

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/278027682>

# Regeneration dynamics of *Euptelea pleiospermum* along latitudinal and altitudinal gradients: Trade-offs between seedling and sprout

ARTICLE *in* FOREST ECOLOGY AND MANAGEMENT · JUNE 2015

Impact Factor: 2.66 · DOI: 10.1016/j.foreco.2015.06.004

---

READS

65

5 AUTHORS, INCLUDING:



**Xinzeng Wei**

Chinese Academy of Sciences

11 PUBLICATIONS 61 CITATIONS

SEE PROFILE



**Hao Wu**

Chinese Academy of Sciences

3 PUBLICATIONS 0 CITATIONS

SEE PROFILE



**Jiang Mingxi**

Chinese Academy of Sciences

43 PUBLICATIONS 237 CITATIONS

SEE PROFILE



Contents lists available at ScienceDirect

## Forest Ecology and Management

journal homepage: [www.elsevier.com/locate/foreco](http://www.elsevier.com/locate/foreco)

## Regeneration dynamics of *Euptelea pleiospermum* along latitudinal and altitudinal gradients: Trade-offs between seedling and sprout

Xinzeng Wei<sup>a</sup>, Hao Wu<sup>a,b</sup>, Hongjie Meng<sup>a,b</sup>, Chunmei Pang<sup>c</sup>, Mingxi Jiang<sup>a,\*</sup>

<sup>a</sup> Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, 430074 Hubei, China

<sup>b</sup> University of Chinese Academy of Sciences, Beijing 100049, China

<sup>c</sup> Administration Bureau of Tianmushan National Nature Reserve, Lin'an, 311311 Zhejiang, China

## ARTICLE INFO

## Article history:

Received 10 April 2015

Received in revised form 28 May 2015

Accepted 3 June 2015

Available online xxxx

## Keywords:

Climate warming

Life history strategy

Range shift

Regeneration dynamics

Sprout

Tertiary relict tree

## ABSTRACT

Poleward and upward range shifts are important strategies for range-restricted tree species in the face of climate warming, but empirical studies of both latitudinal and altitudinal shifts are scarce. We investigated regeneration dynamics of an endemic Tertiary-relict tree (*Euptelea pleiospermum*) along (i) a latitudinal gradient across its range in China and (ii) altitudinal gradients along three mountains at low, middle and high latitudes. Sprouting ratio and relative seedling density present contrasting latitudinal patterns, with more seedlings at the leading edges and more sprouts at the trailing edges. We detected no apparent shift, a downslope shift and an upward shift along mountains located at low, middle and high latitudes, respectively. Sprouting ratio and relative seedling density also show contrasting altitudinal patterns. Our results suggested (i) northward migration along the latitudinal gradient and (ii) disparity in altitudinal shifts of the same tree species along different mountains. Furthermore, we emphasize that sprouting is an important strategy for sprouting tree species to buffer range contraction at the trailing edges in the face of climate warming.

© 2015 Elsevier B.V. All rights reserved.

### 1. Introduction

Poleward and upward migrations are crucial strategies for plants in the face of climate warming (Parmesan, 2006; Chen et al., 2011; Peñuelas et al., 2013). Initial range shifts of long-lived trees are most likely detected in the regeneration layer, because seedling establishment at the leading edges occurs relatively rapidly (Fisichelli et al., 2014). Therefore, one popular way to detect poleward and upward shifts of tree species is comparing regeneration dynamics along latitudinal and altitudinal gradients, respectively (Peñuelas et al., 2007; Dang et al., 2010; Lv and Zhang, 2012; Fisichelli et al., 2014).

Static size structure of tree species is a well-known way to provide information on the regeneration dynamics (Peñuelas et al., 2007; Dang et al., 2010; Dolanc et al., 2013). Furthermore, studies on regeneration dynamics in many forests have also typically

included the analysis of seedling density (Taylor and Qin, 1988; Peñuelas et al., 2007). Therefore, disparities in both size distribution and seedling density along geographic gradients (e.g. latitude and altitude) are early indicators of range shift. There is a growing body of evidence for upward shifts in tree species distributions along altitudinal gradients (Peñuelas et al., 2007; Lenoir et al., 2009; Dang et al., 2010; Lv and Zhang, 2012; Vitasse et al., 2012; Rabasa et al., 2013), whereas only few empirical studies examined latitudinal shifts of tree species and these studies offer conflicting results (Jump et al., 2009; Zhu et al., 2012; Fisichelli et al., 2014). Empirical studies of both latitudinal and altitudinal shifts are scarce (Matias and Jump, 2015).

Range shifts not only refer to expansion at the leading edges of distributions, but also include retraction at the trailing edges (Jump et al., 2006; Peñuelas et al., 2013). In other words, seedling density will gradually decrease toward the trailing (equatorial and lower) edges. However, particular traits of some plants decrease their risk of extinction at the trailing edges (Peñuelas et al., 2013). Sprout is considered to be a key functional trait of woody plants to persist in harsh or unstable environments (Bond and Midgley, 2001; García and Zamora, 2003; Clarke et al., 2013), but too few empirical studies exist to test the hypothesis (Hampe and Petit, 2005). Moreover, there is always a tradeoff between seedling and sprouting

Abbreviation: DBH, diameter at breast height; EM 29°N, Emei Mountains; FP 33°N, Qinling Mountains; NSMSI, the number of sprouts per sprouting individuals; PMSI, the proportion of sprouting individuals among all individuals; RS, ratio of sprout; SNJ 31°N, Shennongjia Mountains.

\* Corresponding author.

E-mail address: [mxjiang@wbcas.cn](mailto:mxjiang@wbcas.cn) (M. Jiang).

<http://dx.doi.org/10.1016/j.foreco.2015.06.004>

0378-1127/© 2015 Elsevier B.V. All rights reserved.

(Bellingham and Sparrow, 2000). Therefore, it is expected that sprouting ratio and seedling density will present contrasting patterns along geographic gradients.

Many studies on range shifts of plants are carried out at tree line (Walther et al., 2005; Wang et al., 2006; Dang et al., 2009) or high latitude (Kullman, 2002; Felde et al., 2012), where organisms are considered to be highly sensitive to climate warming. Recently, some researchers have examined range shifts of plant species below tree line or at low latitude (Parmesan, 2006; Colwell et al., 2008; Matías and Jump, 2015).

South-central China has an impressive diversity of endemic flora (Myers et al., 2000), among which many are rare or endangered Tertiary-relict tree species (López-Pujó et al., 2011). These species include, but are not limited to, *Bretschneidera sinensis*, *Cercidiphyllum japonicum*, *Davidia involucrata*, *Dipteronia sinensis*, *Euptelea pleiospermum*, and *Tetracentron sinense* (Editorial Committee for Vegetation of China, 1980). Most of these species prolifically sprout (Tang and Ohsawa, 2002; Kubo et al., 2005; Wei et al., 2010a). At the continental scale, they occur in a few restricted areas of East Asia (Tang and Ohsawa, 2002; Ying and Chen, 2011). Their main altitudinal ranges are between 1000 and 2000 m, and a bit beyond this range along some mountains (Editorial Committee for Vegetation of China, 1980). As temperate elements of subtropical montane evergreen and deciduous broad-leaved forest, they are likely to migrate to higher latitudes in the face of ongoing global warming. In North America, temperate trees have expanded into adjacent boreal forests (Fisichelli et al., 2014). Although the relict trees mentioned above are not timberline species, climate warming can potentially threaten all montane species with restricted distribution ranges (Parmesan, 2006). It has been reported that upward shifts of plants occurred throughout the elevational gradient and not just at treeline (Kelly and Goulden, 2008; Lenoir et al., 2008; Jump et al., 2012).

Knowledge about whether these relict trees expand at the leading edges or are persistent by sprout at the trailing edges will benefit their further management and conservation. However, it is not feasible to study all relict tree species; an alternative is to use a surrogate species that can represent several others. Therefore, we chose *E. pleiospermum* as surrogate species in this study, because, in China, geographic range of *E. pleiospermum* covers the ranges of all tree species mentioned above (Fu and Jin, 1992; Tang and Ohsawa, 2002).

In this study, we investigated regeneration dynamics of *E. pleiospermum* along latitudinal and altitudinal gradients across its geographic distribution range in China. We compared population size structure, relative seedling density and ratio of sprouts to seedlings along geographic gradients, respectively. Specifically, we examined (i) whether non-timberline tree species present climate warming-induced latitudinal and altitudinal shifts; (ii) whether the same tree species shows the same range shift trend along mountains located at different latitudes; and (iii) whether sprouting ratio and relative seedling density present contrasting patterns along geographic gradients.

## 2. Materials and methods

### 2.1. Study species

*E. pleiospermum* Hook. f. et Thoms (Eupteleaceae) is a deciduous and broad-leaved Tertiary-relict tree species endemic to China, India and Burma (Fu and Jin, 1992). Populations of *E. pleiospermum* are usually scattered in river valleys of remote mountainous areas (Fu and Jin, 1992). Across its range, *E. pleiospermum* always coexists with other Tertiary-relict trees in naturally occurring, uneven-aged montane forests. At maturity, it reaches 12 m in height and 20 cm

in diameter at breast height (DBH). Most individuals produce numerous sprouts, which may contribute to its persistence over long periods (He et al., 2013). The tree produces wind-pollinated flowers and abundant light samaras, which are dispersed by wind and/or water. Seed vigor decreases rapidly after more than one year (Wei et al., 2010b), indicating that this species cannot form persistent soil seed bank.

### 2.2. Study sites and climatic data

The study area was located throughout the geographical distribution range of *E. pleiospermum* in China (Fig. 1), which is determined according to the China Plant Red Data Book (Fu and Jin, 1992). Our investigation area spans montane landscapes from Qinling Mountains in northern China to Hengduan Mountains in southern China (Fig. 1 and Table 1). Data were collected at 21 sites between 25.751°N and 35.271°N latitude, and between 100.017°E and 119.427°E longitude, at elevations ranging from 641 to 2770 m a.s.l. (Fig. 1 and Table 1).

We chose the Emei Mountains (EM 29°N), Shennongjia Mountains (SNJ 31°N), and Qinling Mountains (FP 33°N) to study altitudinal patterns of size structure, seedling density and sprouting ratio. The three mountains are all higher than 3000 m a.s.l. (Emei Mountains, 3099 m; Shennongjia Mountains 3105 m; and Qinling Mountains 3767 m). We choose these mountains because they are the main mountains within the distribution range of *E. pleiospermum* and they are located along a latitudinal gradient with almost equal latitude interval (ca. two degrees). Altitudinal ranges of *E. pleiospermum* along the three mountains are 900–1800 m, 900–2000 m, and 1200–1800 m, respectively.

In mainland China, mean annual temperature has significantly raised in the last few decades, with increases of between 1.16 and 1.56 °C, based on climatic data from 756 meteorological stations across China (Sun et al., 2012). Monthly climatic data series in the last few decades were obtained from the nearest meteorological stations for the three mountains: Foping meteorological station (33.53°N, 107.98°E; 1087.7 m), Badong meteorological station (31.07°N, 110.40°E; 294.5 m) and Yibin meteorological station (28.8°N, 104.60°E; 340.8 m). Based on these climatic data, we demonstrated that mean annual temperature has significantly increased in the last several decades, with an increase of 0.226 °C per decade at the northern latitude, 0.275 °C at the middle latitude, and 0.232 °C at the southern latitude (Fig. 2).

### 2.3. Field investigation

Fieldwork was carried out from May to August in 2013. As *E. pleiospermum*'s distribution is always sporadic, we did not establish plots, but instead used line-transect sampling. The length of transect is not uniform and is decided according to the distribution of this species in the survey area. The direction of transect is along the streamside (usually along slope) because this species always occurs in streamside forest. At each of the 21 sites (hereafter latitudinal site), we surveyed at least 30 individuals (Fig. 1 and Table 1). We investigated almost all individuals along transect at each 100 m altitudinal interval (hereafter altitudinal site) across the species' entire altitudinal range for the three mountains (Appendix A). At each latitudinal or altitudinal site, we measured DBH of each individual with height  $\geq 1.3$  m and height of each individual with height  $< 1.3$  m, respectively. For multi-stemmed individuals, we recorded DBH (for stem with height  $\geq 1.3$  m), height (for stem with height  $< 1.3$  m) and number of stems. In this case, we considered the stem with the largest DBH or height as the main stem and the others as sprouts.

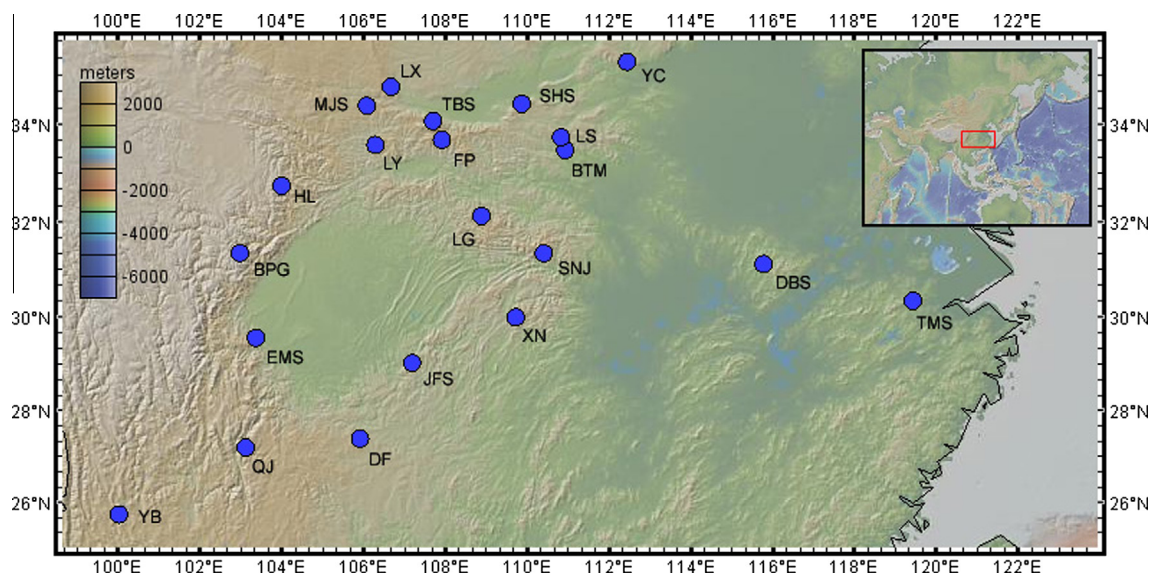


Fig. 1. Location of the 21 study sites across geographical distribution range of *Euptelea pleiospermum* in China. See Table 1 for site names.

Table 1

Site characteristics for the 21 populations of *Euptelea pleiospermum* across its geographical distribution range in China.

Site code	Altitude (m)	Latitude (°N)	Longitude (°E)	Group	N	Location information	Mountains <sup>a</sup>
YB	2690	25.751	100.017	L	54	Yangbi, Yunnan	Henduan
QJ	2770	27.215	103.115	L	67	Qiaojia, Yunnan	Hengduan
DF	1623	27.409	105.909	L	52	Dafang, Guizhou	Wumeng
JFS	1800	29.038	107.184	L	47	Jinfoshan, Nanchuan, Chongqing	Dalou
EMS	1460	29.576	103.366	L	69	Emeishan, Sichuan	Qionglai
XN	1091	30.014	109.716	L	34	Xuanen, Hubei	Wuling
TMS	1030	30.360	119.427	L	40	Tianmushan, Lin'an, Zhejiang	Tianmushan
DBS	1002	31.132	115.776	M	56	Dabieshan, Jinzhai, Anhui	Dabieshan
SNJ	1682	31.356	110.403	M	36	Shennongjia, Hubei	Daba
BPG	2660	31.363	102.973	M	63	Bipenggou, Lixian, Sichuan	Qionglai
LG	1363	32.134	108.879	M	43	Langao, Shaanxi	Daba
HL	2425	32.757	103.992	M	57	Huanglong, Songpan, Sichuan	Minshan
BTM	1239	33.491	110.928	M	88	Baotianman, Neixiang, Henan	Funiu
LY	1538	33.594	106.288	M	46	Lueyang, Shaanxi	Qinling
FP	1553	33.699	107.910	H	35	Foping, Shaanxi	Qinling
LS	1598	33.750	110.825	H	32	Lushi, Henan	Funiu
TBS	1280	34.080	107.693	H	147	Taibaishan, Shaanxi	Qinling
MJS	1538	34.385	106.079	H	96	Maijishan, Tianshui, Gansu	Qinling
SHS	1200	34.427	109.865	H	38	Shaohuashan, Huaxian, Shaanxi	Qinling
LX	1518	34.769	106.665	H	58	Longxian, Shaanxi	Liupanshan
YC	641	35.271	112.440	H	32	Yangcheng, Shanxi	Taihang

L, low latitude; M, middle latitude; N, number of individuals; H, high latitude.

<sup>a</sup> The mountains are determined according to Wang et al. (2004).

#### 2.4. Data analysis

We clustered the 21 sites into three groups based on latitudes (L, low latitude; M, middle latitude; H, high latitude; see Table 1 and Fig. 3a), and then compared size structures along the three latitudinal gradients. Along each of the three mountains, altitudinal sites were also classed into low, middle, and high altitudes (Fig. 5 and Appendix A). We also compared size structures at low, middle and high altitudes along each of the three mountains (Fig. 5). As DBH of *E. pleiospermum* was always smaller than 22.5 cm, we clustered individuals into 10 size classes with a DBH interval of 2.5 cm (e.g. 0–2.5 cm, 2.5–5.0 cm, 5.0–7.5 cm, etc.).

Based on field observations (e.g. flower and fruit), we treated individuals with DBH <2.5 cm as seedlings and the others as adults. Here, seedling is defined as individual that is not big enough to produce flower and fruit, which may include sapling. As an equivalent to sprout (asexual), we used it as seedling (sexual), which

emerges from seed. We defined relative seedling density as proportion of the number of seedlings to the total number of individuals at each site. Relationships between relative seedling density and latitude or altitude were determined using Pearson correlation.

Ratio of sprout (RS) is commonly defined as the ratio of the number of sprouts to the number of main stems. Nanami et al. (2004) proposed two other parameters: the proportion of sprouting individuals among all individuals (PMSI) and the number of sprouts per sprouting individuals (NSMSI). Based on definitions of the three parameters, we can formulate the following equation:  $RS = PMSI \times NSMSI$ . Latitudinal and altitudinal patterns of the three parameters were also examined using Pearson correlations.

Statistical analyses were performed using SPSS 16.0 for Windows (SPSS Inc., Chicago, IL, USA). Prior to Pearson correlation, a Shapiro–Wilk test was used to examine the homogeneity of variance. When required, values were SQRT (relative seedling density of the 21 latitudinal sites), LG (RS and NSMSI of the 21 latitudinal

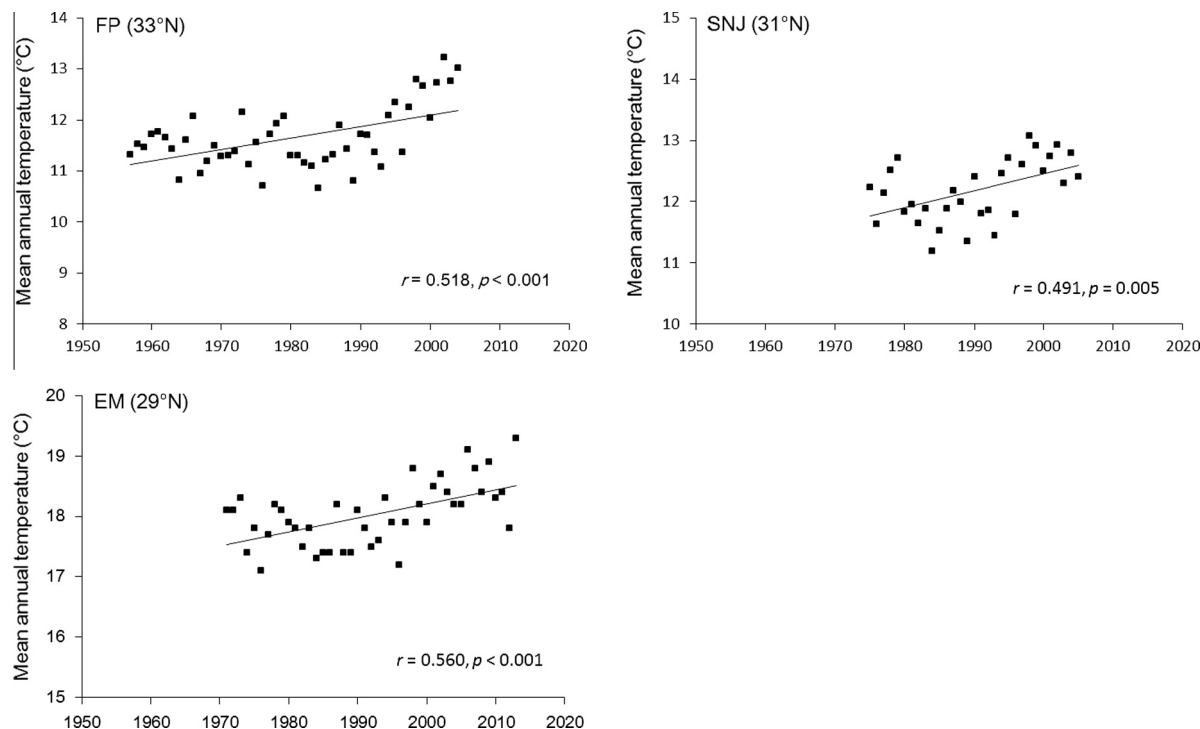


Fig. 2. Temporal patterns of mean annual temperature in the last few decades for the Qinling Mountains (FP), Shennongjia Mountains (SNJ) and Emei Mountains (EM).

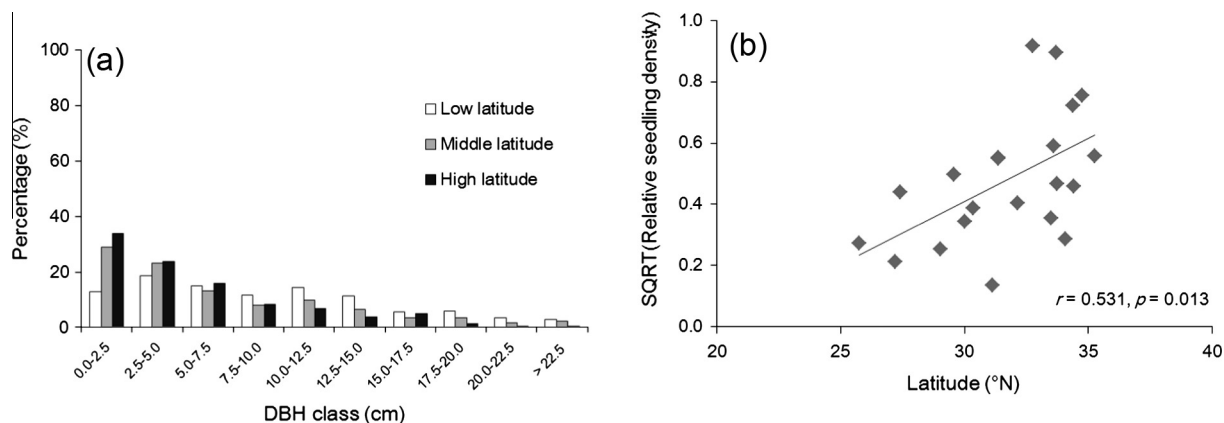


Fig. 3. (a) Size distribution of *Euptelea pleiospermum* at different latitudes across its geographical distribution range in China; (b) Latitudinal pattern of relative seedling density (proportion of the number of seedlings to total number of individuals). See details in Table 1 for the classification of low, middle and high latitudes.

sites), or LN (NSMSI of FP 33°N) transformed to satisfy the assumptions of normality and homogeneity of variance. However, we tried many transformations (including a Box-Cox transformation by using Minitab 15), but RS of SNJ 31°N did not satisfy the assumptions of normality and homogeneity of variance. Therefore, we used Spearman's rho correlation to determine the altitudinal pattern of RS along the Shennongjia Mountains.

### 3. Results

#### 3.1. Regeneration dynamics along latitude

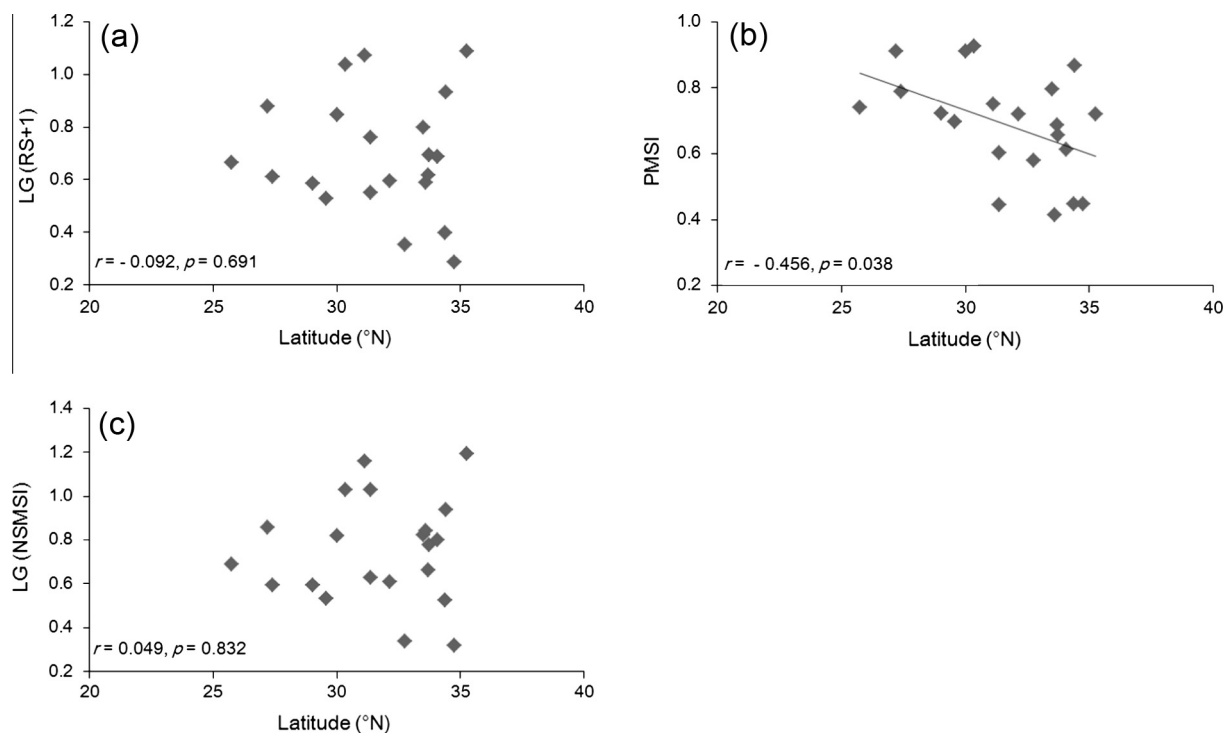
Populations at low latitude showed sporadic size structure, with two or more peaks in size classes (Fig. 3a). Populations at both middle and high latitudes showed inverse-J type of size structure, with the highest frequency in the smallest DBH class (Fig. 3a). The proportions of seedlings (0–2.5 cm) at low, middle and high

latitudes were 12.9%, 29.0% and 33.8%, respectively. Relative seedling density was significantly correlated with latitude (Fig. 3b). Neither RS nor NSMSI were significantly correlated with latitude, whereas PMSI was negatively correlated with latitude (Fig. 4).

#### 3.2. Regeneration dynamics along altitudes

At FP 33°N, seedlings accounted for 63.3%, 75.7% and 83.6% of the total number of individuals at low, middle and high altitudes, respectively (Fig. 5). We detected a marginally positive correlation between relative seedling density and altitude at FP 33°N (Fig. 5). At FP 33°N, both RS and NSMSI were marginally negatively correlated with altitude, whereas PMSI was not related to altitude (Fig. 6).

At SNJ 31°N, all three populations at low, middle and high altitudes showed sporadic size structure (Fig. 5). Contrary to our prediction, percentage of seedlings decreased from low to high



**Fig. 4.** Latitudinal patterns of (a) RS, (b) PMSI and (c) NSMSI. RS, the ratio of the number of sprouts to the number of main stems; PMSI, the proportion of sprouting individuals among all individuals; NSMSI, the number of sprouts per sprouting individual.

altitude at SNJ 31°N (Fig. 5), with 49.5%, 35.0% and 10.6% at low, middle and high altitudes, respectively. Relative seedling density significantly decreased with altitude at SNJ 31°N (Fig. 5). All three sprouting parameters (e.g. RS, PMSI and NSMSI) were significantly positively correlated with altitude at SNJ 31°N (Fig. 6).

At EM 29°N, seedlings accounted for 41.2%, 72.9% and 42.7% of the total number of individuals at low, middle and high altitudes, respectively (Fig. 5). Relative seedling density, RS, PMSI and NSMSI were not significantly correlated with altitude at EM 29°N (Figs. 5 and 6).

## 4. Discussion

### 4.1. Regeneration dynamics along latitude

Our results showed that regeneration dynamics of *E. pleiospermum* varied along the latitudinal gradient. Regeneration trends were generally consistent with predictions, with more seedling establishment at the leading edges. In other words, the closer it gets to the northern edge, the higher the relative seedling density. This indicates that northward migration is occurring in this Tertiary-relict rare tree species across its geographic range. This is consistent with earlier findings reported for temperate trees at the temperate-boreal transition zone in North America (Fischelli et al., 2014) and for about one fifth of the tree species across the eastern United States based on USDA Forest Service's Forest Inventory and Analysis data (Zhu et al., 2012).

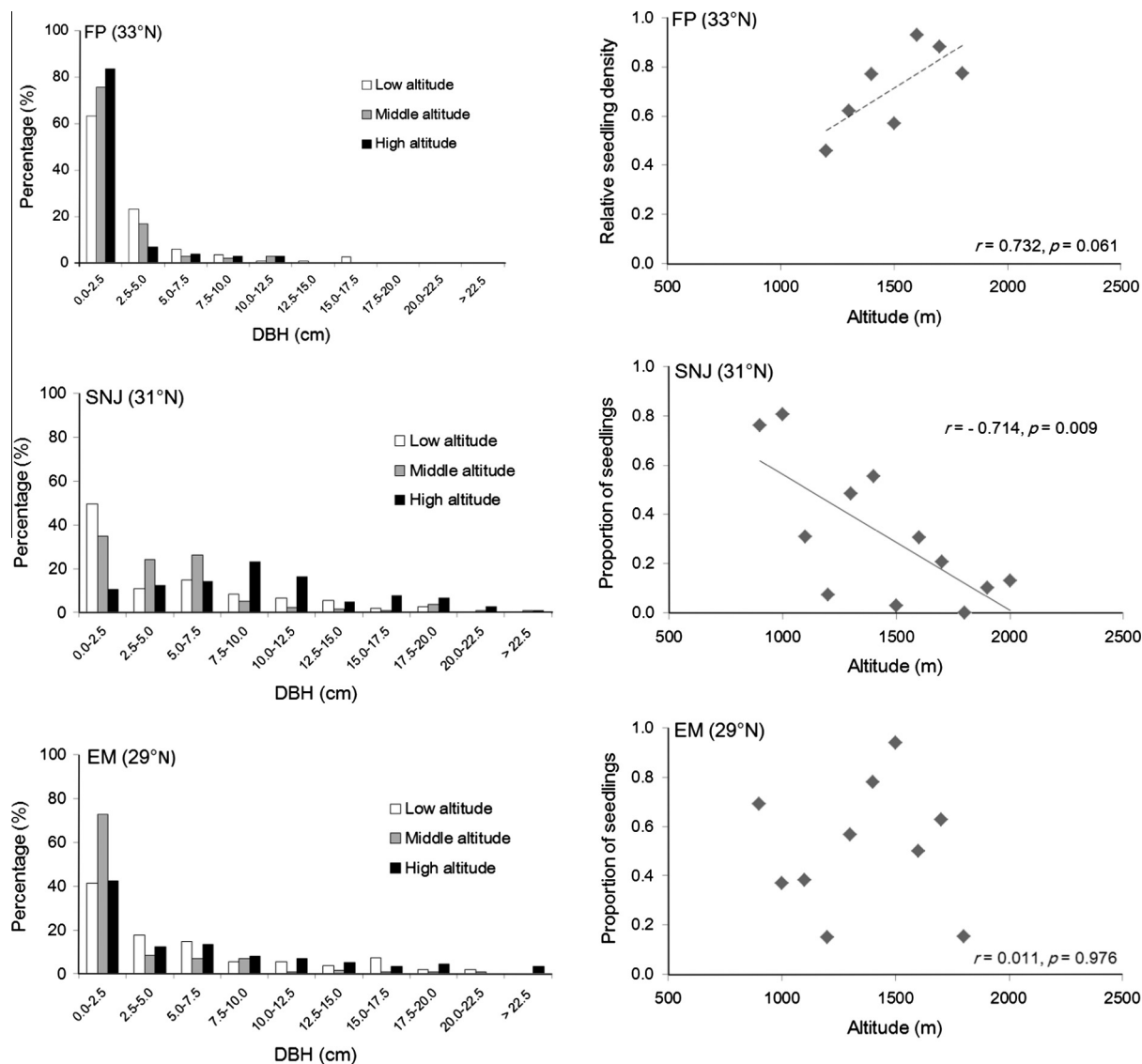
To our knowledge, this is the first study that provides evidence for northward shift of tree species in China. The potential causes of northward migration are the combination of water limitation and hot summers in the south, and elevated temperatures in the north (Jump et al., 2009; Peñuelas et al., 2013). Indeed, based on data from 486 meteorological stations, researchers reported that climate warming was ongoing throughout mainland China during 1960–2000 (Qian and Qin, 2006). However, the underlying

mechanisms (e.g. physiological process) linking northward shift of tree species to climate warming are complex and need further investigation.

In contrast to the increasing relative seedling density along the latitudinal gradient, sprouting ratio gradually decreased from low to high latitude. These results provide evidence for our expectation that sprouting ratio and seedling density present contrasting patterns along latitudinal gradients, and suggest a tradeoff between seedling and sprouting across the range of *E. pleiospermum*. The tradeoff between sexual and asexual reproduction has been shown in long-lived Mediterranean plant species (e.g. *Juniperus communis* and *Pinguicula vallisneriifolia*), which shifted their life-history strategies from regeneration by seeding to vegetative reproduction along gradients of increasing abiotic stress or interspecific competition (García and Zamora, 2003). As persistence is considered to be the most frequent functional role of sprouting in long-lived plants (Bond and Midgley, 2001; Bellingham and Sparrow, 2009; Tanentzap et al., 2012), we emphasize the importance of sprouting for woody plants to persist at their trailing edges. In other words, sprouting is a crucial strategy for long-lived plants to buffer the potential contraction of their distribution ranges in the face of ongoing climate warming.

### 4.2. Regeneration dynamics along altitudes

Our study simultaneously presents altitudinal patterns of relative seedling density and sprouting ratio along latitudinal gradients. Clearly, regeneration dynamics of *E. pleiospermum* along altitudinal gradients of the three mountains are quite different, with no apparent shift along the Emei Mountains, a downslope shift along the Shennongjia Mountains, and upward shift along the Qinling Mountains. These findings suggest that there is disparity in altitudinal shifts of the same tree species along mountains located at different latitudes. However, current theory predicts an upward shift along altitudinal gradients that becomes more



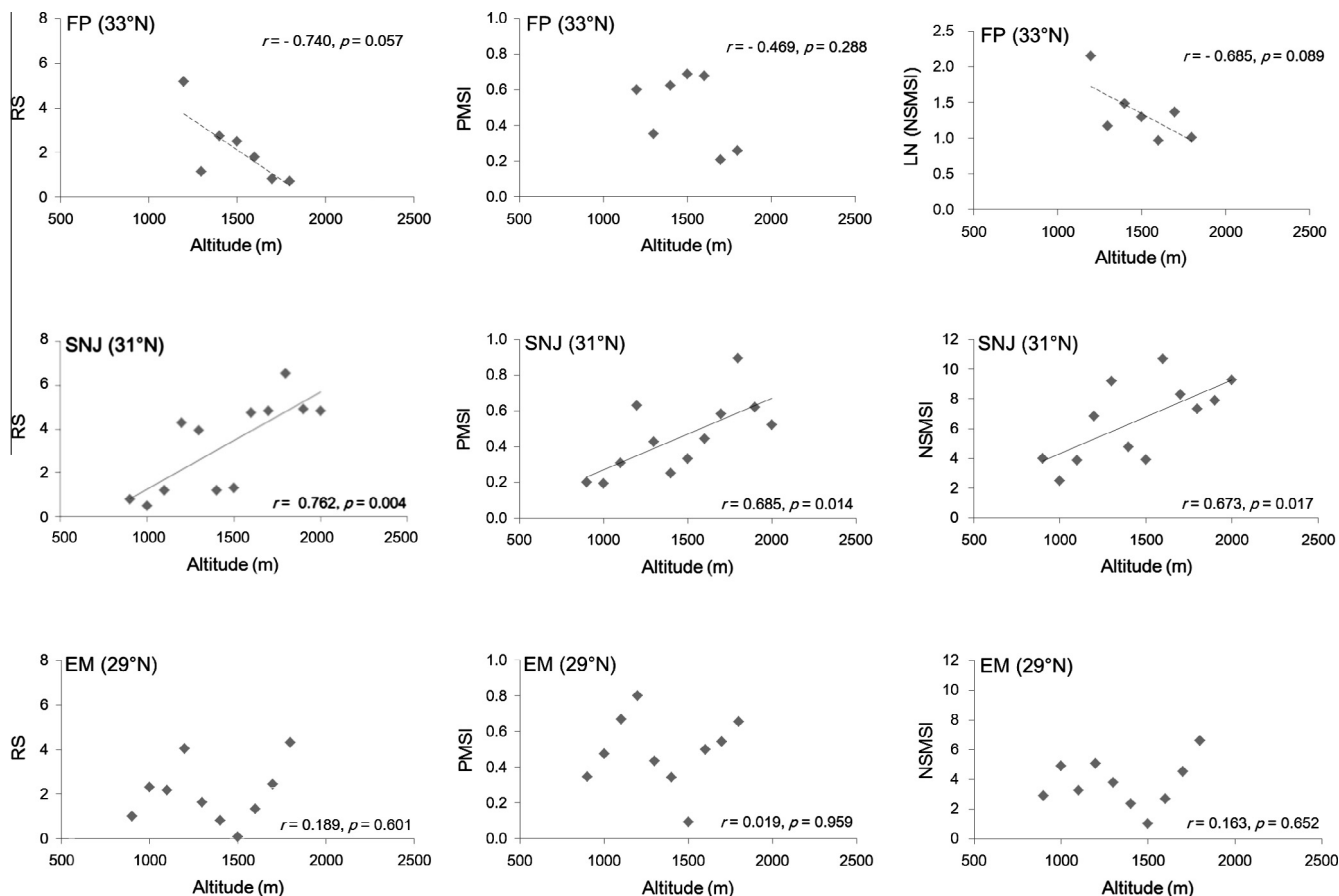
**Fig. 5.** (left) Size distribution of *Euptelea pleiospermum* at different altitudes and (right) altitudinal patterns of relative seedling density along the Qinling Mountains (FP), Shennongjia Mountains (SNJ) and Emei Mountains (EM). Relative seedling density, proportion of the number of seedlings to total number of individuals. See Appendix A for the classifications of low, middle and high altitudes for the three mountains.

obvious from low to high latitude. In contrast to our results, Rabasa et al. (2013) reported that the same tree species showed the same shift trend (e.g. upward shift of *Abies alba*) along mountains located at different latitudes.

Along the Qinling Mountains (33°N), we found an upward shift, although not very remarkable, of *E. pleiospermum*. In line with our result, Dang et al. (2010) reported that recruitment of *Abies fargesii* (2300–2800 m along the Qinling Mountains) was more frequent in populations at the upper altitudes during the last 150 years compared with populations at middle and low altitudes. Similarly, Lv and Zhang (2012) found asynchronous recruitment of *Abies spectabilis* along the Everest Mountains, with more recruitment at higher altitudes over the last three decades. In these remote natural forests, upward shifts along altitudes are likely due to climate change (Peñuelas et al., 2007). Opposite to relative seedling density, we found that sprouting ratio decreased with increasing altitude. This means that, similar to its role at low latitudes, sprouting can reduce the extinction risk of *E. pleiospermum* at lower altitudes along the Qinling Mountains.

Along the Shennongjia Mountains (31°N), contrary to our prediction, we found that seedlings of *E. pleiospermum* gradually

became more frequent from high to low altitude. Interestingly, our results showed that sprouting ratio and seedlings showed the opposite altitudinal pattern (Figs. 5 and 6), which suggests that the tradeoff between seedling (sexual) and sprouting (asexual) is ubiquitous for this species. Although other researchers have found climate-induced downslope shifts in plant species (Lenoir et al., 2010; Crimmins et al., 2011; Rabasa et al., 2013), the downslope shift of *E. pleiospermum* along the Shennongjia Mountains was not likely caused by climate warming. Rather, land use change, one of the potential mechanisms for downslope range shifts (Lenoir et al., 2010), is the most probable explanation. A rapid rate of abandonment of agriculture fields has taken place in the study area since the launch of the Grain to Green Program in 1999 (Liu et al., 2008). This provides a good opportunity for spontaneous vegetation restoration in areas adjacent to old-field forests that offer abundant seeds. In the case of *E. pleiospermum*, a small pioneer tree species, the possibility of seedling establishment (and also the number of abandoned agriculture fields) gradually decreases from low to high across its altitudinal range (900–2000 m), because most residential areas are below 1300 m in the Shennongjia Mountains (Zhu and Song, 1999).



**Fig. 6.** Altitudinal patterns of RS, PMSI and NSMSI along the Qinling Mountains (FP), Shennongjia Mountains (SNJ) and Emei Mountains (EM), respectively. RS, the ratio of the number of sprouts to the number of main stems; PMSI, the proportion of sprouting individuals among all individuals; NSMSI, the number of sprouts per sprouting individual.

Along the Emei Mountains (29°N), we did not detect any significant altitudinal pattern for relative seedling density or sprouting ratio, and thus no detectable shift of *E. pleiospermum*. Likewise, Rabasa et al. (2013) reported three sprouting tree species (e.g. *Quercus ilex*, *Quercus petraea*, and *Acer pseudoplatanus*) did not show any change in distribution along altitudinal gradients. Wang et al. (2006) similarly found that *Picea schrenkiana* did not show an obvious upward shift along the Tianshan Mountains. Researchers have proposed several potential mechanisms (e.g. interspecific competition, seed predation, herbivory, and pathogens) to explain why tree species did not experience upward shift (Lenoir et al., 2010; Speed et al., 2012; Rabasa et al., 2013). Since our study was carried out in natural forests along both the Qinling Mountains and the Emei Mountains and we have found an upward shift of *E. pleiospermum* along the Qinling Mountains, the unchanged distribution along the Emei Mountains may largely be ascribed to interspecific competition at the upper limit. It is reasonable to expect that interspecific competition is more intense at the upper of *E. pleiospermum* along the Emei Mountains compared to the Qinling Mountains, because the number and density of tree species decrease along the latitudinal gradient (Fang, 2004). However, further investigation is needed to exclude the other potential factors mentioned above.

## 5. Conclusions

Our study is unique in that it simultaneously presents regeneration dynamics of *E. pleiospermum* along latitudinal and altitudinal

gradients. We found evidence for northward migration along the latitudinal gradient and an upward shift along a high latitude mountain. This suggests that climate warming is an important driver of northward or upward shift of tree species in subtropical mountain forests. It appears that sprouting is an important strategy for this tree species to buffer range contraction at the trailing edge in the face of climate warming. This study also highlights the disparity in altitudinal shifts of the same tree species along mountains located at different latitudes. This is because range shift along altitudinal gradient can also result from non-climate drivers, which (e.g. interspecific competition) act in concert with climate warming or (e.g. land use change) even mask it. In general, this study emphasizes the complexity of mechanisms underlying regeneration dynamics and range shift along latitudinal and altitudinal gradients.

## Acknowledgements

We thank Haibo Liu, Yili Guo, Cehong Li, Gaodi Dang, Liangmin Wang, Lile Hu, Shijun Li, Wenhui Li, Xiaojing Liu, Zhao Zhang, Zhenyu Liu and Zonglin Peng for their assistance during fieldwork. We are also grateful to Dr. Scott B. Franklin (University of Northern Colorado) for helpful comments on an earlier version of the manuscript. We appreciate Dr. Haishan Dang for providing some of the climatic data. The comments and suggestions of two anonymous reviewers have contributed significantly to improvement of the manuscript. This work was supported by grants from the National Natural Science Foundation of China (Nos. 31270562



and 31470515, 31100344) and the Youth Innovation Promotion Association, Chinese Academy of Sciences (No. 2014314).

## Appendix A. Supplementary material

Number of individuals at each altitudinal site, altitudinal ranges of *Euptelea pleiospermum* and altitudinal boundary of low, middle, and high altitudes along the Emei Mountains, Shennongjia Mountains, and Qinling Mountains, respectively. Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2015.06.004>.

## References

- Bellingham, P.J., Sparrow, A.D., 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* 89, 409–416.
- Bellingham, P.J., Sparrow, A.D., 2009. Multi-stemmed trees in montane rain forests: their frequency and demography in relation to elevation, soil nutrients and disturbance. *J. Ecol.* 97, 472–483.
- Bond, W.J., Midgley, J.J., 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol. Evol.* 16, 45–51.
- Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333, 1024–1026.
- Colwell, R.K., Brehm, G., Cardelús, C.L., Gilman, A.C., Longino, J.T., 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322, 258–261.
- Clarke, P.J., Lawes, M.J., Midgley, J.J., Lamont, B.B., Ojeda, F., Burrows, G.E., Enright, N.J., Knox, K.J.E., 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytol.* 197, 19–35.
- Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T., Mynsberge, A.R., 2011. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science* 331, 324–327.
- Dang, H., Zhang, K., Zhang, Y., Tan, S., Jiang, M., Zhang, Q., 2009. Tree-line dynamics in relation to variability in the Shennongjia Mountains, central China. *Can. J. Forest Res.* 39, 1848–1858.
- Dang, H., Zhang, Y., Zhang, K., Jiang, M., Zhang, Q., 2010. Age structure and regeneration dynamics of subalpine fir (*Abies fargesii*) forests across an altitudinal range in the Qinling Mountains, China. *Forest Ecol. Manage.* 259, 547–554.
- Dolan, C.R., Thorne, J.H., Safford, H.D., 2013. Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007. *Global Ecol. Biogeogr.* 22, 264–276.
- Editorial Committee for Vegetation of China, 1980. *Vegetation of China*. Science Press, Beijing, pp. 279–300.
- Fang, J., 2004. Exploring altitudinal patterns of plant diversity of China's mountains. *Biodivers. Sci.* 12, 1–4.
- Felde, V.A., Kapfer, J., Grytnes, J.A., 2012. Upward shift in elevational plant species ranges in Sikkilisdalen, central Norway. *Ecography* 35, 922–932.
- Fischelli, N.A., Frelich, L.E., Reich, P.B., 2014. Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. *Ecography* 37, 152–161.
- Fu, L.K., Jin, J.M., 1992. *China Plant Red Data Book: Rare and Endangered Plants*. Science Press, Beijing, pp. 680–681.
- García, D., Zamora, R., 2003. Persistence, multiple demographic strategies and conservation in long-lived Mediterranean plants. *J. Veg. Sci.* 14, 921–926.
- Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: the rear edge matters. *Ecol. Lett.* 8, 461–467.
- He, D., Wang, Q.G., Franklin, S.B., Jiang, M.X., 2013. Transient and asymptotic demographics of the riparian species *Euptelea pleiospermum* in the Shennongjia area, central China. *Biol. Conserv.* 161, 193–202.
- Jump, A.S., Huang, T.J., Chou, C.H., 2012. Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. *Ecography* 35, 204–210.
- Jump, A.S., Hunt, J.M., Peñuelas, J., 2006. Rapid climate change-related growth decline at the south range edge of *Fagus sylvatica*. *Global Change Biol.* 12, 2163–2174.
- Jump, A.S., Mátyás, C., Peñuelas, J., 2009. The altitude-for latitude disparity in the range retractions of woody species. *Trends Ecol. Evol.* 24, 694–701.
- Kelly, A.E., Goulden, M.L., 2008. Rapid shifts in plant distribution with recent climate change. *P. Natl. Acad. Sci. USA* 105, 11823–11826.
- Kubo, M., Sakio, H., Shimano, K., Ohno, K., 2005. Age structure and dynamics of *Cercidiphyllum japonicum* sprouts based on growth ring analysis. *Forest Ecol. Manage.* 213, 253–260.
- Kullman, L., 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *J. Ecol.* 90, 68–77.
- Lenoir, J., Gégout, J.C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N.E., Dullinger, S., Pauli, H., Willner, W., Svenning, J.C., 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* 33, 295–303.
- Lenoir, J., Gégout, J.C., Marquet, P.A., de Ruffray, P., Brisse, H., 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320, 1768–1771.
- Lenoir, J., Gégout, J.C., Pierrat, J.C., Bontemps, J.D., Dhote, J.F., 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). *Ecography* 32, 765–777.
- Liu, J., Li, S., Ouyang, Z., Tam, C., Chen, X., 2008. Ecological and socioeconomic effects of China's policies for ecosystems services. *P. Natl. Acad. Sci. USA* 105, 9477–9482.
- López-Pujó, J., Zhang, F.M., Sun, H.Q., Ying, T.S., Ge, S., 2011. Centres of plant endemism in China: places for survival or for speciation? *J. Biogeogr.* 38, 1267–1280.
- Lv, L.X., Zhang, Q.B., 2012. Asynchronous recruitment history of *Abies spectabilis* along an altitudinal gradient in the Mt. Everest region. *J. Plant Ecol.* 5, 147–156.
- Matias, L., Jump, A.S., 2015. Asymmetric changes of growth and reproductive investment herald altitudinal and latitudinal range shift of two woody species. *Global Change Biol.* 21, 882–896.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Nanami, S., Kawaguchi, H., Tateno, R., Li, C., Katagiri, S., 2004. Sprouting traits and population structure of co-occurring *Castanopsis* species in an evergreen broad-leaved forest in southern China. *Ecol. Res.* 19, 341–348.
- Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Syst.* 37, 637–669.
- Peñuelas, J., Ogaya, R., Boada, M., Jump, A.S., 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). *Ecography* 30, 829–837.
- Peñuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M., Barbeta, A., Rivas-Ubach, A., Llusà, J., Garbulsky, M., Filella, I., Jump, A.S., 2013. Evidence of current impact of climate change on life: a walk from genes to the biosphere. *Global Change Biol.* 19, 2303–2338.
- Qian, W., Qin, A., 2006. Spatial-temporal characteristics of temperature variation in China. *Meteorol. Atmos. Phys.* 93, 1–16.
- Rabasa, S.G., Granda, E., Benavides, R., Kunstler, G., Espelta, J.M., Ogaya, R., Peñuelas, J., Scherer-Lorenzen, M., Gil, W., Grodzki, W., Ambroz, S., Bergh, J., Hódar, J.A., Zamora, R., Valladares, F., 2013. Disparity in elevational shifts of European trees in response to recent climate warming. *Global Change Biol.* 19, 2490–2499.
- Speed, J.D.M., Austrheim, G., Hester, A.J., Mysterud, A., 2012. Elevational advance of alpine plant communities is buffered by herbivory. *J. Veg. Sci.* 23, 617–625.
- Sun, C., Shao, Q., Liu, J., 2012. Application analysis of surface air temperature change estimation methods in Chinese mainland. *J. Geo-Inf. Sci.* 14, 14–21.
- Tanentzap, A.J., Mountford, E.P., Cooke, A.S., Coomes, D.A., 2012. The more stems the merrier: advantages of multi-stemmed architecture for the demography of understorey trees in a temperate broadleaf woodland. *J. Ecol.* 100, 171–183.
- Tang, C.Q., Ohsawa, M., 2002. Tertiary relic deciduous forests on a humid subtropical mountain, Mt. Emei, Sichuan, China. *Folia Geobot.* 37, 93–106.
- Taylor, A.H., Qin, Z., 1988. Regeneration patterns in old-growth *Abies-Betula* forests in the Wolong Natural Reserve, Sichuan, China. *J. Ecol.* 76, 1204–1218.
- Vitasse, Y., Hoch, G., Randin, C.F., Lenz, A., Kollas, C., Körner, C., 2012. Tree recruitment of European tree species at their current upper elevational limits in the Swiss Alps. *J. Biogeogr.* 39, 1439–1449.
- Walther, G.R., Beißner, S., Burga, C.A., 2005. Trends in upward shift of alpine plants. *J. Veg. Sci.* 16, 541–548.
- Wang, T., Zhang, Q.B., Ma, K., 2006. Treeline dynamics in relation to climatic variability in the central Tianshan Mountains, northwestern China. *Global Ecol. Biogeogr.* 15, 406–415.
- Wang, X.P., Wang, Z.H., Fang, J.Y., 2004. Mountain ranges and peaks in China. *Biodivers. Sci.* 12, 206–212.
- Wei, X.Z., Jiang, M.X., Huang, H.D., Yang, J.Y., Yu, J., 2010a. Relationships between environment and mountain riparian plant communities associated with two rare tertiary-relict tree species, *Euptelea pleiospermum* (Eupteleaceae) and *Cercidiphyllum japonicum* (Cercidiphyllaceae). *Flora* 205, 841–852.
- Wei, X.Z., Liao, J.X., Jiang, M.X., 2010b. Effects of pericarp, storage conditions, seed weight, substrate moisture content, light, GA3 and KNO3 on germination of *Euptelea pleiospermum*. *Seed Sci. Technol.* 38, 1–13.
- Ying, J., Chen, M., 2011. *Plant Geography of China*. Shanghai Scientific & Technical Publishers, Shanghai.
- Zhu, K., Woodall, C.W., Clark, J.S., 2012. Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biol.* 18, 1042–1052.
- Zhu, Z.Q., Song, C.S., 1999. *Scientific Survey of Shennongjia Nature Reserve*. China Forestry Publishing House, Beijing.