



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

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

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ABSTRACT

Species are changing their elevational distributions in response to climate change, leading to biodiversity loss and changes in community structure. Yet whether native and non-native species have consistent elevational shifts remains to be evaluated. Subtropical mountains are rich in biodiversity, sensitive to climate change, and are experiencing high risks of biological invasion. Hence exploring the changes in species elevational distributions induced by climate change in subtropical mountains is an urgent need. Here, we explored the impact of climate change on the elevational distribution of seed plant species in Jinpo Mountain (Mt. Jinpo), a subtropical mountain in China with rich plant diversity. Notably, we compared the elevational redistributions of native and non-native plants in response to climate change. The results showed that the elevational centroids of native plant species moved downhill, while those of non-native plants shifted upward on average. The upper limit of native plants shifted downward, while the upper limit of non-native plants shifted upward on average. The elevational shifts of non-native plants were dominated by changes in the upper range 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 range size of the non-native plants, but decrease in the elevational range size of native plants, especially in high altitudes. The differences in the directions and magnitudes of elevational shifts between the native and non-native plants are mainly due to differences in their climate adaptation. Changes in temperature and precipitation influenced the 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-native plant species in subtropical mountains, and suggests that climate change has stronger influence on native species than non-native species.**

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

1. Introduction

Mountains play a crucial role for sustaining biodiversity, acting simultaneously as cradles, museums (i.e., refugia) and graves (Rangel et al., 2018; Rahbek et al., 2019). Mountains' biodiversity is vital for the survival and sustainable development of human societies (Perrigo et al., 2019). The steep macroclimatic gradients running from the valley bottom to mountain summits also serve as natural laboratories to assess the 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 regions (Pépin et al., 2015), and future air temperatures will likely be higher than they are today (Nogués-Bravo et al., 2007; Rebetez and Reinhard, 2007). The acceleration of macroclimate warming on mountain summits is already accelerating the rate of species accumulation on mountain summits, with the potential to jeopardize the 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 slopes as global climate warms is essential for effective land management and conservation planning (Beaudrot et al., 2018).

Species are known to have shifted their elevational ranges in response to anthropogenic climate changes (Lenoir et al., 2008; Crimmins et al., 2011; Mamantov 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 loss of ecosystem services (Lenoir and Svenning, 2015). Over the past century, many studies have examined how plants, animals and even fungi shifted their distribution ranges along elevational gradients of mountain regions in response to climatic change (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 direction and magnitude of species elevational range shifts is highly variable and might not only vary with the velocity and direction of climate change, in terms of both temperature and precipitation, but also with baseline environmental conditions (Lenoir et al., 2020). For instance, most vascular plants from temperate forest ecosystems

shifted upslope along elevational gradients in France (Lenoir et al., 2008), while most forest plants from another macroclimatic context in California shifted chiefly downslope (Crimmins et al., 2011). The former may be driven by the velocity and direction of temperature changes, while the latter is affected by the velocity and direction of precipitation changes (Grytnes et al., 2014). Such context dependencies are crucial to understand the huge variability in the direction and magnitude of contemporary range shifts (Lenoir et al., 2020). However, previous studies have been mainly conducted in temperate or Mediterranean mountains, while fewer studies have 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., 2021; Zu et al., 2021). To better understand the redistribution of plant species along the 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 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 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 over the entire range: not only at the centroid of the range but also at the upper and lower elevational limits, in order to assess a potential reduction or expansion of a species elevational range size (Lenoir and Svenning, 2015).

In mountain ecosystems, not only native species are redistributing along mountain 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., 2017; Rew et al., 2020). This redistribution or expansion of non-native plants towards mountain summits possesses an additional threat to native plants, which face increased competition with more adaptive non-native plant species at higher elevations (Bezeng 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 mountain ecosystem as well as accelerate the loss of mountain biodiversity (Hejda et

al., 2009; Pauchard et al., 2009; Pauchard et al., 2015). Native and non-native species have different evolutionary histories and ecological backgrounds leading to different 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 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 over time. Hence, the spatial distribution of each native species along elevational gradients is more likely to be in equilibrium with its realized climatic niche. In contrast, 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 niche (Koide et al., 2017). As already demonstrated for temperate and tropical 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 mountains. However, such comparisons of elevational range shifts between native and non-native plants in subtropical mountains are still lacking.

Herbarium specimens provide accurate information on the collecting time and location of species, and hence provide a unique opportunity to know how species 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 China, where numerous botanists have collected lots of plant specimens throughout the last century (Yi and Huang, 2004). Thus, the collection density along the slopes of Mt. 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 species being invasive at Mt. Jinfo due to the increasing development of tourism in this 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 climate change. Here, using the historical specimen records of plants in one of the biodiversity hotspots in China, Mt. Jinfo, we evaluated and compared the changes in plant elevational distributions between native and non-native plants in response to

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-native plants shift in the same direction and magnitude? (3) What are the driving factors explaining elevational changes in the range of native and non-native plants?

2. Materials and methods

2.1. Study site and vegetation data

The Jinfo Mountain's Nature Reserve (107°00' - 107°22' E, 28°50' - 29°20' N) is located in the Nanchuan District, Chongqing City, China. It is a transitional zone 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 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 conditions for the reproduction and growth of plants in this region. Raw summary 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 (Yi and Huang, 2004).

The species distribution data were collected from the China National Specimen Resources Platform (NSII, <http://www.nsii.org.cn/>), the China Digital Herbarium (CVH, <http://www.cvh.org.cn>), the Global Biodiversity Information Facility (GBIF, <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 geographical coordinates were selected. Duplicate records with similar geographical 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 specimens with georeferenced occurrences collected between 1950 and 2018. We standardized the species names of all records according to the Taxonomic Name Resolution Service (TRNS, <http://tnrs.iplantcollaborative.org/TNRSapp.html>) and the

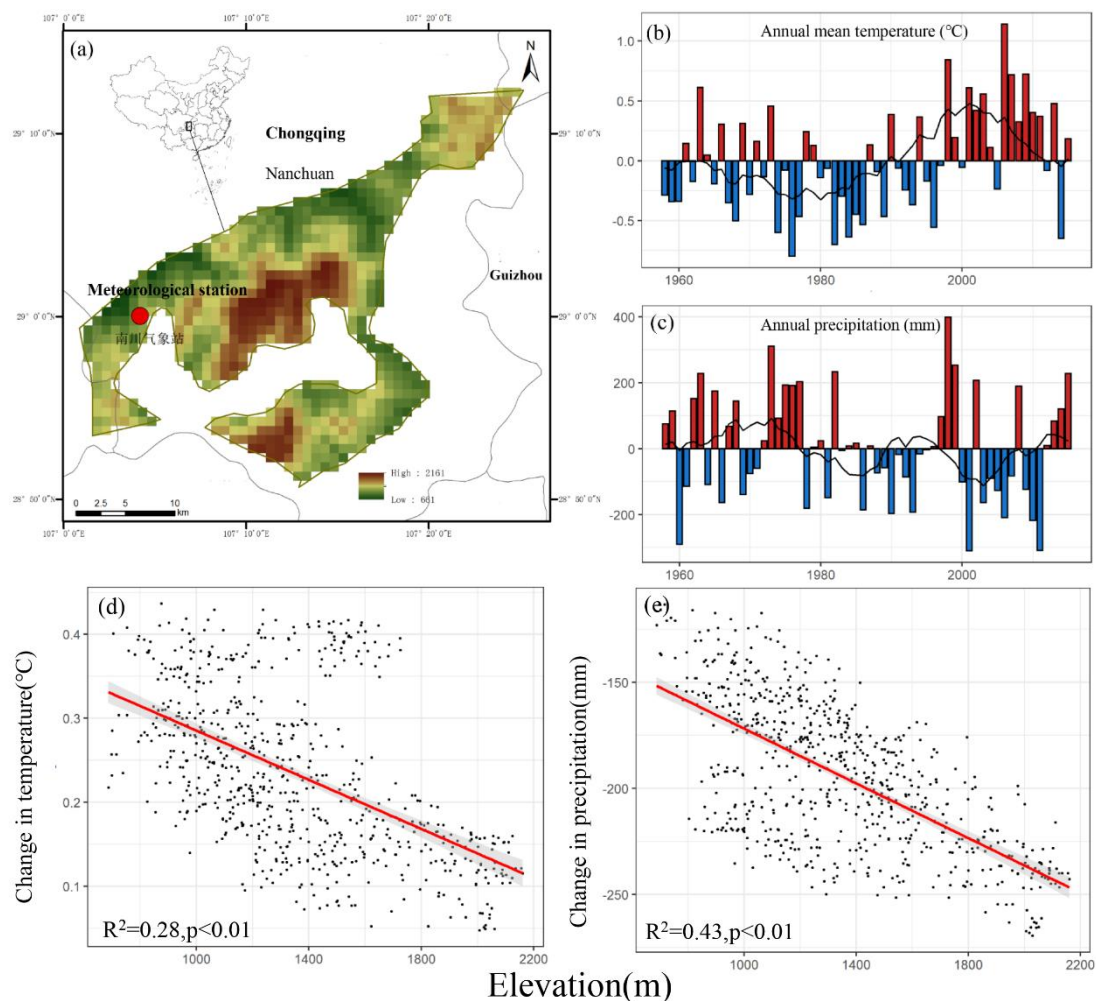


Fig. 1. Geographical location (a) and climate change from 1958 to 2015 in Mt. Jinfo. b: Changes in mean annual temperature (MAT) across the period 1958 - 2015; c: Changes in annual precipitation (AP) across the period 1958 - 2015; d: The changes in mean annual temperature between 1980 - 1988 and 2007 - 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.

2.2. Climate change and human footprint on Mount Jinfo

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

and annual precipitation throughout the past 58 years (1958 - 2015). Based on the meteorological station, we found a warming trend for mean annual temperature (Fig. 1b) but no clear trend for changes in total annual rainfall (Fig. 1c). In addition to extracting data from this specific meteorological station, we also analyzed data 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 the Chinese Academy of Sciences (<http://www.resdc.cn/>). This spatial interpolation is 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 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 km², long-term average 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 mean temperature and annual precipitation between both periods. Then, we analyzed the magnitude of these macroclimatic changes, both in mean annual temperature and annual precipitation, along the elevational gradients available within the study region. 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 negatively correlated with temperature changes between 1980 - 1988 and 2007 - 2015 ($R^2 = 0.28$, $p < 0.01$), which indicates that the magnitude of climate warming is greater in the lowlands of the Jinpo mountain range (Fig. 1d). The change of annual precipitation between 1980 - 1988 and 2007 - 2015 is also negatively correlated with elevation ($R^2 = 0.43$, $p < 0.01$), such that the overall decrease in annual precipitation is greater at high elevations than in the lowlands (Fig 1e). In addition, human activity data were derived from the human footprint (HF) index extracted from "Last of the Wild (V2)" and covering the period 1995 - 2004. We extracted the human footprint (HF) index for each grid cell of 1 km² that range from 0 to 100 (higher number indicate higher human influence) (LWP-2, 2005). Using this information, we found higher human 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).

2.3. Data Analysis

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 the cutoff year 1988 based on the assessment of previous studies relying on climate change time series in China (Wang et al., 2010). We cleaned the species occurrence data during both periods following two principles. First, we selected only those species occurring during both periods. Second, each selected species must occur at least ten times within each of the two studied periods to be able to compute reliable information on each species elevational distribution during a given time period. Following these principles, we focused on 231 species of seed plants, totalling 16,372 and 18,995 occurrence records during 1950 - 1988 and 1989 - 2015, respectively (Figure S2).

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

method works as follows (Zu et al., 2021): first (step 1), we permuted species names of all occurrence records within the two time periods separately to generate randomized positions of each species occurrence for a given time period; then (step 2), we estimated the elevational shift for each species computing the exact same metrics as explained 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 3) of elevational range shifts for each range shift position (centroid and range margins); and finally (step 4), we tested the significance of the observed elevational range shifts of each species against the distribution of the null expectation generated by the 1,000 iterations .

To evaluate how climatic requirements of each native and non-native plant species 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 and 21 non-native plant species. MaxEnt was used to predict species distributions, and the specific parameter setting was based on our past paper (Zu et al., 2021). The species distributions data were obtained from global Biodiversity Information Facility (GBIF, <http://www.gbif.org/>), China National Specimen Resources Platform (NSII, <http://www.nsii.org.cn/>), China Digital Herbarium (CVH, <http://www.cvh.org.cn/>), RAINBIO (Dauby et al., 2016), and plant information with ecological network (BIEN, <http://bien.nceas.ucsb.edu/bien/biendata/>). A total of 14,173 data distribution points 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 spatial biases (Aiello-Lammens et al., 2015). The climate data were obtained from the WorldClim database (<http://www.worldclim.org>) with a spatial resolution of 2.5 arc minutes. Six major bioclimatic variables were finally selected after eliminating the collinearity between climatic variables. GLMs were used to test the relationships between elevation changes of the native and non-native plant species and the climatic factors constraining the distribution range. All analyses were conducted in R version 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.

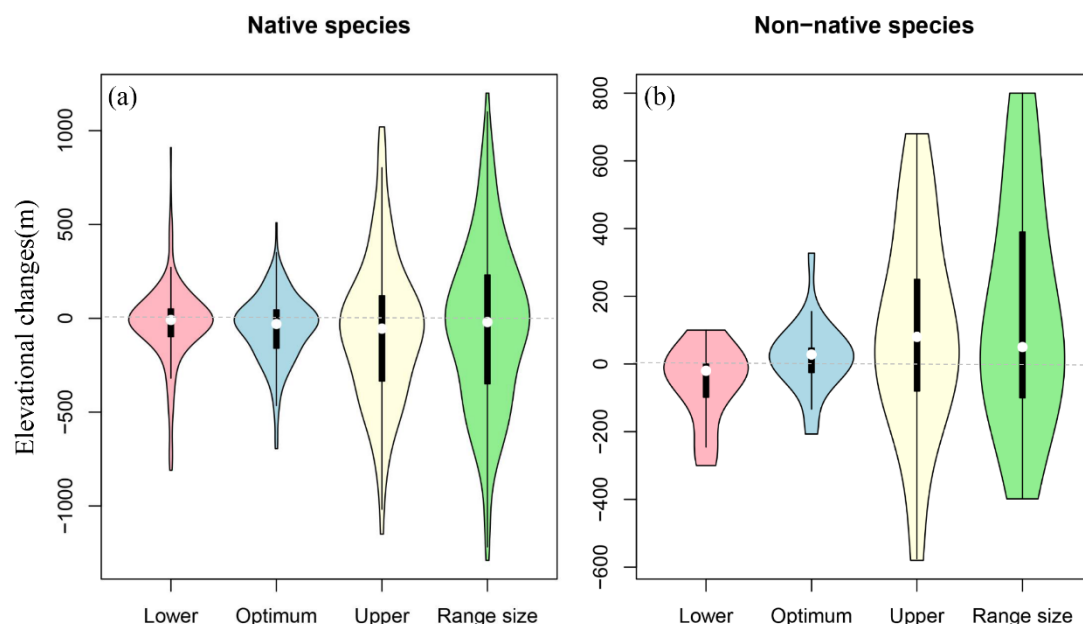


Fig. 2. Changes in range attributes of native (a) and non-native (b) plant species in Mt. Jinfo.

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 magnitude of 56.3 m and 33.44 m (Table S1, Fig.2). The upper and lower range limits of native plants significantly shifted downward, with an average magnitude of -70.6 m and -29.5 m. The magnitude of shifts at both the upper and lower range limits of native plants were significantly correlated with the historical centroid elevation (Fig 3e). However, the upper and lower range limits of non-native plants significantly shifted 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 elevation (Fig. 3f).

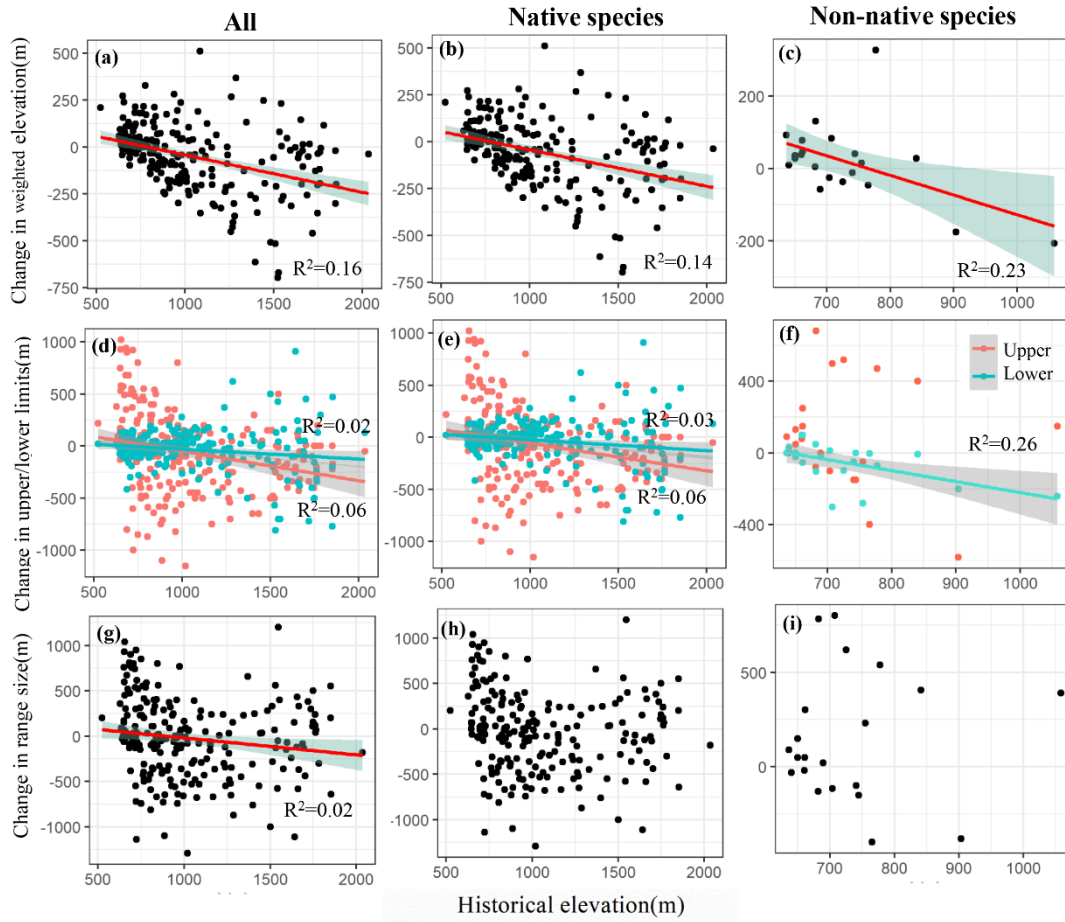


Fig. 3. Relationship between changes in elevation ranges shifts (weighted elevation, upper/lower limits and range size) and their elevations of all plants, native and non-native plant species.

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

The distribution range size of all seed plants shrank about 22.8 m on average, and 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 high-elevation species compared to lowland species (Fig. 3g). The distribution range 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 showed an increasing trend, with an average increase of 149.9 m, while the distribution range size of native plants shrank about 40.1 m (Table S1, Fig.2).

3.4. Relationship between the native/non-native elevational shifts and the 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).

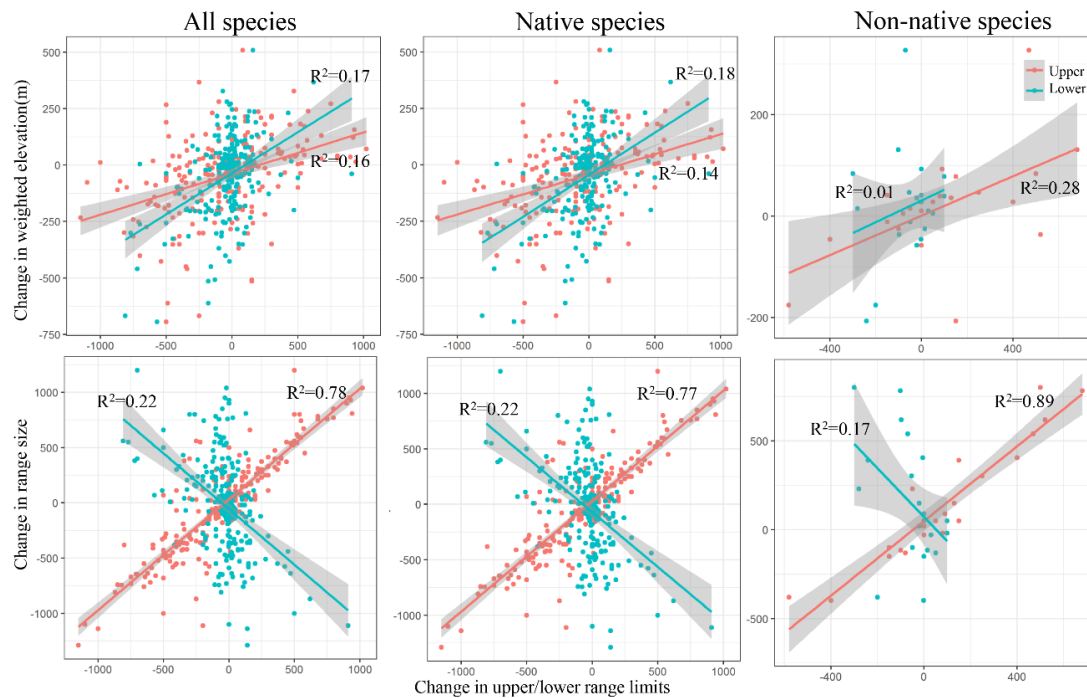


Fig. 4. Relationships of the changes in the weighted elevations and range sizes with the changes in the upper/lower range limits of the native and non-native plant species in Mt. Jinfo from 1950–1988 to 1989–2018. The x-axes represent the changes in upper (red points with red line) and lower (blue points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

confidence intervals of the regression lines are shown in grey.

3.5. The causes of species elevational shifts

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

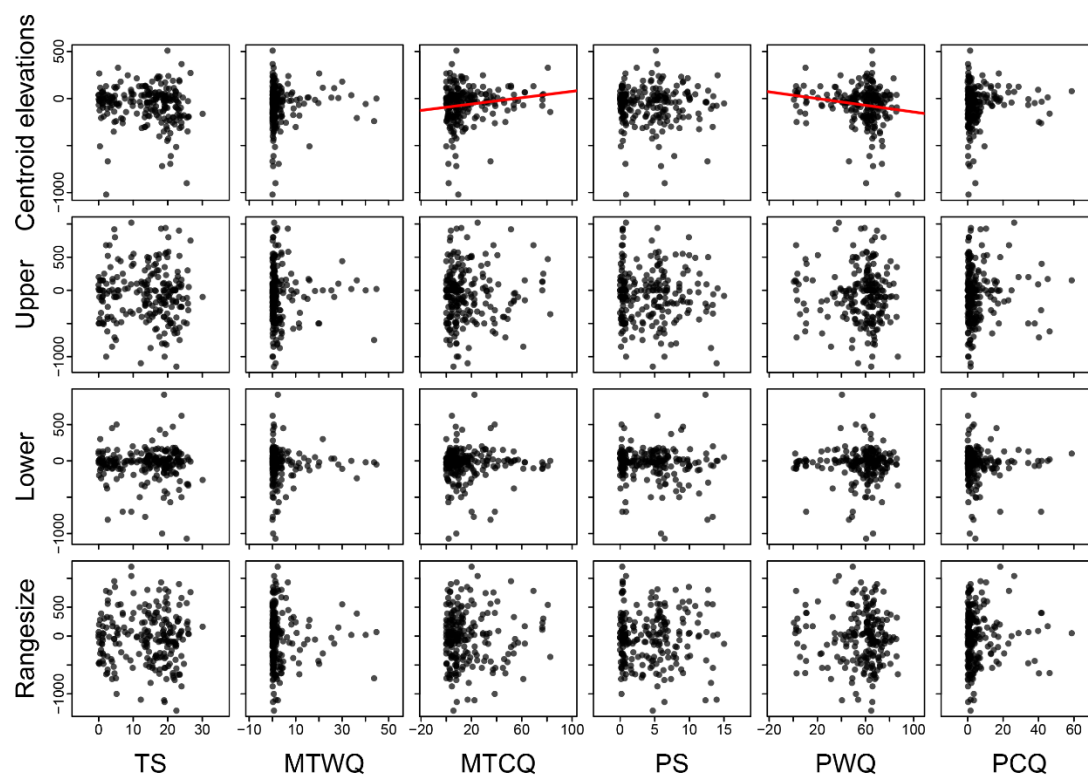


Fig. 5. Relationships of the changes in optimum elevations, upper range limits, lower range limits and range sizes with climatic suitability of all species in Mt. Jinfo. TS, temperature seasonality; MTWQ, mean temperature of the warmest quarter; MTCQ, mean temperature of the coldest quarter; PS, precipitation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

4. Discussion

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 of non-native plants. Moreover, the magnitude and direction of the elevational shifts in 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 limits of non-native plants shifted upward on average. Our results differ from previous studies on vascular plants in Hawaii, where the upper limit of native species remained 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 different mountains led to difference in the elevational shifts of native and non-native plants. **Based on our finding, we conclude that the decrease in precipitation at high-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 mountains. For example, in the mountains of Switzerland, the non-native plants shifted significantly from lowlands to subalpine zones (Petitpierre, 2016). The non-native plants that could move to high elevations globally are not specialists with highly specific climatic tolerance but tend to be generalists with a wide range of climate tolerance (Alexander et al., 2011). In this study, upward shifts of the upper elevational limit were observed in most non-native herbaceous plants, e.g. *Dysphania ambrosioides*, *Capsella bursa-pastoris*, *Cardamine flexuosa*, and *Mirabilis jalapa*. As climate warms, these species could move upward rapidly and threatened the mountain ecosystems at mid-elevations. In this study, we hypothesize that the differences in climate suitability between the native and non-native plants lead to the differences in the magnitude and direction of elevational shifts.

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;

Zu et al., 2021). The reason might be that the changes of temperature and precipitation along the elevation gradient in different mountain regions are different. In Mt. Jinfo, we found that the high-altitude regions show a trend of gradual aridification, causing native plants growing in the high-altitude regions to shift downward. Another possible 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 distribution. But the impact of human activities needs to be further evaluated in future studies. In this study, the lower elevational limits changes were mainly found in the native plants living in the high-altitude regions, such as *Poa Pratensis*, *Aconitum 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. 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 is important.

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

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

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

ecosystems (Bellard et al., 2012; Stubbs et al., 2018). Indeed, our study indicated that the upper range limits of non-native plant species in Mt. Jinfo has significantly moved to a higher altitude, and the expansion of the non-native species range size is mainly due to the upward migration of the upper range limits (Fig. 5). The reason might be that 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 regions (Alexander et al., 2011; Petitpierre, 2016). Previous studies indicated that both human activities and climate factors play an important role in plant invasion in China's 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 regions in Mt. Jinfo (Figure S2), we should pay more attention to the threats induced 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 increases, the incidence of new invaders moving into higher elevation might rise, and thus, the management of non-native species should be strengthened in high elevation regions (Pauchard et al., 2015). This study emphasizes the crucial need to make policy decisions to control non-native species in China's nature reserve.

5. Conclusions

We found that the directions of the elevational redistribution of native and non-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 elevations upward on average during the last seven decades. Both of native and non-native species shifted the lower range limits downhill. However, native and non-native plant species showed differences in their upper range limits and elevational range size. Only the upper elevation limit of non-native species shifted upward, while native plants shifted their upper limits downward on average. The native species shrunk their elevational range sizes, while most non-native species expanded their elevational range sizes. The shifts of centroid elevations of non-native plants were dominated by upper

limit changes, while those of native plants were dominated by lower limit changes. The elevational range size changes of both native and non-native species are mainly influenced by the upper range limits. Changes in temperature and precipitation had significant explanatory power for the elevational range shifts of native plants but not 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-native plant species in the lowland regions, and to prevent their shifts to high elevations. This work provided a new perspective to understand the elevational distribution of native and non-native plant species in other mountains, and also proposed conservation strategies to protect the seed plants in Mt. Jinpo.

CRediT authorship contribution statement

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

Data availability

I have shared the available data within this article.

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

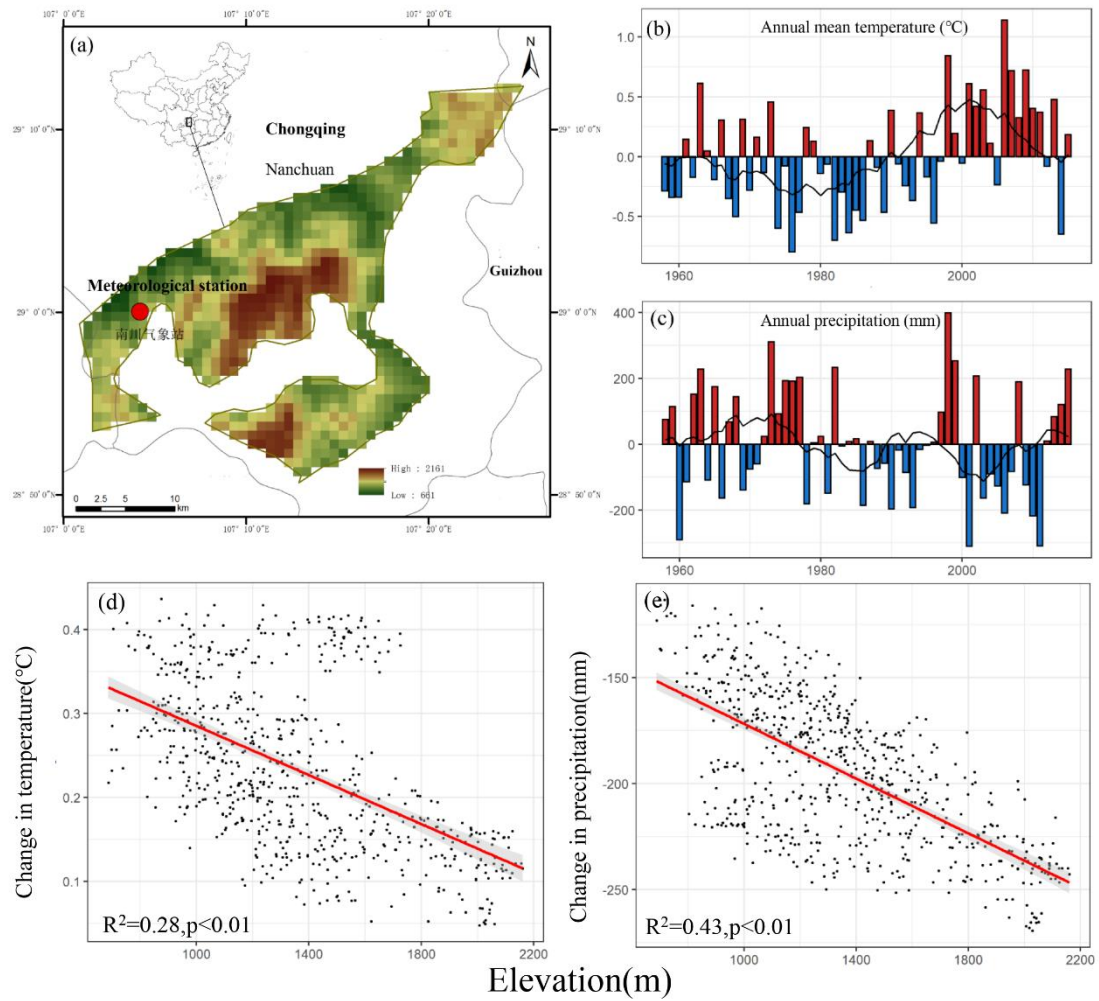


Fig. 1. Geographical location (a) and climate change from 1958 to 2015 in Mt. Jinpo. b: Changes in mean annual temperature (MAT) across the period 1958 - 2015; c: Changes in annual precipitation (AP) across the period 1958 - 2015; d: The changes in mean annual temperature between 1980 - 1988 and 2007 - 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.

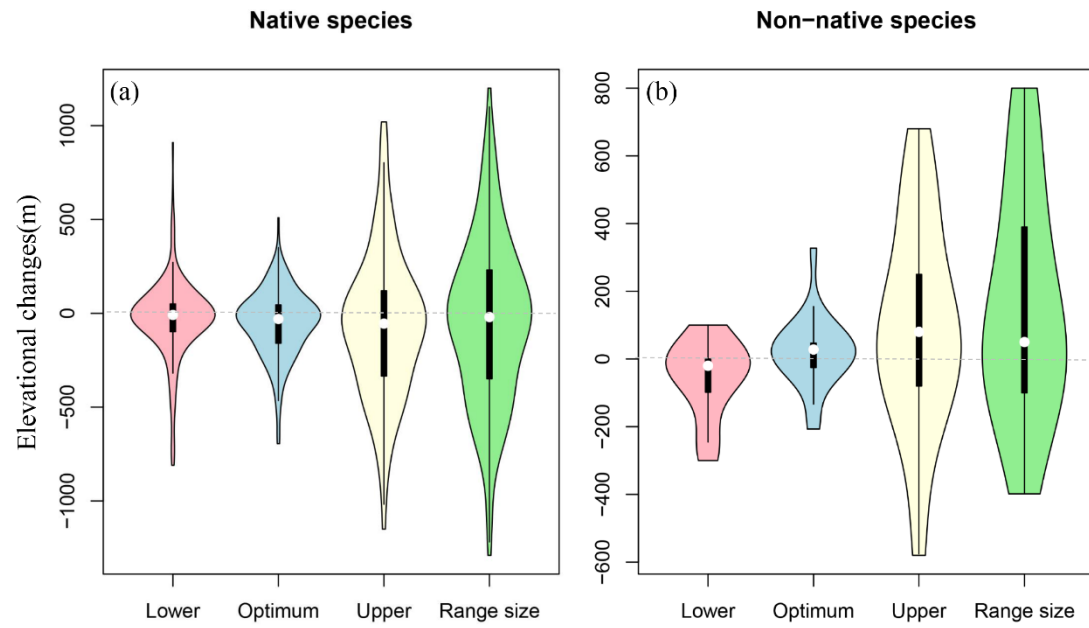


Fig. 2. Changes of range attributes for native (a) and non-native (b) plant species in Mt. Jinfo.

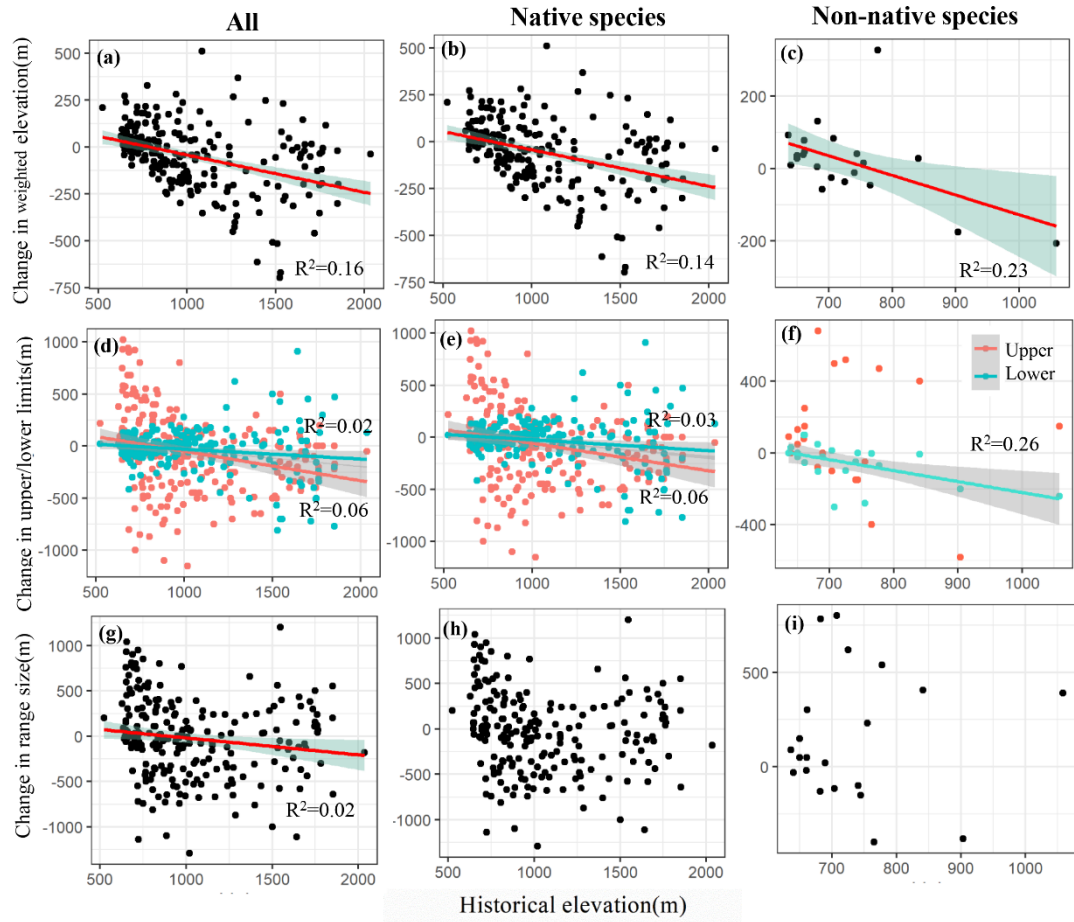


Fig. 3. Relationship between changes in elevation ranges shifts (weighted elevation, upper/lower limits and range size) and their elevations of all plants, native and non-native plant species.

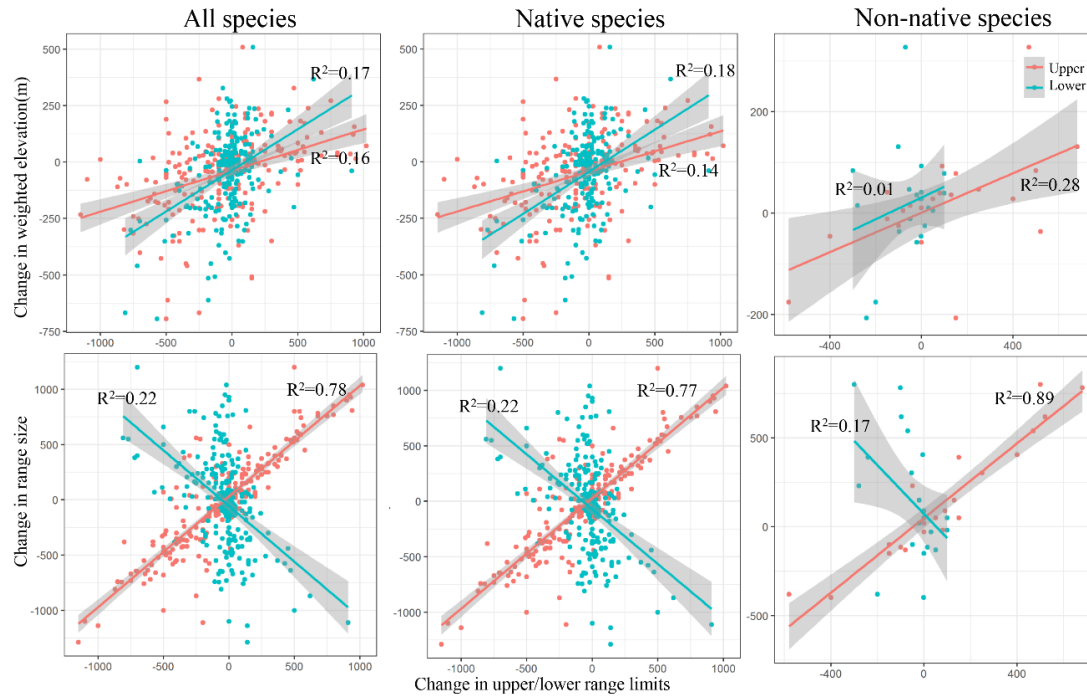


Fig. 4. Relationships of the changes in the weighted elevations and range sizes with the changes in the upper/lower range limits of the native and non-native plant species in Mt. Jinfo from 1950–1988 to 1989–2018. The x-axes represent the changes in upper (red points with red line) and lower (blue points 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.

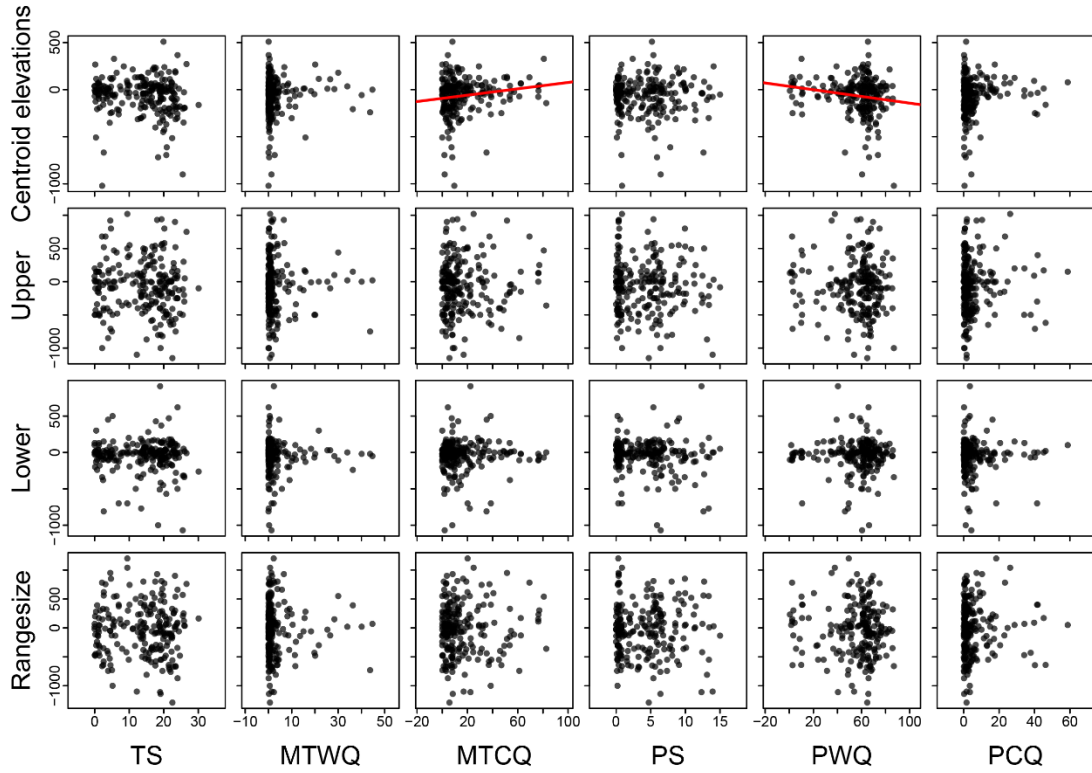


Fig. 5. Relationships of the changes in optimum elevations, upper range limits, lower range limits and range sizes with climatic suitability of all species in Mt. Jinfo. TS, temperature seasonality; MTWQ, mean temperature of the warmest quarter; MTCQ, mean temperature of the coldest quarter; PS, precipitation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