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Title page

Title:

Elevational shift in seed plant distributions in China's mountains over the last 70 years

Running Title : Elevational shifts of plants in China

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Biosketch:

Kuiling Zu is a teacher at Jiangxi Agricultural University, and she did postdoctoral work at Peking University, and interested in macroecology and botany, currently studying the impacts of global changes on plant resources. Her current research interest is to explore the response of species distributions and phenology to climate change.

1 **Abstract**

2 **Aim:** Significant changes in species elevational ranges in mountains have been repeatedly
3 documented, yet the direction, magnitude and drivers of these shifts remain controversial.
4 Presently, there is still lacking evidence about the general nature of species elevational range
5 shifts in eastern Eurasia in response to anthropogenic climate change. By using historical
6 specimen records and recent field observations for 735 seed plant species across 29 China's
7 mountains, we assessed changes in species' elevational centroids and their drivers.

8 **Location:** China.

9 **Time period:** 1950 - 2018.

10 **Major taxa studied:** Seed plant species.

11 **Methods:** The elevation records of all sampled occurrences in each mountain during the two
12 time periods were estimated, and the null models were developed to test the sampling bias.
13 Ecological niche models (ENMs) were used to evaluate the relative importance of climate
14 factors in constraining each species distribution. Generalized linear models (GLMs) to test the
15 relationships between the centroid elevational range shifts of species and different drivers.

16 **Results:** We found that 54% of the species shifting upward and 46% downhill. However,
17 species' elevational shifts significantly differed among species and mountains. Herbaceous and
18 lowland species moved upward faster than woody and high-elevation species. Species in
19 temperate mountains and in mountains with taller elevational gradients moved upward, while
20 species in subtropical mountains and in mountains with shorter elevational gradients moved
21 downward. Precipitation changes experienced by species, species' climatic adaptations, several
22 species' functional traits and mountain size all contributed to explain the magnitude of species'
23 centroid elevational range shifts.

24 **Main conclusions:** Our results highlight complex biodiversity redistribution of seed plants
25 across Chinese mountains, not necessarily conforming to the trend of species upward shifts in
26 elevation. Changes in precipitation regimes may blur the simplistic assumption of isotherm
27 tracking. This study fills an important geographic shortfall for our understanding of biodiversity
28 redistribution under anthropogenic climate change.

29 **KEYWORDS**

30 biodiversity redistribution, climate change, climatic niche, elevational gradients, macroecology,
31 precipitation, upslope range shifts, velocity of species range shift

1 INTRODUCTION

Anthropogenic climate change is a global threat that has the potential to impact species distributions and ecosystem functioning (Pecl et al., 2017). To better understand the possible impacts of climate change on species distributions, studies have examined the responses of individual species in different mountains and taxonomic groups worldwide (Chen et al., 2009; Crimmins et al., 2011; Freeman et al., 2018; Lenoir et al., 2008; Moritz, 2008; Rumpf et al., 2019; Telwala, 2013; Zu et al., 2021). These original reports collectively provide strong evidence that most species moved upward as climate warmed, while some moved downward or did not move (Lenoir et al., 2010; Maggini et al., 2011). Indeed, based on original studies and meta-analyses strictly or partly focusing on species elevational range shifts, we know that: (1) not all species are moving upward; (2) regional differences in species responses exist; and (3) each biotic response depends on local (and sometimes idiosyncratic) drivers (Chen et al., 2009; Freeman et al., 2021; Lenoir et al., 2020; Parmesan, 2003; Vitasse et al., 2021). Although a few recent studies assessed the elevational changes in species distributions (Wen et al., 2017; Zu et al., 2021) and treelines (Liang et al., 2016; Shi et al., 2020) where data is scarce, there is still lacking evidence about the general nature of species elevational range shifts in eastern Eurasia in response to recent climate change. Hence, filling this geographical gap can help reaching a truly global assessment on biodiversity redistribution in mountain ecosystems worldwide (Feeley et al., 2017; Lenoir & Svenning, 2013; Lenoir & Svenning, 2015).

Mountain regions are biodiversity hotspots and their complex and diverse environments provided refugia under past climatic fluctuations since the Quaternary (López-Pujol et al., 2011; Sandel et al., 2011). Recent studies indicated that warming rate in the European Alps is projected to be 1.6 to 2.5 times faster than the average warming rate observed over the northern hemisphere during the 20th century (Vitasse et al., 2021). For most regions of China, temperatures have been observed to have increased by a rate of 0.05°C/yr between 1961 and 2004 (Wang et al., 2010). More importantly, Nogués-Bravo et al. (2007) predicted that air temperature would increase by 0.30 to 0.45°C per decade until 2100. Temperature has long been considered as the most important driver limiting plants' and animals' distributions along elevational gradients in mountain ecosystems (Grinnell, 1917). However, the general and

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4 61 overly simplistic hypothesis that increasing temperature is the main determinant pushing
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6 62 species to shift their elevational range upwards ignores the potential compounding effect of
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8 63 precipitation changes (Crimmins et al., 2011) or other abiotic as well as biotic factors (Lenoir
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10 64 et al., 2010). In line with this result, Grytnes et al. (2014) showed that climate warming alone
11
12 65 had low explanatory power to explain the observed elevational range shifts of alpine plants
13
14 66 across European mountains. However, the relative effects of global warming and precipitation
15
16 67 changes on species range shifts in mountains remain controversial. Moreover, whether the
17
18 68 response of different mountain plants to climate change is consistent across mountains and
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20 69 which factors influence species' elevational redistributions under climate change remains
21
22 70 largely unknown for most Asian mountains.

23 71 The impact of changes in abiotic (e.g., temperature and precipitation) is not enough to
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25 72 explain the direction and magnitude of species elevational range shifts. Indeed, species intrinsic
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27 73 abilities to cope with these changes matter too. Overall, species with different life forms may
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29 74 respond differently to the same amount of change in environmental conditions (Stewart &
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31 75 Dalen, 2010). For instance, Lenoir et al. (2008) reported that short-lived herbaceous plant
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33 76 species shifted farther upward than long-lived woody plants (trees and shrubs), which can be
34
35 77 attributed to the differences in life cycles and the respective capacity to migrate through
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37 78 effective seed dispersal and successful seed germination. Moreover, recent analyses focusing
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39 79 on mountain regions in Europe and worldwide suggests that low-elevation species shifted
40
41 80 upward faster than high-elevation species (Mamantov et al., 2021; Rumpf et al., 2018).
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43 81 Consequently, the velocity of elevational range shifts in response to climate change varied
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45 82 among different life forms and across elevations. Inconsistent responses of different species to
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47 83 climate change imply that species interactions are likely to change over multiple trophic levels
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49 84 (Vitasse et al., 2021), thus affecting the structures and functioning of mountain ecosystems at
50
51 85 different elevations. Hence, more data are needed on species elevational range shifts to forecast
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53 86 these future disruptions within existing ecological networks, especially for understudied regions
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55 87 such as Asian mountains.

56 88 Herbarium specimens are sustainable and persistent, providing accurate information on
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58 89 species distributions during both past and present collecting times (Holmes et al., 2016; Page
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90 & Riccardi, 2015). The collection density of herbarium specimens in China's mountains is
91 considered intensive and complete according to the database of Chinese vascular plant
92 distributions (Yang et al., 2014). Therefore, herbarium specimens are a key resource to improve
93 our understanding of the impacts of climate change on species distributions and redistributions
94 through space and time (James et al., 2018). In this study, we combined old herbarium
95 specimens with recent botanical field surveys to investigate changes in the elevational
96 distributions of 735 seed plant species across 29 mountains in China. We aimed to: (1) assess
97 the direction and magnitude of species centroid elevational shifts along the elevational gradients
98 in China's mountains since the 1950s, assuming a general trend in seed plant species in China
99 to shift upward in elevation (Zu et al., 2021); (2) explore the main determinants of the observed
100 changes in range centroids across the studied mountains, assuming that temperature changes
101 won't be the main or only driver (Grytnes et al., 2014); (3) compare the magnitude of centroid
102 range shifts between herbaceous and woody plants, assuming greater magnitudes of range shifts
103 for short-lived herbs (Lenoir et al., 2008); and (4) compare the difference in centroid range
104 shifts between low- and high-elevation species, expecting greater magnitudes of range shifts
105 for low-elevation species (Mamantov et al., 2021; Rumpf et al., 2018).

106 **2 MATERIALS AND METHODS**

107 **2.1 The study area**

108 The study area covers 29 mountain sites in China (Figure 1; Table S1), which are mainly
109 distributed across 18 distinct mountain ranges, including the Qionglai, Bayankela, Hengduan,
110 Changbai, Yanshan, Wuling, Lvliang, Daba, Wuyi, Dalou, Miaoling, Lushan, Nanling,
111 Himalayan, Qinling, Tianshan, Taihang, and Aertai Mountain Range. These mountain sites are
112 distributed across 15 provinces and 3 climatic zones (Plateau, Temperate and Subtropics) within
113 China.

114 There are 12 mountain sites that are located in the climatic zone of Qinghai-Tibet Plateau in
115 western China. The highest mountain is Mt. Namjagbarwa, which is located at the eastern edge
116 of the Himalayan Mountain Range in the southeast of the Qinghai-Tibet Plateau, reaching its
117 highest elevation at 7782 m. Eight mountain sites are located in the Hengduan Mountain Range,
118 the core biodiversity hotspot in south central China (Myers, 2000). The tallest mountain in that

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4 119 mountainous area is Mt. Gongga with an elevation peaking at 7556 m (Zu et al., 2021). The
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6 120 Hengduan Mountain Range is affected by the Indian and Pacific Ocean monsoon circumfluence,
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8 121 resulting in a distinct wet season during summer and autumn and a dry season during winter
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10 122 and spring. This region is characterized by a sharp elevational gradient from approximately 70
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12 123 to 7556 m, offering an exceptionally long and diverse range of topographical and climatic
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14 124 conditions for studying species elevational range shifts in response to climate change (Wu et
15
16 125 al., 2013). The Qionglai Mountain Range is adjacent to the Hengduan Mountain Range, which
17
18 126 is located in the Sichuan province. Two mountain sites belong to the Qionglai Mountain Range:
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20 127 the Siguniang (SGN) and Balang (BL) site, with the highest elevation being 6250 m and 5072
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22 128 m, respectively.

23 129 There are 10 mountain sites that are located in the climatic zone of the subtropics in southern
24
25 130 China. The lowest mountain ranges are the Lushan and Maoer Mountain Range in southeast
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27 131 China, with the highest elevations being 1474 m and 2142 m, respectively. Mt. Hualong (HL)
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29 132 and Mt. Shennongjia (SNJ) are located in the Daba Mountain Range, which constitute the main
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31 133 body of China's North-South Transitional Zone (Zhang et al., 2021). Mt. Fanjing (FJ), Mt.
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33 134 Fenghuang (FH) and Mt. Leigong (LG) are located in the Guizhou province while Mt. Jinfo
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35 135 (JF) is located at the northeast of the Dalou Mountain Range with the highest elevation being
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37 136 2251 m.

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39 137 Our study region also includes seven mountain sites that are located in the temperature
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41 138 climate zone in the northern part of China. Mt. Taibai is the summit of the Qinling Mountain
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43 139 Range and the highest mountain in eastern China – reaching its highest elevation at 3767 m
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45 140 (Zhang & Chen, 2014). Noteworthy, our study region also covers the Changbai Mountain
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47 141 Range which is located in the northeast of China and is situated on the border between China
48
49 142 and North Korea (Bai et al., 2008). The forested areas in this mountain range is distributed
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51 143 below 2000 m and the typical zonal vegetation is a mixed forest made of Korea pines and broad-
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53 144 leaved tree species.

54 145 **2.2 Data on seed plant species**

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56 146 Plant distribution data across the 29 mountain sites in China were obtained from: (1) historical
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58 147 specimens collected during the past 70 years and available through museum and herbarium
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4 148 collections as well as (2) original field surveys and resurveys carried out during the past 20
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6 149 years. Herbarium records were extracted from the National Specimen Information
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8 150 Infrastructure (NSII, <http://www.nsii.org.cn>, accessed on November 11, 2019) and the Chinese
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10 151 Virtual Herbarium (CVH, <http://www.cvh.ac.cn>). In total, 10918077 herbarium specimens were
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12 152 extracted for all seed plant species in China, covering about 34000 species. Besides, between
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14 153 2000 and 2019, we carried out original botanical surveys in: the Changbai Mountain Range; the
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16 154 Xiaowutai Mountain Range; the Gongga Mountain Range; the Taibai Mountain Range; and in
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18 155 several other mountain ranges of smaller extents. Botanical surveys were carried out in
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20 156 vegetation plots of 600 m² (20 m × 30 m), which were established along elevational transects
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22 157 from low to high elevations with an elevational interval of about 50 m between two subsequent
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24 158 vegetation plots. The vegetation plots selected for each elevation represented the zonal
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26 159 vegetation types in the areas. In each vegetation plot, we also measured the diameter at breast
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28 160 height (DBH) of all tree individuals with a DBH > 3 cm (Fang et al., 2012).

29 161 To ensure data quality, we cleaned the plant species distribution data as following. As a first
30
31 162 step, we extracted the botanical specimen data of each county of the corresponding mountain
32
33 163 site, counted the number of plant specimens in each site and determined the searched area within
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35 164 each mountain site. Then, we cleaned up the geographical names and verified the accuracy of
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37 165 plant distribution points within each mountain site. We excluded duplicate specimens and
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39 166 specimens lacking information on their exact geographical locations, and only included records
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41 167 with correct information (e.g., elevation record and collection year). Finally, over 5000
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43 168 complete records were selected across the 29 mountain sites. The total number of herbarium
44
45 169 specimens we selected for each mountain site are shown in Table 1. As a second step, we
46
47 170 standardized the species names of all records based on the Catalogue of Life (COL,
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49 171 <http://www.catalogueoflife.org/>) which was supplemented with the plant list (TPL,
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51 172 <http://www.theplantlist.org/>) as well as the Taxonomic Name Resolution Service (TNRS,
52
53 173 <http://tnrs.iplantcollaborative.org/>). As a third step, in order to assess changes in species'
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55 174 elevational distributions between the historical and present times, we divided our dataset of
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57 175 species occurrence records into two distinct periods: 1950 - 1988 vs. 1989 - 2018. The threshold
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59 176 time of 1988 / 1989 was chosen because mean annual temperature in China started to
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4 177 significantly increase at this time (Wang et al., 2010). Finally, for statistical reason, we selected
5 178 only seed plant species with at least 10 unique occurrence records for each of the two studied
6
7 179 periods within a given mountain site. The number of the selected seed plant species considered
8
9 180 per site is shown in Table 1 and Figure S1. The occurrence records for the selected seed plant
10
11 181 species per site during the first period (1950 - 1988) and the second period (1989 - 2018) is
12
13 182 displayed in Figure S2. The centroid elevation per species was calculated in each mountain
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15 183 range during the two time periods, using the average summary statistic across all sampled
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17 184 occurrences during a given time period, within a given mountain range and for a given focal
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19 185 species. Because the centroid elevation represents the distribution center of the populations for
20
21 186 each species, and therefore it can represent the elevation shifts.

23 187 **2.3 Climate data**

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25 188 The climate data (daily temperature and precipitation data covering the period 1951 - 2015 and
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27 189 available from the Geographic Data Sharing Infrastructure, College of Urban and
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29 190 Environmental Science, Peking University: <http://geodata.pku.edu.cn>) for all 29 mountain sites
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31 191 were extracted from 54 standard meteorological stations across China (Figure S3). These 54
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33 192 meteorological stations are representative of the macroclimatic conditions experienced within
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35 193 our study areas. For each of the 29 studied mountain sites, we first calculated the mean annual
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37 194 temperature (MAT, °C), the total amount of annual precipitations (AP, mm) and the annual
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39 195 actual evapotranspiration (AET, mm). These three climatic variables were computed for each
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41 196 year during the entire period of 1951 - 2015. Then, we computed the mean of each of the three
42
43 197 variables for the periods 1951 - 1988 and 1989 - 2015 separately before estimating the mean
44
45 198 changes in MAT, AP and AET between the two periods. The climatic variable AET was
46
47 199 calculated following the Thornthwaite and Hare formula (Huntley, 1993), based on the mean
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49 200 monthly temperature and precipitation data. The climatic time series across the 54
50
51 201 meteorological stations showed clear trends of climate warming and precipitation decrease but
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53 202 a less clear trend of change in AET between the two studied periods (Figure S4, S5, and S6).
54
55 203 In addition to that, we also computed seasonal changes by focusing on the change in
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57 204 temperatures and precipitations during summer (May - July) and winter (November - Next
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59 205 January) separately and for each of the 29 mountain sites (Figure S7).
60

2.4 Complementary drivers of changes in species' centroid elevational position

Besides climatic drivers, being the usual culprits responsible for species range shifts under anthropogenic climate change, we extracted information on additional potential drivers to explain the variation we found in species' centroid elevational range shifts of seed plants. First, we downloaded a spatial layer of the human footprint index (HI) at 1km resolution from the Last of the Wild (v2, LWP-2, 2005; <https://sedac.ciesin.columbia.edu>) and extracted HI values across our 29 mountain sites. Then, we extracted data on atmospheric nitrogen deposition from a national dataset providing atmospheric inorganic nitrogen deposition across China from 1996 to 2015 (spatial raster layers at 1 km × 1 km resolution) (Jia et al., 2019). From this raster layer, we calculated the mean nitrogen deposition across each of the 29 mountain sites.

Previous studies suggest that mountain size, in terms of the length of the tallest elevational gradient within a given mountain range, could significantly influence the distribution of treelines and snowlines in southeastern Eurasia (Yao & Zhang, 2014). In order to assess the impact of the mountain size on the observed species' centroid elevational range shifts, we used the difference between the highest and lowest elevation (i.e., the elevation range) within each of the 29 mountain sites to represent the site-specific mountain size. The highest elevation of each mountain were obtained from Wang et al. 2004, and the lowest elevation of each mountain was obtained from literature collections (Table S2).

We also compiled data on several plant species functional traits, including: lifeform (herbaceous vs woody plants), the main reproductive system (SexSyst), and fruit type. These trait data were obtained from Flora of China (<http://www.iplant.cn/foc>), Flora Reipublicae Popularis Bulgaricae (<http://www.iplant.cn/frps>) and other provincial and local floras in China.

2.5 Data analysis

We calculated the centroid elevational position of each species in each of the 29 mountain sites during each time period separately (1950 - 1988 vs. 1989 - 2018) by averaging the elevation records of all sampled occurrences of a given species within a given mountain and during a given time period. The shift in the species' centroid elevation position within each mountain site was computed as the raw difference in the species' centroid position, for the focal mountain site, between the baseline (1950 - 1988) and resurvey period (1989 - 2018): resurvey minus

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4 235 baseline position. Pairwise Student t tests were used to test the significance in the mean
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6 236 difference in species' centroid elevational position between the two studied time periods, for
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8 237 each mountain site separately. We also calculated the proportion of species shifting upward and
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10 238 downward for each mountain site separately. To test whether there is a sampling bias caused
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12 239 by a tendency that current researchers would sample at higher or lower elevations than in the
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14 240 past, we built null models to estimate the null expectation of the elevation change in the centroid
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16 241 position of a given species, for each of the 29 mountains separately, under the actual sampling
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18 242 effort per mountain site. The specific methods and steps to build the null models is the same as
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20 243 the one we used in a previous study focusing on one of the study site: Mt. Gongga (Zu et al.,
21
22 244 2021). To test the influence of species lifeform on species' centroid elevational range shifts, we
23
24 245 used Student t tests to compare the mean elevation shifts of herbaceous and woody plants, for
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26 246 each mountain separately.

27 247 In order to estimate whether climate changes influence species elevational shifts, we
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29 248 estimated the climate changes (Change in MAT and Change in AP) experienced by each species.
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31 249 To assess the effects of several climatic drivers constraining each species distribution and thus
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33 250 potentially explaining the observed magnitude of species' centroid elevational range shifts, we
34
35 251 first collected data on the global distribution of each of the 735 studied species and then
36
37 252 rendered an ecological niche modelling (ENM) approach. To do so, we used the MaxEnt
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39 253 algorithm to estimate the relative importance of six climatic variables in explaining each species
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41 254 distribution. We followed the exact same methodology as described in Zu et al. (2021) for one
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43 255 study site on Mt. Gongga. In short, the global distribution ranges of species were obtained from
44
45 256 online databases including: the Global Biodiversity Information Facility (GBIF,
46
47 257 <http://www.gbif.org/>); the Chinese Virtual Herbarium (CVH, <http://www.cvh.ac.cn/>); the
48
49 258 National Specimen Information Infrastructure (NSII, <http://www.nsii.org.cn/>); RAINBIO
50
51 259 (Dauby et al., 2016); and the Botanical Information and Ecology Network (BIEN,
52
53 260 <http://bien.nceas.ucsb.edu/bien/biendata/>), etc. The climate data were from WorldClim
54
55 261 (<https://www.worldclim.org/data/worldclim21.html>). Then, once the relative importance of
56
57 262 each of the above-mentioned climatic variables were estimated from the ENM approach, we
58
59 263 used generalized linear models (GLMs) to test the strength of the relationship between the
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264 magnitude of species' centroid elevational range shifts and the relative importance of each of
265 the six studied climatic drivers. In addition to these six explanatory variables, we also tested the

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4 266 influence of HI and atmospheric nitrogen deposition. Finally, we also assessed the relationship
5 267 between species' centroid elevational range shifts and the historical mean elevation position
6
7 268 (cf. baseline position) for each species in the 29 mountain sites. All analyses were conducted in
8
9 269 R version 3.5.3 (R Core Team, 2019).

11 270 **3 RESULTS**

13 271 **3.1 Changes in species' centroid elevational position in different mountains**

15 272 Between the periods 1950-1988 and 1989-2018, we found that 54% ($\pm 21\%$) of the studied seed
16
17 273 plant species shifted the centroids of their elevational ranges upward across the 29 mountain
18
19 274 sites. However, the proportion of species with upward centroid elevational shifts significantly
20
21 275 varied among mountain sites. Specifically, 17 of the 29 mountain sites had higher proportions
22
23 276 of species shifting upward ($69\% \pm 9\%$, on average), while 10 mountain sites had lower
24
25 277 proportions of species shifting upward ($29 \pm 10\%$, on average) (Figure 1). The two remaining
26
27 278 mountain sites (Mt. Huanggang and Mt. Tiangeer) had even proportions of species shifting
28
29 279 upward and downward (Figure 1; Table 1). After accounting for the difference in sampling
30
31 280 efforts between time periods, the proportions of species shifting upward vs. downward across
32
33 281 the 29 mountain sites remained similar (Table S3). These results indicate that most plant species
34
35 282 in the 29 studied mountain sites have shifted their elevational distributions during the past 70
36
37 283 years, and that these elevational range shifts were not the result of a sampling bias.

38 284 **3.2 The driving factors of species' centroid elevational range shifts**

40 285 We found that precipitation changes as experienced by species (i.e., the relative importance of
41
42 286 changes in AP between 1951 - 1988 and 1989 - 2015), mean climatic conditions (i.e., the
43
44 287 relative importance of MAT, AP and AET during 1951 - 2015), species' intrinsic characteristics
45
46 288 (i.e., elevational range size, fruit type, family and genus) and mountain sites' properties
47
48 289 (climatic region, longitude and mountain size) all significantly contributed to explain the
49
50 290 magnitude of species' centroid elevational range shifts (Table 2). These variables collectively
51
52 291 explained 66% ($R^2 = 0.66$, $p < 0.001$) of the total variance in species' centroid elevational range
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54 292 shifts across all mountains.

56 293 Specifically, the mean magnitude of species' centroid elevational range shifts were
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58 294 negatively correlated with mean annual temperature and changes in summer and winter
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4 295 precipitation, while positively correlated with mountain size (Figure 1 and Figure S8). In other
5
6 296 words, species tend to move further upward in mountains located in colder regions, within tall
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8 297 mountain ranges and in mountains located in drier regions.

9
10 298 The climatic adaptation of a species was significantly correlated with its shift in centroid
11
12 299 elevation. Specifically, the centroid elevation shifts of species were positively correlated with
13
14 300 the climatic adaptation to mean temperature of coldest quarter (MTCQ) and precipitation
15
16 301 seasonality (PS), but negatively correlated with the climatic adaptation to precipitation of
17
18 302 warmest quarter (PWQ) (Figure 2). Moreover, species with differing fruit types showed
19
20 303 different elevational shifts (Figure S9a). In different climate regions, species centroid
21
22 304 elevational shifts differed. For instance, species in subtropics regions tended to shift downward,
23
24 305 while those inhabiting the Qinghai-Tibet Plateau tended to upward shifts on average (Figure
25
26 306 S9b). The centroid elevation shifts of species were negatively correlated with longitude, and
27
28 307 positively correlated with the relative elevation (Figure 2).

29 308 **3.3 Differences in elevational shifts of herbaceous and woody plants**

30
31 309 The magnitude of species' centroid elevational range shifts differed between herbaceous and
32
33 310 woody plants. Herbs tended to move upward in the Qinghai-Tibet Plateau, while woody plants
34
35 311 tended to move upward in the Temperate zone (Figure S9c). As mean annual temperature
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37 312 decreases, both herbaceous and woody plants shifted further upward (Figure S8). In cold
38
39 313 mountains, upward range shifts of herbs (+90 m, on average) was greater than that of woody
40
41 314 plants (+74 m, on average). In warm mountains, downward range shift of herbs (-170 m, on
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43 315 average) was greater than that of woody plants (-50 m, on average) (Figure 3). Both the
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45 316 elevational range shifts of herbs and woody plants were influenced by the change in
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47 317 precipitation seasonality. However, the elevational shifts of herbs were also significantly
48
49 318 influenced by mountain size (Figure S8).

50 319 **3.4 The relationship between species' centroid elevational range shifts and the historical** 51 52 320 **mean elevation of species distribution**

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54 321 We found that species' centroid elevational range shifts were negatively correlated with the
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56 322 historical mean elevation position of species in nine out of the 29 studied mountain sites (Table
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58 323 S4). The mountains with the strongest negative correlation values are mainly Mt. Xiaowutai
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4 324 (XWT, 0.55) and Mt. Lushan (LS, 0.49) (Figure 4). In these mountains, the high-elevation
5 325 species tended to shift downward, while the low-elevation species tended to shift upward,
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7 326 resulting in a mid-elevation concentration. The results in these mountains support the
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9 327 hypotheses of a negative relationship between the magnitude and direction of elevational range
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11 328 shifts and the historical position of species along the studied elevational gradients, suggesting
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13 329 that lowland species move upward while alpine species move downward. In contrast, the
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15 330 remaining 20 mountains sites did not support this hypothesis (Table S4).

17 331 **4 DISCUSSION**

19 332 We assessed the changes in species' range centroid along elevational gradients using historical
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21 333 and recent (1950 - 1988 vs. 1989 - 2018) occurrence records for 735 seed plant species across
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23 334 29 mountains in China and explored the drivers of these changes in species distribution over
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25 335 time. Similarly to previous meta-analyses (Chen et al., 2011; Lenoir et al., 2020; Mamantov et
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27 336 al., 2021), we found that not all studied species are moving upward along the studied elevational
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29 337 gradients of our 29 mountain sites in China. Yet, we found a much larger proportion of species
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31 338 shifting their centroid elevation position downward in comparison with these former meta-
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33 339 analyses reporting not more than 20% of species shifting downward against 46% based on our
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35 340 findings. Moreover, we found that herbaceous plant species shifted their centroid elevation
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37 341 further upward, by +16 m on average, than woody plants did, which is consistent with a former
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39 342 study reporting faster rates of upward range shifts for herbs than for woody plants in French
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41 343 mountain forests (Lenoir et al., 2008). Centroid shifts show negative relationships with the
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43 344 average elevation of species in 23 mountains, suggesting that lowland species have shifted
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45 345 upward farther than high-elevation species. Overall, our results suggest that species in
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47 346 mountains are not necessarily moving upward following and according to the rather simplistic
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49 347 isotherm-tracking expectation. Instead, species may demonstrate more complex elevational
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51 348 redistribution in response to environmental changes. The elevational redistributions we found
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53 349 in our study are not entirely due to climate change (e.g. climate warming), but are additionally
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55 350 influenced by other factors such as, among others described below, changes in precipitation
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57 351 regimes, which supports former findings (Crimmins et al., 2011; Grytnes et al., 2014). Our
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59 352 results indicate that several factors contribute to the elevational changes of species in Chinese
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4 353 mountains: (1) climate change and species' climatic adaptations; (2) mountain properties; (3)
5 354 the functional traits of different species.

7 355 **4.1 Effect of climate change and species' climatic adaptations on elevational shifts**

9 356 Climatic conditions in Chinese mountains have significantly changed over the past 70 years,
11 357 which has influenced species' elevational distributions. Our results indicate that the amount of
13 358 climate change as experienced by seed plant species significantly influenced the direction and
15 359 magnitude of species' centroid elevational range shifts. This finding is consistent with previous
17 360 studies reporting that changes in temperature and precipitation regimes play an important role
19 361 in species' elevational redistributions (Chen et al., 2009; Grytnes et al., 2014). Previous studies
21 362 suggested that the overall trend of upward range shifts of forest plant species in France is mainly
23 363 driven by climate warming (Lenoir et al., 2008), while the overall trend of downward range
25 364 shifts of woody plants in California is chiefly influenced by precipitation changes (Crimmins
27 365 et al., 2011). However, our study suggests that temperature changes as experienced by seed
29 366 plant species do not necessarily play an important role in explaining the overall trend of
31 367 elevational range shifts in Chinese mountains. In contrast, changes in annual precipitation
33 368 between the two studied periods and as experienced by species had a significant negative effect
35 369 on species elevational range shifts (Figure S8). Our findings regarding the insignificant effect
37 370 of temperature changes over time on the magnitude of species' centroid elevational range shifts
39 371 might stem from a spatial mismatch between climate as measured by weather stations and
41 372 climate as experienced by living organisms. Indeed, air temperatures as measured by
43 373 standardized weather stations normally differ from the actual surface temperatures that low-
45 374 stature alpine plants may experience in-situ, inside their habitats (Daniel & Körner, 2011). This
47 375 suggests that macroclimatic conditions as measured by meteorological stations may to some
49 376 extent lead to low accuracy in predicting species redistributions. Recent studies analyzed multi-
51 377 decadal understory microclimate dynamics in European forests and provided evidence that
53 378 responses of forest community to climate change are most closely related to microclimate rather
55 379 than macroclimate changes (Zellweger et al., 2019). This indicates that local microclimate may
57 380 hold the key to understand biotic responses, such as species elevational range shifts, to
59 381 anthropogenic climate change (Alexander et al., 2018; De Frenne et al., 2013; Devictor et al.,
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4 382 2012).

5 383 In this study, lowland species tended to shift upward faster than high-elevation species in
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7 384 23 mountains. This result is consistent with a recent finding that most lowland species across
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9 385 20 montane transects moved upward farther than the high-elevation species (Mamantov et al.,
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11 386 2021). Our results together with previous studies seem to indicate a general trend for species
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13 387 elevational redistribution to be more pronounced at low elevations than at high elevations in
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15 388 response to anthropogenic climate change. In general, the increase in temperature conditions
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17 389 over time is stronger in highland regions than in the lowlands (Pepin et al. 2015), and the
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19 390 stronger warming and precipitation decrease have negative effects on plant nutrient use and
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21 391 resorption efficiencies for the lowland species (Zu et al., 2021). This might be one of the reasons
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23 392 for the stronger upward shifts of lowland species. Moreover, lowland plant species normally
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25 393 have narrower thermal tolerances (including temperature and precipitation) so that they need to
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27 394 migrate farther upward to track their thermal niche (Smith, 2018).

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29 395 Interestingly, we found that the adaptation of species to climate has significant effects on
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31 396 the elevational changes of species. Specifically, the adaptation of species to winter temperature
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33 397 and precipitation seasonality was positively correlated with species elevational changes, and
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35 398 hence significantly contributed to the upward shifts of species. For instance, the global
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37 399 distribution ranges of two lowland species, *Sorbus discolor* and *Cerastium arvense*, were
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39 400 strongly influenced by both winter temperature and precipitation seasonality, and their
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41 401 elevation distribution ranges shifted 72.5 m and 128.9 m upslope, respectively. In contrast, we
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43 402 found that the adaptation of species to higher summer precipitation was negatively related to
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45 403 the elevation shifts, suggesting that species having strong adaptability to the summer
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47 404 precipitation tends to shifts downhill along the elevation gradients. For instance, the global
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49 405 distribution range of *Paederia foetida* and *Pericampylus glaucus* in subtropical mountains were
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51 406 dominated by summer precipitation, and their elevation range shifted downhill by 177.4 m and
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53 407 94.9 m, respectively. Plant species in these mountains appear to track climatic water balance
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55 408 by shifting their elevational distributions downhill. This is consistent with the previous finding
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57 409 that change in precipitation leads to downward shifts of plant species in California (Crimmins
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59 410 et al., 2011).
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4 411 Our results indicated that some plant species showed no or little elevational shifts.
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6 412 Previous studies suggest that the local persistence of plant populations may be the result of
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8 413 microenvironment on species persistence. Micro-environmental conditions including
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10 414 topography, soil, hydrological characteristics, and microclimate could create a multitude of
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12 415 microhabitats offering refugial persistence to some plant species (Rabasa et al., 2013; Daniel &
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14 416 Körner, 2011). The non-existent or slow migration of some plant species might be also the
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16 417 reason that these species having limited ability to expand into newly climatically suitable
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18 418 habitat due to dispersal and/or recruitment limitation (Feeley, 2012). If this condition continues
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20 419 into the future, these species with little or on elevational shifts will face risks of extinctions due
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22 420 to reduced habit areas and population sizes under future climate changes.

23 421 **4.2 Effect of mountain properties on elevational shifts of species**

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25 422 Our results indicate that in addition to the effects of climate change and species' climate
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27 423 adaptation on species elevational redistributions, the size of the mountains (i.e. measured as the
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29 424 difference between the highest and lowest elevations of a mountain) plays an important role in
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31 425 determining species' elevational distribution shifts. The mean magnitude of upward shifts and
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33 426 the proportions of species with upward shifts were both higher in larger mountains (Figure 2).
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35 427 For instance, the mountains in the Qinghai-Tibet Plateau have higher elevational range (i.e.
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37 428 larger mountains) compared with the mountains in other regions, and the upward movement of
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39 429 the species are larger. Studies indicated that the plant species' optimum elevation movement
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41 430 along the elevational gradient since 1970s was significantly influenced by the mountain
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43 431 topography and summit heights in European Alps (Holmes et al., 2016). Based on studies of
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45 432 516 forest lines in the Northern Hemisphere, a recent meta-analysis indicates that mountains
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47 433 size explains 48.9% of variations in the distribution of forest lines, which also supports our
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49 434 finding that mountains size influences the redistribution of woody plants in response to climate
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51 435 changes (Yao & Zhang, 2014; Zhao et al., 2014). Our results together with previous findings
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53 436 suggest that higher mountains may provide more suitable habitats for species to move upward.

54 437 Moreover, our results showed that species in temperate mountains tended to shift upward,
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56 438 while species in warm and wet mountains (i.e. those in subtropical regions) tended to shift
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58 439 downward. In line with our results, a recent study also demonstrated downward shifts of
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4 440 centroid elevations of plant species living in subtropical mountains (O'Sullivan & Jump, 2020).
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6 441 In subtropical regions, the low seasonal temperature variation reduces overlap in thermal
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8 442 regimes between lowlands and high altitudes, and species tend to have narrow adaptations to
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10 443 temperatures (Shrestha et al., 2018). Lowland species may be restricted to lower elevations
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12 444 because of their limited tolerance to cold stress (Heatwole et al., 1969), while high-elevation
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14 445 species are generally not limited by warm temperature and are therefore able to move to lowland
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16 446 regions (Ghalambor et al., 2006). This explained the results that the high-elevation species in
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18 447 subtropical mountains (e.g. EM, SNJ, BL, HG, JF, LS) tended to shifts downward. Besides, the
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20 448 interaction among species (e.g. species competition), topography and anthropogenic influences
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22 449 may also contribute to the downward elevation shifts of plant species in subtropical mountains
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24 450 (Bhatta, 2018). Recent studies indicate that in subtropical mountains, high-elevation species
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26 451 cannot survive the lowlands because they are often outcompeted by the more competitive
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28 452 lowland species, not due to physiological limitations (Mamantov et al., 2021; Zu et al., 2021).
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30 453 If climate warming reduces the competitive fitness of lowland species, then higher elevation
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32 454 species tend to shift downslope more easily (Rabasa et al., 2013). How species' elevational
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34 455 redistributions may influence species interactions in subtropical regions requires urgent
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36 456 attention.

37 457 **4.3 Effect of functional traits on elevational shifts of species**

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39 458 Our finding demonstrates that the elevational shifts of species in response to climate change
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41 459 may vary among species with different functional traits (including life forms and fruit types).
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43 460 First, several previous studies have demonstrated that the distributions of species with different
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45 461 lifeforms may respond to climate change differently. For example, studies on plants' elevational
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47 462 distributions in the French Alps in Europe (Lenoir et al., 2008) and the Mt. Gongga in China
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49 463 (Zu et al., 2021) and on the forest communities in Switzerland (Küchler, 2014) all showed that
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51 464 herbaceous species had faster upslope shifts than trees and shrubs. In contrast, a recent review
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53 465 on species elevational shifts in the European Alps showed that the optimum elevations of long-
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55 466 lived woody plants were shifting upward at the same rate with non-alpine herbaceous plants
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57 467 (Vitasse et al., 2021). These findings suggest that the conclusions on the responses of woody
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59 468 and herbaceous plants remain controversial. In this study, our result showed that the direction
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4 469 and magnitude of elevational shifts in China' mountains differed between life forms. We found
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6 470 that herbaceous plants shifted their elevational centroids significantly faster than woody plants
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8 471 in 15 mountains. The reason for these differences between the elevational shifts of woody and
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10 472 herbaceous plant species in response to climate change may be partly due to the fact that
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12 473 different lifeforms have different climate adaptation and physiological properties (Grytnes et
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14 474 al., 2014). Generally, the woody plants are long-lived species and have deeper roots, and they
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16 475 seem to be less sensitive to the soil water (Wang et al., 2020). On the contrary, herbaceous
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18 476 species have shorter life cycles and shallower roots than woody species, and they tend to be
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20 477 more sensitive to precipitation changes (Lande, 1993).

21 478 The rate and distance of elevational shifts of species may also be influenced by other
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23 479 functional traits in addition to lifeform (Alexander et al., 2018; Matteodo et al., 2016). In this
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25 480 study, we found that species with different fruit types shifted their centroid elevations in
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27 481 different trends and with different magnitudes. For instance, the species with samara fruits (e.g.,
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29 482 *Acer oliverianum* and *Betula albosinensis*) shifted their centroid elevations upward, while the
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31 483 species with caryopsis fruits (e.g., *Eulalia speciose* and *Bromus remotiflorus*) shifted their
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33 484 centroid elevations downhill. This is because samara fruits are easily dispersed by wind, while
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35 485 caryopsis fruits tend to drop to the ground directly or beneath the parent plants. Moreover,
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37 486 species elevational shifts also significantly different between different genera and families. This
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39 487 is likely because different genera and families normally have different functional traits, climatic
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41 488 adaptation and evolutionary history (Li et al., 2017; Losos, 2011). These results suggest that
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43 489 species distributions of different taxonomic groups may respond differently to environmental
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45 490 changes, and hence may have different risks of local extinction under future environmental
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47 491 change scenarios. In this study, there are only 20 gymnosperm species for which we had
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49 492 sufficient data while we had good time series for 715 angiosperm species in total. Indeed,
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51 493 gymnosperm and angiosperm species have very different traits and climate adaptation, hence
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53 494 we also assumed that the magnitude of elevation range shifts will be different between both
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55 495 taxonomic groups. Yet, we found no significant difference in the magnitude of mean elevational
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57 496 range shifts between gymnosperm and angiosperm species ($t = 1.1132$, $df = 19.754$, $p\text{-value} =$
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59 497 0.279), most likely due to the extremely low sample size for gymnosperms relative to
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4 498 angiosperms.

5 499 Finally, we suggest to consider both regional and species characteristics in future
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7 500 researches related to elevational range shifts. We recommend to focus on the taxon that is more
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9 501 sensitive to climate change and in fragile biodiversity regions. For species that tend to shift
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11 502 upward, those living at high-elevational regions will face more climatic and competitive
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13 503 pressures than lowland species, and thus should be given much more attentions under future
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15 504 climate warming. On the contrary, for species that tend to shift downhill, the lowland species
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17 505 and their natural habitats are more vulnerable to climate change and intensive human pressure
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19 506 (e.g. tourism and recreation). Compared with traditional suggestions to protect or restore species
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21 507 habitats, we recommend to protect dispersal corridors of species to improve their dispersal
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23 508 processes along the elevational or latitudinal gradients. Our study provides essential scientific
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25 509 references for managing protected areas in China's mountain regions.

26 27 510 **COMPETING INTEREST STATEMENT**

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29 511 The authors declare no competing interests.

30 31 512 **DATA AVAILABILITY STATEMENT**

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33 513 The data used in the analyses of the paper are uploaded to the Dryad website
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35 514 (<https://doi.org/10.5061/dryad.r7sqv9sj0>). The data of study regions and the total number of
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37 515 herbarium specimens are provided in the Supporting Information (Table S1); The climate data
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39 516 that support this study are available from the Geographic Data Sharing Infrastructure, College
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41 517 of Urban and Environmental Science, Peking University (<http://geodata.pku.edu.cn>), and
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43 518 WorldClim (<https://www.worldclim.org/data/worldclim21.html>). The distribution data of plant
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45 519 species were from the National Specimen Information Infrastructure (NSII,
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47 520 <http://www.nsii.org.cn>), the Chinese Virtual Herbarium (CVH, <http://www.cvh.ac.cn>), Global
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49 521 Biodiversity Information Facility (GBIF, <http://www.gbif.org/>), and the Botanical Information
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51 522 and Ecology Network (BIEN, <http://bien.nceas.ucsb.edu/bien/biendata/>). The human footprint
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53 523 data is from the Last of the Wild (<https://sedac.ciesin.columbia.edu>).

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TABLES AND FIGURES

TABLE 1. Summary information on the 29 studied mountain sites and the average range shifts of the centroid elevational position across all species occurring in a given mountain site.

Mountain range	Mount	Abbr.	Lat (°N)	Long (°E)	Total_num	N	Up-ratio	Shift(m)
Qionglai(邛崃山)	Balang(巴郎山)	BL	31.167	102.917	13502	114	0.42	-33.12
Bayankela(巴颜喀拉山脉)	Bayankela(巴颜喀拉山)	BYKL	34.204	97.659	11936	18	0.61	50.21
Hengduan(横断山脉)	Baimang(白茫雪山)	BMX	28.183	99.117	13705	21	0.67	53.94
Changbai(长白山脉)	Baitou(白头山)	BT	41.983	128.083	13498	29	0.59	17.56
Yanshan(燕山山脉)	Dongling(东灵山)	DL	39.733	115.5	14267	13	0.38	-86.32
Qionglai(邛崃山脉)	Emei(峨眉山)	EM	29.6	103.5	5451	25	0.8	440.46
Wuling(武陵山脉)	Fanjing(梵净山)	FJ	27.917	108.767	7146	22	0.41	-415.29
Wuling(武陵山脉)	Fenghuang(凤凰山)	FH	28.11	108.68	8188	5	0.6	-37.16
Hengduan(横断山脉)	Gaoligong(高黎贡山)	GLG	25.267	98.783	11047	35	0.2	-173.28
Hengduan(横断山脉)	Gongga(贡嘎山)	GG	29.6	101.883	27669	83	0.64	135.74
Lvliang(吕梁山脉)	Guandi(关帝山孝文山)	GD	37.8	110.8	7123	13	0.69	15.73
Hengduan(横断山脉)	Haba(哈巴雪山)	HB	27.45	100.117	5503	7	0.57	92.84
Daba(大巴山脉)	Hualong(化龙山)	HL	32.054	109.419	5387	5	0.8	116.47
Wuyi(武夷山脉)	Huanggang(黄岗山)	HG	27.8	117.6	11821	54	0.48	15.46
Dalou(大娄山脉)	Jinfo(金佛山)	JF	29.25	108.333	40841	231	0.4	-57.85
Hengduan(横断山脉)	Kagebo(卡格薄峰)	KGB	28.449	98.575	5372	38	0.66	97.76
Hengduan(横断山脉)	Laojun(老君山)	LJ	26.703	99.75	6254	16	0.19	-179.05
Miaoling(苗岭)	Leigong(雷公山)	LG	26.417	108.25	6276	5	0.8	-26.2
Lushan(庐山)	Lushan(庐山)	LS	29.55	115.967	19261	31	0.16	-218.86
Nanling(南岭)	Maoer(猫儿山)	ME	25.918	110.42	7105	22	0.36	-144.65
Himalayas(喜马拉雅山脉)	Nanjiabawa(南迦巴瓦峰)	NJBW	29.633	95.067	5037	6	0.67	-14.38
Hengduan(横断山脉)	Queer(雀儿山)	QE	31.77	99.05	6251	13	0.69	346.99
Daba(大巴山脉)	Shennongjia(神农架)	SNJ	31.667	110.583	59131	61	0.59	134.8
Qionglai(邛崃山脉)	Siguniang(四姑娘山)	SGN	31	103.217	6412	10	0.9	155.53
Qinling(秦岭)	Taibai(太白山)	TB	33.95	107.75	8295	46	0.72	196.38
Tianshan(天山山脉)	Tiangeer(天格尔峰)	TGE	43.168	86.623	8717	18	0.5	18.87
Hengduan(横断山脉)	Wuliang(无量山)	WL	24.45	100.733	6850	7	0.71	153.52
Taihan(太行山脉)	Xiaowutai(小五台山)	XWT	39.967	114.833	5360	12	0.17	-60.97
Aertai(阿尔泰山脉)	Youyi(友谊峰)	YYF	49.1	87.817	5706	6	0.33	1.59

Mount: the name of each of the 29 studied mountain site; Total_num: the total number of herbarium specimens for each of the 29 mountain sites. N: the total number of selected seed plant species in each of the 29 mountain sites; Up-ratio: the percentage of species shifting upward for each mountain site; Shift: the mean range shift of the centroid elevational position across all species of a given mountain site and between the two study periods (1950-1988 vs. 1980-2018).

TABLE 2 The multiple regression model evaluating the relationships between species elevational shifts and climate change experienced by species, the climatic adaptation of species, species properties and mountain properties

Type	Variation	Df	Sum Sq	Mean Sq	F	p
Climate change	Change in tem	1	37051	37051	0.43	0.51
	Change in pre	1	345512	345512	3.99	0.04*
	Importance of TS	1	3304	3304	0.04	0.85
Climatic adaption	Importance of MTWQ	1	46407	46407	0.54	0.46
	Importance of MTCQ	1	414136	414136	4.78	0.03*
	Importance of PS	1	578382	578382	6.68	0.01*
	Importance of PWQ	1	357892	357892	4.13	0.04*
	Importance of PCQ	1	75940	75940	0.88	0.35
	Elevation	1	75603	75603	0.87	0.35
	Range	1	294868	294868	3.40	0.07.
	Life form	2	94746	47373	0.55	0.58
	SexSyst	2	348638	174319	2.01	0.13
	Fruit type	13	1903992	146461	1.69	0.06.
Species properties	Family	109	15435053	141606	1.64	<0.001***
	Genus	224	31068140	138697	1.60	<0.001***
	Re-elevation	1	3235916	3235916	37.37	<0.001***
	Latitude	1	5789	5789	0.07	0.80
	Longitude	1	498763	498763	5.76	0.02*
	Climate regions	2	533050	266525	3.08	0.04*
	Mountain properties	Mountain	23	8981946	390519	4.51
	Residuals	452	39143600	86601		

Change in tem: the temperature changes experienced by each species; Change in pre: the precipitation changes experienced by each species; TS: temperature seasonality; MTWQ: mean temperature of warmest quarter; MTCQ: mean temperature of coldest quarter; PS: Precipitation seasonality; PWQ: precipitation of warmest quarter; PCQ: precipitation of coldest quarter. .p<0.1, *, p < 0.05, **, p < 0.01, ***, p < 0.001.

FIGURE 1 (a) The locations of the 29 study mountains and the ratio of species experiencing upward and downhill elevational shifts in these mountains. (b, c) The changes in the average magnitude of species' elevational shifts as functions of the average temperature (b) and size (c) of the mountains. In (a), blue bars indicated the ratio of species with upward shifts, and red bars indicated the ratios of species with downhill shifts. In (b) and (c), blue circles indicated the average magnitude of upward shifts, red triangles indicated the magnitude of downhill shifts, and white square indicated non-significant elevational shifts. The abbreviations of mountain names are shown in Table 1

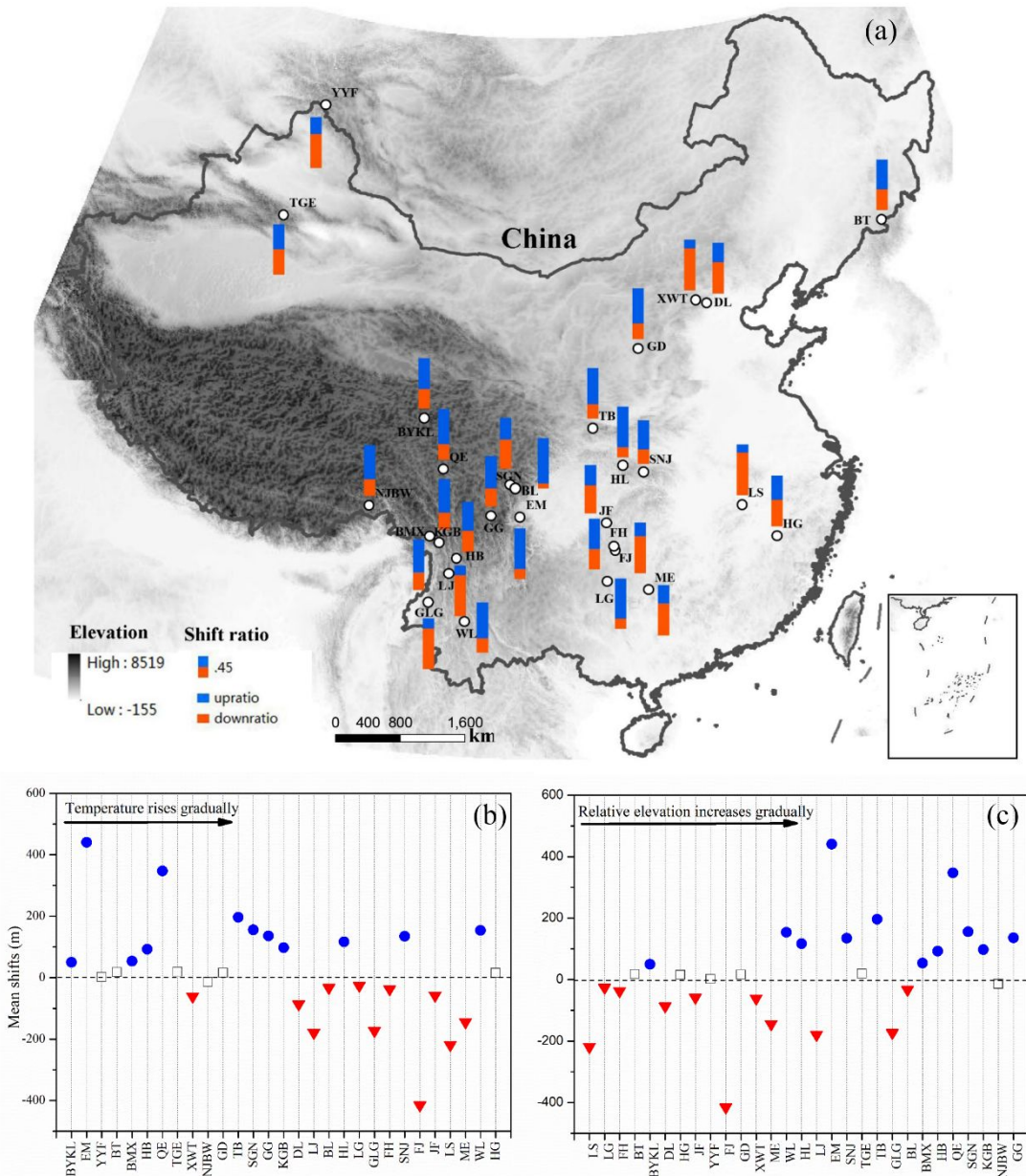


FIGURE 2 Relationships between the changes in optimum elevations and the climatic adaptation of species. The climatic adaptation was represented by the importance of climate factors in determining the global distribution ranges of the studied species (see Methods for details). MTCQ: mean temperature of coldest quarter; PS: Precipitation seasonality; PWQ: precipitation of warmest quarter

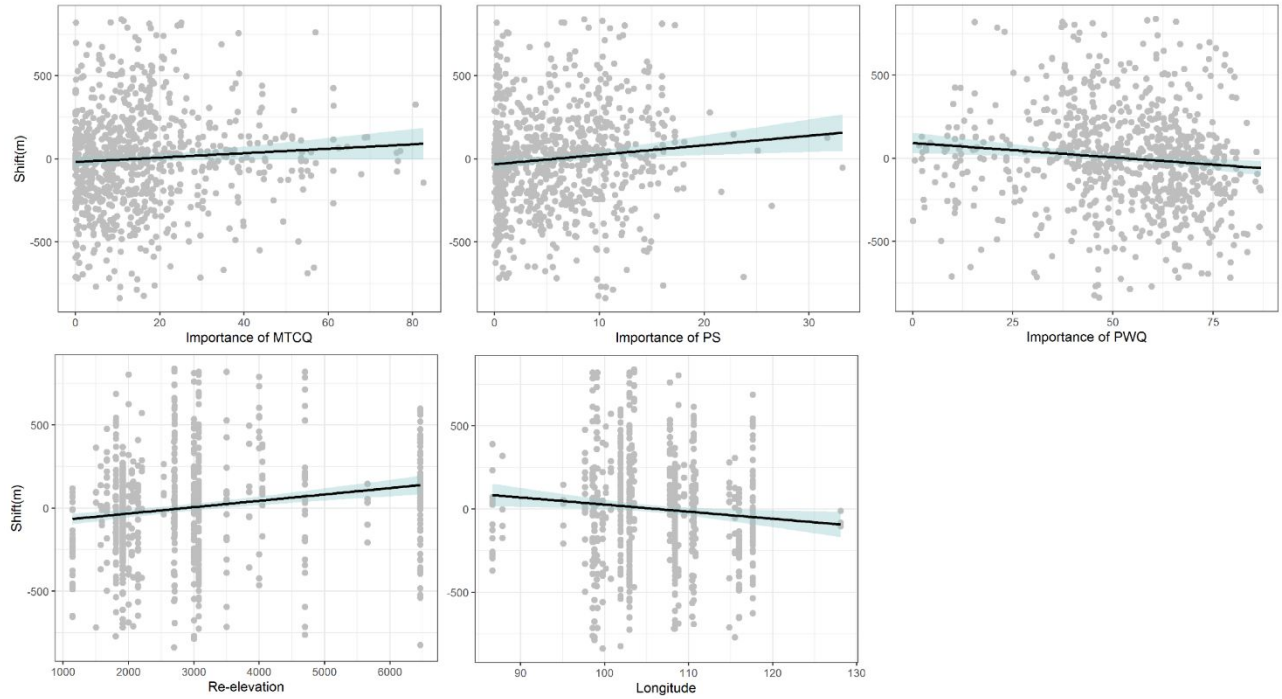


FIGURE 3 The average magnitude of elevational shifts (a) and relative species percentage of upward shifts (b) for herbaceous and woody plant species shown along the gradient of mean temperature of mountains. The abbreviations of mountain names are shown in Table 1

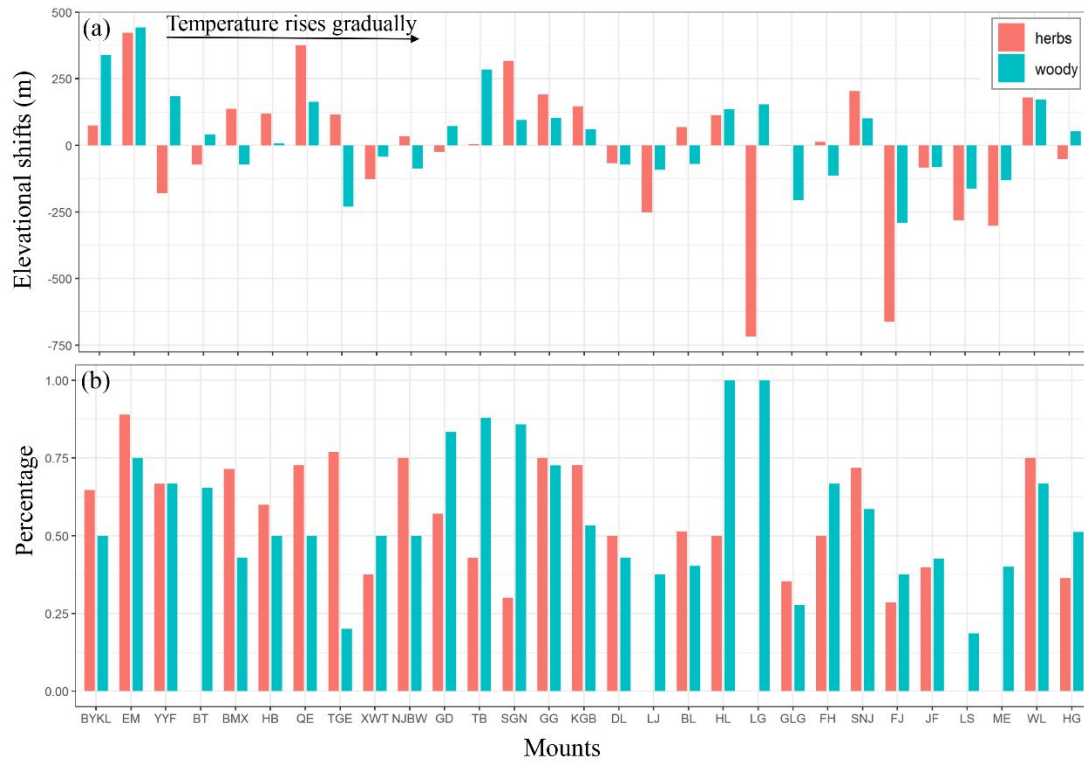
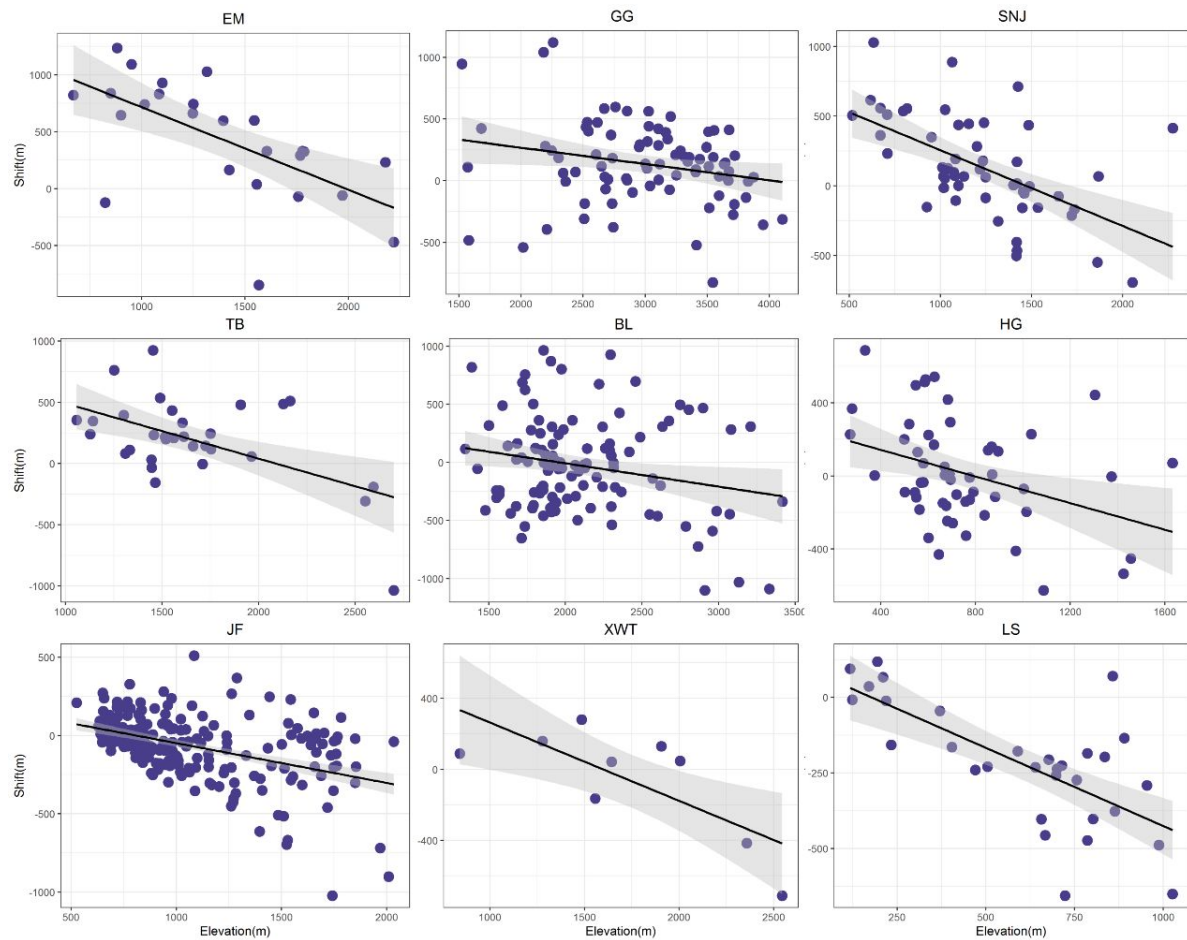


FIGURE 4 The relationship between the centroid elevation shifts and elevational distributions of species in different mountains. The x-axes represent the historical centroid elevation of species, and the y-axes represent the changes in the centroid elevation between the two studied periods. The 95% confidence intervals of the regression lines are shown in grey. The abbreviations of mountain names are shown in Table 1



Supplemental Figures and Tables

Figure S1: The species numbers studied in each mountains.

Figure S2: Elevational distribution of the selected species occurrence records through time for each mountain.

Figure S3: The standard meteorological stations were used in this study.

Figure S4: Change in temperature between historical (1950 - 1988) and present time (1989 - 2015) periods at long-term meteorological stations in China's mountains.

Figure S5: Change in precipitations between historical (1950 - 1988) and present time (1989 - 2015) periods at long-term meteorological stations in China's mountains.

Figure S6: Change in AET between historical (1950 - 1988) and present time (1989 - 2015) periods at long-term meteorological stations in China's mountains.

Figure S7: Change in summer/winter temperatures and precipitations between historical (1950 - 1988) and present time (1989 - 2015) periods at long-term meteorological stations in China' mountains.

Figure S8: Relationships between changes in optimum elevations and the importance of climate factors.

Figure S9: Relationships of the changes in optimum elevations with the functional traits of species, and the elevational shifts of herbs and woody plants in different climate regions (c). The functional traits included fruit types (a), and climate regions (b).

Table S1: The mountain sites located in China.

Tables S2: The lowest elevational data from literature.

Table S3: The random shifts in the species' centroid elevation calculated after the

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6 **Table S4:** The relationship between elevational shifts and elevation. The red indicate
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Supplementary Materials for

Elevational shift in seed plant distributions in China's mountains over the last 70 years

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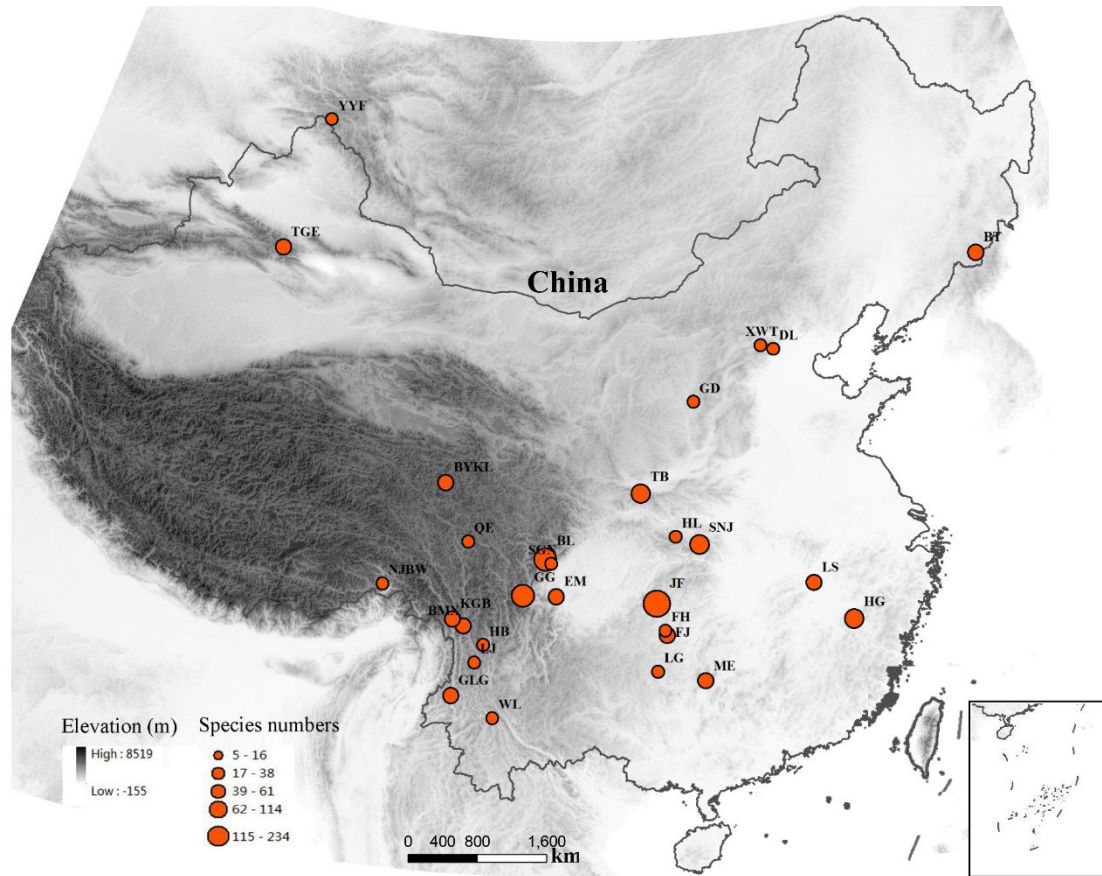
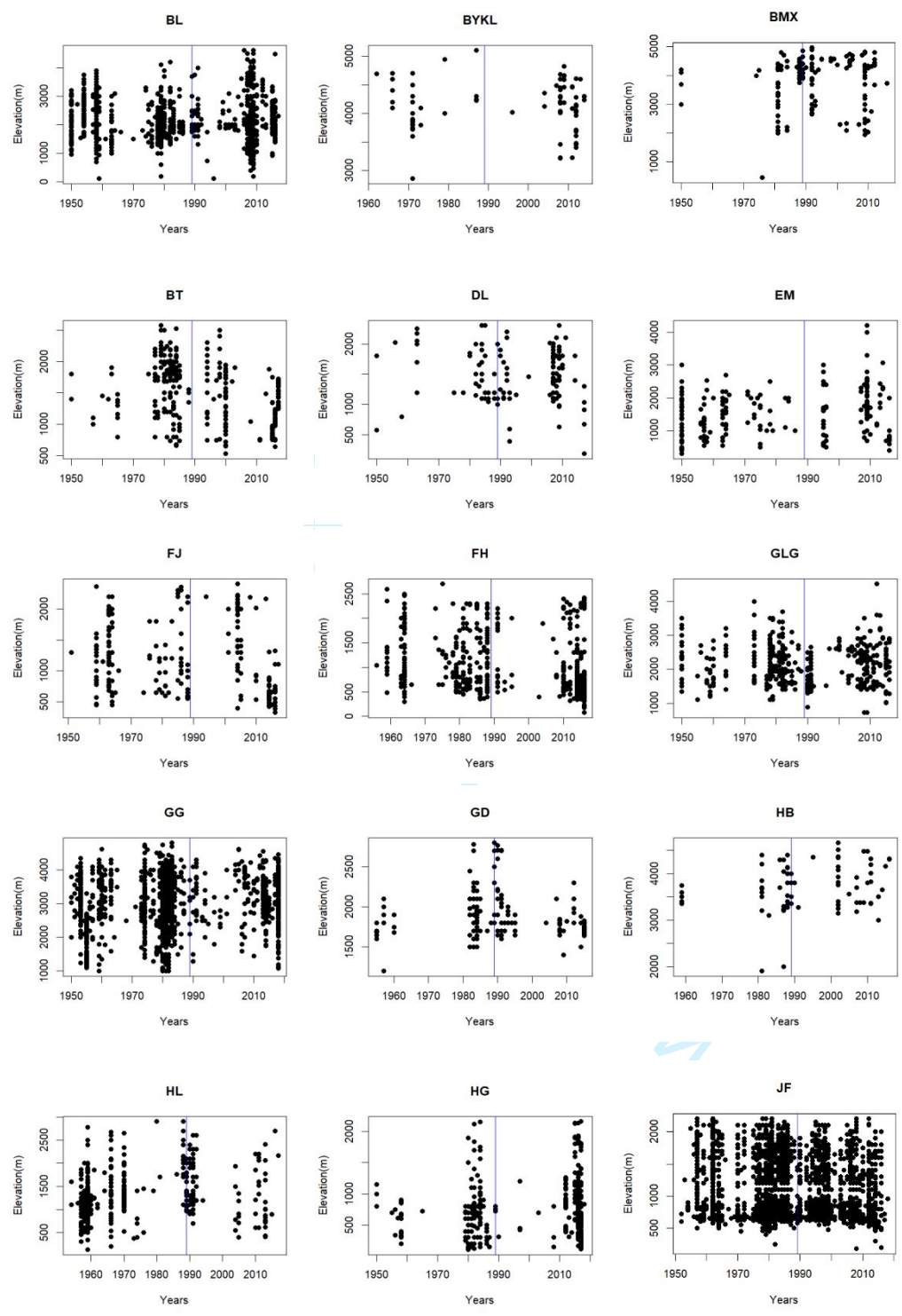


Figure S1: The species numbers studied in each mountains.

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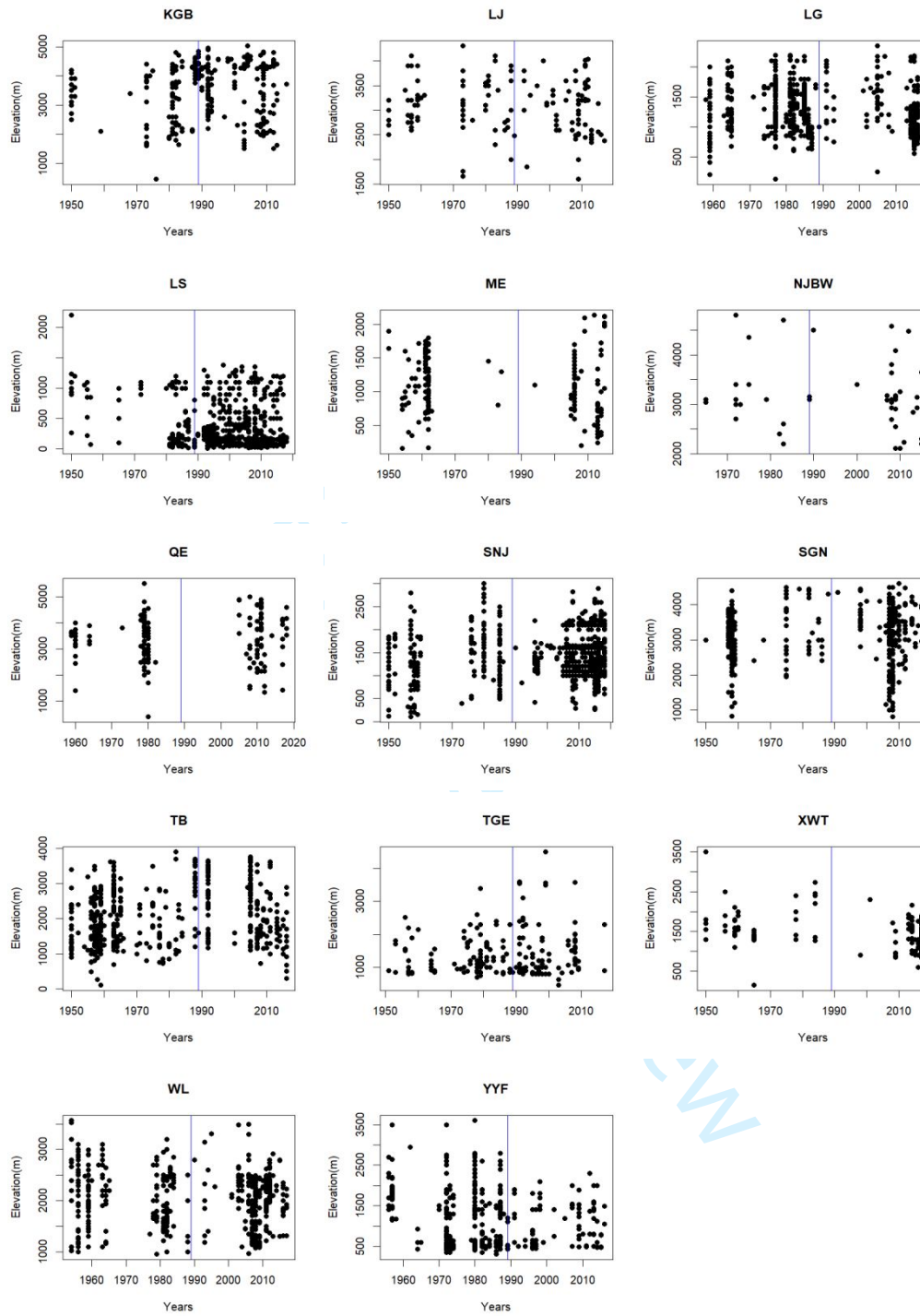


Figure S2: Elevational distribution of the selected species occurrence records through time for each mountain.

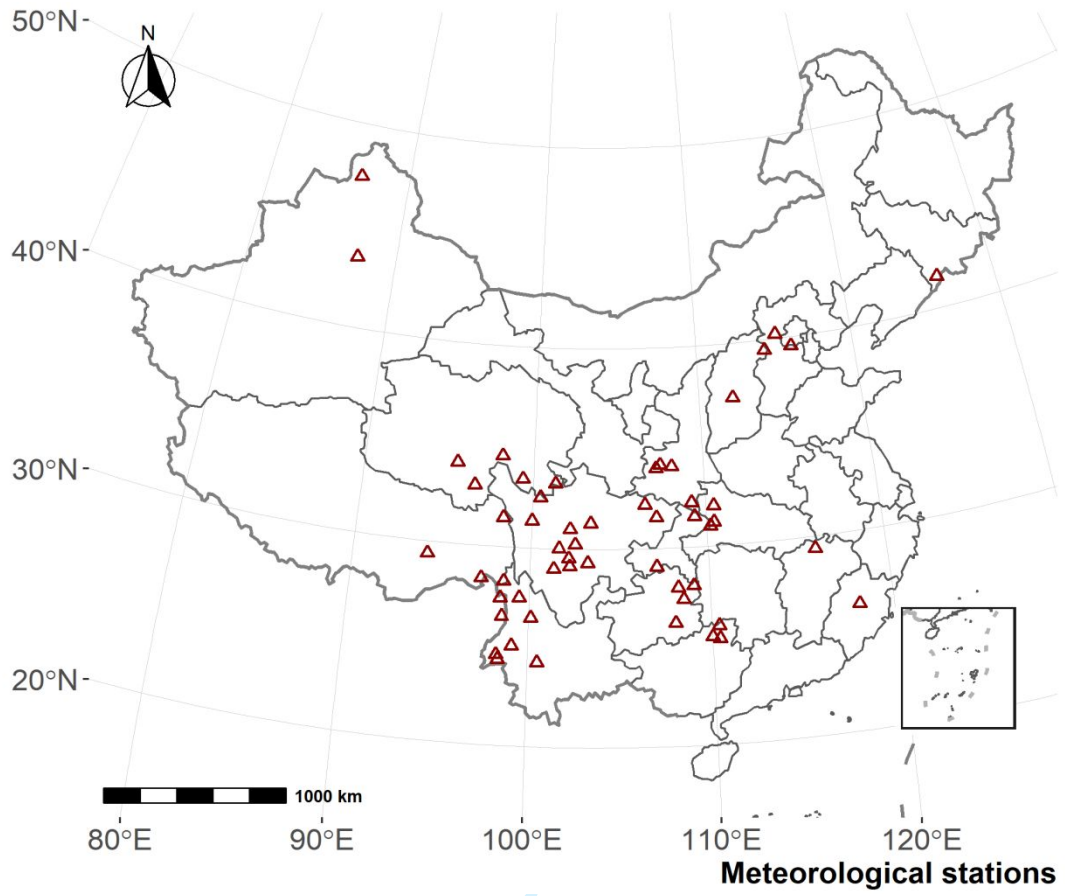


Figure S3: The standard meteorological stations were used in this study.

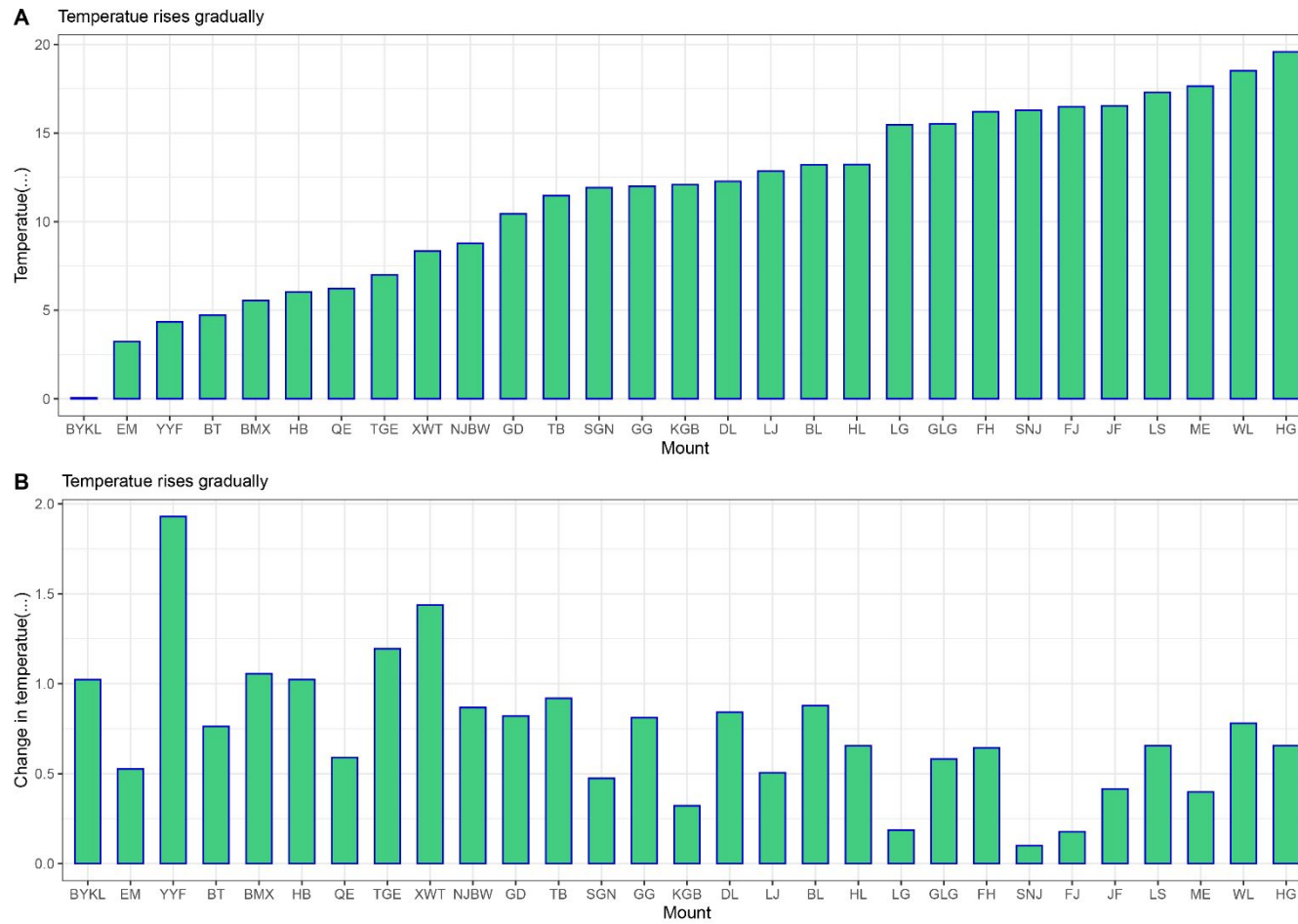
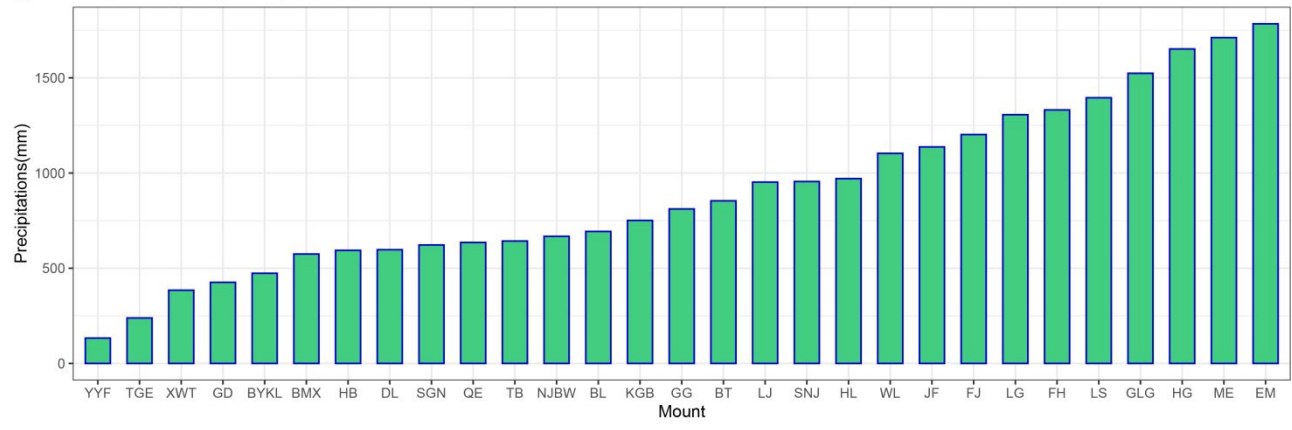


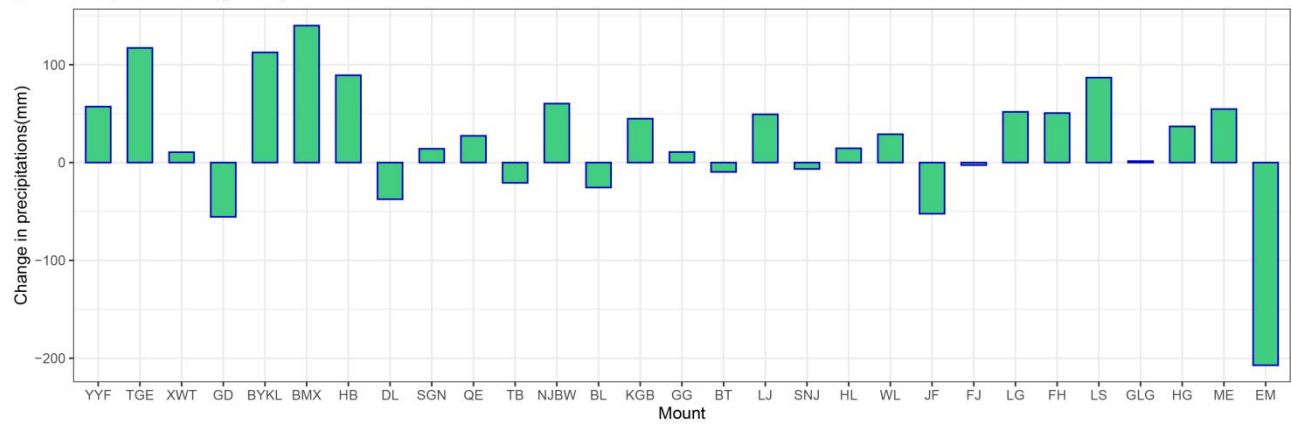
Figure S4: Change in temperature between historical (1950 - 1988) and present time (1989 - 2015) periods at long-term meteorological stations in

China's mountains.

A Precipitations rises gradually



B Precipitations rises gradually



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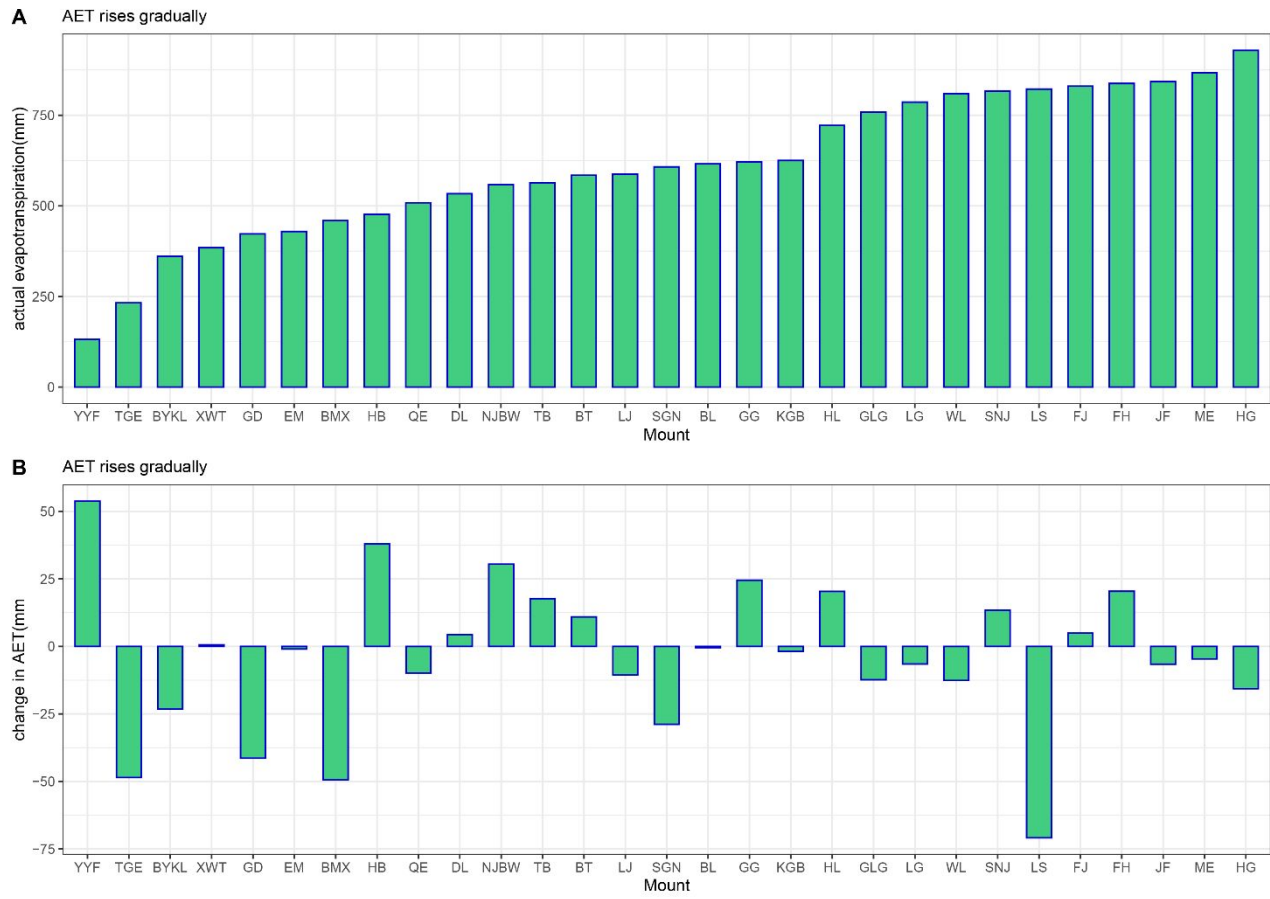


Figure S6: Change in AET between historical (1950 - 1988) and present time(1989 - 2015) periods at long-term meteorological stations in China’s mountains.

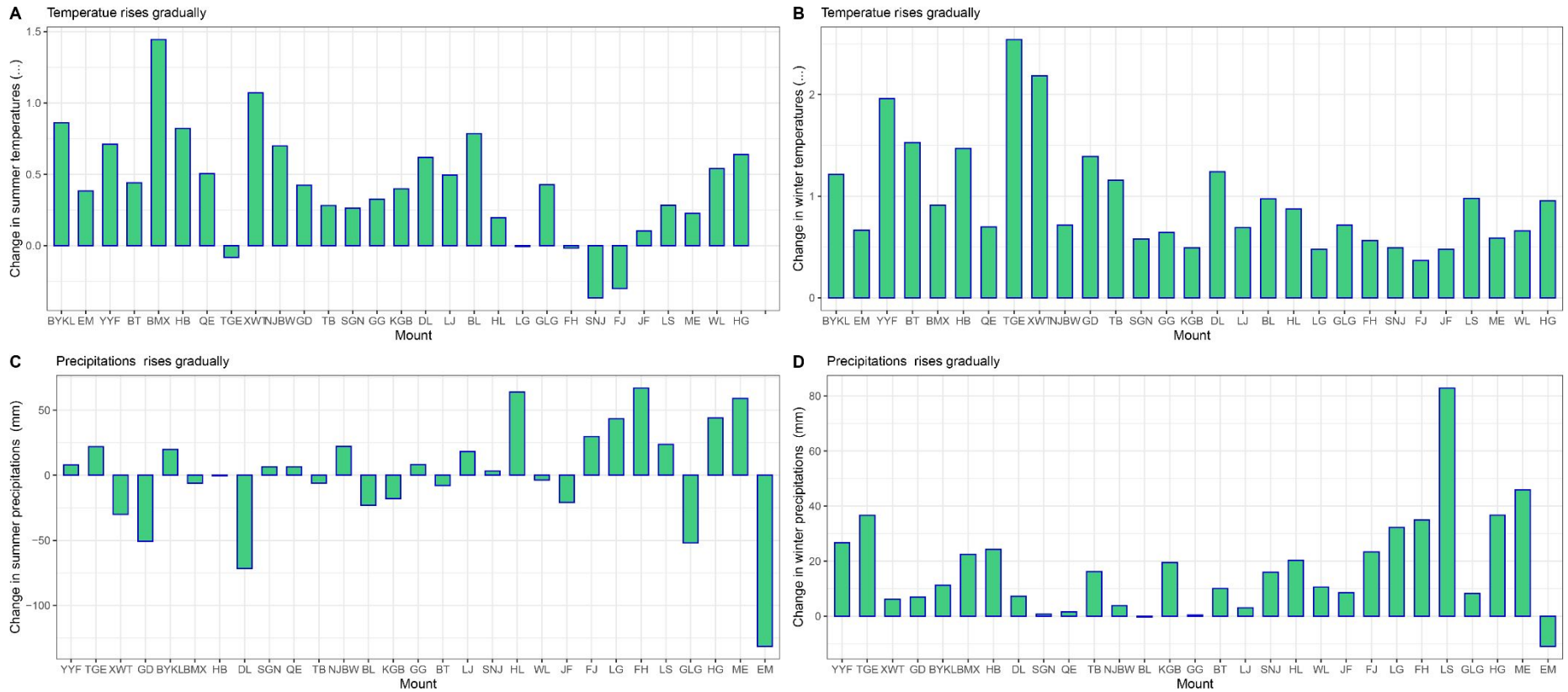


Figure S7: Change in summer/winter temperatures and precipitations between historical (1950 - 1988) and present time (1989 - 2015) periods at

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long-term meteorological stations in China' mountains.

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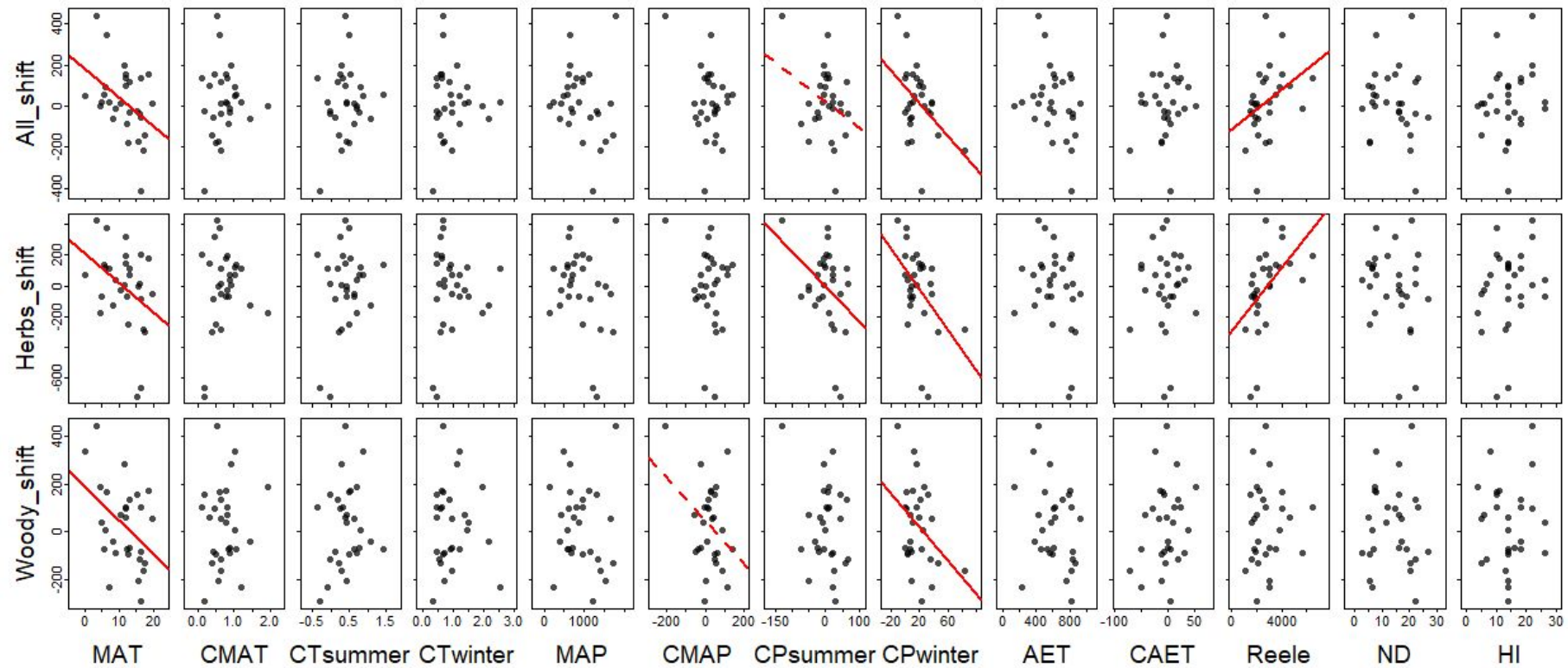


Figure S8: Relationships between changes in optimum elevations and the importance of climate factors. The x-axes are MAT, MAP, AET, changes in MAT, MAP, AET, relative elevation(Reele), Seasonal changes in MAT(CTsummer and CTwinter) and Seasonal changes in MAP(CPsummer and CPwinter), atmospheric nitrogen deposition(ND), and human footprint index (HI). The Y-axes represent changes in optimum elevation for all

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species, the shifts of herbs plants and the shifts of woody.

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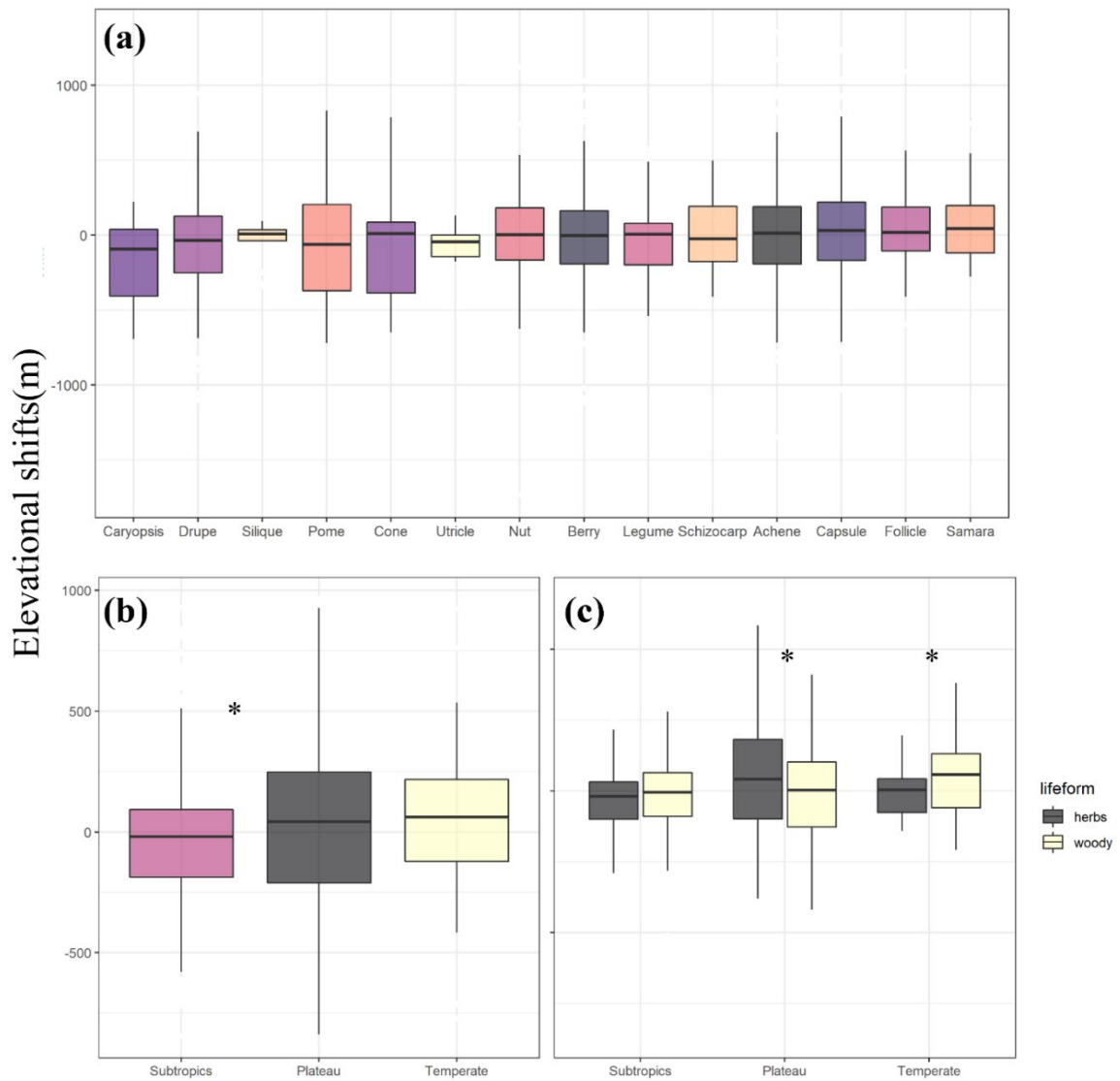


Figure S9: Relationships of the changes in optimum elevations with the functional traits of species, and the elevational shifts of herbs and woody plants in different climate regions (c). The functional traits included fruit types (a), and climate regions (b).

Table S1: The mountain sites located in China.

Mountain range	Mount	Abbr.	Lat (°N)	Long (°E)	The highest elevation	Relevation(max elevation-min elevation)	Province	climate region
Qionglai(邛崃山)	Balang(巴郎山)	BL	31.167	102.917	5072	3072	Sichuan	Plateau
Bayankela(巴颜喀拉山脉)	Bayankela(巴颜喀拉山)	BYKL	34.204	97.659	5267	1667	Qinghai	Plateau
Hengduan(横断山脉)	Baimang(白茫雪山)	BMX	28.183	99.117	5430	3500	Yunnan	Plateau
Changbai(长白山脉)	Baitou(白头山)	BT	41.983	128.083	2691	1591	Jilin	Temperate
Yanshan(燕山山脉)	Dongling(东灵山)	DL	39.733	115.5	2303	1803	Beijing	Temperate
Qionglai(邛崃山脉)	Emei(峨眉山)	EM	29.6	103.5	3099	2700	Sichuan	Subtropics
Wuling(武陵山脉)	Fanjing(梵净山)	FJ	27.917	108.767	2493	2000	Guizhou	Subtropics
Wuling(武陵山脉)	Fenghuang(凤凰山)	FH	28.11	108.68	2572	1572	Guizhou	Subtropics

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5	Hengduan(横断山脉)	Gaoligong(高黎贡山)	GLG	25.267	98.783	3374	3000	Yunnan	Plateau
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8	Hengduan(横断山脉)	Gongga(贡嘎山)	GG	29.6	101.883	7556	6466	Sichuan	Plateau
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11	Lvliang(吕梁山脉)	Guandi(关帝山孝文山)	GD	37.8	110.8	2831	2051	Shanxi	Temperate
12									
13	Hengduan(横断山脉)	Haba(哈巴雪山)	HB	27.45	100.117	5396	3846	Yunnan	Plateau
14									
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16	Daba(大巴山脉)	Hualong(化龙山)	HL	32.054	109.419	2917	2537	Shanxi	Subtropics
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19	Wuyi(武夷山脉)	Huanggang(黄岗山)	HG	27.8	117.6	2158	1808	Fujian	Subtropics
20									
21	Dalou(大娄山脉)	Jinfo(金佛山)	JF	29.25	108.333	2251	1911	Chongqing	Subtropics
22									
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24	Hengduan(横断山脉)	Kagebo(卡格薄峰)	KGB	28.449	98.575	6740	4700	Yunnan	Plateau
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27	Hengduan(横断山脉)	Laojun(老君山)	LJ	26.703	99.75	4247	2697	Yunnan	Plateau
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29	Miaoling(苗岭)	Leigong(雷公山)	LG	26.417	108.25	2179	1500	Guizhou	Subtropics
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32	Lushan(庐山)	Lushan(庐山)	LS	29.55	115.967	1474	1140	Jiangxi	Subtropics
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34	Nanling(南岭)	Maoer(猫儿山)	ME	25.918	110.42	2141.5	1862	Guangxi	Subtropics
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Himalayas(喜马拉雅山脉)	Nanjiabawa(南迦巴瓦峰)	NJBW	29.633	95.067	7782	5682	Xizang	Plateau
Hengduan(横断山脉)	Queer(雀儿山)	QE	31.77	99.05	6168	4000	Sichuan	Plateau
Daba(大巴山脉)	Shennongjia(神农架)	SNJ	31.667	110.583	3106	2706	Hubei	Subtropics
Qionglai(邛崃山脉)	Siguniang(四姑娘山)	SGN	31	103.217	6250	4050	Sichuan	Plateau
Qinling(秦岭)	Taibai(太白山)	TB	33.95	107.75	3767	3000	Shanxi	Temperate
Tianshan(天山山脉)	Tiangeer(天格尔峰)	TGE	43.168	86.623	4562	3000	Xinjiang	Temperate
Hengduan(横断山脉)	Wuliang(无量山)	WL	24.45	100.733	3254	2200	Yunnan	Plateau
Taihan(太行山脉)	Xiaowutai(小五台山)	XWT	39.967	114.833	2870	2070	Hebei	Temperate
Aertai(阿尔泰山脉)	Youyi(友谊峰)	YYF	49.1	87.817	4374	2000	Xinjiang	Temperate

“Relevation (max elevation-min elevation)” means the relative elevation, and it is the value of the highest elevation minus the lowest elevation.

Tables S2: The lowest elevational data from literature.

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Table S3: The random shifts in the species' centroid elevation calculated after the resampling of the historical and current survey records for each mountain.

Mountain range	Mount	Abbr.	downward species			upward species		
			t	df	p	t	df	p
Qionglai(邛崃山)	Balang(巴郎山)	BL	5.7924	63	2.39E-07	-12.142	49	< 2.2e-16
Bayankela(巴颜喀拉山脉)	Bayankela(巴颜喀拉山)	BYKL	2.5854	5	0.04911	-5.4648	11	0.0001964
Hengduan(横断山脉)	Baimang(白茫雪山)	BMX	5.26	6	0.001901	-1.8095	13	0.09354
Changbai(长白山脉)	Baitou(白头山)	BT	1.7506	12	0.1055	-3.4488	4	0.02608
Yanshan(燕山山脉)	Dongling(东灵山)	DL	1.7625	6	0.1285	-5.1134	5	0.003728
Qionglai(邛崃山脉)	Emei(峨眉山)	EM	4.8982	4	0.008055	-2.6158	19	0.017
Wuling(武陵山脉)	Fanjing(梵净山)	FJ	6.2574	12	0.00004208	-3.8442	8	0.004918
Wuling(武陵山脉)	Fenghuang(凤凰山)	FH	4.7051	1	0.1333	-0.6637	2	0.5752
Hengduan(横断山脉)	Gaoligong(高黎贡山)	GLG	2.9785	17	0.008432	-3.3971	6	0.01455
Hengduan(横断山脉)	Gongga(贡嘎山)	GG	10.84	18	< 0.001	-3.97	52	0.0002
Lvliang(吕梁山脉)	Guandi(关帝山孝文山)	GD	5.4114	3	0.01238	-5.804	8	0.0004033
Hengduan(横断山脉)	Haba(哈巴雪山)	HB	2.6428	2	0.1183	-1.5516	3	0.2186
Daba(大巴山脉)	Hualong(化龙山)	HL	—			3.603	3	0.03668
Wuyi(武夷山脉)	Huanggang(黄冈山)	HG	6.5888	27	4.56E-07	-6.1212	25	2.127E-06
Dalou(大娄山脉)	Jinfo(金佛山)	JF	4.1557	133	0.0000577	-21.055	96	< 2.2e-16
Hengduan(横断山脉)	Kagebo(卡格薄峰)	KGB	5.0916	12	0.0002655	-5.4549	24	0.0000132
Hengduan(横断山脉)	Laojun(老君山)	LJ	1.8963	12	0.08225	-3.5976	2	0.06933

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5	Miaoling(苗岭)	Leigong(雷公山)	LG	—			-1.9746	3	0.1428
6	Lushan(庐山)	Lushan(庐山)	LS	0.8541	25	0.4012	-26.477	4	0.00001209
7	Nanling(南岭)	Maoer(猫儿山)	ME	3.6141	13	0.003146	-6.0956	7	0.0004932
8	Himalayas(喜马拉雅山	Nanjiabawa(南迦巴瓦峰)	NJBW	1.7692	1	0.3275	-5.8342	3	0.01003
9	脉)								
10	Hengduan(横断山脉)	Queer(雀儿山)	QE	7.7699	3	0.004435	-3.668	8	0.006328
11	Daba(大巴山脉)	Shennongjia(神农架)	SNJ	3.8511	20	0.0009962	-9.1901	39	2.65E-11
12	Qionglai(邛崃山脉)	Siguniang(四姑娘山)	SGN	-0.478	8	0.6456	—		
13	Qinling(秦岭)	Taibai(太白山)	TB	7.7445	9	0.00002866	7.7175	35	4.64E-09
14	Tianshan(天山山脉)	Tiangeer(天格尔峰)	TGE	8.9414	8	0.00001944	-2.1882	8	0.06009
15	Hengduan(横断山脉)	Wuliang(无量山)	WL	1.4907	1	0.3762	-2.5967	4	0.06026
16	Taihan(太行山脉)	Xiaowutai(小五台山)	XWT	0.1616	9	0.8752	-5.2865	1	0.119
17	Aertai(阿尔泰山脉)	Youyi(友谊峰)	YYF	4.3688	3	0.02218	-3.6829	1	0.1688
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Table S4: The relationship between elevational shifts and elevation. The red indicate the significant relationship.

Mountain range	Mount	Abbr.	slope	r ²	p
Qionglai(邛崃山)	Balang(巴郎山)	BL	-0.23	0.06	0.01
Bayankela(巴颜喀拉山脉)	Bayankela(巴颜喀拉山)	BYKL	-0.33	0.11	0.18
Hengduan(横断山脉)	Baimang(白茫雪山)	BMX	-0.09	0.03	0.50
Changbai(长白山脉)	Baitou(白头山)	BT	-0.12	0.03	0.40
Yanshan(燕山山脉)	Dongling(东灵山)	DL	-0.29	0.08	0.36
Qionglai(邛崃山脉)	Emei(峨眉山)	EM	-0.73	0.39	0.00
Wuling(武陵山脉)	Fanjing(梵净山)	FJ	0.34	0.05	0.44
Wuling(武陵山脉)	Fenghuang(凤凰山)	FH	0.17	0.11	0.58
Hengduan(横断山脉)	Gaoligong(高黎贡山)	GLG	0.03	0.00	0.87
Hengduan(横断山脉)	Gongga(贡嘎山)	GG	-0.13	0.05	0.03
Lvliang(吕梁山脉)	Guandi(关帝山孝文山)	GD	-0.41	0.26	0.08
Hengduan(横断山脉)	Haba(哈巴雪山)	HB	-0.42	0.24	0.26
Daba(大巴山脉)	Hualong(化龙山)	HL	0.15	0.27	0.37
Wuyi(武夷山脉)	Huanggang(黄岗山)	HG	-0.36	0.13	0.01
Dalou(大娄山脉)	Jinfo(金佛山)	JF	-0.25	0.22	0.00
Hengduan(横断山脉)	Kagebo(卡格薄峰)	KGB	-0.06	0.02	0.47
Hengduan(横断山脉)	Laojun(老君山)	LJ	-0.11	0.02	0.58
Miaoling(苗岭)	Leigong(雷公山)	LG	-2.28	0.73	0.06
Lushan(庐山)	Lushan(庐山)	LS	-0.52	0.49	0.00
Nanling(南岭)	Maoer(猫儿山)	ME	-0.37	0.08	0.21
Himalayas(喜马拉雅山脉)	Nanjiabawa(南迦巴瓦峰)	NJBW	-0.01	0.00	0.96
Hengduan(横断山脉)	Queer(雀儿山)	QE	0.50	0.19	0.14
Daba(大巴山脉)	Shennongjia(神农架)	SNJ	-0.54	0.32	0.00
Qionglai(邛崃山脉)	Siguniang(四姑娘山)	SGN	-0.09	0.02	0.68
Qinling(秦岭)	Taibai(太白山)	TB	-0.45	0.29	0.00
Tianshan(天山山脉)	Tiangeer(天格尔峰)	TGE	0.20	0.04	0.41
Hengduan(横断山脉)	Wuliang(无量山)	WL	-0.01	0.00	0.99
Taihan(太行山脉)	Xiaowutai(小五台山)	XWT	-0.44	0.55	0.02
Aertai(阿尔泰山脉)	Youyi(友谊峰)	YYF	-0.39	0.58	0.08