Trees
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ORIGINAL ARTICLE

Sensitivity of seed germination to temperature of a relict tree species from different origins along latitudinal and altitudinal gradients: implications for response to climate change

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Abstract

Key message **Seeds of a relict tree species collected from high latitudes were more sensitive to temperature and warming could accelerate germination.**

Abstract Seed germination is a crucial process in a plant life cycle and is highly vulnerable to environmental change. Studying among-population variation in seed germination in response to environmental and geographic gradients is an important tool, allowing us to understand how plants adapt to different environmental conditions and to predict population dynamics under future climate change. Here, we collected seeds of *Euptelea pleiospermum*, a relict broad-leaved tree species, from six provenances along latitudinal and altitudinal gradients across its distribution in China. We investigated variation in seed germination percentage and germination timing of seeds from these different origins (low, middle, and high latitudes/altitudes) at three incubation temperatures (15 °C, 20 °C and 25 °C). The key results were as follows: first, seeds collected from high latitudes were more sensitive to temperature and was likely to benefit from the higher incubation temperature with increasing germination percentage and shorter germination timing; second, for seeds across latitudes, germination percentage of central populations was lower than that of marginal populations; seed origin and its interaction with temperature were the major drivers of germination percentage variation; germination timing was significantly affected by incubation temperature, and warming could accelerate germination; third, for seeds across altitudes, both germination percentage and germination timing were not significantly affected by seed origin, incubation temperature, or their interaction. Our results indicate that climate warming may influence the population dynamics of relict tree species by altering their seed germination patterns, especially for the leading-edge populations along latitudinal gradient. It is vital to take inter-population variation across species' geographic distribution into account when estimating the impact of environmental changes on plant species' distribution and population persistence.

Keywords Altitude · Climate change · Latitude · Seed germination · Temperature

Introduction

Seed germination is a vital process in a plant life cycle and influences seedling establishment and survival, which can subsequently determine species distribution and population persistence (Hernández-Verdugo et al. 2001; Donohue et al. 2010; Cochrane et al. 2015a). However, the transition from seed to seedling is also often a serious bottleneck in population recruitment (Meyer et al. 1997; Sherry et al. 2007; Cochrane 2016). Climate change has profound and severe implications for all aspects of biodiversity (Thomas et al. 2004; IPCC 2013), and is expected to influence all the aspects of plant life history, including growth, reproduction, phenology, and distribution, and especially the early

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stages of plant regeneration (Walck et al. 2011; Parmesan and Hanley 2015). Seed germination and the transition to the seedling stage appear particularly sensitive to changing climatic conditions (Hovenden et al. 2008; Ooi et al. 2009; Seal et al. 2017). The sensitivity of germination to climate variability depends on the species' phenotypic plasticity, local adaption, and geographic distribution (Nicotra et al. 2010; Cochrane et al. 2015b). Some studies have reported that among-population variation in germination response to environmental conditions resulted in different responses to climate change within species, which can mitigate the species' vulnerability to changing climate and provide opportunities for species adaptation and conservation (Marcora et al. 2008; Cochrane et al. 2015a; Chamorro et al. 2017). Therefore, exploring how germination of seeds from different provenances responds to temperature is helpful to understand the strategies of plants to adapt to environmental gradients and to predict population dynamics under climate warming.

Germination percentage and timing are generally considered to be the two crucial traits of seed germination and they can strongly affect recruitment success (Donohue 2005; Milbau et al. 2009; Baskin and Baskin 2014). Germination is the first step for plants regenerated via seeds to inhabit a specific environment (Donohue et al. 2010). Germination percentage influences the number of seeds that can become seedlings and potentially colonize, and subsequently affects species distribution and community structure (Cochrane et al. 2015a). In addition, germination percentage may vary among populations due to different maternal environmental conditions (Mamo et al. 2006; Harrison et al. 2014; Liu et al. 2017). According to the central–marginal hypothesis (Sagarin and Gaines 2002), seeds from the central population are expected to have higher germination percentage, because the environmental conditions are more favorable and stable at the center than at the edge of a species' geographic range (Abeli et al. 2014). Meanwhile, germination timing determines when a seedling begins to be exposed to environmental factors and sets the context for subsequent development, and thus, it is closely related to species fitness (Donohue et al. 2005, 2010). The seedling establishment, survival, and the onset of growth all can be influenced by seed germination timing (Simons 2009). For example, earlier germination enabled *Arabidopsis thaliana* to attain larger sizes before reproduction, which could increase fecundity (Donohue et al. 2002, 2010). Germination timing itself can be affected by environmental conditions during seed maturation and/or parental habitats (Donohue 2005; Cordeiro et al. 2014; Liu and El-Kassaby 2015). However, there were few studies about among-population variation in the response of seed germination traits to environmental change despite their key roles in plant life history (Cochrane et al. 2015a; Zettlemoyer et al. 2017).

Environmental conditions often vary along latitudinal and altitudinal gradients, especially precipitation and temperature (Körner 2003; Sundqvist et al. 2013; De Frenne et al. 2013). In general, temperature decreases from low to high altitude and latitude; consequently, altitudinal and latitudinal gradients can be used as natural laboratories to investigate plant species' responses to temperature (Körner 2007; De Frenne et al. 2013). Temperature is one of the most important environmental factors that regulate seed germination timing, speed, and percentage (Probert 2000; Fenner and Thompson 2005; Baskin and Baskin 2014). The germination response to temperature may vary among populations across species' geographical distribution because of their adaption to local climatic conditions or habitats (Chamorro et al. 2018). Seed germination temperature can be affected by the climate of a plant's habitat through maternal effects (Gutterman 2000; Rosbakh and Poschlod 2015). For example, Zettlemoyer et al. (2017) reported that seeds from northern populations germinated at cooler temperatures than southern populations. Thus, investigating the germination patterns of seeds collected along geographical gradients under different incubation temperatures is important to estimate among-population variation in germination response to temperature change, which can subsequently improve our power to predict the fate of plants regenerated via seeds under ongoing global warming. This issue is particularly important for mountain woody species (Walck et al. 2011; Cochrane et al. 2015a). However, to date, studies on the response of seed germination to temperature of tree species from different provenances along both latitudinal and altitudinal gradients are scarce.

Euptelea pleiospermum (Eupteleaceae) is a relict tree species of mountain forests with a wide distribution range within China, which provides good material for studying the effects of temperature on seed germination among populations. Here, we collected seeds from different provenances of *E. pleiospermum* along latitudinal and altitudinal gradients. We compared seed germination percentages and germination timing of seeds from different origins (low, middle, and high latitudes/altitudes) at three incubation temperatures (15 °C, 20 °C and 25 °C). Specifically, the aim of this study is to explore the following questions: (1) How does seed germination percentage vary along latitudinal and altitudinal gradients? Is it consistent with what the "central–marginal" hypothesis predicted? (2) How does germination percentage of seeds from different origins respond to temperature? (3) How does germination timing of seeds from different origins respond to temperature?

Materials and methods

Study species

Euptelea pleiospermum Hook. f. et Thoms. (Eupteleaceae), a relict and rare tree species, is a deciduous broad-leaved tree species endemic to China, India, and Burma (Fu and Jin 1992). It is commonly distributed between 760 and 3200 m a.s.l. in mountain riparian forests, with a wide geographic distribution in China (Fu and Jin 1992). Flowers of *E. pleiospermum* bloom in early spring before leaf expansion and are wind-pollinated (Endress 1986). The fruits are indehiscent samaras (in this study referred to as seeds), which scarcely crack under natural conditions. They are dispersed by gravity, wind, and water. The fruits usually contain two seeds but generally only one seed germinates (Wei et al. 2010).

The beginning of seed germination season of *E. pleiospermum* was from March to May for populations from south to north across its geographic distribution in China. The local climatic data showed that mean monthly temperature was about 15–20 °C in March at low latitude provenances, and it was close to 15 °C in April at middle and high latitude provenances, and then, it rose to about 20 °C in May at high latitude provenances (Table 1).

Seed sampling

To examine how seed germination varied with latitude, in October 2016, we collected mature seeds of *E. pleiospermum* from six provenances throughout its geographic range in China, along a latitudinal gradient spanning 1060 km (25.75°N–35.27°N, Table 1). These six provenances were divided into three groups: low latitude (YB, QJ), middle latitude (SNJ, BPG), and high latitude (HX, YC) (referred as seed origin) (Table 1). Seeds were randomly collected from five healthy mother trees in a population at each provenance. The mother trees were separated by at least 50 m within the same population. For each provenance, seeds from all trees were pooled and air-dried for about 1 month in the laboratory, and then, they were stored in plastic bags at 4 °C in a refrigerator until the start of germination experiments. Seed dormancy was present and chilling pre-treatment was an effective method for seeds of this species to break dormancy to germinate (Wan 1988; Wei et al. 2010).

To examine how seed germination varied with altitude, we collected seeds from six provenances along an altitudinal gradient in Shennongjia mountain. It is the highest mountain in the mid-latitude zone of the distribution of *E. pleiospermum* in China. The species is widely distributed

Table 1 Location and climatic condition of sample sites of *Euptelea pleiospermum* along a latitudinal gradient across its geographic distribution in China

Site code	Latitude (°N)	Longitude (°E)	Seed origin	Mean annual temperature (°C)	Mean temperature of coldest quarter (°C)	Mean temperature of warmest quarter (°C)	Mean monthly temperature in March (°C)	Mean monthly temperature in April (°C)	Mean monthly temperature in May (°C)	Mean annual precipitation (mm)	Location information
QJ	27.22	103.12	L	20.8	13.6	26.2	20.3	24.4	25.7	829.2	Qiaojia, Yunnan
YB	25.75	100.02	L	16.4	9.8	21.7	14.3	17.3	20.5	1029.1	Yangbi, Yunnan
SNJ	31.35	110.40	M	12.3	2.2	21.8	7.0	13.0	17.1	951.0	Shennongjia, Hubei
BPG	31.36	102.97	M	11.4	2.3	19.5	7.6	12.2	15.6	619.2	Bipenggou, Lixian, Sichuan
HX	34.43	109.87	H	12.9	0.3	24.6	6.8	14.4	19.4	608.0	Huaxian, Shaanxi
YC	35.27	112.44	H	12.0	−0.6	23.6	6.4	13.7	18.9	578.4	Yangcheng, Shanxi

L low latitude, *M* middle latitude, *H* high latitude in this area across a large range of altitudes. Along the altitude in Shennongjia mountain, seeds of *E. pleiospermum* were collected from low altitude (1100, 1200 m), middle altitude (1500, 1600 m), and high altitude (1900, 2000 m) (referred as seed origin). We collected seeds from five mother trees in one population for each 100 m altitudinal interval and a total of six populations (representing 6 provenances) had been sampled. Seeds were collected and stored as above.

Climatic data

Climatic data of the six provenances along latitudinal gradient were downloaded from China Meteorological Data Network (http://data.cma.cn/site/index.html). They were meteorological observation data obtained from the nearest weather stations in the same county where the seed provenances located (for QJ, YB, SNJ, BPG, YC) or the nearest weather stations in the neighboring county (for HX). These weather stations were Qiaojia meteorological station (26.55°N, 102.55°E), Yangbi meteorological station (25.41°N, 99.57°E), Shennongjia meteorological station (31.45°N, 110.40°E), Lixian meteorological station (31.26°N, 103.10°E), Yangcheng meteorological station (35.29°N, 112.24°E), and Tongguan meteorological station (34.33°N, 110.14°E). Here, mean annual temperature, mean temperature of coldest quarter, mean temperature of warmest quarter, mean monthly temperature in germination season (March, April, and May), and mean annual precipitation were provided (Table 1). These climatic data were the average for the years 1981–2010.

On the other hand, we could not get climatic data along altitudinal gradient in Shennongjia mountain. Seeds were collected along altitude in the same valley at this site. As we known, temperature decreases rapidly with increasing altitude (~ 0.5 to 0.65 °C per 100 m) (Körner 2003; Colwell et al. 2008). Therefore, the altitudinal gradient could be as a proxy for temperature gradient.

Germination test

In April 2017, we examined germination percentages of seeds from each provenance for three different temperature treatments. Prior to the tests, seeds were surface-sterilized with 1% sodium hypochlorite solution for 10 min, and then, they were washed three times with deionized water. For each temperature treatment, three replicates of 50 seeds each were randomly selected from each provenance, and seeds were placed evenly on top of filter paper in 9-cm-diameter Petri dishes. For seeds across latitudes, the experimental design included 50 seeds × 3 replicates × 6 provenances × 3 treatments = 2700 seeds in total. For seeds across altitudes, the experimental design also included 50 seeds × 3 replicates × 6 provenances × 3 treatments = 2700 seeds in total. During the germination test, deionized water was added as necessary to keep the filter paper continuously moist. Seeds were incubated with a white light source (13 h of light:11 h of darkness) in one of the three growth chambers (QHX-300BSH-III, Shanghai, China) set to 15 °C, 20 °C, or 25 °C. Petri dishes were randomized within chambers every day to avoid any effect due to position in the chamber (Yang et al. 1999).

Seed germination was monitored daily from day 1, and germinated seeds were counted and removed. An emerged radicle exceeded 1 mm in length was used as the criterion for germination. The germination tests ended when no germination had occurred for 5 successive days (Grime et al. 1981; Ma et al. 2010). Finally, the seed germination tests lasted for 53, 49, and 36 days when they were conducted at 15 °C, 20 °C, and 25 °C, respectively. Final germination percentage (FGP, total number of seeds germinated divided by the total number of seeds tested × 100), the number of days to the first germination (T_0), and the number of days to 50% of final germination percentage (T_{50}) were recorded for each replicate (Jiménez-Alfaro et al. 2016; Tudela-Isanta et al. 2018). For a small number of replicates with only one seed germinated among the 50 seeds tested, T_{50} was omitted.

Data analysis

We tested the effects of seed origin, temperature, and their interaction on FGP, T_0, and T_{50} using linear mixed-effects models with the "lmer" function in R package "lmerTest" (Kuznetsova et al. 2013). In the model, seed origin (i.e., low, middle, and high latitudes/altitudes), temperature, and their interaction were used as fixed effects, and seed provenances were used as random effects. Prior to the analyses, FGP was Box–Cox-transformed. All analyses were performed in the statistical program R, version 3.1.3 (R Development Core Team 2015; http://www.r-project.org/).

Results

Final germination percentage

Across seed origin by latitude, FGP was significantly affected by the main effect of seed origin (Table 2). There were obvious differences in FGP among origins for seeds under the same temperature treatment (Fig. 1a). No matter whether seeds were incubated at 15 °C, 20 °C, or 25 °C, seeds from middle latitude origin had significant lower FGP than seeds from low and high latitude origins (Table 2; Fig. 1a). Linear mixed-effects model revealed that FGP was not affected by the main effect of temperature, but affected by its interaction with seed origin (Table 2). We found that FGP of seeds from high latitude was lower when seeds incubated at 15 °C than that incubated at 20 °C and 25 °C (Fig. 1b).

Across seed origin by altitude, the trend of variation in FGP was similar to that of seeds collected along latitudinal gradient, with seeds from middle altitude having a lower but not significant FGP than that from low and high altitudes (Fig. S1A; Table 2). According to the results of linear mixed-effects model, FGP was not significantly affected by seed origin, temperature, or their interaction (Table 2). However, FGP of seeds from high altitude exhibited a highest value at 20 °C (Fig. S1B).

The timing of seed germination

For latitude, seeds from high latitude origin were the first to germinate at 17, 11, and 10 days at 15 °C, 20 °C, and 25 °C, respectively (Fig. 2a–c). Both mean T_0 and T_{50} were only significantly affected by the main effect of temperature, and germination was quicker under higher temperature incubation (Table 3; Fig. 3). No matter whether seeds were collected from low, middle, or high latitude, both T_0 and T_{50} decreased with the increase of incubation temperature (Fig. 3).

Table 2 Effects of seed origin, temperature, and their interaction on final germination percentage of *Euptelea pleiospermum* seeds from different latitudes and altitudes, respectively

Factor	Latitude			Altitude		
	t value	*p*	R^2	*t* value	*p*	R^2
Origin (ori)	−2.274	**0.050**		−0.514	0.610	
Temperature (temp)	−1.535	0.130		−0.182	0.856	
Ori × temp	3.125	**0.003**		0.610	0.545	
			0.844			0.198

The significant *p* values were shown in bold ($p < 0.05$)

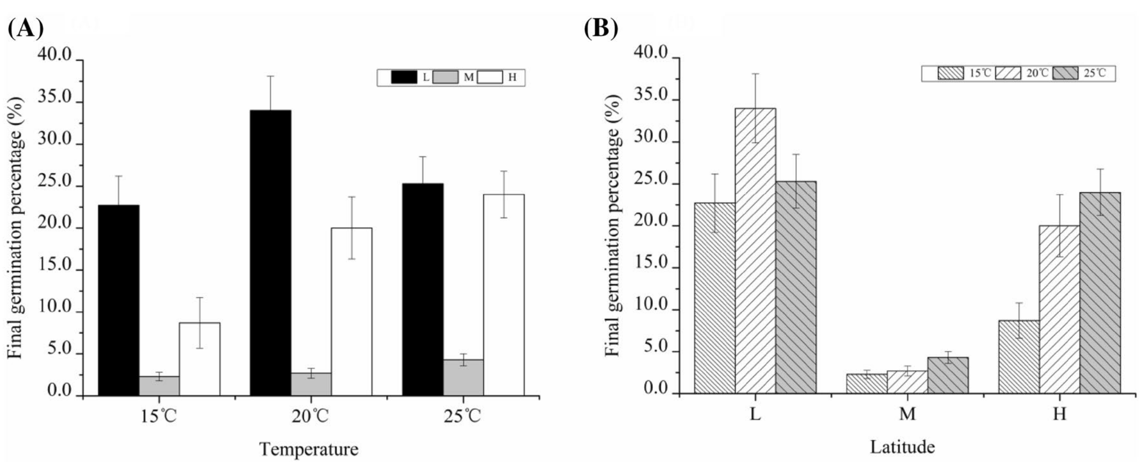

Fig. 1 Variation in the final germination percentage of *Euptelea pleiospermum* from low, middle, and high latitudes under different temperature treatments (mean ± SE). *L* low latitude, *M* middle latitude, *H* high latitude

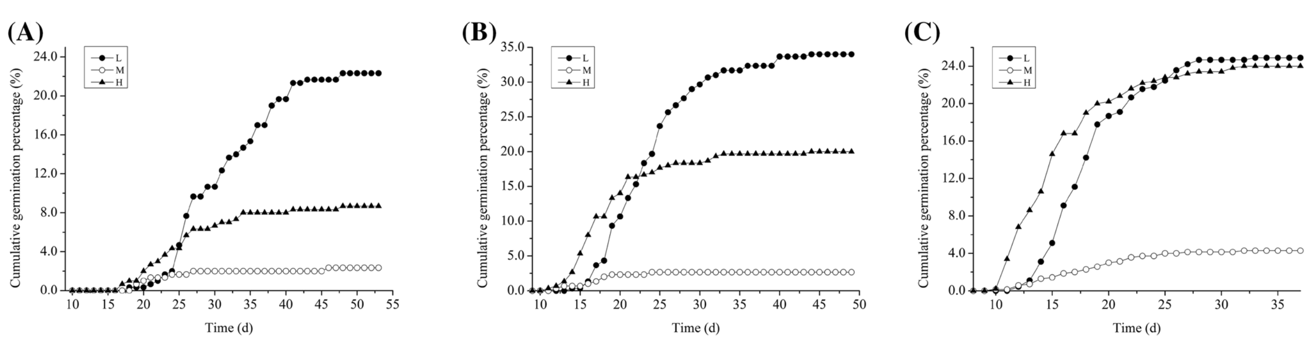

Fig. 2 Cumulative germination percentage of *Euptelea pleiospermum* from low, middle, and high latitudes under different temperature treatments. Panel **a** 15 °C; panel **b** 20 °C; panel **c** 25 °C. *L* low latitude, *M* middle latitude, *H* high latitude

For altitude, seeds from high altitude origin were the first to germinate at 15 °C (day 14; Fig. 4a), but they were the last to germinate at 25 °C (day 13; Fig. 4c). Interestingly, seeds from high altitude germinated earlier than that from low altitude at 15 °C, while they needed more time to initiate germination than seeds from low altitude at 25 °C (Fig. 4). Similar to FGP, both T_0 and T_{50} of seeds collected along altitudinal gradient were not significantly affected by seed origin, temperature, or their interaction (Table 4), despite that germination timing exhibited a decreasing trend from 15 to 20 °C and 25 °C (Fig. S2).

Table 3 Effects of seed origin, temperature, and their interaction on T_0 and T_{50} of *Euptelea pleiospermum* seeds from different latitudes, respectively

Factor	T_0			T_{50}		
	t value	*p*	R^2	*t* value	*p*	R^2
Origin (ori)	−0.323	0.747		−1.810	0.075	
Temperature (temp)	−3.071	**0.003**		−3.971	**<0.001**	
Ori × temp	−0.130	0.897		0.831	0.409	
			0.563			0.645

The significant *p* values were shown in bold ($p<0.05$). T_0 number of days of the first germination from the beginning of germination test; T_{50} number of days required to reach 50% of final germination percentage

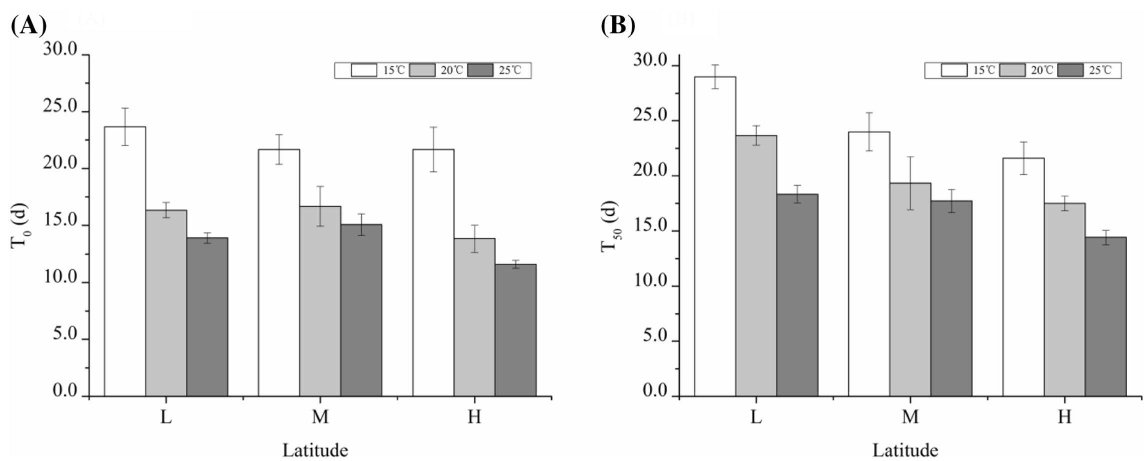

Fig. 3 T_0 and T_{50} of *Euptelea pleiospermum* from low, middle, and high latitudes under different temperature treatments (mean ± SE). Panel **a** T_0; panel **b** T_{50}. *L* low latitude, *M* middle latitude, *H* high latitude. T_0 number of days of the first germination from the beginning of germination test; T_{50} number of days required to reach 50% of final germination percentage

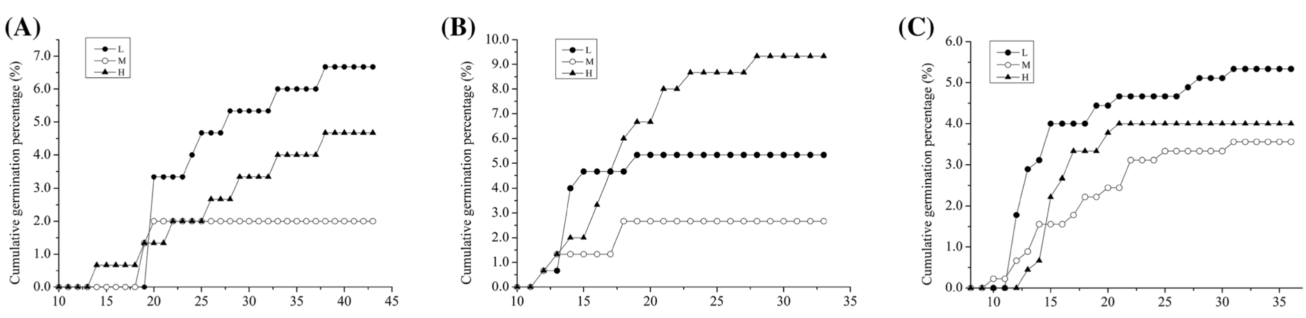

Fig. 4 Cumulative germination percentage of *Euptelea pleiospermum* from low, middle; and high altitudes under different temperature treatments. Panel **a** 15 °C; panel **b** 20 °C; panel **c** 25 °C. *L* low altitude, *M* middle altitude, *H* high altitude

Table 4 Effects of seed origin, temperature, and their interaction on T_0 and T_{50} of *Euptelea pleiospermum* seeds from different altitudes, respectively

Factor	T_0			T_{50}		
	t value	*p*	R^2	*t* value	*p*	R^2
Origin (ori)	− 0.346	0.731		0.496	0.622	
Temperature (temp)	− 1.797	0.080		− 1.587	0.120	
Ori × temp	0.433	0.667		− 0.284	0.777	
			0.290			0.373

T_0 number of days of the first germination from the beginning of germination test; T_{50} number of days required to reach 50% of final germination percentage

Discussion

Seed germination patterns along latitudinal and altitudinal gradients

Our study found that germination percentages of central populations (i.e., seeds from middle latitudes) were lower than that of marginal populations along latitudinal gradient, and a similar but not significant trend along altitudinal gradient. This result is not consistent with the other studies, which have documented a monotonic relationship between seed germination percentage and latitude or altitude. For examples, seed germination percentage of *Cyananthus* species was positively correlated with altitude (Chen et al. 2017) and seeds of *Calluna vulgaris* and *Erica cinerea* collected from the highest altitudes had higher germination percentages than seeds from lower altitudes (Vera 1997). In contrast, some studies found a negative relationship between germination and latitude/altitude (Miller and Cummins 2001; Bu et al. 2007).

However, according to the central–marginal hypothesis, species performance (demography, growth, and regeneration) of populations from the center of a species' distribution range should be better than that of the marginal populations, because habitat suitability declines from the center towards the edge of the range (Brown 1984; Sexton et al. 2009; Kiełtyk 2018). In contrast to this hypothesis, seed germination percentages of *E. pleiospermum* in our study were exactly the opposite, with lower germination in middle latitude origin seeds. One possible explanation is that *E. pleiospermum* may have higher seed production in central populations and worse in the marginal regions; consequently, marginal populations may have enhanced seed germination somehow to compensate for their disadvantage in seed production. Some instances of a strong decline in seed production from the center toward the range margin along latitude or altitude have been found (Jump and Woodward 2003; Vaupel and Matthies 2012). Therefore, quantification of seed production (and indeed other components of fitness) is necessary to fully understand the selection pressures on species populations in response to variation in climate.

On the other hand, plants growing under suboptimal environmental conditions or resource-limited habitats usually improve their efficiency in energy utilization and resource allocation to ensure their fitness and persistence (Hall et al. 1992). Similar to this study, Wei et al. (2015) also found higher seedling establishment of *E. pleiospermum* at the leading edges across its geographic range. Thus, we speculated that *E. pleiospermum* populations at the margin range may have evolved an efficient regeneration strategy. However, even though the underlying mechanisms for the germination patterns that we observed in this study were not entirely clear, these patterns appear beneficial to the maintenance and expansion of population at the edge of this species' geographical distribution.

Seed germination percentage of different origins in response to temperature

Our results revealed that temperature had a limited effect on germination percentage of seeds from different origins, except seeds collected from high latitudes. In general, populations growing on the margin of species' distribution range are considered to be more vulnerable to environmental changes (Thomas et al. 2001; Mimura et al. 2014). Accordingly, we found that FGP increased with incubation temperature for seeds from high latitudes. Therefore, we inferred that seed germination of populations near the upper limits of this species' geographic distribution was more sensitive to various temperatures and the ongoing climate warming. In addition, FGP of seeds from high latitudes increased with incubation temperature, which indicates that population recruitment at higher latitudes may benefit from warmer climate in terms of germination. Graae et al. (2008) also demonstrated that seeds of two dwarf shrub from arctic and boreal sites would increase their germination in response to warmer climatic conditions. However, we observed that FGP of seeds from high altitudes reached the peak under middle temperature treatment (Fig. S1B), although FGP of seeds along altitudinal gradient was not significantly affected by temperature. To some extent, it indicates that slightly warmer conditions may enhance germination at higher altitudes, but more intense warming will have a negative effect.

On the other hand, some studies demonstrated that seed germination percentage of populations spanning the geographic gradient varied under different incubation temperatures (Mariko et al. 1993; Vandelook et al. 2008; Zettlemoyer et al. 2017). For example, Ross et al. (2012) found that seeds of two *Senecio* species from high altitude populations germinated better under low temperatures (9–13 °C) than those from low altitude populations. Similarly, Weng and Hsu (2006) showed that seeds of *Lilium formosanum* from lower latitude populations had significantly higher FGP than seeds from the higher latitude populations at high temperature (25 °C). However, our results showed that neither the FGP of seeds from high altitude or latitude was higher under low temperature (15 °C), nor that of seeds from low altitude or latitude was higher under high temperature (25 °C).

FGP of *E. pleiospermum* was affected by seed origin and its interaction with temperature for seeds collected along latitudinal gradient, but not for seeds collected along altitudinal gradient. Similarly, Zettlemoyer et al. (2017) found that latitude and its interaction with temperature had significant effects on germination across populations of *Campanula americana* spanning a latitudinal gradient throughout eastern North America. Thus, the response of seed germination to temperature varied significantly among seed origins along geographic gradient, and we should take inter-population variation into account when predicting the impact of climate warming on seed germination. In general, seed germination is affected not only by environmental condition of germination process, but also by seed quality (i.e., seed size, mass, and nutrients) (Hantsch et al. 2013; Carón et al. 2014), which was strongly related to the parental growing environments (e.g., temperature, light, and precipitation) of seed origins (Murray et al. 2004; De Frenne et al. 2011). In addition, it was curious that incubation temperature had a significant interaction with seed origin affecting FGP for latitudinal origin seeds, but there was no similar effect for altitudinal origin seeds, given that we expect temperature to vary similarly across latitude and altitude. Therefore, we suggest caution in extrapolating the seed germination patterns and their response to different environmental conditions between latitude and altitude despite their similar environmental gradients (Montesinos-Navarro et al. 2011; De Frenne et al. 2013).

Seed germination timing of different origins in response to temperature

Germination timing of seeds collected along latitudinal gradient was significantly affected by temperature in our study, and increasing temperature from climate change could advance the onset of germination and speed the whole process of seed germination, since T_0 and T_{50} of seeds incubated under higher temperatures were significantly lower than that of seeds incubated under lower temperature. Similarly, other studies demonstrated that incubation temperature can strongly affect the timing of germination and warming substantially accelerated germination (Milbau et al. 2009; Zettlemoyer et al. 2017). Chamorro et al. (2013) also found that germination speed (reflected by T_{50}) was faster at warmer temperatures for three Mediterranean shrubs. These results all indicate that seed germination timing will likely be affected by a future warmer climate. As temperatures increase, the advance of seedling emergence can be favorable to prolong the growing season for high latitude populations (Milbau et al. 2009). However, if warming could accelerate seed germination and shorten the germination duration for high altitude populations, the risk of frost damage would increase. Because late frosts in spring are frequent in high altitude areas, if most seeds germinate simultaneously in a relatively short time, the seedlings may be completely destroyed by an unpredictable late frost (Shimono and Kudo 2005; Vitasse et al. 2013).

During the germination experiments, seeds from high altitude were the first and the last to be observed to germinate under low and high incubation temperature, respectively, in line with the other studies. For instance, Mariko et al. (1993) showed that upland populations of *Reynoutria japonica* had quicker germination times than lowland populations under the lowest temperature regime. These patterns of seed germination timing may be related to the environmental conditions of their habitats (Weng and Hsu 2006). Shimono and Kudo (2005) also revealed that alpine plants experiencing colder climate had lower temperature requirements for germination. On the other hand, as the temperature and growing season declined with increasing altitude, seeds of the populations growing at high altitude must be adapted to earlier germination under low temperature to maximize the length of growing season to ensure their growth and reproduction (Körner 2003; Giménez-Benavides et al. 2005; Montesinos-Navarro et al. 2011). Interestingly, De Luis et al. (2008) detected that fitness (survival, growth, or fecundity) benefits acquired by early seedling emergence could be maintained throughout the life cycle of four woody species.

Conclusions

In this study, we found that seed germination percentage of *E. pleiospermum* was lower for central populations along latitudinal gradient, contrary to predictions of the central–marginal hypothesis. We inferred that higher germination percentage of marginal populations may be an effective strategy to maintain species persistence and population expansion at the edge of the species' geographic distribution. On the other hand, our results demonstrated that seed origin and its interaction with temperature were the major drivers of germination percentage variation for seeds across latitudes, but not for seeds across altitudes. Thus, we should be cautious about extrapolating the results from latitudinal gradient to altitudinal gradient. Moreover, we found that temperature can alter the timing of seed germination of *E. pleiospermum* along latitudinal gradient, but it had limited effects on germination percentage of seeds from most origins. However, seed germination percentage of high latitudinal populations was more sensitive to temperature and may benefit from a warmer climate.

Although the intrinsic physiological mechanism for seed germination patterns and their response to temperature along latitudinal and altitudinal was not clearly revealed in this study, our results will help to predict the fate of this relict species in future climate change. Here, we suggest that it is necessary to carry out experiments under more natural conditions to explore how seed germination responds to climate warming. In addition, we suggest that it is increasingly important to take inter-population variation across species' geographic distribution into account when analyzing the impact of environmental changes on plant species' demography.

Author contribution statement HW, XW, and MJ conceived the ideas and designed experiments; HW, SW, and XW conducted fieldwork and performed the experiments; HW analyzed the data and prepared the manuscript. All authors provided valuable suggestions for the improvement of the final manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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