribution

Comparing the present distribution of A. morrisonense with the postdictions in the LGM and the HTO suggested that a cool climate is more suitable for A. morrisonense (Figure 5). During the middle of the Holocene, the warmer climate compared with the LGM caused severe shrinkage of distribution areas in the north and south. The narrow latitudinal range of Taiwan Island reduces horizontal temperature advection on the local temperature, but the temperature changes rapidly with altitude (Sun et al., 1990). The rapid downhill range expansion of A. morrisonense since the mid-Holocene reflects the severe cooling of alpines more than the monsoon effect (cf. Sun et al., 1990). A drastic change in vegetation type even from tropical to subtropical forests at 650 m a.s.l. has also been recorded for Salix L. in central Taiwan based on pollen evidence (Liew et al., 2006). Therefore, both population genetic patterns and species distributions are influenced mostly by altitude rather than latitude since the post-LGM warming and post-HTO cooling periods.

Spatial expansion of A. morrisonense after the habitat-range shrinkage was inferred from ENM. The genetic diversity remained high even after the range-size decline in the HTO, with population differentiation between the north and south parts (Figure 5). However, the mountains in the north and south Taiwan are relatively low in altitude, limiting the altitude distribution and causing noticeable climatic differences at short distances. At short geographic distances, both nDNA and cpDNA exhibited an apparent IBD pattern. By contrast, chloroplast differentiation increased with decreasing environmental distance (Figure 3d).

4.3 Historical demographics and the Massenerhebung effect affect genetic diversity patterns

The genetic diversity of peripheral populations of anemophilous species could be supplemented by core populations via frequent pollen flow (Shi & Chen, 2012). The increasing estimates of the pollen-to-seed migration ratio with geographic distance were attributed to higher genetic divergence of cpDNA than nDNA. The former reflects seed dispersal only, while the latter reflects both seed and pollen dispersal. The more homogeneous genetic composition of nDNA can be attributed to the longer dispersal distance of pollen than seed. By contrast, cpDNA exhibited various pattern of genetic diversity among populations, which can be explained by three possible mechanisms.

The first is historical colonization events after the HTO. Based on ENM, the extreme altitudinal climate change prompted range expansion from the central toward the peripheral mountain range after the HTO. The central and high-altitude populations were refugia and preserved more ancestral polymorphism. In comparison, the north and south populations were likely the last-colonized habitats, resulting in stronger founder effects and lower genetic diversity. The second is edge effects. The north and south populations located at the ends of the mountain ranges in Taiwan are the leading-edge populations. Although these populations probably carry more evolutionary and ecological value, the edge distributions will undergo stronger selective pressure or lower gene flow, diminishing genetic diversity, and strengthening the population structure (Eckert et al., 2008). After expansion from HTO refugia (Figure 5b), the populations at the peripheral regions (northern SMR and two ends of CMR) are expected to share similar low genetic diversity patterns. Furthermore, secondary contact led to the genetic mixing between the two isolated HTO refugia, resulting in higher genetic diversity in the central CMR (Figure 5a and b).

Third, in addition to the two demography-related effects outlined above, the population genetic patterns of cpDNA may also be influenced by the current altitudinal distribution. Mountain ridges can serve as potential barriers to sporopollen dispersal (García-Mozo et al., 2004). Hence, wind-mediated seed dispersal may be negatively influenced by topography. In this study, the mountain-barrier hypothesis was well-supported by the constrained seed flow of A. morrisonense. That is, the higher the elevation, the lower the montane barrier. The rugged topography inhibited the seed flow, causing the strong structuring and large variance of pollen-to-seed migration ratios. Under Massenerhebung distribution patterns, high-altitudinal populations will spread seeds more distantly and will easily colonize to the south and north at lower elevations. In addition, vegetation compression narrowed the vertical distribution of A. morrisonense in the lowland edges, resulting in small population size. The rapid genetic drift of these peripheral populations with the selection at a suboptimal condition would reduce the genetic diversity (Ohsawa & Ide, 2007). These features would facilitate colonization, homogenize
the population structure, and maintain higher genetic diversity in the central high elevation area (Figure 4a).

4.4 | Environmental heterogeneity affects supplementation of genetic variation

According to ENM, precipitation in March (43.2% contribution) and August (32.9% contribution) and collinear factors are crucial determinants of the current distribution of *A. morrisonense*. Early spring and midsummer are the peak of the flowering and deciduous seasons, respectively. Precipitation in these seasons may affect pollen dispersal, the onset of vegetation growth, and nutrient accumulation before winter (Chang et al., 2013; Liu et al., 2017). Precipitation differences with altitude enhance the environmental heterogeneity among populations. Furthermore, the negative correlation between genetic and environmental distances implies phylogenetic overdispersion (Beltrán et al., 2012; Emerson & Gillespie, 2008; Pianka, 1974). This may correspond to recent stronger population migrations from high to low altitudes. The higher mountains restrict recent gene flow from low-altitude populations to high altitude, indicating the difficulties for pollen and seed ascending dispersal. Species with broader fundamental climate niches have a greater opportunity for colonization because novel environments may not necessarily require an evolutionary response (Dellinger et al., 2016; Prentis et al., 2008). Pre-adaptive genes of *A. morrisonense* might have spread by gene flow along environmental gradients after population establishment (e.g. Hahn et al., 2012; Matter et al., 2013).

5 | CONCLUSION

Space constraints and local climate heterogeneity are two factors structuring population genetics within an island. The Massenerhebung effect may explain the range-size reduction in peripheral populations in the north and south Taiwan due to vegetation compression. In addition to finding neutral colonization processes or edge effects, this study is the first to demonstrate a case of Massenerhebung-driven genetic patterns in Taiwan, with evidence of post-HTO expansion from central mountain populations and a change in chloroplast genetic diversity along latitude and altitude. However, frequent long-distance pollen flow and the rapid evolutionary rate of nuclear SSRs counterbalanced the drift effect of small populations, thus homogenizing the genetic differentiation among populations. To conserve genetic diversity, low- and high-elevation populations warrant different approaches. For the former, the lower genetic connectivity and genetic supplements from distinct environments signify the importance of dispersal corridors between core and marginal populations. For the latter, alpine refugia retain ancestral polymorphisms and hence should be targeted for habitat preservation.

This study of the Massenerhebung effect on the genetics of a montane maple on an island revealed that (1) the altitudinal distribution and the relative distance to mountain edge are determinants of genetic diversity for montane plants; (2) past and current climates determine the source of genetic variation and influence the distribution range; (3) spacious areas at high elevations effectively prompt long-distance dispersal and genetic admixture among relict populations (refugia); (4) mountains function as barriers that interrupt long-distance dispersal of seed by low-elevation plants; and (5) the patterns of gene flow associated with mountain barriers implicate different conservation concerns for low- and high-elevation populations. Low-elevation populations were more isolated and prone to diversity loss at the fringes; high-elevation populations contained more ancestral diversity and may play a key role in supplementing genetic diversity. Therefore, populations at different elevations are distinct management units in terms of conservation of genetic diversity and could be generalized to the species distribution across a wide altitudinal range. Although restricted to an island, this study also provides insights into changes in the range and genetic diversity of continental vegetation under climate change.

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DATA AVAILABILITY STATEMENT

The EST-SSR genotypes have been deposited as Supplementary Data and also uploaded in Dryad with https://doi.org/10.5061/dryad.ghx3fbbng. The obtained cpDNA sequences have been deposited in GenBank (accession numbers: MK258201-MK258681).

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REFERENCES


**BIOSKETCH**

Jui-Tse Chang is interested in the role ecological factors play on the microevolutionary processes, especially for the plants among the heterogeneous (sky) island landscape. Min-Xin Luo’s research interests include the population genetics and the trait evolution of island species after colonization. Our laboratory also focuses on landscape genetics and phylogeography, species diversification with trait evolution, and population and community ecology.

Authors’ contribution: PCL conceived and designed the project. JTC, MXL, and PCL interpreted the data and wrote the manuscript; MXL, HPL, and YTT collected field samples and performed laboratory experiments; HPL, YTT, and PCL performed statistical analyses; and JTC, MXL, and PCL critically reviewed and provided constructive suggestions on the first draft. All authors read and approved the final manuscript.

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