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1 **Title: Different range shifts and determinations of elevational**
2 **redistributions of native and non-native plant species in Jinfo**
3 **Mountain of subtropical China**

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23 **ABSTRACT**

24 Species are changing their elevational distributions in response to climate change,
25 leading to biodiversity loss and changes in community structure. Yet whether native
26 and non-native species have consistent elevational shifts remains to be evaluated.
27 Subtropical mountains are rich in biodiversity, sensitive to climate change, and are
28 experiencing high risks of biological invasion. Hence exploring the changes in species
29 elevational distributions induced by climate change in subtropical mountains is an
30 urgent need. Here, we explored the impact of climate change on the elevational
31 distribution of seed plant species in Jinfo Mountain (Mt. Jinfo), a subtropical mountain
32 in China with rich plant diversity. Notably, we compared the elevational redistributions
33 of native and non-native plants in response to climate change. The results showed that
34 the elevational centroids of native plant species moved downhill, while those of non-
35 native plants shifted upward on average. The upper limit of native plants shifted
36 downward, while the upper limit of non-native plants shifted upward on average. The
37 elevational shifts of non-native plants were dominated by changes in the upper range
38 limits, while those of native plants were affected by the lower limits. These opposite
39 elevational shifts of native vs. non-native species led to the increase in the elevational
40 range size of the non-native plants, but decrease in the elevational range size of native
41 plants, especially in high altitudes. The differences in the directions and magnitudes of
42 elevational shifts between the native and non-native plants are mainly due to differences
43 in their climate adaptation. Changes in temperature and precipitation influenced the
44 elevational range shifts of native plants but not of non-native ones. **This study provides
45 a new perspective for understanding the elevational redistribution of native and non-
46 native plant species in subtropical mountains, and suggests that climate change has
47 stronger influence on native species than non-native species.**

48 **Keywords:** Elevational shifts; Climate change; Non-native plants; Range size;
49 Elevational distribution

50 **1. Introduction**

51 Mountains play a crucial role for sustaining biodiversity, acting simultaneously as
52 cradles, museums (i.e., refugia) and graves (Rangel et al., 2018; Rahbek et al., 2019).
53 Mountains' biodiversity is vital for the survival and sustainable development of human
54 societies (Perrigo et al., 2019). The steep macroclimatic gradients running from the
55 valley bottom to mountain summits also serve as natural laboratories to assess the
56 impact of climate change on biodiversity (Körner, 2000; Myers et al., 2000). Mountain
57 regions globally have experienced climate warming at a much faster pace than lowland
58 regions (Pépin et al., 2015), and future air temperatures will likely be higher than they
59 are today (Nogués-Bravo et al., 2007; Rebetz and Reinhard, 2007). The acceleration
60 of macroclimate warming on mountain summits is already accelerating the rate of
61 species accumulation on mountain summits, with the potential to jeopardize the
62 mountains' primary function to act as long-term refugia for biodiversity (Steinbauer et
63 al., 2018). Assessing the velocity at which species are redistributing along mountain
64 slopes as global climate warms is essential for effective land management and
65 conservation planning (Beaudrot et al., 2018).

66 Species are known to have shifted their elevational ranges in response to
67 anthropogenic climate changes (Lenoir et al., 2008; Crimmins et al., 2011; Mamantov
68 et al., 2021; Zu et al., 2021). Changes in mountain biodiversity distribution may
69 influence the structure and functioning of mountain ecosystems and lead to significant
70 loss of ecosystem services (Lenoir and Svenning, 2015). Over the past century, many
71 studies have examined how plants, animals and even fungi shifted their distribution
72 ranges along elevational gradients of mountain regions in response to climatic change
73 (Lenoir et al., 2008; Moritz et al., 2008; Freeman et al., 2018; Rumpf et al., 2019; Diez
74 et al., 2020; Vitasse et al., 2021; Zu et al., 2021). Current evidence suggests that the
75 direction and magnitude of species elevational range shifts is highly variable and might
76 not only vary with the velocity and direction of climate change, in terms of both
77 temperature and precipitation, but also with baseline environmental conditions (Lenoir
78 et al., 2020). For instance, most vascular plants from temperate forest ecosystems

79 shifted upslope along elevational gradients in France (Lenoir et al., 2008), while most
80 forest plants from another macroclimatic context in California shifted chiefly
81 downslope (Crimmins et al., 2011). The former may be driven by the velocity and
82 direction of temperature changes, while the latter is affected by the velocity and
83 direction of precipitation changes (Grytnes et al., 2014). Such context dependencies are
84 crucial to understand the huge variability in the direction and magnitude of
85 contemporary range shifts (Lenoir et al., 2020). However, previous studies have been
86 mainly conducted in temperate or Mediterranean mountains, while fewer studies have
87 examined the changes in the distribution of plants in tropical mountains and even less
88 in subtropical mountains, where plant diversity is extremely rich (Mamantov et al.,
89 2021; Zu et al., 2021). To better understand the redistribution of plant species along the
90 slopes of subtropical mountains, repeated and long-term field studies over time are
91 crucial. In addition, studies reporting species elevational range shifts in response to
92 climate change tend to focus almost exclusively on the changes in the centroid of
93 elevation range (Lenoir et al., 2008; Crimmins et al., 2011) or changes in upper range
94 limit (Pauli et al., 2012; Grytnes et al., 2014). However, to better understand the
95 responses of species to climate change, it is necessary to simultaneously assess changes
96 over the entire range: not only at the centroid of the range but also at the upper and
97 lower elevational limits, in order to assess a potential reduction or expansion of a
98 species elevational range size (Lenoir and Svenning, 2015).

99 In mountain ecosystems, not only native species are redistributing along mountain
100 slopes but non-native plants also tend to shift and expand their elevational range upward
101 to colonize new habitats (Dainese et al., 2017; Koide et al., 2017; Lembrechts et al.,
102 2017; Rew et al., 2020). This redistribution or expansion of non-native plants towards
103 mountain summits possesses an additional threat to native plants, which face increased
104 competition with more adaptive non-native plant species at higher elevations (Bezeng
105 et al., 2017). Besides competition for space, the invasion risk associated to exotic
106 species expanding their range upward in elevation could alter the functioning of
107 mountain ecosystem as well as accelerate the loss of mountain biodiversity (Hejda et

108 al., 2009; Pauchard et al., 2009; Pauchard et al., 2015). Native and non-native species
109 have different evolutionary histories and ecological backgrounds leading to different
110 distribution patterns along elevational gradients (Sandoya et al., 2017; Guo et al., 2018)
111 and thus different patterns in the expected direction and magnitude of elevational range
112 shifts under macroclimate warming (Dainese et al., 2017; Koide et al., 2017). **Native**
113 **species have been evolving in response to the local changes in environmental conditions**
114 **over time. Hence, the spatial distribution of each native species along elevational**
115 **gradients is more likely to be in equilibrium with its realized climatic niche. In contrast,**
116 **non-native species introduced to a new environment are more likely to be in a process**
117 **of range filling and thus, not likely to be in equilibrium with their realized climatic**
118 **niche (Koide et al., 2017).** As already demonstrated for temperate and tropical
119 mountains (Dainese et al., 2017; Koide et al., 2017), Therefore, we speculate that the
120 direction and magnitude of native and non-native plants will also differ for subtropical
121 mountains. However, such comparisons of elevational range shifts between native and
122 non-native plants in subtropical mountains are still lacking.

123 Herbarium specimens provide accurate information on the collecting time and
124 location of species, and hence provide a unique opportunity to know how species
125 distributed in the past and endure the potential of evaluating how species responded to
126 historical climate change. Mount Jinfo is located in the subtropical region of Southwest
127 China, where numerous botanists have collected lots of plant specimens throughout the
128 last century (Yi and Huang, 2004). Thus, the collection density along the slopes of Mt.
129 Jinfo is among the most intensive and complete across all China's mountains (Yang et
130 al., 2014; Page et al., 2015). Currently, there are many reports of non-native plant
131 species being invasive at Mt. Jinfo due to the increasing development of tourism in this
132 region of China (Sun et al., 2009). Thus, Mt. Jinfo provides a unique opportunity to
133 compare the dynamics of range shifts of native and non-native species in response to
134 climate change. Here, using the historical specimen records of plants in one of the
135 biodiversity hotspots in China, Mt. Jinfo, we evaluated and compared the changes in
136 plant elevational distributions between native and non-native plants in response to

137 climate change over the last 70 years. The following questions were addressed: (1) How
138 did the centroid elevations, the upper and lower elevational limits, and the elevational
139 range sizes of both native and non-native plant species change? (2) Did native and non-
140 native plants shift in the same direction and magnitude? (3) What are the driving factors
141 explaining elevational changes in the range of native and non-native plants?
142

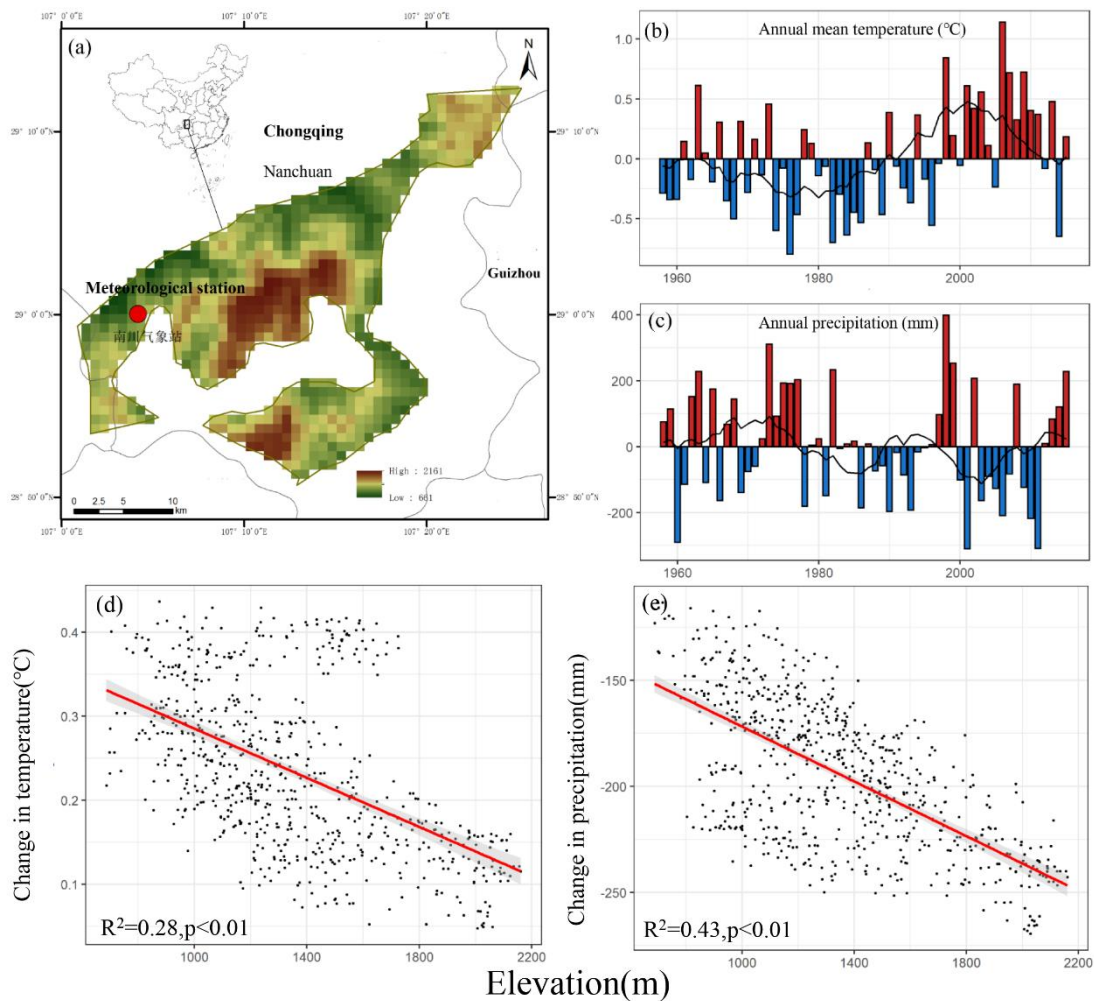
143 **2. Materials and methods**

144 *2.1. Study site and vegetation data*

145 The Jinfo Mountain's Nature Reserve (107°00' - 107°22' E, 28°50' - 29°20' N) is
146 located in the Nanchuan District, Chongqing City, China. It is a transitional zone
147 between the southeastern margin of Sichuan Basin and Yunnan-Guizhou Plateau with
148 a typical limestone karst landform. Mount Jinfo is located at the northeast end of the
149 Dalou mountain range with the highest summit reaching 2251 m (Fig. 1a). The study
150 area is located in the subtropical humid monsoon climate zone and provides good
151 conditions for the reproduction and growth of plants in this region. Raw summary
152 statistics show that there are 4,764 species of seed plants in this region, belonging to
153 1,256 genera from 183 families, accounting for about 16.67% of seed plants in China
154 (Yi and Huang, 2004).

155 The species distribution data were collected from the China National Specimen
156 Resources Platform (NSII, <http://www.nsii.org.cn/>), the China Digital Herbarium (CVH,
157 <http://www.cvh.org.cn>), the Global Biodiversity Information Facility (GBIF,
158 <http://www.gbif.org/>) and the Botanical Information and Ecology Network (BIEN,
159 <http://bien.nceas.ucsb.edu/bien/biendata/>). For the analysis, only data with precise
160 geographical coordinates were selected. Duplicate records with similar geographical
161 coordinates but extracted from different sources were removed to reduce geographical
162 bias and spatial autocorrelation. Finally, we retrieved a total of 35,367 seed plant
163 specimens with georeferenced occurrences collected between 1950 and 2018. We
164 standardized the species names of all records according to the Taxonomic Name
165 Resolution Service (TRNS, <http://tnrs.iplantcollaborative.org/TNRSapp.html>) and the

166 Asian Plant Synonym Lookup (APSL, <http://phylodiversity.net/fsl/synonym>
 167 [lookup.htm](#)).



168
 169 **Fig. 1.** Geographical location (a) and climate change from 1958 to 2015 in Mt. Jinfo. b:
 170 Changes in mean annual temperature (MAT) across the period 1958 - 2015; c: Changes
 171 in annual precipitation (AP) across the period 1958 - 2015; d: The changes in mean
 172 annual temperature between 1980 - 1988 and 2007 - 2015 along the elevation gradients;
 173 e: The changes in annual precipitation between 1980 - 1988 and 2007 - 2015 along the
 174 elevation gradients. Each dot in d and e represents climate changes within each 1×1
 175 km grid cell along elevation gradients between the two periods.

176 *2.2. Climate change and human footprint on Mount Jinfo*

177 Using climatic data from the Nanchuan meteorological station located in Chongqing,
 178 within the Jinfo mountain range, we assessed changes in both mean annual temperature

179 and annual precipitation throughout the past 58 years (1958 - 2015). Based on the
180 meteorological station, we found a warming trend for mean annual temperature (Fig.
181 1b) but no clear trend for changes in total annual rainfall (Fig. 1c). In addition to
182 extracting data from this specific meteorological station, we also analyzed data
183 extracted from climatic grids provided on a yearly basis and at a spatial resolution of 1
184 km by the climate dataset of the Resources and Environmental Data Cloud Platform of
185 the Chinese Academy of Sciences (<http://www.resdc.cn/>). This spatial interpolation is
186 based on daily observations from more than 2,400 meteorological stations across China
187 (Hutchinson, 1998). We chose the cutoff year 1988 as the breaking points based on the
188 temperature changes along the long-term dataset for the study sites (Fig 1b). From these
189 gridded products, we first computed, for each grid cell of 1 km², long-term average
190 values of annual mean temperature and annual precipitation during two time periods
191 (1980 - 1988 vs. 2007 - 2015) before computing the difference or change in annual
192 mean temperature and annual precipitation between both periods. Then, we analyzed
193 the magnitude of these macroclimatic changes, both in mean annual temperature and
194 annual precipitation, along the elevational gradients available within the study region.
195 We considered the difference between the two periods as changes in temperature and
196 precipitation (Fig 1d, e). According to these climatic data, we found that elevation is
197 negatively correlated with temperature changes between 1980 - 1988 and 2007 - 2015
198 ($R^2 = 0.28$, $p < 0.01$), which indicates that the magnitude of climate warming is greater
199 in the lowlands of the Jinpo mountain range (Fig. 1d). The change of annual
200 precipitation between 1980 - 1988 and 2007 - 2015 is also negatively correlated with
201 elevation ($R^2 = 0.43$, $p < 0.01$), such that the overall decrease in annual precipitation is
202 greater at high elevations than in the lowlands (Fig 1e). In addition, human activity data
203 were derived from the human footprint (HF) index extracted from "Last of the Wild
204 (V2)" and covering the period 1995 - 2004. We extracted the human footprint (HF)
205 index for each grid cell of 1 km² that range from 0 to 100 (higher number indicate higher
206 human influence) (LWP-2, 2005). Using this information, we found higher human
207 pressures on the environment at lower elevations (Figure S1). When analyzing the

208 elevational patterns of annual mean temperature changes, annual precipitation changes
209 and human footprint index, we used an improved T-test to account for the influence of
210 spatial autocorrelation on the significance of the model (Dutilleul, 1993).

211 *2.3. Data Analysis*

212 In order to evaluate the changes in species elevational distribution, we divided our
213 dataset of species occurrences into two periods: 1950 - 1988 and 1989 - 2018. We chose
214 the cutoff year 1988 based on the assessment of previous studies relying on climate
215 change time series in China (Wang et al., 2010). We cleaned the species occurrence data
216 during both periods following two principles. First, we selected only those species
217 occurring during both periods. Second, each selected species must occur at least ten
218 times within each of the two studied periods to be able to compute reliable information
219 on each species elevational distribution during a given time period. Following these
220 principles, we focused on 231 species of seed plants, **totalling** 16,372 and 18,995
221 occurrence records during 1950 - 1988 and 1989 - 2015, respectively (Figure S2).

222 To assess distribution changes over time, we calculated the centroid of the range
223 as well as the upper and lower limits for each time period and for each species (both
224 native and non-native) separately. Specifically, the centroid elevation per species in
225 each time period was calculated as the average elevation of all sampled occurrences,
226 and the lower and upper elevational limits of a species were calculated as the 5%
227 quantile and 95% quantile of all sampled occurrences, respectively. We used Student's
228 pairwise *t*-tests to assess the significance of the elevational changes between the two
229 periods, running a separate test for the native and non-native plants. **The hypothesis of**
230 **the t-test for the elevational changes of native and non-native plants is satisfied, and**
231 **they are normally distributed (Figure S3).** Generalized linear model (GLMs) were used
232 to analyze the relationship between elevational changes and changes in the upper/lower
233 limits of the non-native and native plant species.

234 In order to test whether there is sampling bias caused by specimen gatherers, we
235 developed a null-model approach to estimate the null expectation of the elevational
236 shifts of a species between the two studied periods (1950 - 1988 and 1989 - 2018). The

237 method works as follows (Zu et al., 2021): first (step 1), we permuted species names of
238 all occurrence records within the two time periods separately to generate randomized
239 positions of each species occurrence for a given time period; then (step 2), we estimated
240 the elevational shift for each species computing the exact same metrics as explained
241 above for the empirical data but based on the randomized dataset generated by step 1;
242 we repeated steps 1 and 2 for 1,000 times to generate 1,000 randomized iterations (step
243 3) of elevational range shifts for each range shift position (centroid and range margins);
244 and finally (step 4), we tested the significance of the observed elevational range shifts
245 of each species against the distribution of the null expectation generated by the 1,000
246 iterations .

247 To evaluate how climatic requirements of each native and non-native plant species
248 influence the magnitude of elevational range shifts at the centroid of the range and at
249 both margins, we fitted species distribution models (SDMs) for each of the 210 native
250 and 21 non-native plant species. MaxEnt was used to predict species distributions, and
251 the specific parameter setting was based on our past paper (Zu et al., 2021). The 231
252 species distributions data were obtained from global Biodiversity Information Facility
253 (GBIF, <http://www.gbif.org/>), China National Specimen Resources Platform (NSII,
254 <http://www.nsii.org.cn/>), China Digital Herbarium (CVH, <http://www.cvh.org.cn/>),
255 RAINBIO (Dauby et al., 2016), and plant information with ecological network (BIEN,
256 <http://bien.nceas.ucsb.edu/bien/biendata/>). A total of 14,173 data distribution points
257 were obtained after clearing the distribution records. We then thinned the occurrence
258 records to a spatial resolution of 2.5 arc minutes to reduce the potential influences of
259 spatial biases (Aiello-Lammens et al., 2015). The climate data were obtained from the
260 WorldClim database (<http://www.worldclim.org>) with a spatial resolution of 2.5 arc
261 minutes. Six major bioclimatic variables were finally selected after **eliminating** the
262 collinearity between climatic variables. GLMs were used to test the relationships
263 between elevation changes of the native and non-native plant species and the climatic
264 factors constraining the distribution range. All analyses were conducted in R version
265 3.4.1 (Team, 2017).

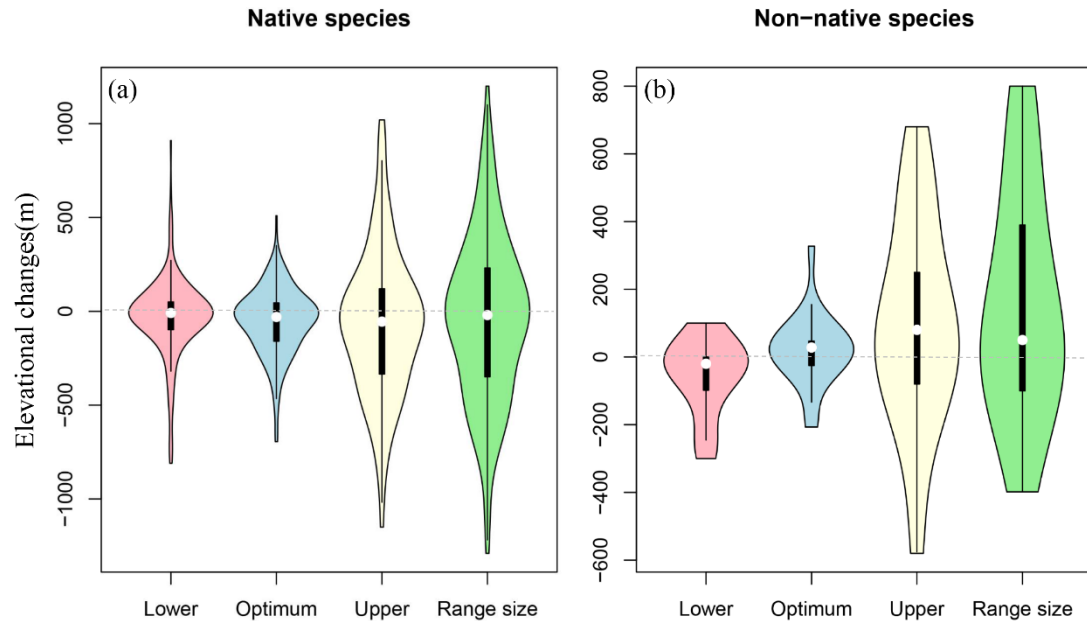
266

267 **3. Results**

268 *3.1. Elevational migration of native and non-native plants in Mt. Jinfo*

269 Among the 231 seed plants, 32.03% (74 sp) showed significant upward shifts in their
270 centroid elevations, 47.62% (110 sp) showed downward shifts, and 20.35% (47 sp)
271 remained unchanged in their elevational distributions (Fig. S2a). Specifically, among
272 the 21 non-native plants species, the proportion of upward and downward shifts
273 accounted for 47.62% (10 sp) and 33.33% (7 sp), respectively (Fig. S2b). Among the
274 210 native plant species, the proportion of upward and downward shifts accounted for
275 30.95% (65 sp) and 50.00% (105 sp), respectively (Fig. S2c). The centroids elevation
276 of all species shifted 47.6 m downward on average, the non-native plants species shifted
277 19.2 m upward on average, and the native species shifted 53.8 m downward on average
278 (Table S1; Fig. 2). After resampling, both of the native and non-native plant species
279 showed significant differences in the historical and current survey records (see Table
280 S2).

281 Moreover, the magnitude of species' centroid elevation shifts of both native and
282 non-native plants were negatively related to their historical centroid elevations (Fig. 3b,
283 c). Specifically, the non-native species and native species in lowland (e.g. species living
284 below 800 m) tended to shift upward 42 ± 85 m and 54 ± 83 m on average, respectively.
285 However, two non-native species living about 1000 m tend to downhill shifts, and most
286 native species living above 1400m downhill shifts.

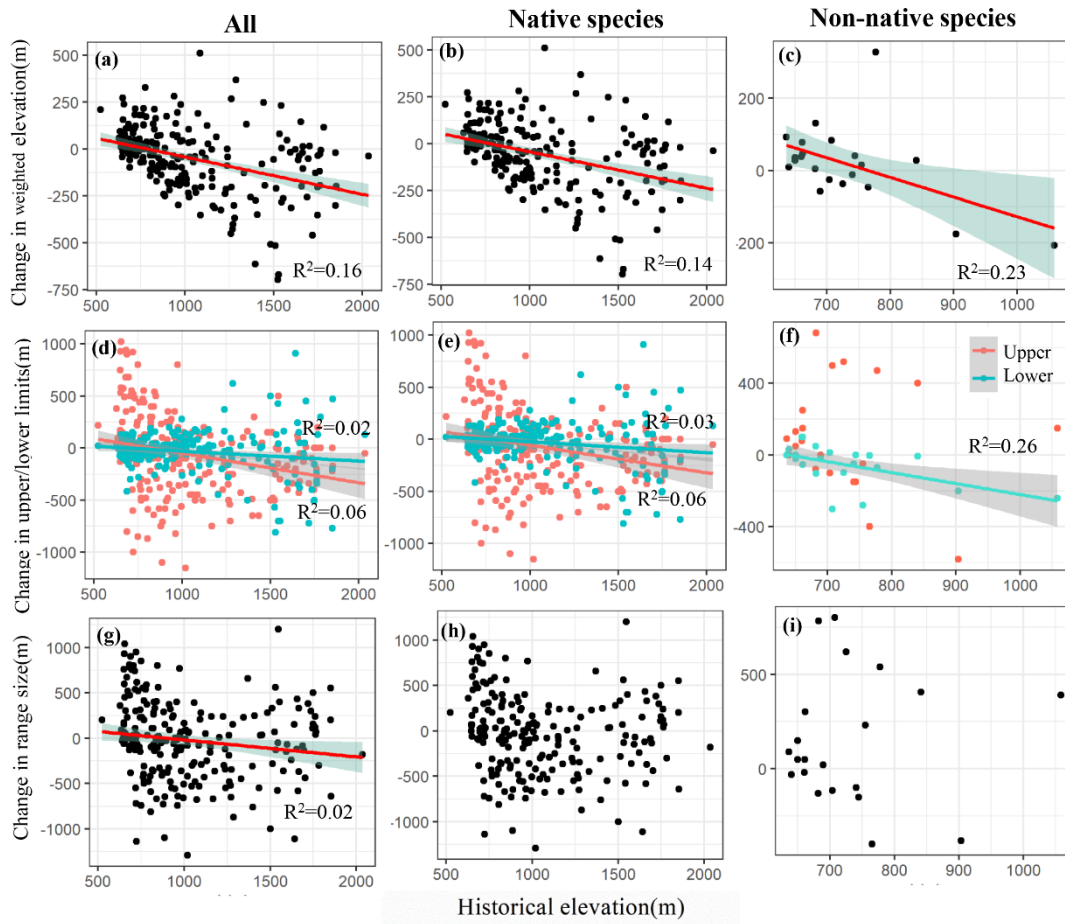


287

288 **Fig. 2.** Changes in range attributes of native (a) and non-native (b) plant species in Mt.
 289 Jinfo.

290 **3.2. Changes in upper and lower limits of native and non-native plants**

291 Both the upper and lower range limits of all species shifted downhill with an average
 292 magnitude of 56.3 m and 33.44 m (Table S1, Fig.2). The upper and lower range limits
 293 of native plants significantly shifted downward, with an average magnitude of -70.6 m
 294 and -29.5 m. The magnitude of shifts at both the upper and lower range limits of native
 295 plants were significantly correlated with the historical centroid elevation (Fig 3e).
 296 However, the upper and lower range limits of non-native plants significantly shifted
 297 93.3 m upward and shifts 54.6 m downhill. Only the magnitude of shifts at lower range
 298 limits of non-native plants were significantly correlated with the historical centroid
 299 elevation (Fig. 3f).



300

301 **Fig. 3.** Relationship between changes in elevation ranges shifts (weighted elevation,
 302 upper/lower limits and range size) and their elevations of all plants, native and non-
 303 native plant species.

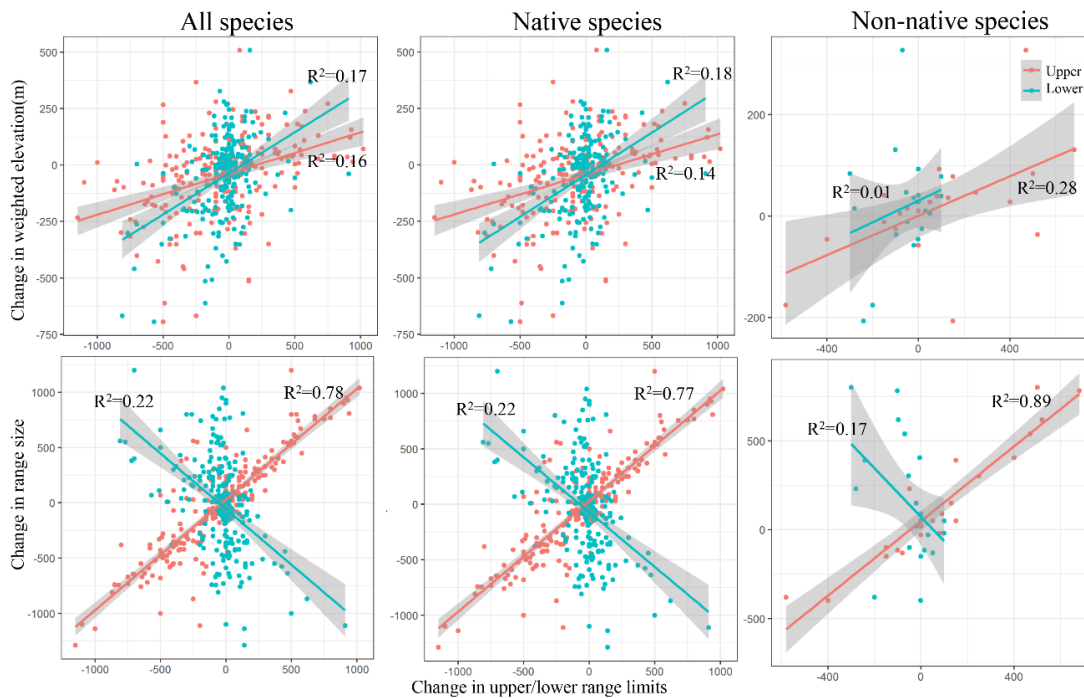
304 **3.3. Changes in the elevational distribution range size of seed plants**

305 The distribution range size of all seed plants shrank about 22.8 m on average, and
 306 showed a significant negative correlation with the historical centroid elevation (Table
 307 S1, Fig. 2; Fig. 3g). The decrease in elevational range size was more pronounced in
 308 high-elevation species compared to lowland species (Fig. 3g). The distribution range
 309 size of both non-native and native species showed no significant correlation with their
 310 historical centroid elevation (Fig. 3h, i). The distribution range size of non-native plants
 311 showed an increasing trend, with an average increase of 149.9 m, while the distribution
 312 range size of native plants shrank about 40.1 m (Table S1, Fig.2).

313 **3.4. Relationship between the native/non-native elevational shifts and the**
314 **upper/lower range limits**

315 The centroid elevations changes of all species were positively correlated with the
316 change in upper/lower range limits. For the native species, the correlations between
317 centroid elevation changes and lower limit changes were consistently stronger than
318 those with upper limit changes, while the non-native plants showed an opposite
319 correlation (Fig. 4).

320 For all species, changes in elevational range size had a negative correlation with
321 the changes in lower range limits ($R^2 = 0.22$, $p < 0.001$), while a stronger positive
322 correlation with the changes in the upper range limits ($R^2 = 0.78$, $p < 0.001$). For both
323 the non-native and native species, change in upper range limits had higher explanatory
324 power for the elevational range size than changes in the lower ranges limits (Figure S4,
325 5).

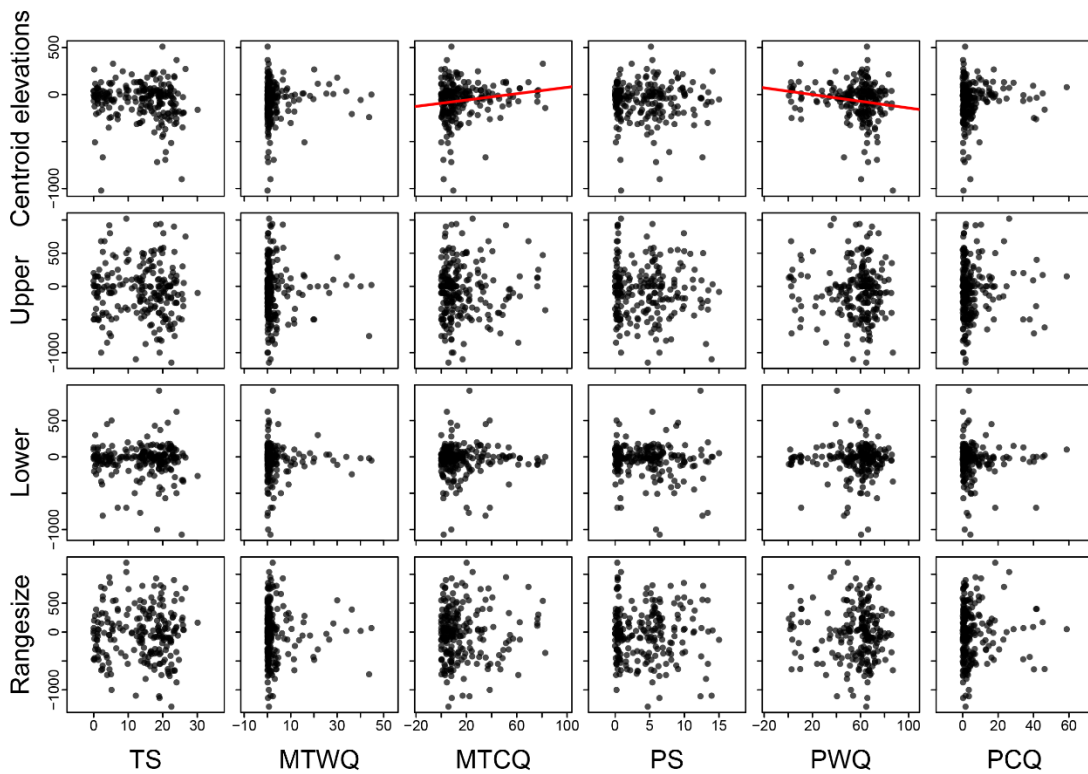


326
327 **Fig. 4.** Relationships of the changes in the weighted elevations and range sizes with the
328 changes in the upper/lower range limits of the native and non-native plant species in
329 Mt. Jinfo from 1950–1988 to 1989–2018. The x-axes represent the changes in upper
330 (red points with red line) and lower (blue points with blue line) range limits. The y-axes
331 represent the changes in weighted elevation and the elevational range size. The 95%

332 confidence intervals of the regression lines are shown in grey.

333 3.5. The causes of species elevational shifts

334 The elevational range shifts of all species were significantly positive correlated
335 with the importance of mean temperature of coldest quarter (MTCQ) ($R^2 = 0.24$), while
336 negatively correlated with the importance of precipitation of warmest quarter (PWQ)
337 ($R^2 = 0.30$) (Fig. 5). Specifically, native species showed a similar pattern with the all
338 species, suggesting that changes in temperature ($R^2 = 0.26$) and precipitation ($R^2 = 0.31$)
339 influenced the elevational shifts of native plants (Figure S4). However, for non-native
340 species, only the change in lower limits was significantly positively correlated with the
341 importance of MTCQ ($R^2 = 0.24$) (Figure S5).



342

343 **Fig. 5.** Relationships of the changes in optimum elevations, upper range limits, lower
344 range limits and range sizes with climatic suitability of all species in Mt. Jinfo. TS,
345 temperature seasonality; MTWQ, mean temperature of the warmest quarter; MTCQ,
346 mean temperature of the coldest quarter; PS, precipitation seasonality; PWQ,
347 precipitation of the warmest quarter; PCQ precipitation of the coldest quarter.

348

349 **4. Discussion**

350 ***4.1. Different elevational shifts of native and non-native species***

351 We reported that the proportion of upward shifts in native plants is lower than that
352 of non-native plants. Moreover, the magnitude and direction of the elevational shifts in
353 both upper and lower elevational limits are opposite between the native and non-native
354 plants. Specifically, the upper limits of native plants shifted downward, while the upper
355 limits of non-native plants shifted upward on average. Our results differ from previous
356 studies on vascular plants in Hawaii, where the upper limit of native species remained
357 unchanged, while the upper limit of non-native plants shifted upward (Koide et al.,
358 2017). It is likely that differences in the ecological and environmental conditions in
359 different mountains led to difference in the elevational shifts of native and non-native
360 plants. **Based on our finding, we conclude that the decrease in precipitation at high-**
361 **altitude regions leads to downward shift of species.** However, there is a consistent trend
362 in the upward shifts of the upper elevational limit for non-native plants in different
363 mountains. For example, in the mountains of Switzerland, the non-native plants shifted
364 significantly from lowlands to subalpine zones (Petitpierre, 2016). The non-native
365 plants that could move to high elevations globally are not specialists with highly
366 specific climatic tolerance but tend to be generalists with a wide range of climate
367 tolerance (Alexander et al., 2011). In this study, upward shifts of the upper elevational
368 limit were observed in most non-native herbaceous plants, e.g. *Dysphania ambrosioides*,
369 *Capsella bursa-pastoris*, *Cardamine flexuosa*, and *Mirabilis jalapa*. As climate warms,
370 these species could move upward rapidly and threatened the mountain ecosystems at
371 mid-elevations. In this study, we hypothesize that the differences in climate suitability
372 between the native and non-native plants lead to the differences in the magnitude and
373 direction of elevational shifts.

374 On the other hand, we found that the optimal elevations of native species shifted
375 downhill, which is likely due to downward shifts of their lower elevational limits. This
376 result is different from the significant upward shifts of the lower limit of seed plants in
377 Mt. Gongga in southwest China and in the mountains in Europe (Gottfried et al., 2012;

378 Zu et al., 2021). The reason might be that the changes of temperature and precipitation
379 along the elevation gradient in different mountain regions are different. In Mt. Jinfo,
380 we found that the high-altitude regions show a trend of gradual aridification, causing
381 native plants growing in the high-altitude regions to shift downward. Another possible
382 reason for the lower limit of native species is the ecological restoration of the lowland
383 regions, which reflects changes in human activities and their impact on species
384 distribution. But the impact of human activities needs to be further evaluated in future
385 studies. In this study, the lower elevational limits changes were mainly found in the
386 native plants living in the high-altitude regions, such as *Poa Pratensis*, *Aconitum*
387 *Scaposum*, *Sedum oligospermum*, and *Cotoneaster horizontalis*. The downward shifts
388 of the lower limits for these plants may be affected by severe drought stress (e.g.
389 reduced precipitation at high elevations) (Figure 1). This finding suggest that in order
390 to avoid species extinction at high elevations, protecting habitats at middle elevations
391 is important.

392 ***4.2. Different changes in elevational range size of native and non-native species***

393 Previous studies on the changes in species range sizes have mostly employed
394 species distribution modeling. Moreover, few studies have compared the differences in
395 the range changes of native and non-native plants in mountains (Datta et al., 2019;
396 Ahmad et al., 2021). Based on the detailed distribution information of species over the
397 past few decades, we found that the elevational range sizes of most native plant species
398 in Jinfo Mountain shrank, while the range sizes of non-native plant species expanded.
399 The proportion of non-native plant species with range size expansion was higher than
400 that of native species (Figure 4). These findings support the niche breadth hypothesis,
401 which states that non-native species with broad niches are better adapted to local
402 environments, and hence are able to extend their elevational ranges (Polechova and
403 Barton, 2015).

404 Previous studies have predicted that non-native plants tend to migrate to the high-
405 altitude regions due to climate warming and habitat fragmentation, and the elevational
406 distributions changes of non-native species will become a severe threat to the alpine

407 **ecosystems** (Bellard et al., 2012; Stubbs et al., 2018). Indeed, our study indicated that
408 the upper range limits of non-native plant species in Mt. Jinfo has significantly moved
409 to a higher altitude, and the expansion of the non-native species range size is mainly
410 due to the upward migration of the upper range limits (Fig. 5). The reason might be that
411 non-native species have high drought tolerance. Moreover, these non-native species
412 also tend to have broad climatic niches and can live both in lower and higher elevation
413 regions (Alexander et al., 2011; Petitpierre, 2016). Previous studies indicated that both
414 human activities and climate factors play an important role in plant invasion in China's
415 natural forests (Wang et al., 2021). Although our result showed that the human influence
416 and temperature changes are stronger in the lowland regions than in the high-elevation
417 regions in Mt. Jinfo (Figure S2), we should pay more attention to the threats induced
418 by non-native species at higher elevations, where warm and humid climate is conducive
419 to the reestablishment of non-native species. As globalization and human activities
420 increases, the incidence of new invaders moving into higher elevation might rise, and
421 thus, the management of non-native species should be strengthened in high elevation
422 regions (Pauchard et al., 2015). This study emphasizes the crucial need to make policy
423 decisions to control non-native species in China's nature reserve.

424

425 **5. Conclusions**

426 We found that the directions of the elevational redistribution of native and non-
427 native species were opposite. The native seed plant species in Mt. Jinfo have shifted
428 their centroid elevations downhill, and non-native species have shifted their centroid
429 elevations upward on average during the last seven decades. Both of native and non-
430 native species shifted the lower range limits downhill. However, native and non-native
431 plant species showed differences in their upper range limits and elevational range size.
432 Only the upper elevation limit of non-native species shifted upward, while native plants
433 shifted their upper limits downward on average. The native species shrunk their
434 elevational range sizes, while most non-native species expanded their elevational range
435 sizes. The shifts of centroid elevations of non-native plants were dominated by upper

436 limit changes, while those of native plants were dominated by lower limit changes. The
437 elevational range size changes of both native and non-native species are mainly
438 influenced by the upper range limits. Changes in temperature and precipitation had
439 significant explanatory power for the elevational range shifts of native plants but not
440 non-native ones, suggesting that climate change might have serious impacts on the
441 native plants. It is an urgent need to improve the monitoring and management of non-
442 native plant species in the lowland regions, and to prevent their shifts to high elevations.
443 This work provided a new perspective to understand the elevational distribution of
444 native and non-native plant species in other mountains, and also proposed conservation
445 strategies to protect the seed plants in Mt. Jinfo.

446 **CRedit authorship contribution statement**

447 ZW and KZ collected the data, conceived the idea and wrote the manuscript. JL and KZ
448 conducted the analyses. JL, ZS, FC and NS provided ideas and suggestions. All authors
449 contributed to the writing.

450 **Data availability**

451 I have shared the available data within this article.

452 **Declaration of Competing Interest**

453 We declare that we have no competing financial and personal relationships with other
454 people or organizations that could inappropriately influence our work reported in this
455 paper.

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Figures and tables

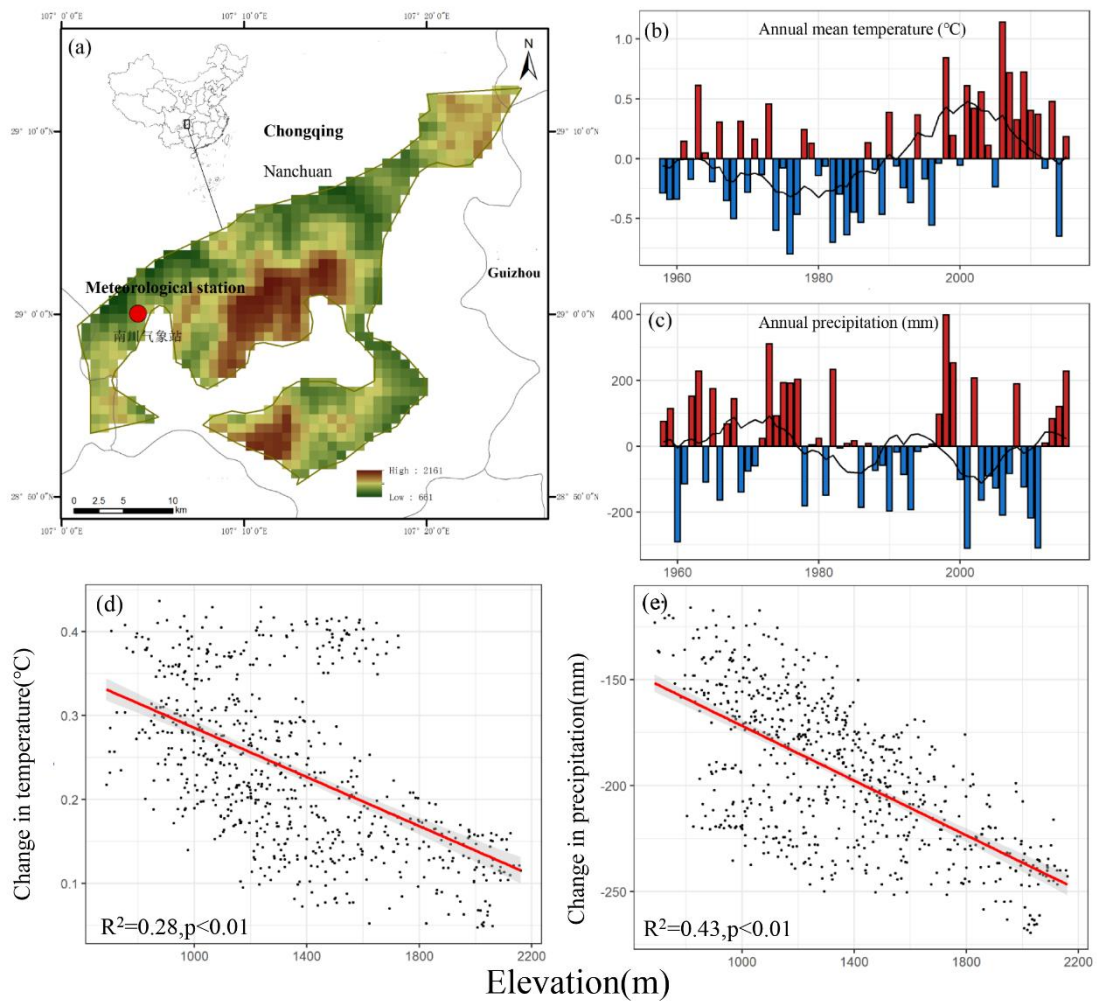


Fig. 1. Geographical location (a) and climate change from 1958 to 2015 in Mt. Jinfo. b: Changes in mean annual temperature (MAT) across the period 1958 - 2015; c: Changes in annual precipitation (AP) across the period 1958 - 2015; d: The changes in mean annual temperature between 1980 - 1988 and 2007 - 2015 along the elevation gradients; e: The changes in annual precipitation between 1980 - 1988 and 2007 - 2015 along the elevation gradients. Each dot in d and e represents climate changes within each 1×1 km grid cell along elevation gradients between the two periods.

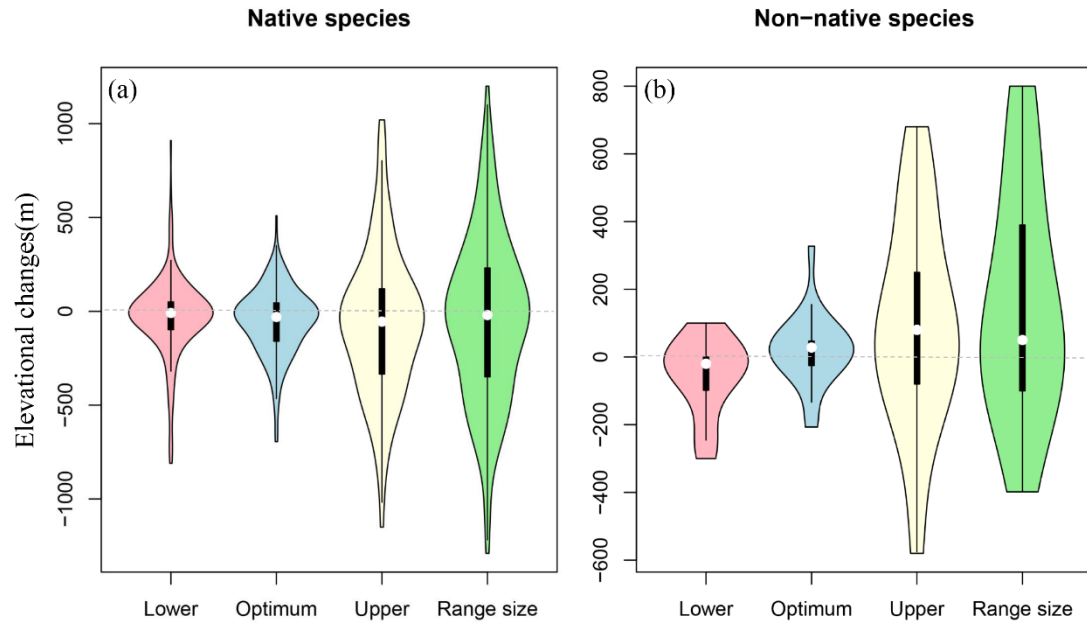


Fig. 2. Changes of range attributes for native (a) and non-native (b) plant species in Mt. Jinfo.

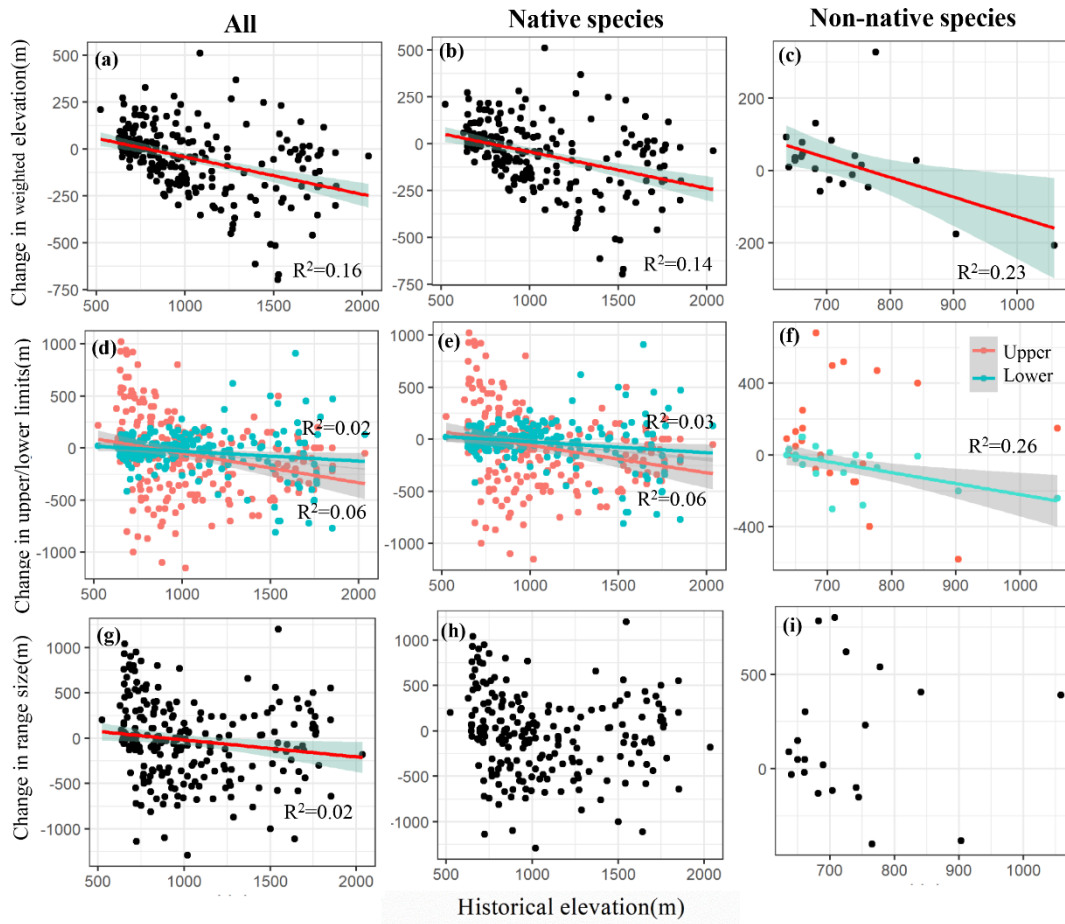


Fig. 3. Relationship between changes in elevation ranges shifts (weighted elevation, upper/lower limits and range size) and their elevations of all plants, native and non-native plant species.

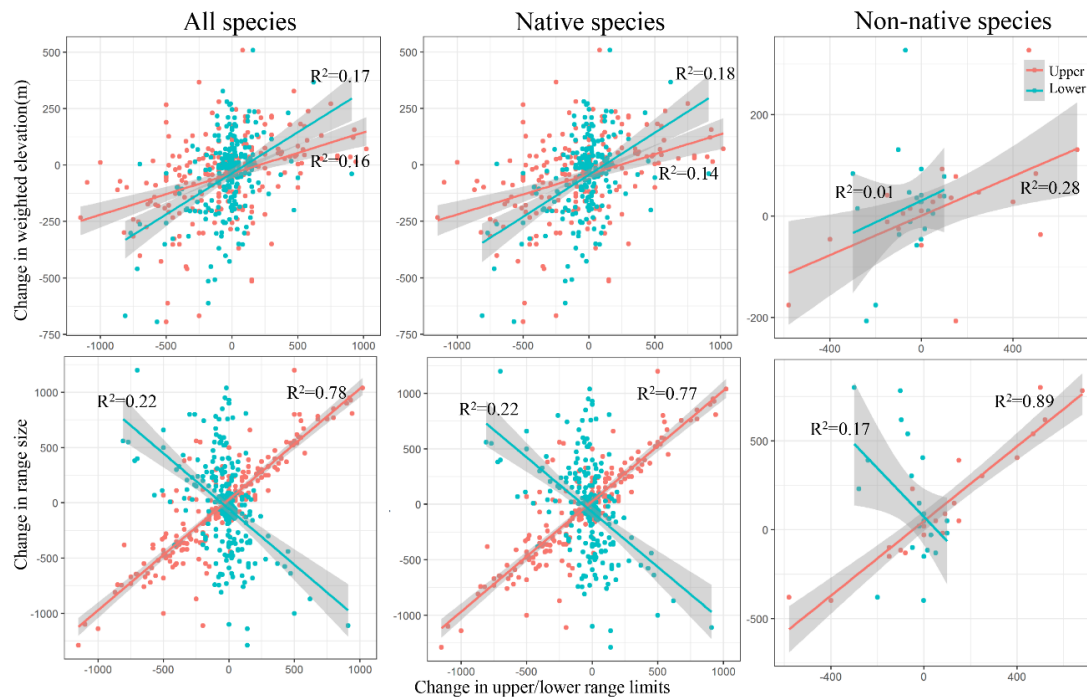


Fig. 4. Relationships of the changes in the weighted elevations and range sizes with the changes in the upper/lower range limits of the native and non-native plant species in Mt. Jinfo from 1950–1988 to 1989–2018. The x-axes represent the changes in upper (red points with red line) and lower (blue points with blue line) range limits. The y-axes represent the changes in weighted elevation and the elevational range size. The 95% confidence intervals of the regression lines are shown in grey.

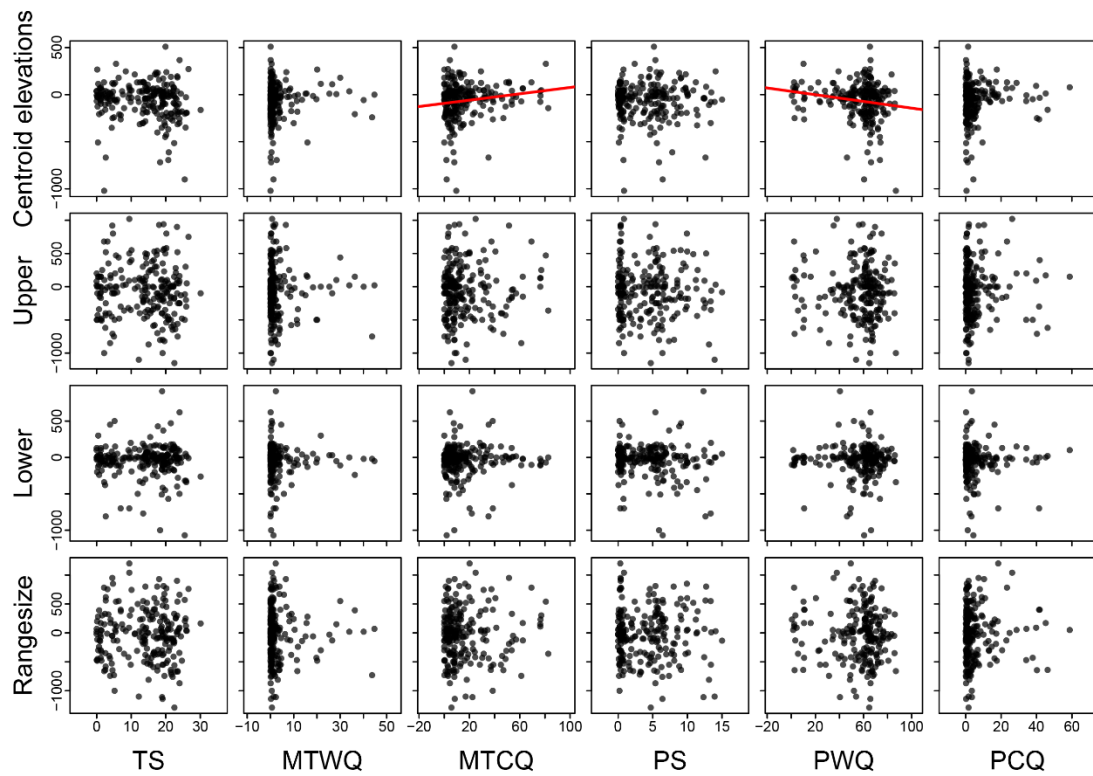


Fig. 5. Relationships of the changes in optimum elevations, upper range limits, lower range limits and range sizes with climatic suitability of all species in Mt. Jinfo. TS, temperature seasonality; MTWQ, mean temperature of the warmest quarter; MTCQ, mean temperature of the coldest quarter; PS, precipitation seasonality; PWQ, precipitation of the warmest quarter; PCQ precipitation of the coldest quarter.