Genetic variation characterization of the boreal tree *Acer ginnala* population in response to environmental change of Northern China

Yiling Wang

Shanxi Normal University <https://orcid.org/0000-0002-0358-0851>

Jiahui Wu

Shanxi Normal University

Zhi Wang

Shanxi Normal University

Hang Ye

Shanxi Normal University

Huimin Hou

Shanxi Normal University

Yue Gao

Shanxi Normal University

Wei Han

Shanxi Normal University

Wenming Ru

Changzhi University

Genlou Sun (✉ genlou.sun@smu.ca)

Research article

Keywords: *Acer ginnala*, genetic differentiation, climate factors, environmental heterogeneity

Posted Date: September 7th, 2019

DOI: <https://doi.org/10.21203/rs.2.14043/v1>

License: This work is licensed under a Creative Commons Attribution 4.0 International License. [Read Full License](#)

Abstract

Background: *Acer ginnala* is a deciduous shrub/small tree that primarily distributed across the northern regions of China. It comprises a foundation species in many terrestrial ecosystems and has significant ornamental and economic value. Owing to its increased use as an economic resource, overexploitation and environmental destruction have resulted in the vulnerability of this species. Thus, the elucidation of the genetic differentiation and influence of environmental factors on *A. ginnala* is very critical for its management and future utilization strategies.

Results: Our results revealed that high genetic variation occurred in *A. ginnala* species while low genetic diversity was observed at the population level. Most differentiation has found among populations. A significant correlation existed between genetic and environmental distances. Seven climate variables (bio1, bio2, bio3, bio4, bio13, bio15 and bio18) might explain the substantial levels of genetic variation (> 40%) in populations. The most suitable areas of this species appeared in Shaanxi, Shanxi, Anhui Provinces, and Northeastern China based on ENM results. Compared to the last interglacial (LIG) period, *A. ginnala* migrated toward Northern and Northeastern China, and extended to the most suitable areas during the last glacial maximum (LGM) period. Shanxi and Anhui Provinces might have served as refugium owing to their relatively high genetic variation.

Conclusions: Low genetic diversity at the population level that may be the source of its vulnerability. Climate heterogeneity would play an important role in the pattern of genetic differentiation in *A. ginnala* populations. The *A. ginnala* population was isolated by a heterogeneous climate and subsequently began to adapt to local selection processes resulted in high genetic divergence.

Background

Genetic diversity and variation are manifested through phenotypic, chromosomal, and proteomic variations, which are revealed particularly through spatio-temporal environmental heterogeneity. These exist as evolutionarily viable units to adapt to changing environmental conditions over protracted temporal scales [1–3]. Investigating the genetic diversity and extent of genetic differentiation within/between populations, while estimating the impact of environmental factors and understanding the processes that maintain these variations are very useful toward gaining deeper insights into evolutionary history. Further, these genetic resources are critical for the prudent formulation of conservation, management and utilization strategies [1–2, 4–6].

Acer ginnala (Aceraceae) is a deciduous shrub/small tree that has monoecious and anemophilous pollination and an outcrossing breeding system [7–9]. It is a foundation species in many terrestrial ecosystems, distributing in Korea, Japan, Russia, Siberia, and China [8]. In China, this species is primarily distributed in the northern regions, including Inner Mongolia, Hebei, Henan, Shanxi, and Anhui provinces. It is able to grow on cloudy slopes, gullies and valleys, and occupies a wide ecological range due to high adaptability and cold resistance [8]. Considering its ecological benefits, such as low light requirements and anti-chimney growth, *A. ginnala* is often employed for precise greening plant landscaping worldwide [8]. The leaves of *A. ginnala* also have important economic value as the abundant gallic acid within them is not only used for making dyes and ink, but also keeps the leaves fresh, which are UV radiation resistant and uptake heavy metals for environmental remediation [10–13]. Galloyl derivatives extracted from this species have potential as a functional material or novel herbal medicine for the treatment of diabetes mellitus [14]. This elegant and beautiful maple with its upright branching structure has become an important ornamental plant in many cities [7, 8]. However, the increased use of this plant as an economic resource has accelerated the degradation of *A. ginnala* populations to the point that this species has been listed as a vulnerable in a recent nationwide biodiversity report [15].

Previous studies on *A. ginnala* have focused primarily on its physiological characteristics [16–18], tissue culture [19], cultivation management [8], population structure and space pattern [20], community characteristics [21], and secondary metabolites [11, 13]. Its genetic diversity and differentiation were examined along an altitude gradient at Qiliyu in Shanxi Province. In Qiliyu, significant differences in phenotypic variation occurred between and within populations along an altitude gradient, where high phenotypic diversity was found within *A. ginnala* populations. The variation within -populations comprised a majority of the total phenotypic variation [22]. The genetic diversity and structure of *A. ginnala* at different elevation were also estimated in Qiliyu of Shanxi Province using inter-simple sequence repeat (ISSR) markers and a high genetic diversity was found in this species. The level of genetic variation of the studied populations was observed to increase along an elevation gradient. The genetic variation between populations was less than that within populations [23]. Although these studies revealed the level of genetic diversity in *A. ginnala*, they were conducted using a small number of individuals from a small-scale district; thus, the results provided very limited information on the genetic diversity and variations of this species. The extent and pattern of genetic differentiation of *A. ginnala* at relatively wide geographic scales remain

unknown. Being an important element of the forest community in northern regions of China, knowledge of genetic variation *A. ginnala* may reveal the evolutionary history and existing factors associated with this plant species [24–26]. Therefore, a comprehensive analysis of the genetic variation of *A. ginnala* may be invaluable, not only for the identification and development of this species, but also for its sustainable conservation and commercial utilization.

For this study, we presented the first investigation of the genetic variation of *A. ginnala* across a wide range in China. The main objectives were to: estimate the genetic variability of *A. ginnala* populations and geographical groups; analyze the genetic structures and relationships of *A. ginnala* populations; verify the potential influences of spatial and environmental factors on detected population differentiation patterns. The combined analysis of molecular markers and eco-geographical data provided beneficial data for the utilization and conservation of this wild plant germplasm.

Results

Genetic variation of *A. ginnala* populations

A total of 170 bands were amplified with the sequence-related amplified polymorphism (SRAP) marker, and 100% of the bands were polymorphic. For the simple sequence repeats (SSR) markers, there were 177 polymorphic loci in 179 putative genetic loci, with the percentage of polymorphic bands (*PPB*) being 98.99%. According to the SRAP markers, the HHG population had the highest genetic diversity, followed by QLY and BYS. Based on the SSR markers, the highest genetic diversity was present in the PQG population, followed by XTS and BYS (Table 1).

At the species level, *A. ginnala* exhibited a high level of genetic diversity using the two types of markers ($I_{SSR} = 0.561$, $I_{SRAP} = 0.5044$; $He_{SSR} = 0.384$, $He_{SRAP} = 0.3366$), which was higher than the mean values at the population level ($I_{SSR} = 0.086$, $I_{SRAP} = 0.057$; $He_{SSR} = 0.056$, $He_{SRAP} = 0.038$) (Table 1).

Through the STURCTURE results, we further analyzed the level of genetic diversity of the different groups. We combined two types of markers, Group I presented a relative genetic diversity, where the Shannon's Information index I was 0.087_{SSR} and 0.059_{SRAP} , and the expected heterozygosity He was 0.056_{SSR} and 0.039_{SRAP} , respectively (Table 1), following Group III and Group II (Table 1).

To further elucidate the relationships between the populations, a cluster analysis was implemented. The dendrogram constructed from the SRAP markers divided the 19 populations into three main clusters (Fig. 1A). Similar results were obtained with the SSR markers (Fig. 1B). Within these three clusters, eight populations (BDG, HJG, YDS, PQG, QLY, HHG, XTS, and JMLC) from Shanxi Province were gathered into a cluster. Three populations (WCLC, FZL, and TTZ) from Anhui Province formed a group, whereas the eight other populations (SFS, MLG, TBD, TBS, BYSM LJL, LJS, and LTG) from Beijing, Inner Mongolia, and Henan Provinces were clustered together.

To reveal the patterns of genetic distribution of this species, we performed a population structure analysis using STURCTURE. The STRUCTURE results suggested that the best grouping number (K) was based on the ΔK , where all of the populations were divided into three groups, which was consistent with the cluster analysis (Fig. 2). Additionally, there were some admixed individuals among populations, which indicated that gene exchange occurred between them.

With SRAP markers, AMOVA analysis revealed that 88% ($\Phi_{ST\ SRAP} = 0.88$) of the total genetic variation was found between the populations ($P = 0.01$), whereas the remaining 12% of the total variation occurred within the populations (Table 2). According to the SSR markers, the genetic differentiation between the populations was 84% ($\Phi_{ST\ SSR} = 0.84$, $P = 0.01$), indicating that 16% of the total variance occurred within the populations. The two markers indicated a high level of interpopulation genetic differentiation and low level of intrapopulation genetic differentiation in *A. ginnala* (Table 2). Among the different groups, the variation was ~ 40% ($\Phi_{ST\ SSR} = 0.40$, $\Phi_{ST\ SRAP} = 0.42$, $P = 0.01$) of the total variation, while there was ~ 60% variation within the groups (Table 2).

In the DAPC analysis, which employed one discriminant function to distinguish five principal components (PCs), three groups were present on the two main axes and a scatter plot of the discriminant analysis (Fig. 3). Every cluster was clearly differentiated using the two main DA eigenvalues and were represented according the provinces of origin. The DAPC results were similar to the STRUCTURE results; however, it was possible to assign admixed individuals to multiple clusters [27].

Predicted spatial distribution areas

Within the 19 bioclimative variables, seven variables were selected. They were bio1 (Annual Mean Temperature), bio2 (Mean Diurnal Range), bio3 (Isothermality), bio4 (Temperature Seasonality), bio13 (Precipitation of Wettest Month), bio15 (Precipitation Seasonality), and bio18 (Precipitation of Warmest Quarter). Among these seven bioclimatic variables, the first four (bio1, bio2, bio3, and bio4) were associated with the temperature dimension, while the last three (bio13, bio15, and bio18) were associated with the precipitation dimension. The explanatory percentage of the first two PCs of the temperature dimension was estimated to be higher than that of the precipitation dimension, which suggested that the temperature might be more relevant in explaining the geographic distribution.

Ecological niche modeling (ENM) was further employed to predict the suitable distributions of *A. ginnala*, as well as to examine the key climatic variables in the prediction. Distribution models showed high discrimination performance (Fig. 4). The cross-validation area under the curve (AUC) value for all models was 0.989, indicating that 98.9% of the records were correctly predicted.

The ranges predicted by the seven bioclimatic variables (bio1, bio2, bio3, bio4, bio13, bio15, and bio18) were roughly consistent with the currently known distributions (Fig. 4A). The large areas of Shanxi and Shaanxi Provinces were high suitable regions for *A. ginnala*. Some areas of Jiangsu, Anhui, and Hubei were also the most suitable habitat for this species. Aside from these areas, there were small regions Northeast China that were suitable for the growth of *A. ginnala*.

In LIG, the potential distribution range expanded, compared with the current distribution. The most suitable areas (> 0.50) in Northeast China disappeared (Fig. 4B). The additional most suitable areas still existed and their extent was broader than currently. Compared with the LIG, the most suitable areas (> 0.50) increased significantly during the LGM, particularly in Shanxi and Shaanxi Provinces (Fig. 4 C and D). There were large suitable areas in the southern portions of Shanxi and Shaanxi Provinces. Moreover, some of the most suitable areas appeared in the Ningxia Autonomous Region. In Northeastern China, the most suitable areas were also expanded compared with that of the present day and LIG.

Influence of environmental factors

To assess whether geographic or environmental differences drove genetic divergence between populations, isolation-by-distance (IBD) and isolation-by-environment (IBE) tests were conducted using the Mantel test. The Spearman correlation showed no significant association between geographic and environmental distances ($\rho_{\text{SRAP}} = -0.1532$, $P = 0.284$; $\rho_{\text{SSR}} = -0.0133$, $P = 0.474$), or between genetic and geographic distances ($\rho_{\text{SRAP}} = 0.1943$, $P = 0.051$; $\rho_{\text{SSR}} = 0.1549$, $P = 0.125$). However, a significant relationship between genetic and environmental distances was found ($\rho_{\text{SRAP}} = 0.4068$, $P = 0.001$; $\rho_{\text{SSR}} = 0.2647$, $P = 0.02$). The partial Mantel test did not detect a significant correlation between genetic and geographic distance when conditioning on the environmental effect ($\rho_{\text{SRAP}} = 0.2187$, $P = 0.307$; $\rho_{\text{SSR}} = 0.1643$, $P = 0.101$). Nevertheless, there was a significant association between genetic and environmental distances, when the geographic distance was considered as a covariate in the partial Mantel test ($\rho_{\text{SRAP}} = 0.2187$, $P = 0.037$; $\rho_{\text{SSR}} = 0.2701$, $P = 0.014$). In terms of the joint effects of geographic and environmental distances, the geographic distance did not have an impact, while the environmental distance did impact the genetic distance significantly ($r_{\text{SRAP}}^2 = 0.1686$, $\beta_{\text{geo}} = 0.4709$, $P = 0.052$, $\beta_{\text{env}} = 0.3865$, $P = 0.001$; $r_{\text{SSR}}^2 = 0.1344$, $\beta_{\text{geo}} = 0.2847$, $P = 0.215$, $\beta_{\text{env}} = 0.1728$, $P = 0.003$). These results revealed that the genetic variation, or gene flow, of the populations were linearly correlated with climatic differentiation, but not geographic differentiation.

When conditioned on the geographic distribution, we found that more 40% of the variation (45.71% by SRAP data, 40.42% by SSR data) could be explained by climatic variables (Table 3). The ANOVA further indicated that seven predictors (bio1, bio2, bio3, bio4, bio13, bio15, and bio18) significantly explained the genetic components of the population ($P < 0.0001$), and that bio2 and bio3 had the highest explanatory proportions for predicting the genetic variation of the population. Three bioclimatic variables (bio1, bio2, and bio3) of the temperature dimension had significant F statistics (adjusted $R^2 = 0.0259$, 0.0400 , and 0.0386 , $P < 0.05$, Table 3) through SRAP data. According to the SSR data, two temperature variables (bio1 and bio3) had significant F statistics (adjusted $R^2 = 0.0067$ and 0.0065 , $P < 0.05$, Table 4). Only three variables (bio3, bio4, and bio13) were significantly correlated with the ordination axis1, while the other four variables (bio1, bio2, bio15, and bio18) were significantly correlated with axis 2 of dbRDA (Table 3).

Discussion

Population genetic variation of *A. ginnala*

A. ginnala contained a high genetic diversity at the species level (Table 1). Genetic diversity is the culmination of the long-term evolution of species or populations [28–29], which might be affected by multiple factors, such as the size of the geographical range, genetic exchange, environmental conditions, and species characteristics [30–31]. As relates to geographical distribution, *A. ginnala* has a relatively extensive distribution area, from Southwest to Northeast China. Within a larger distribution area, species can generally possess higher genetic diversity [31]. Being a perennial tree, longlived *A. ginnala* could provide more opportunities to accumulate mutations or specialized microstructures in different populations. Further, genetic diversity at the species level is also related to the breeding system, where *A. ginnala* is an insect-pollinated species [32–33] through sexual propagation through seeds. These reproductive characteristics have significance for maintaining genetic diversity in populations [31], which likely resulted in higher genetic diversity in this species.

However, genetic diversity at the population level was relatively lower (Table 1), which might have been initiated through two possible scenarios. Firstly, the inbreeding of plants can lower genetic diversity, which results from a reduction in population size, and leads to inbreeding depression [31, 34]. Owing to human disturbance and destruction, *A. ginnala* population continued to dwindle, becoming smaller than previously. A degree of inbreeding of this species population could reduce plant fitness, while promoting a further drop in abundance. Although *A. ginnal* is primarily insect-pollinated, self-pollination can occur. There are reports that some plants have suffered from a general decline in pollinator insects; a phenomenon referred to a pollination crises [35–37]. From the spring season, when *A. ginnala* flowers, one might expect an elevated rate of self-pollination due to the presumable lack of effective pollinators [31]. Secondly, based on our field investigations, more adults and fewer seedlings were found in *A. ginnala* communities. Those populations might be exposed to greater genetic drift effects, resulting in the observed low level of genetic diversity. Aside from anthropogenic factors, climate change may also be considered as a factor in the decline of this species. Low levels of genetic diversity might restrict the ability of a population to respond to changing environmental conditions [1, 31, 38]. Environmental heterogeneity at an over-all scale among *A. ginnala* populations was suggested by the Mantel test and Spearman correlation between genetic and environmental distances. Habitat isolation or immigrant non-viability may have arisen from the local optimal for the environment; limiting the survival and reproduction of migrants [1, 39–40].

Most genetic variation (> 80%) was observed between populations, whereas ~10% of the differentiation existed within populations. This significant genetic variation among populations could be related to low gene flow ($N_{m\text{ SSR}} = 0.085$, $N_{m\text{ SRAP}} = 0.063$). The seeds of *A. ginnala* have a large wing and can be dispersed by the wind; the potential for exchange may be more sensitive to geographic barriers than that of wind-pollinated and wind-dispersed species. In the *A. ginnala* distribution areas, the discontinuous distribution of mountains, such as Taihang Mountains and Wuling Mountains, provide a complex landscape that likely blocks gene exchange among between populations [41–42]. These factors presumably isolated populations; thus, promoting population differentiation by limiting the potential for gene exchange. Interestingly, the Mantel test and Spearman correlation revealed no significant relationship between genetic and geographical distances. High genetic variation values (Table 2) pointed to habitat fragmentation and the presence of barriers to gene flow between populations. For *A. ginnala*, gene flow might also be obstructed by the pollination method. Being an insect pollinated species, pollen-mediated gene flow was generally limited, as the range of most pollinators can be less than 20 km [31], and they tend to visit neighboring plants [43]. *A. ginnala* populations may be geographically and/or ecologically too isolated to be connected via pollen exchange. The considerable genetic differences between populations might also be attributed to the absence of generative reproduction [44–45]. Field observations found that some populations ruled out generative reproduction, due to the absence of flowering individuals, or their inability to produce fruit. The above factors might have inhibited gene flow and exacerbated genetic differences.

STRUCTURE, UPGMA, and DPAC analyses suggested that all of the studied populations were divided into three clusters (Fig. 1, 2, and 3). The observed genetic differences between the three groups were relatively large and statistically significant. Low levels of migration between populations was reported above, thus efficient genetic exchange between the populations studied may be excluded. Discontinuous mountains and/or climate heterogeneity can segment large populations into multiple-small fragmented populations, and enhance differentiation between populations and groups [42].

Population structure and dynamic history

Historical events leave an indelible mark on patterns of genetic diversity found within plant species [46–47]. As hypothesized, Central and Western populations in China harbored relatively higher levels of genetic variation compared to Eastern populations. Further, the former areas served as large LGM refugia for many species in China; mainly boreal and temperate plants [47–49]. For this study, Group

I and III contained relative genetic diversity among all examined populations (Table 1). The Group I populations were located in the North Qinling Mountains and West Taihang Mountains, while the Group III populations were located in the South Qinling Mountains. These mountainous regions comprised areas that were not heavily influenced by the LGM [50]. In general, large portions of Central and Southwestern China served as plant refugia [47, 48], due to their relatively stable climatic conditions [51]. All populations in the above-mentioned areas were genetically more variable (Table 1).

The ENM results provided a historical perspective for the interpretation of genetic data. During the LGM period, suitable habitats for *A. ginnala* were mainly in Shaanxi, Shanxi, and Anhui Provinces. Following the LGM period, suitable habitats for *A. ginnala* decreased dramatically in the regions indicated above, particularly in the Shanxi and Anhui provinces, which were regarded as refugia for *A. ginnala* (Fig. 4). Northern China once hosted temperate forests; however, this was replaced by tundra and taiga forests during the LGM period [52]. These temperate forests likely retreated to the South, and below 30°N [47, 53]. Compared with the LIG, *A. ginnala* did not retreat to Southern China, but instead extended toward North and Northeastern China. Data reveals that Northern China was considered to be an important source of postglacial expansion to the Northeastern region of China for many studied temperate forest species [50, 54–57]. In STRUCTURE analysis, there were admixtures of individuals between Group I and Group II, as well as between Group II and Group III, respectively. This result also supported that the northward expansion of *A. ginnala*. Meanwhile, physiographic heterogeneity might have also contributed to the dynamic history of *A. ginnala*. The Northern areas of China are characterized by mountains, isolated hills, and valleys [58–60]. The diversity of this terrain favored the survival of plants within isolated refugia during periods of glaciation [58–61].

Influence of environmental heterogeneity

The genetic divergence of populations should be correlated with both geographic distance and environmental heterogeneity [40]. In the present study, geographic distance was not correlated with environmental distance. A significant correlation was found between genetic and environmental distances by Mantel test and Spearman correlation (Table 3). When considering the combined effects of environmental and geographic distances using MMRR, environmental distance was found to affect genetic distance significantly (Table 3). These results suggested that IBE (Isolation by Environment) might have played an important role in shaping the genetic divergence and adaptive divergence of populations, corresponding to the environmental heterogeneity that occurred for *A. ginnala*.

Seven environmental variables (bio1, bio2, bio3, bio4, bio13, bio15, and bio18) were separated into two categories: temperature and precipitation, and found to be a critical environmental factor that substantially explained the genetic variation of *A. ginnala*. Having significant *F* statistics, three temperature variables (bio1, bio2, and bio3) were the most important environmental factors that influenced adaptive variation in *A. ginnala*. However, the second most important set of environmental factors, including bio4, bio13, bio15, and bio18, could also be important environmental elements that may have played key roles in driving adaptive divergence in this species. Based on dbRDA analysis, three variables (bio3, bio4 and bio13) were significantly correlated with the ordination axis, whereas the other four variables (bio1, bio2, bio15, and bio18) were significantly correlated with axis2.

Temperature and precipitation are frequently found to play prominent roles as selective drivers for adaptive variation in various plant species [40, 62–68]. Being an ecological factor, temperature can cause an increase in genetic divergence. Among four temperature variables, the highest adjusted R^2 value was bio2 (Mean diurnal range), followed by bio3, Isothermality (Table 3). Within the studied populations, each was located in areas under different environment conditions. The maximum of bio2 was 116 in the MLG population, and the minimum was 78 in the FZL population. For bio3, it was from 270 in the BYS population, to 236 in the BDG population. On the other hand, monsoon rainfall may occurred due to the orientation of different mountains (such as Qinling and Taihang Mountains) in the geographical distribution of *A. ginnala* [58–61, 69]. Bio15 had the highest adjusted R^2 value between three major precipitation ranges (Table 3), which is Precipitation seasonality. Therefore, populations that are demographically isolated by environmental climate heterogeneity respond to local selection and may promote genetic divergence among *A. ginnala* populations. It should be noted that rather than individual environmental variables acting independently to shape the distribution patterns of the genetic variation of species, it was most likely that the interdependencies of environmental variables exerted direct and indirect effects on genetic divergence within and between species.

Conclusions

Multiple factors can affect the genetic variation of plant populations. *A. ginnala* in Northern China has high genetic diversity and abundant genetic differentiation at the species level. Nevertheless, the low genetic diversity found at the population level, may be a reason for the vulnerable status of this species. Pollination crises, species characteristics, and extensive geographical range might drive the patterns of genetic variation of *A. ginnala*. Seven climate variables, particularly bio2, bio3, and bio15, can explain the significant degree of genetic variation in these populations. Climatic heterogeneity was suggested as a critical driver leading to population differentiation. For this species, isolated populations can respond to the local selection that caused by heterogeneous climate rather than the geographical barriers resulting from mountain ranges. During the LGM period, *A. ginnala* migrated toward Northern and Northeastern China, where the most suitable areas appeared in Shaanxi, Shanxi and Anhui Provinces. Through relatively high genetic differentiation *A. ginnala* found refugia in the areas of Shanxi and Anhui Provinces and subsequently began to adapt to the warm temperate continental climate.

Methods

Sample collection

Our study was conducted in accordance with the laws of the People's Republic of China, and field collection was approved by Chinese Government. All researchers received permission letters from the College of Life Science, Shanxi Normal University, to collect the samples. The samples were taxonomically identified by Junxia Su (Associate Professor of systematic botany) at the Shanxi Normal University. The voucher specimens were deposited in the herbarium of College of Life Science, Shanxi Normal University (No: 20150105001–20150105010; 20170105001–20170105020).

Nineteen *A. ginnala* populations were collected based on their geographical distribution (Table 4, Fig. 5), which covered almost its entire distribution across Northern China. Among these populations, 20–30 individuals were sampled from each population, with a minimum distance of 30 m between any two individuals. Healthy young leaves were collected and immediately preserved with silica gel for DNA extraction, with the sampled populations being primarily from six provinces or regions. Eight *A. ginnala* populations were located in Shanxi Province, six in Henan Province, three in Anhui Province, one in Beijing City, and one in Inner Mongolia. The longitude, latitude, and altitude of each sample site were quantified using a global position system.

PCR amplification

Genomic DNA from the sampled individuals was extracted using the modified CTAB method [70]. The quality of the DNA was determined using an ultraviolet spectrophotometer and the electrophoresis on 0.8 % agarose gel [71]. Following extraction, the DNA was stored at –20 °C for further use.

Ten pairs of polymorphic SSR primers [42] with distinct bands and high stability were selected to amplify all individuals of the *A. ginnala* populations. The 20 µL reaction contained 20 ng/L DNA templates, 2 µL Mg²⁺, 2.5 µL dNTPs, 2 µL each primer, 1 µL *Taq* DNA polymerase, and double-distilled water. The reaction procedure included 95 °C modification (5 min), 94 °C denaturation (30 s), 55 (56, 57, 58) °C annealing (45 s), 72 °C extension (65 s), 36 cycles, and a final extension for 9 min at 72 °C.

For SRAP markers, ten pairs of primers [72] with clear and stable bands were selected. The 20 µL PCR reaction system contained 50 ng/L of DNA templates, 2 µL 10 × PCR buffer, 2.5 µL dNTPs (0.5 µmol/L), 2 µL each primer (0.2 µmol/L), 1 µL *Taq* DNA polymerase (0.08 U/µL; Takara, Shiga, Japan), and 12.5 µL double-distilled water. The reaction procedure included initial denaturation at 94 °C (5 min), followed by 36 cycles at 94 °C (40 s), annealing at T_m temperature under different primers (25 s), extension at 72 °C (65 s), and final extension at 72 °C (10 min).

The PCR amplified products were separated by polyacrylamide gel electrophoresis (12 %), with an electrophoresis time of ~ 2.5 h at 200 V, and the fragments were visualized by silver staining.

Data analysis

Distinct and reproducible bands of each marker were scored as either 1 (present) or 0 (absent). The genetic diversity parameters, such as the percentage of polymorphic bands (*PPB*), Shannon's Information index (*I*) and expected heterozygosity (*He*) were calculated using GENALEX [73].

STRUCTURE analysis [74], underlying the model Bayesian methods, was often used to delineate the clusters of genetically similar individuals. The presumed number of populations (K) was set from 2 to 19. For each run, the initial burn-in period was set to 100,000 with 500,000 Monte Carlo Markov Chain interactions. Ten independent runs were completed for each K value. The number of populations was determined using the DeltaK method (ΔK statistic).

According to the STRUCTRE results, the hierarchical analysis of molecular variance (AMOVA) was performed in GENALEX [73] to elucidate the extent of genetic variation between and within populations or groups.

Based on Nei's genetic distance, the phylogenetic relationship of populations was constructed by the unweighted pair-group method of arithmetic averages (UPGMA) using Molecular Evolutionary Genetics Analysis MEGA software [75].

To further confirm the cluster analysis and population genetic structure, a discriminant analysis of principal components (DAPC) was conducted using the R package ADEGENET [76]. For this study, the genetic data was initially transformed according Principal Component Analysis (PCA). These components explained most of the genetic variation, which was then used to perform linear Discriminant Analysis (DA), which provided variables that described the genetic groups that minimized the genetic variance within populations, while maximizing the variation between populations.

To investigate the influence of the environment on *A. ginnala* variation, we extracted the environmental factors with DIVA-GIS software [77] and determined the key environmental factors by principal component analysis with SPSS. Variables with a high variance inflation factor (VIF) [78–79] were removed to reduce multicollinearity. Additionally, the VIF values of all the remaining variables were < 10 , where finally seven bioclimatic variables were retained for further analyses.

To predict the potential habitats of this plant, species distribution models were developed under the maximum entropy model implemented in MAXENT [80] and the R package DISMO [81]. The topographical data from LIG (120,000–140,000 years BP) and current climate data was downloaded from the WorldClim website (<http://www.worldclim.org>), whereas LGM (21,000 years BP) data were obtained from the Model for Interdisciplinary Research on Climate (MIROC) (<https://pmip2.lsce.ipsl.fr/>) and the Community Climate System Model (CCSM) [82].

The Mantel test of Spearman correlation [83] was performed between genetic, geographic, and environmental (climatic) distances, for testing the geographic distance and environmental differences that affected genetic variation. Pairwise F_{ST} was calculated between populations based on Nei's [84] method, then using $F_{ST} / (1 - F_{ST})$ to estimate the genetic distance metric. Geographic distances were estimated using Euclidean distances, according to three dimensional factors (latitudes, longitudes, and altitudes). Environmental distances were also calculated using Euclidean distances, with the variables having high contribution rate in PCA. A partial Mantel test between genetic and environmental distances controlled for the geographic distance was also performed. Further, multiple matrix regression with randomization (MMRR) [85] was performed to test whether genetic distances responded to variations in geographic and/or environmental distances. The joint impacts of both geographic and environmental distances on the genetic distances was also examined. Regression coefficients of the Mantel test (ρ) and MMRR (β), and their significance, were determined based on 9,999 random permutations.

Finally, partial distance-based redundancy analyses (partial dbRDA) were performed to explain the effects of climatic variables on the genetic distribution of populations. MLGR was employed to test the effects of bioclimatic variables on populations. The type-II ANOVA Wald χ^2 test was used to test the significance of each bioclimatic factor.

Abbreviations

CTAB: Cetyl trimethyl ammonium bromide; SSR: Simple sequence repeats; SRAP: Sequence-related amplified polymorphism; H_e : expected heterozygosity; I : Shannon's information index; PPB : the percentage of polymorphic bands; AMOVA: Analysis of molecular variance; UPGMA: unweighted pair-group method of arithmetic averages; DAPC: discriminant analysis of principal components; PCA: Principal Component Analysis; DA: linear Discriminant Analysis; VIF: variance inflation factor; LIG: last interglacial; LGM: last glacial period; MIROC: Interdisciplinary Research on Climate; CCSM: Community Climate System Model; MMRR: multiple matrix regression with randomization; dbRDA: distance-based redundancy analyses; ANOVA: Analysis of variance; IBD: isolation-by-distance; IBE: isolation-by-environment

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors approved the manuscript and consent for publication.

Availability of data and materials

All data used are available upon request.

Competing interests

The authors declare that no competing interest exist.

Funding

This work was financially supported by Chinese National Natural Science Foundation (31970358 to YW) and Hundred Talents Program of Shanxi Province (to GS).

Authors' contributions

YW, WR and GS conceived the ideas; YW wrote the manuscript; JW, HH, HY and YG analyzed the data; ZW and WH collected the data; GS and WR reviewed and edited the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

The authors thank Junxia Su for her assistance with the sample identification. This study was supported by Chinese National Natural Science Foundation (31970358 to YW) and Hundred Talents Program of Shanxi Province (to GS).

Author details

¹College of Life Science, Shanxi Normal University, Linfen 041000, People's Republic of China.²Changzhi University, Changzhi 046011, People's Republic of China.³Department of Biology, Saint Mary's University, Halifax B3H3C3, Canada.

References

1. Yang S, Xue S, Kang W, Qian Z, Yi Z. Genetic diversity and population structure of *Miscanthus lutarioriparius*, an endemic plant of China. *PLoS ONE*. 2019; 14(2): e0211471.
2. Zhang Y, Zhang XJ, Chen X, Sun W, Li J. Genetic diversity and structure of tea plant in Qinba area in China by three types of molecular markers. *Hereditas*. 2018; 155: 22.
3. Sreekanth PM, Balasundaran M, Nazeem PA, Suma TB. Genetic diversity of nine natural *Tectona grandis* L.f. populations of the Western Ghats in Southern India. *Conserv Genet*. 2012; 13: 1409–19.
4. Cohen JI, Williams JT, Plucknett D, Shands H. Ex situ conservation of plant genetic resources: Global development and environmental concerns. *Science*. 1991; 253: 866–72.
5. Li M, Zhao Z, Miao XJ, Zhou JJ. Genetic diversity and population structure of Siberian apricot (*Prunus sibirica* L.) in China. *Int J Mol Sci*. 2014; 15: 377–400.
6. Bao W, Wuyun T, Li T, Liu H, Jiang Z, Zhu X, Du H, Bai Y. Genetic diversity and population structure of *Prunus mira* (Koehne) from the Tibet plateau in China and recommended conservation strategies. *PLoS ONE*. 2017; 12(11): e0188685.

7. Tian X, Jin QJ, Li DZ, Wei ZX, Xu TZ. Pollen morphology of Aceraceae and its systematic implication. *Acta Bot Yunnan*. 2001; 23(4): 457–65.
8. Zhang XS. Vegetation regionalization map of China. Geological Publishing House, Beijing, China. 2007.
9. Huang D, Wang J, Li DL. Biological characteristics and planting technology of *Acer ginnala* Maxim. *Modren Agri Sci*. 2009; 16(4): 112–14.
10. Zhou Y, Zhang ZQ, Zhang JJ, Gu JQ, Gu XZ, Xu GL. Inhibiting effects of 3 antioxidants on contamination and browning of tissue culture of *Acer ginnala* Maxim. *Acta Agri Shanghai*. 2007; 23(1): 5–7.
11. Li HY, Song JY, Dong J, Zhan YG. Establishment of callus regeneration system for *Acer ginnala* Maxim and determination of gallic acid in callus. *Chinese Bull Bot*. 2008; 25(2): 212–19.
12. Wang RB, Wang CQ, Liu XL, Li LH. Advance in the research of chemical constituents and medicine and edible function of *Acer ginnala*. *J Anhui Agri Sci*. 2011; 9: 5387–88, 17.
13. Xie YF, Li J, Zou H, Yuan HL. Analysis of polyphenols from the leaves of *Acer ginnala* Maxim by reversed-phase high performance liquid chromatography. *J Ana Sci*. 2011; 27 (4): 443–6.
14. Park KH, Yoon KH, Yin J, Le TT, Ahn HS, Yoon SH, Lee MW. Antioxidative and Anti-Inflammatory Activities of Galloyl Derivatives and Antidiabetic Activities of *Acer ginnala*. *Evid. Based Complement Alternat Med*. 2017; 2017: 6945912.
15. Ma ZH, Zhang MS, Ma CE, Qi YH. Cultivation technology of economic forest of *Acer ginnala* Maxim. *Spec Ecol Anim Plant*. 2005; 5(28): 22.
16. Wang HJ, Meng YE, Zhao XS, Zhang Q, Li YM, Li XY. Effects of different fertilization levels on growth, photosynthesis and physiological characteristics of *Acer ginnala*. *Plant Nutri Fert Sci*. 2008; 14(5): 1023–6.
17. Li YC, Liang YL, Wang QC Influence of cadmium on photosynthesis and chlorophyll fluorescence characteristics in *Acer ginnala* and *Acer mono*. *Acta Bot Boreal Occident Sin* 2009; 29(9): 1881–6.
18. Li YC, Liang YL, Wang QC. Influence of Pb pollution on photosynthesis and chlorophyll fluorescence characteristics in *Acer ginnala* and *Acer mono*. *J Hunan Agri Univ*. 2012; 38 (2): 168–72.
19. Dong J, Zhan YG, Ren J. Kinetics in suspension culture of *Acer ginnala*. *Sci Silv Sin*. 2012; 48 (10): 18–23.
20. Wang YL, Zhang QD, Hao XJ, Yan GQ. Structure and spatial distribution of *Acer ginnala* population in Qiliyu, shanxi. *Acta Bot Boreal-Occident Sin*. 2012; 32(5): 1027–35.
21. Wang YL, Hao XJ, Yan GQ. Community characteristics and species diversity research of *Acer ginnala* in Qiliyu, Shanxi. *Guihaia*. 2012; 32 (3): 326–32.
22. Wang D, Pang CH, Gao YH, Hao XJ, Wang YL. Phenotypic diversity of *Acer ginnala* (Aceraceae) populations at different altitude. *Acta Bot Yunnan*. 2010; 32(2): 117–25.
23. Yan N, Wang D, Gao YH, Hao XJ, Wang YL. Genetic diversity of *Acer ginnala* populations at different elevation in Qiliyu based on ISSR markers. *Sci Silv Sin*. 2010; 46(10): 50–6.
24. Kramer AT, Havens K. Plant conservation genetics in a changing world. *Trends Plant Sci*. 2009; 14: 599–607.
25. Allendorf FW, Luikart G. Conservation and the genetics of populations. Wiley, New York, 2009.
26. Abebe TD, Bauer AM, Léon J. Morphological diversity of Ethiopian barleys (*Hordeum vulgare* L.) in relation to geographic regions and altitudes. *Hereditas*. 2010; 147: 154–64.
27. Gioia T, Logozzo G, Marzario S, Spagnoletti Zeuli P, Gepts P. Evolution of SSR diversity from wild types to U.S. advanced cultivars in the Andean and Mesoamerican domestications of common bean (*Phaseolus vulgaris*). *PLoS ONE*. 2019; 14(1): e0211342.
28. Masmoudi MB, Chaoui L, Topçu NE, Hammami P, Kara MH, Aurelle D. Contrasted levels of genetic diversity in a benthic Mediterranean octocoral: consequences of different demographic histories? *Ecol Evol*. 2016; 6: 8665–78.
29. Li X, Li M, Zhang Z, Pang X, Li Y. De novo transcriptome assembly and population genetic analyses for an endangered Chinese endemic *Acer miaotaiense* (Aceraceae). *Genes*. 2018; 9: 378.
30. Goudarzi F, Hemami M, Rancilhac L, Malekian M, Fakheran S, Elmer KR, Steinfartz S. Geographic separation and genetic differentiation of populations are not coupled with niche differentiation in threatened Kaiser's spotted newt (*Neurergus kaiseri*). *Sci Rep*. 2019; 9: 6239.
31. Szczecińska M, Sramko G, Wołosz K, Sawicki J. Genetic diversity and population structure of the rare and endangered plant species *Pulsatilla patens* (L.) Mill in east central Europe. *PLoS ONE*. 2016; 11(3): e0151730.

32. Matsui K. Pollination ecology of four *Acer* species in Japan with special reference to bee pollinators. *Plant Species Biol.* 1991; 6:117–20.
33. Rosado A, Vera-Vélez R, Cota-Sánchez JH. Floral morphology and reproductive biology in selected maple (*Acer* L.) species (Sapindaceae). *Braz J Bot.* 2018; 41(2): 361–74.
34. Lönn M, Prentice H. Gene diversity and demographic turnover in central and peripheral populations of the perennial herb *Gypsophila fastigiata*. *Oikos.* 2003; 99: 489–98.
35. Kearns CA, Inouye DW, Waser NM. Endangered mutualisms: the conservation of plant-pollinator interactions. *Annu Rev Ecol Evol Syst.* 1998; 29: 83–112.
36. Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science.* 2006; 313: 351–4.
37. Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. Global pollinator declines: trends, impacts and drivers. *Trends Ecol Evol.* 2010; 25: 345–53.
38. Booy G, Hendriks RJJ, Smulders MJM, Van Groenendael JM, Vosman B. Genetic diversity and the survival of populations. *Plant Biol.* 2000; 2: 379–95.
39. Nosil P, Funk DJ, Ortiz-Barrientos D. Divergent selection and heterogeneous genomic divergence. *Mol Ecol.* 2009; 18: 375–402.
40. Shih KM, Chang CT, Chung JD, Chiang YC, Hwang SY. Adaptive genetic divergence despite significant isolation-by-distance in populations of Taiwan Cow-Tail Fir (*Keteleeria davidiana* var. *formosana*). *Front Plant Sci.* 2018; 9: 92.
41. Lu ZX, Wang YH, Peng YH, Korpelainen H, Li CY. Genetic diversity of *Populus cathayana* Rehd. populations in southwestern China revealed by ISSR markers. *Plant Sci.* 2006; 170: 407–12, 71.
42. Liu C, Tsuda Y, Shen H, Hu L, Saito Y, Ide Y. Genetic structure and hierarchical population divergence history of *Acer* mono var. *mono* in South and Northeast China. *PLoS ONE.* 2014; 9(1): e87187.
43. Rasmussen IR, Brodsgaard B. Gene flow inferred from seed dispersal and pollinator behaviour compared to DNA analysis of restriction site variation on patchy population of *Lotus corniculatus* L. *Oecologia.* 1992; 89: 278–83.
44. Šmídová A, Münzbergová Z, Plačková I. Genetic diversity of a relict plant species, *Ligularia sibirica* (L.) Cass. (Asteraceae). *Flora.* 2011; 206: 151–7.
45. Ilves A, Lanno K, Sammul M, Tali K. Genetic variability, population size and reproduction potential in *Ligularia sibirica* (L.) populations in Estonia. *Conserv Genet.* 2013; 14: 661–9.
46. Godt MJW, Hamrick JL. Genetic diversity in rare southeastern plants. *Nat Areas J.* 2001; 21: 61–70.
47. Qiu YX, Fu CX, Comes HP. Plant molecular phylogeography in China and adjacent regions: tracing the genetic imprints of Quaternary climate and environmental change in the world's most diverse temperate flora. *Mol Phylogenet Evol.* 2011; 59: 225–44.
48. López-Pujol J, Zhang FM, Sun HQ, Ying TS, Ge S. Centres of plant endemism in China: places for survival or for speciation? *J Biogeogr.* 2011; 38: 1267–80.
49. Tian HZ, Han LX, Zhang JL, Li XL, Kawahara T, Yukawa T, López-Pujol J, Kumar P, Chung MG, Chung MY. Genetic diversity in the endangered terrestrial orchid *Cypripedium japonicum* in East Asia: insights into population history and implications for conservation. *Sci Rep.* 2018; 8: 6467.
50. Bai WN, Liao WJ, Zhang DY. Nuclear and chloroplast DNA phylogeography reveal two refuge areas with asymmetrical gene flow in a temperate walnut tree from East Asia. *New Phytol.* 2010; 188: 892–901.
51. Tian ZP, Jiang DB. Revisiting last glacial maximum climate over China and East Asian monsoon using PMIP3 simulations. *Palaeogeogr Palaeoclimatol Palaeoecol.* 2016; 453: 115–26.
52. Wang SH, Bao L, Wang TM, Wang HF, Ge JP. Contrasting genetic patterns between two coexisting *Eleutherococcus* species in northern China. *Ecol Evol.* 2016; 6 (10): 3311–24.
53. Cao X, Herzschuh U, Ni J, Zhao Y, Böhmert T. Spatial and temporal distributions of major tree taxa in eastern continental Asia during the last 22,000 years. *Holocene.* 2015; 25: 79–91.
54. Hu LJ, Uchiyama K, Shen HL, Saito Y, Tsuda Y, Ide Y. Nuclear DNA microsatellites reveal genetic variation but a lack of phylogeographical structure in an endangered species, *Fraxinus mandshurica*, across North-east China. *Ann Bot.* 2008; 102: 195–205.
55. Bai WN, Wang WT, Zhang DY. Phylogeographic breaks within Asian butternuts indicate the existence of a phytogeographic divide in East Asia. *New Phytol.* 2015; 209: 1757–72.

56. Guo XD, Wang HF, Bao L, Wang TM, Bai WN, Ye JW, Ge JP. Evolutionary history of a widespread tree species *Acer mono* in East Asia. *Ecol Evol.* 2014; 4 (22): 4332–45.
57. Zeng YF, Wang WT, Liao WJ, Wang HF, Zhang DY. Multiple glacial refugia for cool-temperate deciduous trees in northern East Asia: the Mongolian oak as a case study. *Mol Ecol.* 2015; 24: 5676–91.
58. Xue X, Li W, Liu L. The northward shift of Weihe River and the uplift of Qinling Mountains. *J Northeast University.* 2002; 32: 451–4.
59. Zhang Y, Yang N, Ma Y. Neotectonics in the southern part of the Taihang uplift, North China. *J Geomech.* 2003; 9: 313–29.
60. Xue X, Li H, Li Y, Liu H. The new data of the uplifting of Qinling Mountains since the Middle Pleistocene. *Quaternary Sci.* 2004; 24: 82–7.
61. Zhang TC, Comes HP, Sun H. Chloroplast phylogeography of *Terminalia franchetii* (Combretaceae) from the eastern Sino-Himalayan region and its correlation with historical river capture events. *Mol Phylogenet Evol.* 2011; 60: 1–12.
62. Manel S, Poncet BN, Legendre P, Gugerli F, Holderegger R. Common factors drive adaptive genetic variation at different spatial scales in *Arabis alpina*. *Mol Ecol.* 2010; 19: 3824–35.
63. Manel S, Gugerli F, Thuiller W, Alvarez N, Legendre P, Holderegger R, Gielly L, Taberlet P, IntraBioDiv Consortium. Broad scale adaptive genetic variation in alpine plants is driven by temperature and precipitation. *Mol Ecol.* 2012; 21: 3729–38.
64. Bothwell H, Bisbing S, Therkildsen NO, Crawford L, Alvarez N, Holderegger R, Stéphanie M. Identifying genetic signatures of selection in a non-model species, alpine gentian (*Gentiana nivalis* L.), using a landscape genetic approach. *Conser Genet.* 2013; 14: 467–81.
65. Fang JY, Chung JD, Chiang YC, Chang CT, Chen CY, Hwang SY. Divergent selection and local adaptation in disjunct populations of an endangered conifer, *Keteleeria davidiana* var. *formosana* (Pinaceae). *PLoS ONE.* 2013; 8: e70162.
66. Hsieh YC, Chung JD, Wang CN, Chang CT, Chen CY, Hwang SY. Historical connectivity, contemporary isolation and local adaptation in a widespread but discontinuously distributed species endemic to Taiwan, *Rhododendron oldhamii* (Ericaceae). *Heredity.* 2013; 111: 147–56.
67. Huang CL, Chang CT, Huang BH, Chung JD, Chen JH, Chiang YC, Hwang SY. Genetic relationships and ecological divergence in *Salix* species and populations in Taiwan. *Tree Genet Genom.* 2015; 11: 39.
68. Li YL, Xue DX, Zhang BD, Liu JX. Population genomic signatures of genetic structure and environmental selection in the catadromous roughskin sculpin *Trachidermus fasciatus*. *Genome Biol Evol.* 2019; 11(7): 1751–64.
69. Ye JW, Zhang ZK, Wang HF, Bao L, Ge JP. Phylogeography of *Schisandra chinensis* (Magnoliaceae) reveal multiple refugia with ample gene flow in Northeast China. *Front Plant Sci.* 2019; 10: 199.
70. Doyle J, Doyle J. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin.* 1987; 19: 11–5.
71. Sambrook J, Russell D. *Molecular Cloning: A Laboratory Manual*, 3rd edn. Cold Spring Harbor, Cold Spring Harbor Laboratory Press, New York. 2001.
72. Li G, Quiros C. Sequence-related amplified polymorphism (SRAP), a new marker system based on a simple PCR reaction: its application to mapping and gene tagging in *Brassica*. *Theor Appl Genet.* 2001; 103: 455–61.
73. Peakall R, Smouse PE. GenAEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update. *Bioinformatics* 2012; 28(19): 2537–9.
74. Evanno G, Regnaut S, Goudet J. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Mol Ecol.* 2005; 14: 2611–20.
75. Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S. MEGA5: Molecular Evolutionary Genetics Analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol Biol Evol.* 2011; 28: 2731–9.
76. Jombart T, Ahmed I. adegenet 1.3–1: new tools for the analysis of genome-wide SNP data. *Bioinformatics* 2011; 27(21): 3070–1.
77. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol.* 2005; 25: 1965–78.
78. Borcard D, Gillet F, Legendre P. *Numerical Ecology with R*. New York. 2011.
79. Naimi B, Hamm NAS, Groen TA, Skidmore AK, Toxopeus AG. Where is positional uncertainty a problem for species distribution modelling? *Ecography.* 2014; 37: 191–203.
80. Phillips SJ, Dudik M. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography.* 2008; 31: 161–75.

81. Hijmans RJ, Phillips S, Leathwick J, Elith J. Dismo: Species Distribution Modeling. R Package Version 0.8–17. Available online at: [http:// CRAN.R-project.org/package = dismo](http://CRAN.R-project.org/package=dismo). 2013.
82. Collins WD, Bitz CM, Blackmon ML, Bonan GB, Bretherton CS, Carton JA, Chang P, Doney SC, Hack JJ, Henderson TB, Kiehl JT, Large WG, McKenna DS, Santer BD, Smith RD. The Community Climate System Model Version 3 (CCSM3). J Climate. 2006; 19: 2122–43.
83. Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, ÓHara RB, Simpson GL, Solymos P. Vegan: Community Ecology Package. R package version 2.4–4. 2017.
84. Nei M. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics. 1978; 89: 583–90.
85. Wang IJ. Examining the full effects of landscape heterogeneity on spatial genetic variation: a multiple matrix regression approach for quantifying geographic and ecological isolation. Evolution. 2013; 67: 3403–11.

Tables

Table 2 Analysis of molecular variance (AMOVA) within/among *Acer ginnala* populations/ groups

Source	df	SS	MS	Est. Var	%	Φ_{ST}	<i>P</i>
		SSR/SRAP	SSR/SRAP	SSR/SRAP	SSR/SRAP	SSR/SRAP	SSR/SRAP
Among populations	18	9033.59/8103.67	501.87/450.20	30.70/27.63	84/88	0.84/0.88	0.01
Within populations	289	1733.90/1101.43	6.00/3.81	6.00/3.81	16/12		0.01
Total	307	10767.50/9205.10		31.45	100		
Among groups	2	2222.34/3106.76	1111.17/1553.38	15.75/15.08	40/42	0.40/0.44	0.01
Within groups	305	8545.16/6098.34	28.02/20.00	23.63/20.99	60/58		0.01
Total	307	10767.50/9205.10		39.38/36.07			

Table 3 Summary of partial dbRDA, showing the significance of climatic variables (constrained factors) for explaining the variation in the genetic components

	Var (SRAP/SSR)	Proportion(SRAP/SSR)	Adj R^2 (SRAP/SSR)	<i>F</i> (SRAP/SSR)	<i>P</i> (SRAP/SSR)	Axis 1(SRAP/SSR)	Axis 2(SRAP/SSR)
Conditional	0.0122/0.0096	0.2055/0.1713					
Unconstrained	0.0321/0.0333	0.5429/0.5958					
Constrained	0.0271/0.0226	0.4571/0.4042					
bio1	0.0047/0.0035	0.0800/0.0619	0.0259/0.0067	1.6214/1.1431	0.006/0.017	-0.0352/-0.0230	-0.0157/-0.0003
bio2	0.0042/0.0032	0.0933/0.0637	0.0400/0.0087	1.4390/1.0573	0.034/0.151	-0.9014/-0.0723	0.2185/0.7319
bio3	0.0055/0.0035	0.0919/0.0616	0.0386/0.0065	1.8694/1.1417	0.001/0.013	0.4888/-0.1502	0.0370/-0.3001
bio4	0.0033/0.0031	0.0905/0.0599	0.0370/0.0046	1.1418/1.0135	0.210/0.382	0.0077/-0.0002	-0.0019/-0.0034
bio13	0.0029/0.0031	0.0605/0.0588	0.0052/0.0034	0.9943/1.0311	0.438/0.264	0.0533/0.0777	-0.0633/-0.0473
bio15	0.0036/0.0031	0.0891/0.0587	0.0354/0.0034	1.2450/1.0643	0.109/0.116	-0.0622/-0.0296	0.0559/-0.1175
bio18	0.0028/0.0333	0.0679/0.0599	0.0131/0.0047	0.9492/1.0120	0.530/0.420	-0.0258/-0.0296	0.0205/0.0238
Total	0.0592/0.0559	1.0000/1.0000					

Table 4 Sampled populations of *Acer ginnala*

Population	Latitude	Longitude	Altitude/m
BDG, Badaogou, Shanxi	41°08'31.16"	114°08'16.09"	1580
HJG, Haojiagou, Shanxi	38°32'11.08"	111°26'17.16"	1450
HHG, Houhuigou, Shanxi	36°48'01.16"	111°45'05.51"	1200
JMLC, Jiemiaolinchang, Shanxi	36°49'41.07"	111°56'59.42"	1450
PQG, Pangquangou, Shanxi	37°52'17.67"	111°27'12.89"	1800
QLY, Qiliyu, Shanxi	36°36'53.80"	111°14'03.80"	1560
XTS, Xingtangsi, Shanxi	36°25'06.48"	111°46'27.15"	1530
YDS, Yundingshan, Shanxi	37°53'18.38"	111°34'36.70"	1000
SFS, Shangfangshan, Beijing	39°40'35.24"	115°49'17.37"	1420
MLG, Meiligeng, Inner Mongolia	40°40'16.10"	109°26'29.39"	1273
BYS, Baiyunshan, Henan	33°40'13.43"	111°49'50.34"	1479
LJL, Laojieling, Henan	33°37'11.03"	111°43'44.91"	1482
LJS, Laojunshan, Henan	33°44'47.46"	111°38'13.26"	952
LTG, Longtangou, Henan	33°31'01.88"	111°36'43.34"	1560
TBD, Taibaiding, Henan	33°30'50.50"	111°36'40.67"	1440
TBS, Tongbaishan, Henan	32°23'53.80"	113°09'37.80"	960
TTZ, Tiantanzai, Anhui	31°10'17.44"	115°46'04.85"	560
FZL, Foziling, Anhui	31°20'58.53"	116°16'32.11"	700
WCLC, Wochuanlinchang, Anhui	31°14'33.80"	115°50'13.80"	760

Table 1

Due to technical limitations, the table is only available as a download in the supplemental files section

Figures

Figure 1

Cluster analysis of all populations of *Acer ginnala*. A: based on SRAP data. B: based on SSR data

Figure 2

Genetic structure of *Acer ginnala* populations obtained by Bayesian analysis through Structure software

A **B**

Figure 3

Genetic structure of the sampled populations as estimated by discriminant analysis of principal components (DAPC). (Cluster 1: Group I in STRUCTURE, Cluster 2: Group II in STRUCTURE, Cluster 3: Group III in STRUCTURE)

Figure 4

The predicted distribution areas of *Acer ginnala*. A: the current; B: LIG period; C: LGM-CCSM; D: LGM-MIROC. The obtained distribution map of 19 bioclimatic variables was tailored at 1:1000000 onto a Chinese administrative map, which was downloaded from the National Geomatics Center of China (<http://www.ngcc.cn/ngcc/>, NGCC) with a scale of 1:400, edited by ARCGIS 10.4 software Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 5

Sampled distribution sites of *Acer ginnala* populations in this study. Chinese administrative zoning map downloaded from the National Geomatics Center of China (<http://www.ngcc.cn/ngcc/>, NGCC) Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Table1.docx](#)