

1 Multiple glacial refugia across northern and southern China and unexpected patterns  
2 of spatial genetic diversity in *Betula albosinensis*: a widespread temperate deciduous  
3 tree species

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21

22 **Abstract**

23 The central-marginal hypothesis (CMH) predicts high genetic diversity at the species'  
24 geographic centre and low genetic diversity at the species' geographic margins.  
25 However, most studies examining the CMH have neglected potential effect of past  
26 climate. Here, we test six hypotheses, representing effects of past climate and  
27 contemporary range position, for their ability to explain the spatial patterns of genetic  
28 diversity in 37 populations of *Betula albosinensis*. Ecological niche modelling (ENM)  
29 revealed large and continuous suitable habitats in north, southwest and southeast  
30 China during the last glacial maximum (LGM) but a contraction of suitable habitats  
31 since the LGM. Pollen records further confirmed the existence of multiple refugia in  
32 north and south China. The spatial pattern of genetic diversity (i.e., expected  
33 heterozygosity, gene diversity and allele richness) were best explained by distance to  
34 the southern edge and distance to the range edge but also showed longitudinal and  
35 latitudinal gradients. Hypotheses accounting for the effects of climate (climatic  
36 suitability, climatic stability and climatic variability) had comparatively little support.  
37 Our findings show partial support for the CMH and illustrates that the existence of  
38 multiple LGM refugia, and suggests species abundance and past species movement  
39 play a role in shaping genetic diversity across species' ranges.

40 **Keywords** birch, ecological niche modelling, microsatellite markers, pollen record,  
41 refugia

42

43 **Introduction**

44

45 Developing an understanding of the factors shaping the spatial pattern of genetic  
46 diversity in species ranges will be important in predicting the response of populations  
47 to future climate change and informing population conservation. Populations' position  
48 within a species' range has been thought to impact the distribution of genetic diversity  
49 (Eckert, et al. 2008). For example, one of the most commonly tested hypotheses posits  
50 that populations located at the centre of the range tend to have a higher level of  
51 genetic diversity than populations at the geographic margin (Eckert, et al. 2008,  
52 Micheletti and Storfer 2015). This has been referred as the “central-marginal  
53 hypothesis” (CMH), and is thought to result from central populations having higher  
54 population abundance, larger effective population size, stronger gene flow and being  
55 nearer the ecological optimum compared to marginal populations (Sagarin and Gaines  
56 2002). As a consequence, central populations are expected to have higher genetic  
57 diversity within populations and lower genetic differentiation among populations  
58 compared with marginal populations (Eckert, et al. 2008, Swaegers, et al. 2013).

59 However, the “central-marginal hypothesis” is often violated as the underlying pattern  
60 thought to result in the CMH, i.e. high population abundance in the centre of species'  
61 range is not consistently found (Dallas, et al. 2017, Sagarin and Gaines 2002).

62 Historical climate and species' response to the changing climate may also impact the  
63 spatial pattern of genetic diversity. For example, temperature shifts during the glacial  
64 and inter-glacial cycles, especially the last glacial maximum (LGM), often required

65 forest trees to retreat southward into geographically isolated refugia (Hewitt 1999,  
66 2004). As a consequence of this southern retreat and eventual northward  
67 recolonisation, many species exhibit a latitudinal decrease in genetic diversity (Petit,  
68 et al. 1997); although cryptic refugia and admixture zones are known to obscure  
69 simple latitudinal gradients (Petit, et al. 2003). Species' dispersal ability may also  
70 impact the distribution of genetic diversity. For example, species with high dispersal  
71 ability sometimes leave a more obvious genetic gradient than species with low  
72 dispersal ability (Wang, et al. 2016, Ye, et al. 2019).

73 The LGM is thought to have had a more minor impact on the distribution of forest  
74 trees in East Asia compared to other regions in the northern hemisphere (Qian and  
75 Ricklefs 2001, Qiu, et al. 2011). Based on pollen fossil records, it has been proposed  
76 that most temperate forest trees in East Asia retreated to between 25 and 30 N during  
77 the LGM (Qian and Ricklefs 2001). However, an increasing number of  
78 phylogeographic studies indicate the existence of a single refugium in northeast China  
79 (NEC) or multiple isolated refugia in NEC and/or north China (NC) for temperate  
80 cold-tolerant trees (Hou, et al. 2018, Hu, et al. 2008, Liu, et al. 2012, Zeng, et al. 2015,  
81 Zhang, et al. 2005). Several studies indicate an expansion from a single refugium into  
82 northeastern China, resulting in a decrease in genetic diversity with increasing latitude  
83 (Hu, et al. 2008). Other studies favor multiple isolated refugia in north China, despite  
84 a decrease in genetic diversity (Zeng, et al. 2015, Zhang, et al. 2005), or a mixed  
85 pattern of genetic diversity, with populations in NEC showing a latitudinal decrease in  
86 genetic diversity and a latitudinal increase in genetic diversity in south China (Liu, et

87 al. 2012).

88 Hence, understanding the drivers of genetic diversity in species ranges requires  
89 incorporating information about past climate and demographic history in the frame of  
90 CMH. However, to date, only a small number of studies consider past climate  
91 (Gougherty, et al. 2020, Jin, et al. 2020). By doing so, some studies have shown that  
92 the effects of past climate are relatively minor, while others indicate that historical  
93 factors strongly influences the spatial patterns of genetic variation. In addition, many  
94 studies do not disentangle historical and contemporary range position and do not  
95 account for range-wide spatial auto-correlation.

96

97 In this study, we tested whether historical processes affect spatial patterns of genetic  
98 diversity in the context of the CMH in China (Wei, et al. 2016). Using *Betula*  
99 *albosinensis* as our study species, we compared six hypotheses for their ability to  
100 describe the patterns of genetic diversity across 37 populations. *Betula* is an  
101 ecologically important genus that consists of approximately 65 species and subspecies  
102 (Ashburner and McAllister 2016, Wang, et al. 2016), widely distributed across the  
103 Northern Hemisphere. *Betula* species are wind-pollinated and self-incompatible, often  
104 resulting in a high level of genetic diversity within populations (Ashburner and  
105 McAllister 2016). Some *Betula* species are pioneers, colonising new habitats and  
106 providing shelter for other trees.

107

108 Our focal species, *B. albosinensis*, is a deciduous broad-leaved temperate species,

109 growing in mountains at an altitude between 1800~3800m according to our field  
110 observations. In China, it extends from northwestern Yunnan province to northern  
111 Hebei province, between 25° and 40° latitude and between 99° and 116° longitude.  
112 *Betula albosinensis* is a pioneer species and can grow up to 35 meters. Its  
113 regeneration depends on habitat disturbances as evidenced by the observations that  
114 seedlings are only found in open habitats caused by tree gaps (Guo, et al. 2019).

115

116 Here, we used 16 microsatellite markers to investigate the spatial distribution of  
117 genetic diversity of *B. albosinensis*. We used ENM and pollen records to robustly  
118 infer its suitable habitats since the LGM, and based on these paleo reconstructions of  
119 its distribution, we further explored factors impacting the distribution of its population  
120 genetic diversity. The specific questions we sought to address are: (1) Does *B.*  
121 *albosinensis* have multiple LGM refugia in China? (2) Does *B. albosinensis* form  
122 different genetic clusters? (3) What is the spatial distribution of genetic diversity? (4)  
123 What factors impact the spatial distribution of genetic diversity?

124

## 125 **Materials and Methods**

126

### 127 **Field sampling**

128

129 *Betula albosinensis* samples were collected from natural populations over four years  
130 (2016-2019), covering nearly its entire distribution in China. Within each population,

131 samples were chosen at random and separated by at least 20 meters. A GPS system  
132 (UniStrong) was used to record sampling locations. Herbarium specimens were  
133 collected from most individuals and, for a subset of individuals where twigs were out  
134 of our reach, cambial tissue was collected and stored in coffee bags and dried using  
135 silica gel. A total of 815 individuals were collected from 37 populations, with 3-56  
136 individuals sampled from each population (Table S1).

137

### 138 **Species distribution model**

139

140 To predict the potential distribution of *B. albosinensis*, we used occurrence records  
141 from our own field work recorded with a GPS system (UniStrong), and collected  
142 additional occurrence records from the literature published since the year 2000. If *B.*  
143 *albosinensis* was recorded in a particular certain region, but lacked a geographic  
144 coordinate, a random point was selected to represent its occurrence within the region.  
145 To avoid spatial autocorrelation due to geographic aggregation, only one point was  
146 kept every 5 km. A total of 264 points data were obtained and after filtering, 132  
147 records were retained for ecological niche modelling.

148 Nineteen bioclimatic variables were downloaded from WorldClim  
149 (<http://www.worldclim.org>) for the four periods: the Last Glacial Maximum (LGM),  
150 the Middle Holocene (MID), Present (1970-2000) and Future (2050-2070) (Hijmans,  
151 et al. 2005). Present climate variables are derived from monthly mean precipitation  
152 and temperature data from the World Meteorological Station from 1970 to 2000 (Fick

153 and Hijmans 2017). Simulated climate data were selected for the other three periods  
154 under the Community Climate System Model (CCSM4) (Gent, et al. 2011), in which  
155 the data of Representative Concentration Pathways 85 (RCP 85) were selected for  
156 FUTURE climate variables. The current and past distribution of *B. albosinensis* were  
157 estimated based on an ensemble species model, performed using the R package  
158 “BiodiversityR” (Kindt 2018). We selected six bioclimatic variables that lacked strong  
159 correlation (<0.75), identified using “ENMTools” (Warren, et al. 2010), to include in  
160 subsequent analyses: BIO01 (annual mean temperature), BIO03 (isothermality),  
161 BIO07 (temperature annual range), BIO13 (precipitation of wettest month), BIO14  
162 (precipitation of driest month) and BIO15 (precipitation seasonality).

163

164 Maximum entropy (MAXENT), generalized boosted regression modeling (GBM),  
165 random forest (RF), generalized linear models (GLM) and support vector machines  
166 (SVM) were selected for niche model integration simulation test, setting five  
167 cross-validations using “BiodiversityR” (Kindt 2018). The five algorithms included in  
168 the integrated model had equivalent weights (0.20) for each model. Models were  
169 evaluated by splitting data into training and testing datasets with 80% of the data  
170 being used to train and 20% to test the models. The true skill statistic (TSS) and the  
171 area under the receiver operating characteristics (ROC) curve were used to assess the  
172 performance of the models. TSS scores range from -1 to 1, where +1 indicates a  
173 perfect ability to distinguish suitable from unsuitable habitat, while values of zero (or  
174 less) indicate a performance no better than random. For the ensemble modelling, only



175 those models with a TSS value greater than 0.85 were considered.

176

### 177 **Pollen records**

178

179 To infer the past distribution of *B. albosinensis* in China, we collected pollen records  
180 of *Betula* species from the published literature. For most pollen cores, paleobotanists  
181 identified pollen only to the genus level; however, *Betula* pollen in this region is  
182 likely *B. albosinensis* as it is currently the dominant *Betula* species. We mapped these  
183 pollen sites using coordinates given in the literature. We grouped pollen records into  
184 two time periods to coincide with projections from the distribution model: the LGM  
185 (22Ka-19Ka) and the Early to Middle Holocene (19Ka-4Ka). The detailed pollen  
186 records are listed in table S2.

187

### 188 **DNA extraction and microsatellite genotyping**

189

190 Genomic DNA was extracted from cambial tissue using a previously modified 2×  
191 CTAB (cetyltrimethylammoniumbromide) protocol (Wang, et al. 2013). The quality  
192 of genomic DNA was assessed with 1.0 % agarose gels and then was diluted to a  
193 concentration of ~10 ng/ul for microsatellite genotyping. Sixteen microsatellite loci  
194 developed from closely-related species (Kulju, et al. 2004, Truong, et al. 2005, Tsuda,  
195 et al. 2008, Wu, et al. 2002) were used to genotype our samples. The 5' terminus of  
196 the forward primers was labeled with FAM, HEX or TAM fluorescent probes. Each

197 microsatellite locus was amplified individually prior to being artificially combined  
198 into four multiplexes. In order to avoid errors caused by size overlapping, loci with  
199 significant length differences were labeled using the same dye. PCR procedures were  
200 provided in supplementary data. PCR products were delivered to Personal (Shanghai)  
201 for microsatellite genotyping. Microsatellite alleles were scored using the software  
202 GENEMARKER 2.4.0 (Softgenetics) and checked manually. Individuals with more  
203 than three missing loci were excluded, resulting in 815 individuals in the final dataset.

204

#### 205 **Microsatellite data analyses**

206

207 Microsatellite data of *B. albosinensis* was analyzed in STRUCTURE 2.3.4 (Pritchard,  
208 et al. 2000) to identify the most likely number of genetic clusters (K) and estimate  
209 genetic admixture. As *B. albosinensis* is a tetraploid species, we set ploidy to four in  
210 STRUCTURE. Ten replicates of the STRUCTURE analysis were performed with  
211 1,000,000 iterations and a burn-in of 100,000 for each run at each value of K from 1  
212 to 6. We used the admixture model, with an assumption of correlated allele  
213 frequencies among populations. Individuals were assigned to clusters based on the  
214 highest membership coefficient averaged over the ten independent runs. The number  
215 of biologically-meaningful genetic clusters was estimated using the “Evanno test”  
216 (Evanno, et al. 2005) and the program Structure Harvester (Earl and vonHoldt 2011).  
217 Gene diversity (Nei 1987) and allelic richness (El Mousadik and Petit 1996) were  
218 calculated in the software FSTAT 2.9.4 (Goudet 1995). The tetraploid genotypes were

219 treated as two diploid individuals as described by Tsuda et al. (2017) and Hu et al.  
220 (2019). A principal coordinate analysis (PCoA) was also performed on microsatellite  
221 data of *B. albosinensis* using POLYSAT (Clark and Jasieniuk 2011) implemented in R,  
222 ver. 4.0.2 (R Core Team 2020), based on pairwise genetic distances calculated  
223 according to Bruvo et al. (2004).

224

### 225 **Geographic and climatic centrality**

226

227 We used eight variables as predictors of gene diversity (*Gd*), allele richness (*Ar*) and  
228 expected heterozygosity (*He*). These include: (a) distance from the geographic range  
229 centre (geoCentre), (b) distance from the southern range edge (southernEdge), (c)  
230 distance from the range edge (geoEdge), (d) current climatic suitability, (e) climatic  
231 distance from the climatic niche centroid (climDist), (f) climatic stability, (g) climatic  
232 variability since the LGM, and (h) population structure/genetic admixture. In order to  
233 estimate the distribution of *B. albosinensis*, we generated an alpha hull (Rodríguez  
234 and Pateiro 2010) around the 264 occurrence records representing the minimum  
235 convex polygons (Burgman and Fox 2003) and calculated the distance between each  
236 population and the nearest edge. To calculate distance from the geographic range  
237 centre, we located the centroid of the alpha hull using “rgeos” (Bivand and Rundel  
238 2018) and then calculated the geographic distance between each population and the  
239 centroid (Dallas, et al. 2017, Lira-Noriega and Manthey 2014). The alpha hull was  
240 also used to calculate population distance from the southern edge and the distance of

241 each population from the nearest geographic edge (Gougherty, et al. 2020). If  
242 populations were located exactly on the geographic boundary or the southern edge,  
243 we set the distance to one kilometer.

244

245 We calculated the climatic niche centroid by averaging values of the six climatic  
246 variables of the 264 coordinate points used for ecological niche modelling. We used  
247 Mahalanobis distance as an index to measure the climatic distance between each  
248 population and the climatic niche centroid using “statmatch” (D’Orazio 2015). We  
249 calculated climatic stability as the sum of suitability of LGM, MID and present  
250 (Ortego, et al. 2015, Yannic, et al. 2013); and climatic variability as the standard  
251 deviation of suitability of the three time scales (Gougherty, et al. 2020).

252

253 In addition to effects of geographic/climatic centrality and past climate, we also tested  
254 for effects of population structure and admixture among genetic clusters on *He*, *Gd*  
255 and *Ar*. Using admixture proportions, we calculated a population-level index of  
256 admixture. To do so, first we averaged admixture proportions across individuals  
257 within populations. We defined populations with genetic admixture between 0.4 and  
258 0.6 as admixed.

259

260 We measured the spatial autocorrelation of *He*, *Gd* and *Ar* using Moran's Index (I),  
261 with  $-1.0$  and  $1.0$  indicating perfect dispersion and perfect clustering, respectively.  
262 Correlograms of Moran's I for *He*, *Gd* and *Ar* were estimated in 200 km increments.

263 Significance was determined for both the correlograms and global statistic by  
264 comparing the observed statistic to 999 random permutations following Gougherty et  
265 al. (2020). Using the eight variables, we compared statistical support for models  
266 representing six hypotheses (Table 1). For each hypothesis, we created conditional  
267 autoregressive (CAR) models to account for the potential effects of spatial  
268 autocorrelation in genetic diversity. CAR models use a weighted estimate of the  
269 response variable at neighbouring locations, in addition to the explanatory variables,  
270 to parameterise the models (Lichstein, et al. 2002). Neighbourhoods were defined as  
271 all populations within 600 km of one another as this distance ensured each population  
272 had at least one neighbour and was the approximate maximum distance of continuous  
273 positive spatial autocorrelation. Models were compared using Nagelkerke R<sup>2</sup>, Akaike  
274 information criterion (AIC) and Akaike weights (Wagenmakers and Farrell 2004).  
275 Each explanatory variable was scaled to a mean of 0 and a standard deviation of 1, to  
276 facilitate the comparison of coefficient estimates (Schielzeth 2010).

277

## 278 **Results**

279

### 280 **Ecological niche modelling**

281

282 A final ensemble model was created by incorporating weighted runs from the  
283 MAXENT, GBM, RF, GLM and SVM models, with TSS ranging from  $\square$  0.89 to 0.92  
284 (TSS average  $\square$  =  $\square$  0.90) and AUC ranging from 0.96 to 0.98 (AUC average = 0.97).

285 The ensemble model predicts high habitat suitability during the LGM in the  
286 Qinling-Daba Mountains, northwestern Yunnan and southeastern China (Fig. 1A).  
287 During the Holocene, suitable habitat for *B. albosinensis* expanded from the Qinling  
288 Mountains into some parts of Shaanxi province and contracted from southeastern  
289 China (Fig. 1B). Suitable habitat for *B. albosinensis* seems to have been stable from  
290 the Holocene to the present (Fig. 1BC) and is predicted to shift westward in the future  
291 (Fig. 1D).

292

### 293 **Pollen records**

294

295 During the LGM (22 to 19 Ka), eleven pollen records of *Betula* species existed in  
296 southwest, central and north China (Fig. 1A). However, pollen records of *Betula*  
297 species became more widespread since the beginning of the Holocene (19 to 4 Ka)  
298 and appeared in regions representing the current distribution of *B. albosinensis* (Fig.  
299 1B).

300

### 301 **Genetic structure and admixture**

302

303 Our STRUCTURE analyses identified two clusters ( $K = 2$ ) as the optimal grouping,  
304 according to the  $\Delta K$  criterion (Fig. S1A). Cluster I, termed hereafter the northern  
305 cluster, included populations from the Qinling Mountains and the north (Fig. 2AB).  
306 Cluster II, termed the southern cluster hereafter, included several populations from

307 northwestern Yunnan (DQ, JS, LJA, LJS, LP and WX) and southern Sichuan (DC, JD,  
308 JLX, LFG, SDX and YJA) (Fig. 2AB). Seven populations (RTX, BMX, MEK, BX,  
309 EBY and SLS) located mainly in western Sichuan province showed roughly equal  
310 genetic admixture between the northern and southern clusters (Fig. 2AB). The  
311 northern and southern clusters were geographically separated by the Sichuan Basin.  
312 At higher K values (three to six), populations located at the southern margin in  
313 northwest Yunnan provinces (LP, LJS, LJA, JS, WZ and DQ) and on the northwest  
314 periphery in Qinghai and Gansu provinces (DTX and XMX) remain genetically  
315 distinct (Fig. S1B).

316

317 We treated individuals with genetic admixture greater than 0.9 from the northern  
318 cluster as “northern individuals” and individuals with genetic admixture greater than  
319 0.9 from the southern cluster as “southern individuals”. We treated individuals with  
320 genetic admixture in between as admixed. Principal coordinate analysis (PCoA) based  
321 on Bruvo’s genetic distances among all samples showed that the “northern  
322 individuals” can be separated from the “southern individuals” by PC1 (Fig. 3).  
323 Admixed individuals bridged the gap between the “northern individuals” and  
324 “southern individuals” and overlapped substantially with individuals from the two  
325 clusters. PC1, PC2 and PC3 could not distinguish admixed individuals from  
326 individuals from either the northern cluster or the southern cluster. PC1, PC2 and PC3  
327 explained 7.0%, 3.8% and 3.4% of the total variation, respectively (Fig. 3).

328

329 **Spatial patterns of genetic diversity**

330 *Gd*, *Ar* and *He* ranged from 0.72 to 0.83, from 4.04 to 5.07 and from 0.69 to 0.82,  
331 respectively. Moran's *I* showed moderate but significant spatial correlations for *He* ( $I$   
332 = 0.19,  $P < 0.001$ ), *Gd* ( $I = 0.22$ ,  $P < 0.001$ ) and *Ar* ( $I = 0.32$ ,  $P < 0.001$ ) in the 37  
333 populations, indicating similar levels of genetic diversity among adjacent populations.  
334 Correlograms of Moran's *I* for the three metrics of genetic diversity were positively  
335 autocorrelated up to ~200 km, and negatively correlated at 1500 and 2000 km (Fig.  
336 4).

337

338 In general, populations with high *He*, *Gd* and *Ar* tend to be situated in the northern  
339 portion of the range and the geographic centre whereas populations with low *He*, *Gd*  
340 and *Ar* tend to be located near the southern margin. *He*, *Gd* and *Ar* were positively  
341 correlated with both latitude and longitude (Fig. 5). Moreover, we found that climatic  
342 distance from the climatic niche centroid was significantly positively correlated ( $r =$   
343 0.49,  $P < 0.01$ ) with distance from the geographic range centre and significantly  
344 negatively correlated with distance from the range edge ( $r = - 0.64$ ,  $P < 0.01$ ),  
345 indicating that the geographic centre substantially overlapped with the climatic niche  
346 centroid.

347

348 **Spatial models of genetic diversity**

349

350 The best performing model for *Gd*, *He* and *Ar* included distance from the range edge



351 and distance from the southern edge. This model had the highest Akaike weights and  
352 highest Nagelkerke R<sup>2</sup> (Table 1) for each of the diversity metrics. The spatial models  
353 incorporating past climate (climate stability, variability, current suitability and climate  
354 distance) tended to have less support, and had Akaike weights near zero (Table 1).

355

## 356 **Discussion**

357

### 358 **Range dynamics and its implications**

359

360 In our study, three lines of independent evidence jointly point towards multiple  
361 refugia and cryptic refugia throughout the current distribution of *B. albosinensis*. First,  
362 ecological niche models (ENM) predict large and continuous suitable habitats for *B.*  
363 *albosinensis* situated in north, south and southeast China during LGM. Second, the  
364 presence of *Betula* pollen dated to the LGM in north and south China further confirms  
365 the existence of *Betula* species in these regions. Third, the high genetic diversity  
366 within populations in northern China suggests the existence of refugia near these  
367 populations. Interestingly, although the ENM does not predict high suitability at LGM  
368 at the northern range margin of *B. albosinensis*, high genetic diversity within northern  
369 populations (ie., XLA, BA, PQG, LS and SWP) supports the existence of cryptic  
370 LGM refugia in this region. This finding, together with several previous studies (Tian,  
371 et al. 2009, Zeng, et al. 2015), refutes the hypothesis that temperate forests migrated  
372 to the south (25–30 N) during the LGM (Cao, et al. 2014, Harrison, et al. 2001).

373 Instead, our findings favor the “multiple refugia hypothesis” that some temperate trees  
374 had multiple refugia in north China (Chen, et al. 2008, Hao, et al. 2018, Wang, et al.  
375 2016).

376

377 Unexpectedly, our ENM shows that the suitable habitats for *B. albosinensis* are  
378 comparable or even larger than its current distribution, indicating that the LGM may  
379 have had little effect on the distribution of *B. albosinensis*. This is possibly due to  
380 some unusual characteristics of this species. First, *B. albosinensis* is cold-tolerant and  
381 has a broad distribution across north, central and south China. Second, *B. albosinensis*  
382 populations occupy a broad altitudinal range between 1800 and 2800m in the Qinling  
383 Mountains according to our own field observations. Together, these could indicate  
384 that *B. albosinensis* responded to the glacial and interglacial cycles by shifting its  
385 range altitudinally, rather than latitudinally. In addition, *B. albosinensis*, like some  
386 other *Betula* species, is wind-pollinated and produces a large number of tiny winged  
387 seeds (Ashburner and McAllister 2016). This would help *B. albosinensis* disperse  
388 long distances and occupy open habitats. Moreover, regeneration of *B. albosinensis*  
389 depends on disturbance. Previous studies of *B. albosinensis* in the Qinling Mountains  
390 show that its seedlings only grow in open habitats caused by tree gaps (Guo, et al.  
391 2019). These characteristics may have enabled *B. albosinensis* to not only tolerate  
392 LGM but may also have allowed it to colonise unglaciated habitats quickly.

393

394 Surprisingly, our ENM reveals large suitable habitats for *B. albosinensis* in eastern

395 China during the LGM and disappearance of suitable habitats since the Holocene.  
396 *Betula albosinensis* is presently absent from eastern China and *B. luminifera* is the  
397 dominant species there. If *B. albosinensis* historically existed in eastern China, one  
398 possible scenario for its disappearance is due to its hybridisation with *B. luminifera*,  
399 given the extensive hybridisation between *Betula* species documented elsewhere  
400 (Anamthawat-Jónsson and Thórsson 2003, Bona, et al. 2018, Eidesen, et al. 2015,  
401 Tsuda, et al. 2017, Wang, et al. 2014). Further research characterizing patterns of the  
402 genetic admixture between the two species may help to understand this.

403

#### 404 **Distinct genetic clusters**

405

406 Both PCoA and STRUCTURE grouped *B. albosinensis* into two genetic clusters: a  
407 northern cluster from the Qinling-Daba Mountains and the regions to the north and  
408 northwest, and a southern cluster from northwestern Yunnan and southern Sichuan  
409 province. Several populations located in between, such as populations MYL, BX,  
410 MEK and EBY showed genetic admixture between the two clusters, indicating  
411 regions in between may serve as a contact zone. As expected, the Sichuan Basin is  
412 currently a geographic and genetic barrier for *B. albosinensis*, consistent with some  
413 previous studies (Qiu, et al. 2009, Wei, et al. 2016). Interestingly, the ENM showed  
414 that the Sichuan Basin has been unsuitable for *B. albosinensis* since the LGM,  
415 suggesting that it may be partially responsible for genetic differentiation of *B.*  
416 *albosinensis* populations located on both sides of the Sichuan Basin. The absence of

417 *Betula* pollen records from the Sichuan Basin during LGM further indicates the  
418 inhospitable habitats for *Betula* species (Fig. 1). Although *Betula* pollen records  
419 appeared during the Holocene in Sichuan Basin, it was possibly dispersed from  
420 adjacent mountainous ranges, or may belong to *B. luminifera*, which currently has a  
421 broad distribution around the Sichuan Basin. In contrast, for *B. albosinensis*, the  
422 Qinling-Daba Mountains seems to be a dispersal corridor as populations at both sides  
423 of the Qinling-Daba Mountains were not divided into genetically different groups (Fig.  
424 2). Similar results have been observed for other plant species, such as *Fagus sylvatica*  
425 (Magri, et al. 2006) and *Fraxinus mandshurica* (Hu, et al. 2008). If mountainous areas  
426 are barriers to dispersal, it may depend on several aspects: orientation of mountain  
427 range and species dispersal ability (Reeves and Richards 2014). The Taihang  
428 Mountains and Lvliang Mountains in north China are of a north-south orientation and  
429 the Qinling-Daba Mountains are of a west-east orientation, facilitating the dispersal of  
430 *B. albosinensis* along the mountains. Furthermore, the ability of *B. albosinensis* to  
431 disperse across the mountains is confirmed by our own observations that it grows on  
432 the top of mountains in north China. In general, mountain ranges are more likely to be  
433 dispersal barriers for lowland plant species with low dispersal ability. In our case of *B.*  
434 *albosinensis*, its occupation of high altitude and strong dispersal via pollen and seed  
435 could allow this species to easily spread across mountains at a broad scale. This  
436 explains the low genetic differentiation among populations from north and central  
437 China. The northern cluster and the southern cluster of *B. albosinensis* may also  
438 reflect local adaptation to different environments, as has been reported for *Quercus*

439 *aquifolioides* (Du, et al. 2020). It is noteworthy that every individual from the  
440 southern cluster has genetic traces from the northern cluster and vice versa, a pattern  
441 mirroring incomplete lineage sorting.

442

#### 443 **Geographic pattern of genetic diversity**

444 A key finding of our study is that the spatial pattern of genetic diversity of *B.*  
445 *albosinensis* can best be explained by distance from the southern edge and distance  
446 from the range edge. Our results partially support the CMH and largely fit the  
447 proposed pattern of genetic diversity(Guo 2012). However, the latitudinal effect on  
448 genetic diversity is opposite that from most previous studies(Guo 2012). In our study,  
449 genetic diversity shows a latitudinal increase whereas many other studies show a  
450 latitudinal decrease in genetic diversity. For example, a latitudinal decrease of genetic  
451 diversity has been reported for tree species distributed in NEC and subtropical areas  
452 due to northward colonisation events (Ye, et al. 2019). Our study also differs with the  
453 proposed pattern that genetic diversity decreases from the geographic centre towards  
454 both the southern and the northern range (Wei, et al. 2016). Two mutually inclusive  
455 hypotheses likely explain a latitudinal increase in genetic diversity: the existence of  
456 the northern LGM refugia and a southward movement of *B. albosinensis*. The  
457 existence of northern refugia is very likely for *B. albosinensis* as evidenced by ENM  
458 results and pollen records and a southward colonisation is also likely due to the  
459 dispersal corridor of the Qinling-Daba Mountains.

460

461 Interestingly, population HHG, located close to the geographic centre, harbors the  
462 highest level of genetic diversity, possibly due to a high abundance of *B. albosinensis*.  
463 Based on our field observations, population HHG seemed to be much larger than  
464 other populations and had numerous stands of *B. albosinensis*. Hence, we suggest that  
465 population abundance may partly account for genetic diversity for *B. albosinensis* in  
466 the Qinling Mountains. Although the ENM and pollen records indicate that  
467 northwestern Yunnan also served as LGM refugia, populations there had low genetic  
468 diversity. Two hypotheses may explain such a pattern: isolated small populations with  
469 low species abundance and a southward or an eastward movement of *B. albosinensis*.  
470 Unlike populations from the Qinling Mountains where *B. albosinensis* is the dominant  
471 species and formed very large and near pure stands in the HHG population, *B.*  
472 *albosinensis* from northwestern Yunnan grows sparsely among other tree species. This  
473 may result in the reduced genetic diversity due to genetic drift. Another possibility is  
474 that a southward or eastward movement of *B. albosinensis* from the geographic centre  
475 or southeastern Tibet, respectively, resulting in loss of genetic diversity due to  
476 bottleneck effects. Further inclusion of some populations from Tibet may help to  
477 clarify these points. The genetic diversity of *B. albosinensis* is also positively  
478 correlated with longitude, with higher levels of genetic diversity residing in more  
479 eastern populations. This may indicate a westward dispersal of *B. albosinensis* from  
480 central China along the Qinling-Daba Mountains.

481

482 Our work also shows that past climate by itself does not explain the patterns of

483 genetic diversity of *B. albosinensis*. For example, the model with past climate stability  
484 and variability and model with current climate suitability and climatic distance had  
485 low support, with AIC weights being zero and 0.001, respectively. This is somewhat  
486 counterintuitive given that *B. albosinensis* seems a demanding species for moisture  
487 and temperature. This is possibly due to the fact that the geographic centre of *B.*  
488 *albosinensis* coincides with its climatic centre whereas its peak climatic suitability is  
489 not in the geographic centre of the range but in other regions, in particular the western  
490 Sichuan and northwestern Yunnan province. Another plausible explanation is that  
491 distribution of suitable habitats for *B. albosinensis* did not vary much since the LGM  
492 as evidenced by our ENM results. In conclusion, genetic diversity could be related to  
493 abundance whereas suitability from ENMs tends not to be associated with patterns of  
494 abundance (Dallas and Hastings 2018), resulting in a mismatch between genetic  
495 diversity and climatic suitability.

496

#### 497 **Acknowledgement**

498 This work was funded by the National Natural Science Foundation of China  
499 (31600295 and 31770230) and Funds of Shandong ‘Double Tops’ Program  
500 (SYL2017XTTD13).

501

#### 502 **Author contributions**

503 NW and AD conceived the project. LL, LW, FW and NW collected samples. LL  
504 carried out lab work. LL and AD analyzed the results. NW and AD edited the draft.

505

506 **Reference**

- 507 Anamthawat-Jónsson, K. and Thórrsson, A. T. 2003. Natural hybridisation in birch:  
508 triploid hybrids between *Betula nana* and *B. pubescens*. - Plant Cell, Tissue Organ  
509 Cult. 75: 99-107.
- 510 Ashburner, K. and McAllister, H. A. 2016. The genus *Betula*: a taxonomic revision of  
511 birches. - Kew Publishing.
- 512 Bivand, R. and Rundel, C. 2018. rgeos: interface to geometry engine-open source  
513 (GEOS). R package version 0.3-28.
- 514 Bona, A. et al. 2018. Unfavourable habitat conditions can facilitate hybridisation  
515 between the endangered *Betula humilis* and its widespread relatives *B. pendula* and *B.*  
516 *pubescens*. - Plant Ecol. Divers. 11: 295-306.
- 517 Bruvo, R. et al. 2004. A simple method for the calculation of microsatellite genotype  
518 distances irrespective of ploidy level. - Mol. Ecol. 13: 2101-2106.
- 519 Burgman, M. A. and Fox, J. C. 2003. Bias in species range estimates from minimum  
520 convex polygons: implications for conservation and options for improved planning. -  
521 Anim. Conserv. 6: 19-28.
- 522 Cao, X. Y. et al. 2014. Spatial and temporal distributions of major tree taxa in eastern  
523 continental Asia during the last 22,000 years. - Holocene 25: 79-91.
- 524 Chen, K. et al. 2008. Phylogeography of *Pinus tabulaeformis* Carr. (Pinaceae), a  
525 dominant species of coniferous forest in northern China. - Mol. Ecol. 17: 4276-4288.
- 526 Clark, L. V. and Jasieniuk, M. 2011. POLYSAT: an R package for polyploid  
527 microsatellite analysis. - Mol. Ecol. Resour. 11: 562-566.
- 528 D'Orazio, M. 2015. Integration and imputation of survey data in R: the StatMatch  
529 package. - Int. Stat. Rev. 63: 57-68.
- 530 Dallas, T. et al. 2017. Species are not most abundant in the centre of their geographic  
531 range or climatic niche. - Ecol. Lett. 20: 1526-1533.
- 532 Dallas, T. A. and Hastings, A. 2018. Habitat suitability estimated by niche models is  
533 largely unrelated to species abundance. - Glob. Ecol. Biogeogr. 27: 1448-1456.
- 534 Du, F. K. et al. 2020. Contrasted patterns of local adaptation to climate change across



535 the range of an evergreen oak, *Quercus aquifolioides*. - *Evol. Appl.* 13: 2377-2391.

536 Earl, D. A. and vonHoldt, B. M. 2011. STRUCTURE HARVESTER: a website and  
537 program for visualizing STRUCTURE output and implementing the Evanno method.  
538 - *Conserv. Genet. Resour.* 4: 359-361.

539 Eckert, C. G. et al. 2008. Genetic variation across species' geographical ranges: the  
540 central-marginal hypothesis and beyond. - *Mol. Ecol.* 17: 1170-1188.

541 Eidesen, P. B. et al. 2015. Comparative analyses of plastid and AFLP data suggest  
542 different colonization history and asymmetric hybridization between *Betula*  
543 *pubescens* and *B. nana*. - *Mol. Ecol.* 24: 3993-4009.

544 El Mousadik, A. and Petit, R. J. 1996. High level of genetic differentiation for allelic  
545 richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic  
546 to Morocco. - *Theor. Appl. Genet.* 92: 832-839.

547 Evanno, G. et al. 2005. Detecting the number of clusters of individuals using the  
548 software STRUCTURE: a simulation study. - *Mol. Ecol.* 14: 2611-2620.

549 Fick, S. E. and Hijmans, R. J. 2017. WorldClim 2: new 1-km spatial resolution  
550 climate surfaces for global land areas. - *Int. J. Climatol.* 37: 4302-4315.

551 Gent, P. R. et al. 2011. The Community Climate System Model version 4. - *J. Clim.*  
552 24: 4973-4991.

553 Goudet, J. 1995. FSTAT (version 1.2): a computer program to calculate F-statistics. -  
554 *Heredity* (Edinb) 86: 485-486.

555 Gougherty, A. V. et al. 2020. Contemporary range position predicts the range-wide  
556 pattern of genetic diversity in balsam poplar (*Populus balsamifera* L.). - *J. Biogeogr.*  
557 47: 1246-1257.

558 Guo, Q. 2012. Incorporating latitudinal and central–marginal trends in assessing  
559 genetic variation across species ranges. - *Mol. Ecol.* 21: 5396-5403.

560 Guo, Y. et al. 2019. Canopy disturbance and gap partitioning promote the persistence  
561 of a pioneer tree population in a near-climax temperate forest of the Qinling  
562 Mountains, China. - *Ecol. Evol.* 9: 7676-7687.

563 Hao, Q. et al. 2018. The critical role of local refugia in postglacial colonization of

- 564 Chinese pine: joint inferences from DNA analyses, pollen records, and species  
565 distribution modeling. - *Ecography* 41: 592-606.
- 566 Harrison, S. P. et al. 2001. The role of dust in climate changes today, at the last glacial  
567 maximum and in the future. - *Earth Sci. Rev.* 54: 43-80.
- 568 Hewitt, G. M. 1999. Post-glacial re-colonization of European biota. - *Biol. J. Linn.*  
569 *Soc. Lond.* 68: 87-112.
- 570 Hewitt, G. M. 2004. Genetic consequences of climatic oscillations in the Quaternary. -  
571 *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 359: 183-195.
- 572 Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for  
573 global land areas. - *Int. J. Climatol.* 25: 1965-1978.
- 574 Hou, Z. et al. 2018. Phylogeographic analyses of a widely distributed *Populus*  
575  *davidiana*: further evidence for the existence of glacial refugia of cool-temperate  
576 deciduous trees in northern east Asia. - *Ecol. Evol.* 8: 13014-13026.
- 577 Hu, L. J. et al. 2008. Nuclear DNA microsatellites reveal genetic variation but a lack  
578 of phylogeographical structure in an endangered species, *Fraxinus mandshurica*,  
579 across north-east China. - *Ann. Bot.* 102: 195-205.
- 580 Hu, Y. N. et al. 2019. Population structure of *Betula albosinensis* and *Betula*  
581  *platyphylla*: evidence for hybridization and a cryptic lineage. - *Ann. Bot.* 123:  
582 1179-1189.
- 583 Jin, P. Y. et al. 2020. Geography alone cannot explain *Tetranychus truncatus* (Acari:  
584 Tetranychidae) population abundance and genetic diversity in the context of the  
585 center-periphery hypothesis. - *Heredity (Edinb)* 124: 383-396.
- 586 Kindt, R. 2018. Ensemble species distribution modelling with transformed suitability  
587 values. - *Environ. Model. Softw.* 100: 136-145.
- 588 Kulju, K. K. M. et al. 2004. Twenty-three microsatellite primer pairs for *Betula*  
589  *pendula* (Betulaceae). - *Mol. Ecol. Notes* 4: 471-473.
- 590 Lichstein, J. W. et al. 2002. Spatial autocorrelation and autoregressive models in  
591 ecology. - *Ecol. Monogr.* 72: 445-463.
- 592 Lira-Noriega, A. and Manthey, J. D. 2014. Relationship of genetic diversity and niche  
593 centrality: a survey and analysis. - *Evol.* 68: 1082-1093.

- 594 Liu, J. Q. et al. 2012. Phylogeographic studies of plants in China: advances in the past  
595 and directions in the future. - J. Syst. Evol. 50: 267-275.
- 596 Magri, D. et al. 2006. A new scenario for the quaternary history of European beech  
597 populations: palaeobotanical evidence and genetic consequences. - New Phytol. 171:  
598 199-221.
- 599 Micheletti, S. J. and Storfer, A. 2015. A test of the central-marginal hypothesis using  
600 population genetics and ecological niche modelling in an endemic salamander  
601 (*Ambystoma barbouri*). - Mol. Ecol. 24: 967-979.
- 602 Nei, M. 1987. Molecular evolutionary genetics. - Columbia university press.
- 603 Ortego, J. et al. 2015. Climatically stable landscapes predict patterns of genetic  
604 structure and admixture in the Californian canyon live oak. - J. Biogeogr. 42:  
605 328-338.
- 606 Petit, R. et al. 2003. Glacial refugia: hotspots but not melting pots of genetic diversity.  
607 - Science 300: 1563-1565.
- 608 Petit, R. J. et al. 1997. Chloroplast DNA footprints of postglacial recolonization by  
609 oaks. - PNAS 94: 9996-10001.
- 610 Pritchard, J. K. et al. 2000. Inference of population structure using multilocus  
611 genotype data. - Genetics 155: 945-959.
- 612 Qian, H. and Ricklefs, R. E. 2001. Palaeovegetation (Communications arising):  
613 diversity of temperate plants in east Asia. - Nature 413: 130-131.
- 614 Qiu, Y. X. et al. 2009. Did glacials and/or interglacials promote allopatric incipient  
615 speciation in east Asian temperate plants? Phylogeographic and coalescent analyses  
616 on refugial isolation and divergence in *Dysosma versipellis*. - Mol. Phylogenet. Evol.  
617 51: 281-293.
- 618 Qiu, Y. X. et al. 2011. Plant molecular phylogeography in China and adjacent regions:  
619 tracing the genetic imprints of Quaternary climate and environmental change in the  
620 world's most diverse temperate flora. - Mol. Phylogenet. Evol. 59: 225-244.
- 621 R Core Team 2020. R: A language and environment for statistical computing. R  
622 Foundation for Statistical Computing, Vienna, Austria.
- 623 Reeves, P. A. and Richards, C. M. 2014. Effect of a geographic barrier on adaptation

624 in the dwarf sunflower (*Helianthus pumilus* Nutt.). - Int. J. Plant Sci. 175: 688-701.

625 Rodríguez, C. A. and Pateiro, L. B. 2010. Generalizing the convex hull of a sample:  
626 the R package alphahull. - J. Stat. Softw.

627 Sagarin, R. D. and Gaines, S. D. 2002. The 'abundant centre' distribution: to what  
628 extent is it a biogeographical rule? - Ecol. Lett. 5: 137-147.

629 Schielzeth, H. 2010. Simple means to improve the interpretability of regression  
630 coefficients. - Methods Ecol. Evol. 1: 103-113.

631 Swaegers, J. et al. 2013. Rapid range expansion increases genetic differentiation while  
632 causing limited reduction in genetic diversity in a damselfly. - Heredity (Edinb) 111:  
633 422-429.

634 Tian, B. et al. 2009. Phylogeographic analyses suggest that a deciduous species  
635 (*Ostryopsis davidiana* Decne., Betulaceae) survived in northern China during the Last  
636 Glacial Maximum. - J. Biogeogr. 36: 2148-2155.

637 Truong, C. et al. 2005. Isolation and characterization of microsatellite markers in the  
638 tetraploid birch, *Betula pubescens* ssp. *tortuosa*. - Mol. Ecol. Notes 5: 96-98.

639 Tsuda, Y. et al. 2008. Development of 14 EST-SSRs for *Betula maximowicziana* and  
640 their applicability to related species. - Conserv. Genet. 10: 661-664.

641 Tsuda, Y. et al. 2017. Multispecies genetic structure and hybridization in the *Betula*  
642 genus across Eurasia. - Mol. Ecol. 26: 589-605.

643 Wagenmakers, E. J. and Farrell, S. 2004. AIC model selection using Akaike weights. -  
644 Psychon. Bull. Rev. 11: 192-196.

645 Wang, N. et al. 2013. Genome sequence of dwarf birch (*Betula nana*) and  
646 cross-species RAD markers. - Mol. Ecol. 22: 3098-3111.

647 Wang, N. et al. 2014. Molecular footprints of the Holocene retreat of dwarf birch in  
648 Britain. - Mol. Ecol. 23: 2771-2782.

649 Wang, N. et al. 2016. Molecular phylogeny and genome size evolution of the genus  
650 *Betula* (Betulaceae). - Ann. Bot. 117: 1023-1035.

651 Wang, W. T. et al. 2016. Phylogeography of postglacial range expansion in *Juglans*  
652 *mandshurica* (Juglandaceae) reveals no evidence of bottleneck, loss of genetic  
653 diversity, or isolation by distance in the leading-edge populations. - Mol. Phylogenet.

- 654 Evol. 102: 255-264.
- 655 Warren, D. L. et al. 2010. ENMTools: a toolbox for comparative studies of  
656 environmental niche models. - *Ecography* 33: 607-611.
- 657 Wei, X. Z. et al. 2016. Genetic evidence for central-marginal hypothesis in a Cenozoic  
658 relict tree species across its distribution in China. - *J. Biogeogr.* 43: 2173-2185.
- 659 Wu, B. et al. 2002. Development of microsatellite markers in white birch (*Betula*  
660 *platyphylla* var. *japonica*). - *Mol. Ecol. Notes* 2: 413-415.
- 661 Yannic, G. et al. 2013. Genetic diversity in caribou linked to past and future climate  
662 change. - *Nat. Clim. Chang.* 4: 132-137.
- 663 Ye, J. W. et al. 2019. Phylogeography of *Schisandra chinensis* (Magnoliaceae) reveal  
664 multiple refugia with ample gene flow in northeast China. - *Front. Plant Sci.* 10: 199.
- 665 Zeng, Y. F. et al. 2015. Multiple glacial refugia for cool-temperate deciduous trees in  
666 northern east Asia: the Mongolian oak as a case study. - *Mol. Ecol.* 24: 5676-5691.
- 667 Zhang, Q. et al. 2005. Phylogeography of the Qinghai-Tibetan Plateau endemic  
668 *Juniperus przewalskii* (Cupressaceae) inferred from chloroplast DNA sequence  
669 variation. - *Mol. Ecol.* 14: 3513-3524.

670

671 **Conflicts of interest**

672 There is no conflict of interest in this study.

673

674 **Figure legends**

675 **Figure 1** The predicted climatic suitability for *B. albosinensis* and pollen records of  
676 *Betula* species. (a) Suitable climate during the LGM, (b) the mid-Holocene, (c)  
677 present and (d) in the future (2070). Orange and blue points represent pollen records  
678 of *Betula* species during LGM and the Holocene, respectively. Red points represent  
679 coordinate points used for ecological niche modelling.

680 **Figure 2** STRUCTURE results for K=2 based on microsatellite markers and a map  
681 showing sampling sites. Pie charts indicate the admixture of each population.

682 **Figure 3** A principal component analysis (PCoA) of *B. albosinensis* at 16  
683 microsatellite markers. Green, yellow and blue points represent “northern individuals”,  
684 “southern individuals” and admixed individuals between the northern cluster and the  
685 southern cluster, respectively.

686 **Figure 4** Maps and correlograms (a, b) of genetic diversity (expected heterozygosity  
687 =  $He$ ; gene diversity =  $Gd$ ; allele richness =  $Ar$ ) among *B. albosinensis* populations.  
688 Circle size in the correlograms is proportional to the number of records within each  
689 distance class and filled circles indicate significant autocorrelation at particular  
690 distance class (two sided,  $p > .975$  or  $p < .025$ ).

691 **Figure 5** Linear model fit of genetic diversity (expected heterozygosity =  $He$ ; gene  
692 diversity =  $Gd$ ; allele richness =  $Ar$ ) with latitude and longitude, respectively.

693 **Figure S1** The optimal number of clusters inferred using the “Evanno test” method (A)  
694 and (B) STRUCTURE results at K values between 2 and 6 based on microsatellite  
695 markers.

696 **Table legends**

697 **Table 1** Summary statistics for conditional autoregressive models for genetic diversity

698 (*He*, *Gd* and *Ar*) in *B. albosinensis*.

699 **Table S1** Detailed information of populations used in the present study.

700 **Table S2** Detailed information of pollen records used in the present study.

701

702

703 **Table 1.** Summary statistics for conditional autoregressive models for a range-wide  
704 sample of *He*, *Gd* and *Ar* in *Betula albosinensis*, ranked by relative support.

Model	<i>He</i>			<i>Gd</i>		
	Nagelkerke R <sup>2</sup>	AIC	AIC weight	Nagelkerke R <sup>2</sup>	AIC	AIC weight
southernEdge+GeoEdge	0.464	-171.099	0.978	0.644	-200.621	0.997
southernEdge	0.289	-162.655	0.014	0.479	-188.459	0.002
geoEdge+geoCenter	0.291	-160.769	0.006	0.417	-182.317	0.000
suitability+climDist	0.184	-157.946	0.001	0.253	-182.793	0.000
admixture+maxCluster	0.227	-155.560	0.000	0.443	-182.008	0.000
stability+variability	0.067	-155.361	0.000	0.070	-178.550	0.000

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706











