

# Different range shifts and determinations of elevational redistributions of native and non-native plant species in Jinfo Mountain of subtropical China

Kuiling Zu, Zhiheng Wang, Jonathan Lenoir, Zehao Shen, Fusheng Chen,

Nawal Shrestha

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Title: Different range shifts and determinations of elevational 1 redistributions of native and non-native plant species in Jinfo 2 3 **Mountain of subtropical China List of Authors:** 4 Kuiling Zu<sup>a, b, c</sup>, Zhiheng Wang<sup>a</sup>\*, Jonathan Lenoir<sup>d</sup>, Zehao Shen<sup>a</sup>, Fusheng Chen<sup>b, c</sup>, 5 Nawal Shrestha<sup>e</sup> 6 **Institutional affiliations:** 7 <sup>a</sup>Institute of Ecology, and Key Laboratory for Earth Surface Processes of the Ministry 8 9 of Education, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China 10 11 <sup>b</sup>Key Laboratory of National Forestry and Grassland Administration on Forest 12 Ecosystem Protection and Restoration of Poyang Lake Watershed, College of Forestry, 13 Jiangxi Agricultural University, Nanchang 330045, China <sup>c</sup>Jiangxi Provincial Key Laboratory of Silviculture, College of Forestry, Jiangxi 14 Agricultural University, Nanchang 330045, China 15

- <sup>16</sup> <sup>d</sup>UMR CNRS 7058 "Ecologie et Dynamique des Systèmes Anthropisés" (EDYSAN),
- 17 Université de Picardie Jules Verne, 1 Rue des Louvels, 80000 Amiens, France
- <sup>18</sup> <sup>e</sup>State Key Laboratory of Grassland Agro-Ecosystems, College of Ecology, Lanzhou
- 19 University, Lanzhou 730000, China

## 20 Author for correspondence:

- 21 \*Email: zhiheng.wang@pku.edu.cn
- 22 Telephone: 010-62745157

#### 23 ABSTRACT

24 Species are changing their elevational distributions in response to climate change, leading to biodiversity loss and changes in community structure. Yet whether native 25 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 elevational shifts of native vs. non-native species led to the increase in the elevational 39 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 a new perspective for understanding the elevational redistribution of native and non-45 46 native plant species in subtropical mountains, and suggests that climate change has stronger influence on native species than non-native species. 47

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

2

## 50 **1. Introduction**

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

Species are known to have shifted their elevational ranges in response to 66 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 influence the structure and functioning of mountain ecosystems and lead to significant 69 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 et al., 2020; Vitasse et al., 2021; Zu et al., 2021). Current evidence suggests that the 74 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 downslope (Crimmins et al., 2011). The former may be driven by the velocity and 81 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 crucial to understand the huge variability in the direction and magnitude of 84 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 in subtropical mountains, where plant diversity is extremely rich (Mamantov et al., 88 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 crucial. In addition, studies reporting species elevational range shifts in response to 91 92 climate change tend to focus almost exclusively on the changes in the centroid of elevation range (Lenoir et al., 2008; Crimmins et al., 2011) or changes in upper range 93 94 limit (Pauli et al., 2012; Grytnes et al., 2014). However, to better understand the responses of species to climate change, it is necessary to simultaneously assess changes 95 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 to colonize new habitats (Dainese et al., 2017; Koide et al., 2017; Lembrechts et al., 101 102 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 species expanding their range upward in elevation could alter the functioning of 106 107 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) and thus different patterns in the expected direction and magnitude of elevational range 111 112 shifts under macroclimate warming (Dainese et al., 2017; Koide et al., 2017). Native species have been evolving in response to the local changes in environmental conditions 113 114 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 of range filling and thus, not likely to be in equilibrium with their realized climatic 117 niche (Koide et al., 2017). As already demonstrated for temperate and tropical 118 119 mountains (Dainese et al., 2017; Koide et al., 2017), Therefore, we speculate that the direction and magnitude of native and non-native plants will also differ for subtropical 120 121 mountains. However, such comparisons of elevational range shifts between native and non-native plants in subtropical mountains are still lacking. 122

123 Herbarium specimens provide accurate information on the collecting time and location of species, and hence provide a unique opportunity to know how species 124 125 distributed in the past and endure the potential of evaluating how species responded to historical climate change. Mount Jinfo is located in the subtropical region of Southwest 126 127 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 al., 2014; Page et al., 2015). Currently, there are many reports of non-native plant 130 131 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 compare the dynamics of range shifts of native and non-native species in response to 133 climate change. Here, using the historical specimen records of plants in one of the 134 biodiversity hotspots in China, Mt. Jinfo, we evaluated and compared the changes in 135 136 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

did the centroid elevations, the upper and lower elevational limits, and the elevational

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

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

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



- 166 Asian Plant Synonym Lookup (APSL, <u>http://phylodiversity.net/fslik/synonym\_</u>
- 167 *lookup.htm*).



169Fig. 1. Geographical location (a) and climate change from 1958 to 2015 in Mt. Jinfo. b:170Changes in mean annual temperature (MAT) across the period 1958 - 2015; c: Changes171in annual precipitation (AP) across the period 1958 - 2015; d: The changes in mean172annual temperature between 1980 - 1988 and 2007 - 2015 along the elevation gradients;173e: The changes in annual precipitation between 1980 - 1988 and 2007 - 2015 along the174elevation gradients. Each dot in d and e represents climate changes within each 1 × 1175km 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 km by the climate dataset of the Resources and Environmental Data Cloud Platform of 184 185 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 (Hutchinson, 1998). We chose the cutoff year 1988 as the breaking points based on the 187 188 temperature changes along the long-term dataset for the study sites (Fig 1b). From these gridded products, we first computed, for each grid cell of 1 km<sup>2</sup>, long-term average 189 190 values of annual mean temperature and annual precipitation during two time periods (1980 - 1988 vs. 2007 - 2015) before computing the difference or change in annual 191 192 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 precipitation (Fig 1d, e). According to these climatic data, we found that elevation is 196 negatively correlated with temperature changes between 1980 - 1988 and 2007 - 2015 197  $(R^2 = 0.28, p < 0.01)$ , which indicates that the magnitude of climate warming is greater 198 199 in the lowlands of the Jinfo mountain range (Fig. 1d). The change of annual precipitation between 1980 - 1988 and 2007 - 2015 is also negatively correlated with 200 elevation ( $R^2 = 0.43$ , p < 0.01), such that the overall decrease in annual precipitation is 201 202 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) index for each grid cell of 1 km<sup>2</sup> that range from 0 to 100 (higher number indicate higher 205 206 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

elevational patterns of annual mean temperature changes, annual precipitation changes
and human footprint index, we used an improved T-test to account for the influence of
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 dataset of species occurrences into two periods: 1950 - 1988 and 1989 - 2018. We chose 213 214 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.

In order to test whether there is sampling bias caused by specimen gatherers, we developed a null-model approach to estimate the null expectation of the elevational 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; we repeated steps 1 and 2 for 1,000 times to generate 1,000 randomized iterations (step 242 243 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 iterations . 246

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 both margins, we fitted species distribution models (SDMs) for each of the 210 native 249 and 21 non-native plant species. MaxEnt was used to predict species distributions, and 250 the specific parameter setting was based on our past paper (Zu et al., 2021). The 231 251 252 species distributions data were obtained from global Biodiversity Information Facility (GBIF, http://www.gbif.org/), China National Specimen Resources Platform (NSII, 253 http://www.nsii.org.cn/), China Digital Herbarium (CVH, http://www.cvh.org.cn), 254 RAINBIO (Dauby et al., 2016), and plant information with ecological network (BIEN, 255 256 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 records to a spatial resolution of 2.5 arc minutes to reduce the potential influences of 258 spatial biases (Aiello-Lammens et al., 2015). The climate data were obtained from the 259 260 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 collinearity between climatic variables. GLMs were used to test the relationships 262 between elevation changes of the native and non-native plant species and the climatic 263 264 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

Among the 231 seed plants, 32.03% (74 sp) showed significant upward shifts in their 269 270 centroid elevations, 47.62% (110 sp) showed downward shifts, and 20.35% (47 sp) remained unchanged in their elevational distributions (Fig. S2a). Specifically, among 271 272 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 30.95% (65 sp) and 50.00% (105 sp), respectively (Fig. S2c). The centroids elevation 275 of all species shifted 47.6 m downward on average, the non-native plants species shifted 276 277 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 showed significant differences in the historical and current survey records (see Table 279 280 S2).

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



287

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

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

Both the upper and lower range limits of all species shifted downhill with an average 291 magnitude of 56.3 m and 33.44 m (Table S1, Fig.2). The upper and lower range limits 292 293 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 limits of non-native plants were significantly correlated with the historical centroid 298 299 elevation (Fig. 3f).



300

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

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

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

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





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%

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

## 333 3.5. The causes of species elevational shifts

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



342

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.

348

## 349 **4. Discussion**

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

We reported that the proportion of upward shifts in native plants is lower than that 351 of non-native plants. Moreover, the magnitude and direction of the elevational shifts in 352 353 both upper and lower elevational limits are opposite between the native and non-native plants. Specifically, the upper limits of native plants shifted downward, while the upper 354 355 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., 2017). It is likely that differences in the ecological and environmental conditions in 358 different mountains led to difference in the elevational shifts of native and non-native 359 360 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 in the upward shifts of the upper elevational limit for non-native plants in different 362 363 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 plants that could move to high elevations globally are not specialists with highly 365 specific climatic tolerance but tend to be generalists with a wide range of climate 366 367 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 direction of elevational shifts. 373

On the other hand, we found that the optimal elevations of native species shifted downhill, which is likely due to downward shifts of their lower elevational limits. This result is different from the significant upward shifts of the lower limit of seed plants in 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 regions, which reflects changes in human activities and their impact on species 383 384 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 of the lower limits for these plants may be affected by severe drought stress (e.g. 388 389 reduced precipitation at high elevations) (Figure 1). This finding suggest that in order to avoid species extinction at high elevations, protecting habitats at middle elevations 390 is important. 391

#### 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 species distribution modeling. Moreover, few studies have compared the differences in 394 395 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 high405 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 also tend to have broad climatic niches and can live both in lower and higher elevation 412 413 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 and temperature changes are stronger in the lowland regions than in the high-elevation 416 regions in Mt. Jinfo (Figure S2), we should pay more attention to the threats induced 417 418 by non-native species at higher elevations, where warm and humid climate is conducive to the reestablishment of non-native species. As globalization and human activities 419 420 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 their centroid elevations downhill, and non-native species have shifted their centroid 428 429 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 native plants. It is an urgent need to improve the monitoring and management of non-441 442 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

We declare that we have no competing financial and personal relationships with other people or organizations that could inappropriately influence our work reported in this 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  $1 \times 1$ 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.