diversity

Article

Asymmetric Effects of Temperature Change on Herbaceous Seed Germination: Implications for Climate Warming

Kai Chen [1,2,3,4,*], Zi-Hong Chen [1,2,3,4] and Zhong-Hua Jiang [4]

[1] Construction Projects about the Key Laboratory of Entomogenous Fungi Resources Conservation and Green Development in Gaoligong Mountains, Baoshan University, Baoshan 678000, China; zhchen78@163.com
[2] Research Institute of Gaoligong Mountains, Baoshan University, Baoshan 678000, China
[3] Baoshan Key Laboratory of Biodiversity Conservation and Utilization of Gaoligong Mountains, Baoshan University, Baoshan 678000, China
[4] School of Resources and the Environment, Baoshan University, Baoshan 678000, China; jiangzh_95@163.com
* Correspondence: kchen1985@163.com

Abstract: Seed germination is a critical ecological process that governs both the establishment and maintenance of plant diversity and is highly sensitive to temperature fluctuations. As climate change accelerates, particularly through increasing temperatures, the disruption to seed germination could pose significant risks to plant diversity. Therefore, understanding how temperature fluctuations affect seed germination is essential for predicting the future recruitment of mountain plants and for conserving biodiversity in the context of ongoing climate warming scenarios. In this study, we collected seeds from 14 *Impatiens* species (Balsaminaceae) in the Gaoligong Mountains (Southwest China) at an elevation of approximately 2000 m. Germination tests were conducted on seeds subjected to cold stratification (42 days at 4 °C) across a range of alternating temperatures (6/1, 11/6, 16/11, 21/16, 26/21, and 31/26 °C). We used generalized linear mixed-effects models (random intercept) with temperature and its higher-order terms as the fix-effect terms to construct four models describing the relationship between germination percentage and temperature. Results indicated that (1) the germination percentage varied significantly among species and temperature treatments; (2) the nonlinear and asymmetrical model, incorporating temperature and its quadratic and cubic terms, best fit the germination data; and (3) the decline in germination percentage above the optimum temperature (T_o) was significantly steeper than the increase below based on the best model. Overall, these findings suggest that seed plants at low elevations in mountain ecosystems may be particularly vulnerable to future climate warming due to the sharp decline in germination percentage at temperatures above T_o. Thus, protecting low-elevation plants should be a key priority in biodiversity conservation efforts as global temperatures continue to rise.

Keywords: Gaoligong Mountains; *Impatiens* species; germination percentage; GLMMs; nonlinear

Citation: Chen, K.; Chen, Z.-H.; Jiang, Z.-H. Asymmetric Effects of Temperature Change on Herbaceous Seed Germination: Implications for Climate Warming. *Diversity* **2024**, *16*, 649. https://doi.org/10.3390/d16100649

Academic Editor: Mario A. Pagnotta

Received: 14 September 2024
Revised: 9 October 2024
Accepted: 15 October 2024
Published: 21 October 2024

1. Introduction

Seed germination is crucial for maintaining plant diversity in mountain ecosystems, which host a substantial proportion of the world's seed plants. This process is highly sensitive to environmental hazards, particularly temperature fluctuations [1,2]. Temperature is a critical environmental factor governing seed germination, and even minor fluctuations can significantly impact plant survival by affecting germination success rates [3–5]. As climate warming increases temperatures in mountain habitats, it is likely to exert strong selective pressure on seed germination and plant regeneration [6]. However, our understanding of how climate warming will influence seed germination and plant diversity in these ecosystems remains limited. As such, quantitative analysis of germination sensitivity to temperature is essential for predicting the germination characteristics of mountain plants and ensuring the protection of plant diversity in the context of climate warming [7].

Cardinal temperatures are valuable for predicting seed germination under temperature change scenarios [5]. Seeds germinate within a specific range, defined by a minimum (T_{min}) and maximum (T_{max}) threshold temperature, outside of which germination does not occur, with the highest germination percentage reached at the optimal temperature (T_o) [8,9]. These cardinal temperatures can vary spatiotemporally, serving as an efficient adaptation strategy to different ecological factors [10,11]. For instance, Mediterranean low-elevation plants have lower T_{min} values compared to high-elevation plants, enabling them to avoid seed germination during brief warm periods in winter [10]. The T_{max} values for *Peltophorum dubium* seeds are higher in the northern provenance of Brazil, which experiences higher temperatures compared to other provenances [12]. The T_o values for *Corymbia calophylla* increase with the seed origin temperatures, aiding in maintaining germination success under warmer habitats [13]. The three cardinal temperatures are closely linked to environmental temperatures during seed development [12] and can be quantified using thermal models, which are useful for characterizing germination responses to temperature changes [8].

Various thermal models, such as intersected lines, quadratic polynomial, and five-parameter beta models, have been developed and extensively used to investigate seed germination responses to temperature fluctuations in both cultivated and wild species. These studies suggest that nonlinear models are effective for assessing and predicting shifts in seed germination due to temperature variations [10,14–18]. Conversely, linear models have been successfully employed to quantify the effects of temperature on logit or arcsine-transformed germination percentages, indicating that the relationships can be significantly positive, negative, or non-correlated, depending on the temperature tolerance of plants [4,14,19,20]. However, comparative studies on the effectiveness of nonlinear versus linear models in capturing seed germination responses to temperature are limited, with Watt et al. (2010) reporting that nonlinear models generally provide a more accurate fit [21].

Nonlinear models, used to describe seed germination responses to temperature, can be categorized into two main types based on the rate of change in germination percentage. The first type, represented by models like intersected lines [8,18], assumes a linear relationship between germination percentage (GP) and temperature (T) within the range from $T_{min/max}$ to T_o (i.e., $d(GP)/dT = \text{constant}$). The second type, including models such as quadratic polynomial [16,18], suggests that the rate of change in germination percentage is more abrupt near $T_{min/max}$ than near T_o (i.e., $d(GP)/dT = \beta_0 + \beta_1 \times T$). Nevertheless, beyond these general trends, there remains a significant gap in our detailed understanding of how temperature variations affect seed germination.

Seed germination responses to temperature changes are indirectly regulated by synthetase, hydrolase, and antioxidant enzymes, which govern various key metabolic reactions involved in the germination process [22,23]. These enzyme proteins are susceptible to degradation at temperatures exceeding the optimal range (T_o), and thus, warming may cause irreversible damage to proteases, unlike cooling [22,24]. According to the enzyme kinetics theory, the rate of enzyme activity decline between T_o and T_{max} is more rapid than the rate of activity increase between T_{min} and T_o [25]. Research also suggests that crop seed production increases gradually with temperature up to T_o, then sharply declines at temperatures above T_o, indicating a nonlinear and asymmetric relationship between crop seed production and temperature [26]. Based on these theories and empirical findings, we hypothesize that the relationship between seed germination and temperature is nonlinear and asymmetric, with a steeper decline in germination percentage above T_o compared to the incline below. To test these hypotheses, we addressed the following questions: (1) Are nonlinear models more effective than linear models in describing the relationship between germination percentage and temperature? (2) Is the reduction in germination percentage due to temperatures increasing above T_o greater than the reduction caused by temperatures decreasing below T_o?

2. Materials and Methods

2.1. Species and Seed Collection

The genus *Impatiens* L. in the Balsaminaceae family is one of the largest among seed plants and is widely distributed in subtropical and temperate zones of the Northern Hemisphere [27]. Consequently, *Impatiens* species serve as representative herbs in mountain ecosystems. Fully mature seeds from 14 *Impatiens* species were collected at the onset of natural dispersal between 10 August and 20 October 2023 in the Gaoligong Mountains (97°30′–98°30′ E, 24°40′–25°30′ N), Southwest Yunnan Province, China. For each species, seeds were collected from a single site but from more than 15 individual plants, then packed in paper envelopes and transported to the laboratory within 3 days. All collection sites were distributed within a narrow elevational range of 1930 to 2180 m in similar wet understory habitats on the eastern slopes of the Gaoligong Mountains to minimize maternal seed effects. The maximum distance between the two collection sites was approximately 500 m, while the shortest distance was about 0.5 m. The collection area is influenced by the Indian Ocean monsoon, with an annual rainfall of 648–1591 mm and a mean temperature of 5.4–14.9 °C [28].

2.2. Germination Experiments

Physiological dormancy is a common trait of *Impatiens* seeds in Southwest China and can be alleviated by the cold–moist stratification [3,29]. To address this, fresh *Impatiens* seeds were sown five days post-harvest on seven layers of damp filter paper in 90 mm diameter Petri dishes, then placed in a 4 °C refrigerator for 42 days to break dormancy. Cold stratification at 4 °C does not harm *Impatiens* seeds, and the 42-day period represents the maximum time required for *Impatiens* seeds at 2200 m elevation to overcome dormancy.

Prior to conducting germination tests, the seeds, having undergone dormancy breaking, were macerated in 0.3% sodium hypochlorite solution (NaClO) for 5 min, then rinsed three times with distilled water to prevent fungal contamination. Three replicates of 30 seeds per species were sown on the surface of five layers of damp filter paper in 90 mm diameter Petri dishes and incubated under alternating temperature regimes (6/1, 11/6, 16/11, 21/16, 26/21, and 31/26 °C) and a 12 h light/dark cycle, with light (4000 Lux) applied during the warm phase. These temperatures included the highest and lowest temperatures of the growing season in the sampling sites. Germination was monitored daily, with seeds displaying visible radicles ($\geq$1 mm) considered germinated. The trials lasted for 30 days until no further germination was observed. Non-germinated seeds were dissected, and those showing complete and hard embryos were considered viable [29,30]. The percentage of germinated seeds was calculated after discarding nonviable seeds. The final dataset contained 252 germination records.

2.3. Data Analysis

The seed germination percentage does not follow a normal distribution. Consequently, a nonparametric two-way analysis of variance (ANOVA) was employed to assess differences in germination percentages among species and temperatures using the “aov” function in the R *stats* package. Germination percentage was converted to ranks as the response variable using the “rank” function in *stats*, and temperature was converted to a categorical variable using the “factor” function in *stats* before performing ANOVA.

Generalized linear mixed-effects models (GLMMs), with a logit link function and binomial error structure, were used to quantify the relationship between seed germination and temperature changes. In each random intercept model, species was included as the random-effect term to account for germination variation among *Impatiens* species not explained by the fixed-effect terms. To consider possible nonlinear responses of seed germination to temperature changes, the average of day/night temperatures (i.e., 3.5, 8.5, 13.5, 18.5, 23.5, and 28.5 °C) and their higher-order terms (i.e., quadratic, cubic, and quartic) were used as fix-effect terms to construct four alternative models. Model 1 used the average of day/night temperature as a fix-effect term ($\text{logit(GP)} = \beta_0 + \beta_1 \times \text{T} + \varepsilon_{\text{species}} + \varepsilon_0$, $\varepsilon \sim$

N(0, σ^2)); model 2 used the average of day/night temperature and its quadratic term as fix-effect terms (logit(GP) = $\beta_0 + \beta_1 \times T + \beta_2 \times T^2 + \varepsilon_{species} + \varepsilon_0$, $\varepsilon \sim N(0, \sigma^2)$); model 3 used the average temperature and its quadratic and cubic terms as fix-effect terms (logit(GP) = $\beta_0 + \beta_1 \times T + \beta_2 \times T^2 + \beta_3 \times T^3 + \varepsilon_{species} + \varepsilon_0$, $\varepsilon\sim N(0, \sigma^2)$); model 4 used the average temperature and its quadratic, cubic, and quartic terms as fix-effect terms (logit(GP) = $\beta_0 + \beta_1 \times T + \beta_2 \times T^2 + \beta_3 \times T^3 + \beta_4 \times T^4 + \varepsilon_{species} + \varepsilon_0$, $\varepsilon \sim N(0, \sigma^2)$). GLMM analysis was performed using the “glmer” function in the R package *lme4*. To compare independent variables, temperature values were transformed to Z scores (mean = 0, SD = 1) before GLMM analysis.

Model selection was conducted through a comprehensive evaluation of the Akaike information criterion (AIC), collinearity, and the coefficient of determination (R^2). AIC estimates information loss when a specific model is used to describe the data-generating process [31]. A model with an AIC value at least 2 units lower than another is considered significantly better. The “anova” function in *stats* was used to compare AIC values among models. Collinearity was assessed using the variance inflation factor (VIF) through the “vif” function in the *car* package, with VIF values greater than 10 indicating high collinearity among independent variables [32,33]. In addition, marginal and conditional R^2 values were calculated using the “r.squaredGLMM” function in the *MuMIn* package.

To determine the potential asymmetric effects of temperature change on seed germination, we used the best model, denoted as GP = f(T), to find the optimum germination temperature (T_o) for *Impatiens* seeds using the “optimize” function in *stats*. We then adjusted the temperature unit at T_o (i.e., $T = T_o \pm 1$) and compared the germination differences between the two adjusted temperatures using the best model (i.e., $\Delta GP = f(T_o + 1) - f(T_o - 1)$; Figure 1). To estimate the distribution of ΔGP, we employed the bootstrap method, involving two steps. First, we used the “sample” function in *stats* to sample 252 records with replacement from the original dataset and 1000 repeats. Second, we calculated ΔGP for each bootstrap sample. The normality of ΔGP was determined using the Shapiro–Wilk normality test with the “shapiro.test” function in *stats*. One-sample Student’s *t*-test was performed using the “t.test” function in *stats* to determine whether the mean of the ΔGP distribution differed from zero. All statistical analyses were conducted using R v.4.2.1 [34].

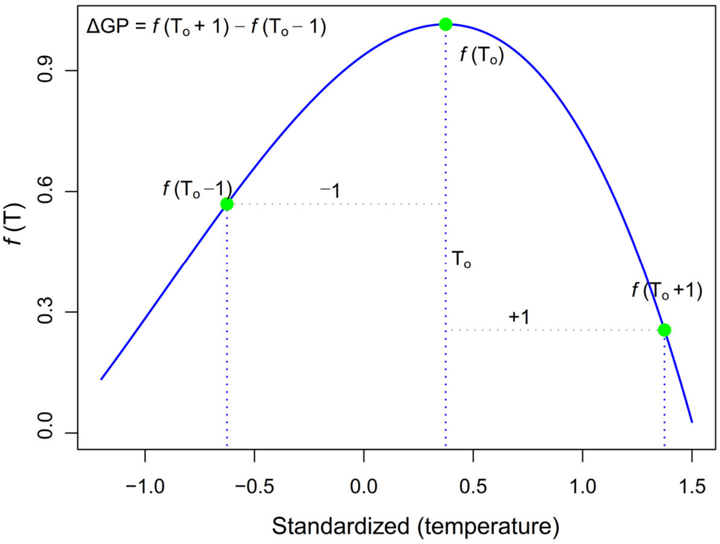
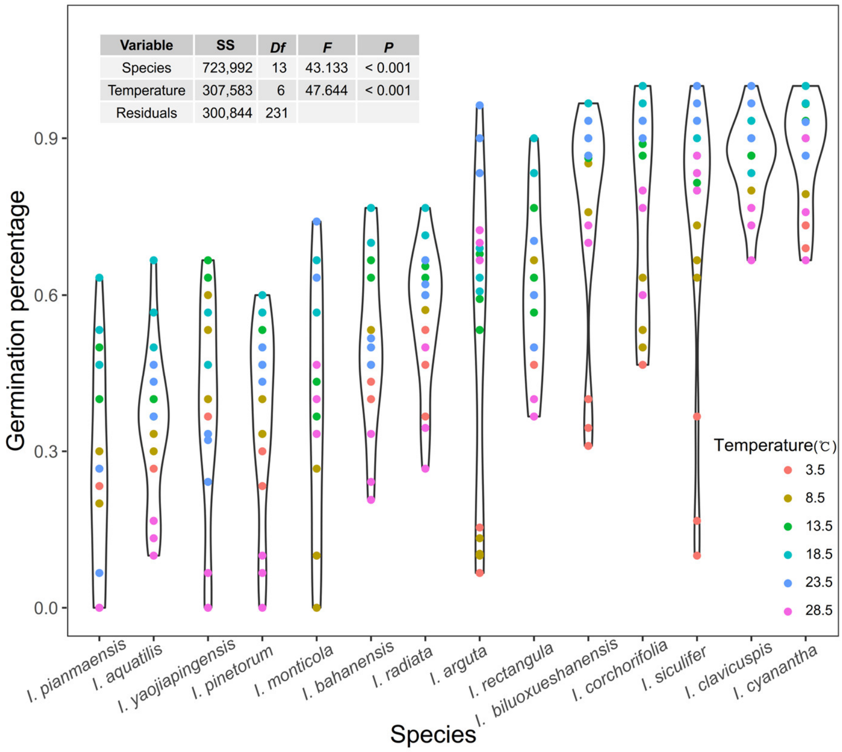


Figure 1. Method for calculating ΔGP. Solid blue line represents germination as a function of temperature, and three green dots from left to right represent values of the function at $T = T_o - 1$, $T = T_o$, and $T = T_o + 1$, respectively.

3. Results

3.1. Seed Germination Differences among Species and Germination Temperatures

Variation in germination percentages was observed among the 14 *Impatiens* species, with *I. cyanantha* exhibiting the highest germination percentage (average = 87.62%; Figure 2) and *I. pianmaensis* exhibiting the lowest (average = 26.3%; Figure 2). Significant differences in germination percentages were observed among the *Impatiens* species when controlling for germination temperature ($F_{(13, 231)} = 43.13$, $p < 0.001$; Figure 2).



Variable	SS	*Df*	*F*	*P*
Species	723,992	13	43.133	< 0.001
Temperature	307,583	6	47.644	< 0.001
Residuals	300,844	231		

Figure 2. Differences in germination percentage among *Impatiens* species and germination temperatures. Outlines are violin plots showing distribution of values across the data. Thicker sections represent higher probability, while thinner sections represent lower probability. Points show germination percentage at different temperatures. Top left is a nonparametric two-way ANOVA table showing variance of seed germination attributed to species, germination temperature, and residuals.

The T_o for the germination of most *Impatiens* seeds was around 18.5 °C (Figure 2). For example, *I. siculifer* had a germination percentage exceeding 80% at 18.5 °C but less than 40% at 3.5 °C, while *I. yaojiapingensis* showed 66.67% germination at 13.5 °C and no germination at 28.5 °C (Figure 2). Significant differences in germination percentages were also noted among different germination temperatures for the same *Impatiens* species ($F_{(6, 231)} = 47.64$, $p < 0.001$; Figure 2).

3.2. Modeling the Relationship between Germination Percentage and Temperature

The GLMMs were all significant ($p < 0.05$) and explained at least 86.21% of the variation in germination percentage, which was largely attributable to the random effect (Table 1). Model 1 had the highest AIC value (2283.9) and explained less variation than the other models, indicating that a simple linear regression was not a good predictor of germination response to temperature change (Table 1 and Figure 3a). Model 4 exhibited severe collinearity with a VIF value of 21.01 (Table 1 and Figure 3d) despite having the lowest AIC value (1710.9) and the highest R^2 value (91.15%). Based on the AIC and VIF values, Model 3 (AIC = 1713.3, VIF = 8.02; Table 1) was preferred over Model 2 (AIC = 1753.9, VIF = 1; Table 1). This suggests that the cubic regression model with asymmetry (logit(GP) = $\beta_0 + \beta_1 \times \mathrm{T} +$

$\beta_2 \times T^2 + \beta_3 \times T^3 + \varepsilon_{species} + \varepsilon_0$, $\varepsilon \sim N(0, \sigma^2)$; Figure 3c) better described the relationship between germination percentage and temperature than the quadratic regression model with symmetry ($\text{logit(GP)} = \beta_0 + \beta_1 \times T + \beta_2 \times T^2 + \varepsilon_{species} + \varepsilon_0$, $\varepsilon \sim N(0, \sigma^2)$; Figure 3b).

Table 1. Comparison of four generalized linear random intercept models explaining the relationships between logit germination percentage and temperature, including higher-order terms (i.e., quadratic, cubic, and quartic) using various model selection criteria. GP: germination percentage; T: temperature; AIC: Akaike information criterion; BIC: Bayesian information criterion; R^2: coefficient of determination; VIF: variance inflation factor; *p*: error probability; $\varepsilon \sim N(0, \sigma^2)$.

Model	AIC	BIC	Marginal R^2	Conditional R^2	Max VIF	*p*-Value
$\text{logit(GP)} = \beta_0 + \beta_1 \times T + \varepsilon_{species} + \varepsilon_0$	2283.9	2294.5	3.26%	86.21%		
$\text{logit(GP)} = \beta_0 + \beta_1 \times T + \beta_2 \times T^2 + \varepsilon_{species} + \varepsilon_0$	1753.9	1768.1	26.86%	90.9%	1	<0.001
$\text{logit(GP)} = \beta_0 + \beta_1 \times T + \beta_2 \times T^2 + \beta_3 \times T^3 + \varepsilon_{species} + \varepsilon_0$	1713.3	1731	28.18%	91.12%	8.02	<0.001
$\text{logit(GP)} = \beta_0 + \beta_1 \times T + \beta_2 \times T^2 + \beta_3 \times T^3 + \beta_4 \times T^4 + \varepsilon_{species} + \varepsilon_0$	1710.9	1732.1	28.38%	91.15%	21.01	0.036

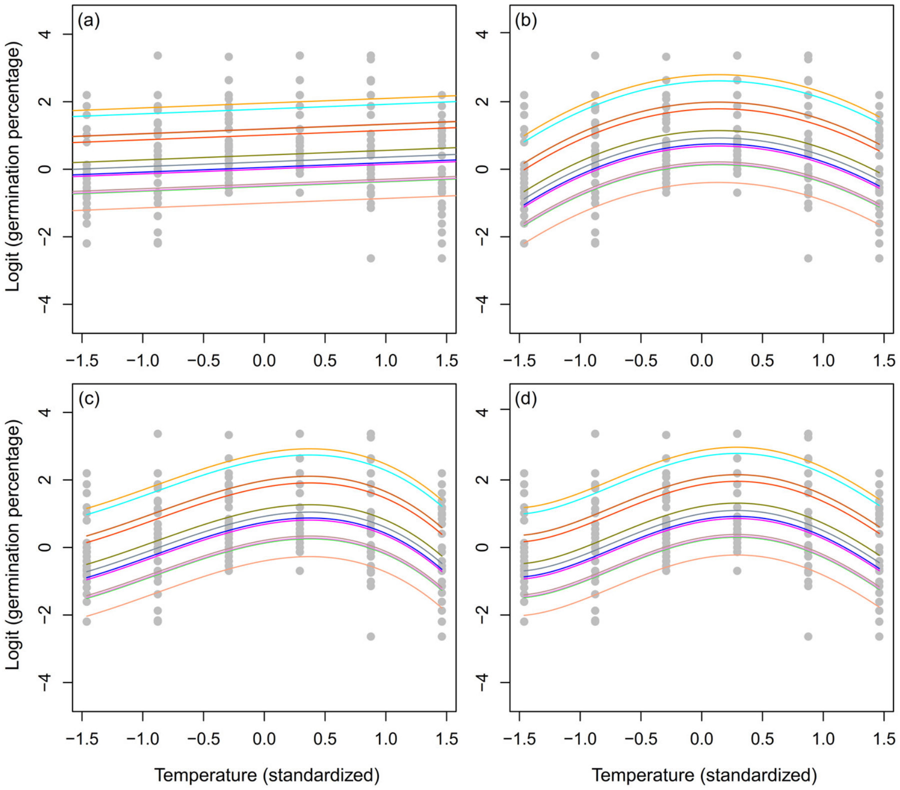


Figure 3. Relationship between germination percentage and temperature fitted by linear model (**a**), quadratic polynomial model (**b**), cubic polynomial model (**c**), and quartic polynomial model (**d**), respectively. Lines in (**a**–**d**) represent fitted models for each species, distinguished by different colors.

Model 3 revealed that the germination percentage decreased nonlinearly with temperatures at both the sub-optimal ($<T_o$) and supra-optimal ($>T_o$) levels (Table 2 and Figure 3c). Specifically, the change in *Impatiens* seed germination percentage was less pronounced between T_{min} and T_o than between T_o and T_{max} ($d(GP)/dT = 0.64 + 2 \times (-0.71) \times T + 3 \times (-0.26) \times T^2$; Table 2 and Figure 3c).

Table 2. Results of generalized linear random intercept model estimating the relationship between logit (GP) with T, T^2, and T^3; GP: germination percentage; T: temperature.

Term	Variable	Estimate	Standard Error	*p*-Value
Fixed effect	Intercept	1.06	0.27	<0.001
	T	0.64	0.07	<0.001
	T^2	−0.71	0.03	<0.001
	T^3	−0.26	0.04	<0.001
Random effect	Variable		Variance	
	Species		0.97	
	Residual		3.21	

3.3. Germination Percentage with Temperatures Above and Below T_O

The ΔGP values ranged from −1.07 to 0.24 (average = −0.43) and followed a normal distribution ($w = 1$, $p = 0.159$; Figure 4). One-sample Student's *t*-test showed that the mean value of ΔGP was significantly less than zero ($t = -15.6$, $p < 0.001$; Figure 4). This suggests that increasing the temperature by 1 unit above the optimal temperature had a greater inhibitory effect on germination than decreasing the temperature by 1 unit.

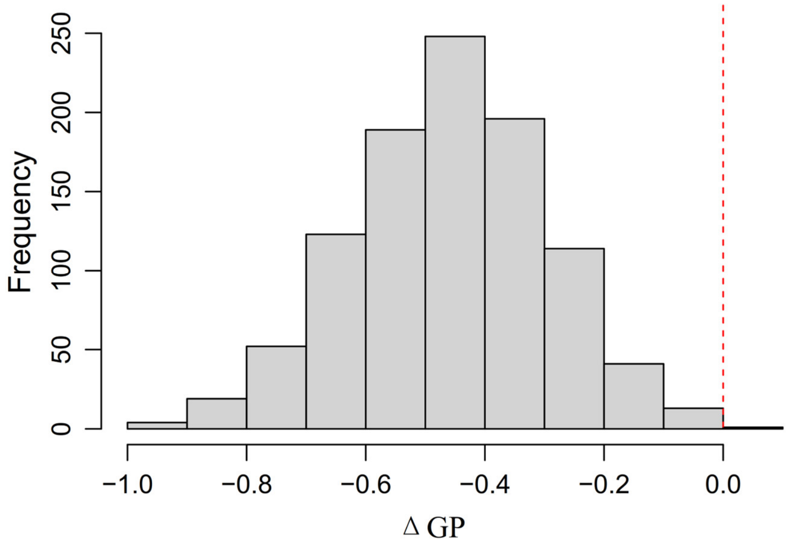


Figure 4. Histogram of ΔGP values for each bootstrap sample. ΔGP is the difference in germination percentage between the best model at temperatures $T_o + 1$ and $T_o - 1$. Red dotted line shows a ΔGP of 0 for reference.

4. Discussion

4.1. Seed Germination Variation among Impatiens Species

All 14 *Impatiens* species exhibited heritability in seed germination, with germination percentages significantly influenced by species. This finding is consistent with Perglová et al. (2009), who reported marked differences in seed germination among four *Impatiens* species [35]. This observed variation could be attributed to a phylogenetic pattern in seed germination behavior across seed plants globally [11,36]. Our results highlight the necessity of considering genetic differences among species in seed germination studies, even for closely related species.

4.2. Nonlinear and Asymmetric Relationship between Seed Germination and Temperature

An initially increasing and then decreasing trend in *Impatiens* seed germination percentage with incubation temperature was observed, consistent with previous reports for various cultivated and wild species [4,14,30]. This pattern suggests the existence of a thermal threshold beyond which germination percentages decline in *Impatiens* species. Seed germination behavior is an adaptation to the climatic conditions of a plant's natural habitat [3]; therefore, all 14 *Impatiens* species were able to germinate at 13.5 °C, corresponding to the low temperatures before the rainy season in the Gaoligong Mountains. This indicates convergent adaptation among *Impatiens* species, ensuring that subsequent seedling establishment occurs when sufficient water is available.

Nonlinear models more accurately captured the relationship between germination percentage and temperature compared to linear models, suggesting that the germination percentage of *Impatiens* seeds increases with temperature until reaching an optimum, after which it declines. While linear models are straightforward and can be helpful for predicting germination responses to temperature fluctuations, they are generally more prone to bias than nonlinear models [12]. Accumulating evidence has indicated that the relationship between seed germination and temperature exhibits a significant curve, passing through T_o [18,21,37]. Nonlinear models, such as quadratic polynomial models, intersected-lines models, beta models, and Dent-like models, have been shown to fit germination data well [15,16,18,37]. The suitability of a particular nonlinear model depends on the germination behavior of the species or ecotype [18,37].

The relationship between germination percentage and temperature in *Impatiens* species was also asymmetric, with the decline in germination percentage above T_o, which was found to be significantly steeper than the incline below. This may be because temperatures above T_o can cause seed death through protein denaturation [22]. As temperatures increase above T_o, the enzyme activity controlling various seed metabolic processes decreases sharply, eventually halting enzyme-catalyzed reactions as enzymes lose their ability to function [25]. Additionally, asymmetric models are more adaptable than symmetric models, as their curvilinear nature allows for a gradual transition between phases, producing a smoother and more realistic curve [37]. This finding partially aligns with previous research showing a gradual increase in corn, soybean, and cotton yields with rising temperatures up to T_o, followed by a sharp decline beyond that point [26], indicating severe damage to both agricultural seed production and wild plant propagation under climate warming. To the best of our knowledge, this is the first report documenting a nonlinear and asymmetric response of seed germination to temperature changes.

4.3. Implications for Plant Diversity Conservation Under Climate Warming Scenarios

Climate change, particularly rising temperatures, strongly influences seed germination, plant recruitment, and species diversity [38]. Consequently, nonlinear and asymmetric models that describe the relationship between seed germination and temperature are essential tools for predicting the germination characteristics and seedling establishment of mountain plants in the context of global climate change [6]. Plants in the mountains of Southwest China, a global biodiversity hotspot, are generally restricted to specific climatic conditions and are particularly vulnerable to climate warming [39]. The asymmetric effects of temperature on seed germination suggest that rising temperatures due to climate warming could make it difficult for seeds to germinate at low elevations in these mountains, where plants are already near their upper germination temperature limits [5,17]. While most previous studies on plant diversity conservation have focused primarily on the germination responses of alpine plants to climate warming in the mountains of Southwest China [40–43], our results suggest that plants at low elevations should also be of concern due to the sharp decline in germination percentage at temperatures above the optimum.

5. Conclusions

Nonlinear and asymmetric models more accurately capture the relationship between seed germination and temperature compared to nonlinear and symmetric models, indicating that warming is more detrimental to seed germination than cooling above the optimum temperature. In a warming world, plants are increasingly pushed toward their upper germination temperature limits. This study highlights the importance of conserving plant diversity at low elevations in mountain ecosystems, where many species are already approaching their upper germination temperature limits and experience substantial declines in germination percentage at temperatures above their optimum. To the best of our knowledge, this research is the first to reveal the nonlinear and asymmetric response of seed germination to temperature changes.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16100649/s1.

Author Contributions: K.C. and Z.-H.C. designed this study. Z.-H.J. carried out the germination experiments. K.C., Z.-H.C. and Z.-H.J. conducted fieldwork. K.C. performed statistical analysis, generated the graphs, and wrote this manuscript. Z.-H.C. revised this manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the National Natural Science Foundation of China (32160078 and 32060638), Middle–Young-Aged Academic and Technical Leader Reserve Talents Projects of Yunnan, China (202205AC160061), and Lower Nu River, Mountain Agroecosystem, Observation, and Research Station of Yunnan Province (202305AM340031).

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The datasets used in the study are attached in the Supplementary Materials.

Acknowledgments: We are grateful to Yuan-Yuan Huang, Lin-Yuan Shi, and Xian-Qi Bai for their assistance in fieldwork.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Abdellaoui, R.; Boughalleb, F.; Zayoud, D.; Neffati, M.; Bakhshandeh, E. Quantification of *Retama raetam* seed germination response to temperature and water potential using hydrothermal time concept. *Environ. Exp. Bot.* **2019**, *157*, 211–216. [CrossRef]
2. Antonelli, A.; Kissling, W.D.; Flantua, S.G.A.; Bermúdez, M.A.; Mulch, A.; Muellner-Riehl, A.N.; Kreft, H.; Linder, H.P.; Badgley, C.; Fjeldså, J.; et al. Geological and climatic influences on mountain biodiversity. *Nat. Geosci.* **2018**, *11*, 718–725. [CrossRef]
3. Baskin, C.C.; Baskin, J.M. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*, 2nd ed.; Academic Press: San Diego, CA, USA, 2014. [CrossRef]
4. Cochrane, A. Modelling seed germination response to temperature in *Eucalyptus* L'Her. (Myrtaceae) species in the context of global warming. *Seed Sci. Res.* **2017**, *27*, 99–109. [CrossRef]
5. Hsu, H.W.; Stuke, M.; Bakker, J.D.; Kim, S.H. A time-to-event analysis for temperature dependence of seed germination in four conifers: Ecological niche and environmental gradients. *For. Ecol. Manag.* **2024**, *562*, 121972. [CrossRef]
6. Elsen, P.; Tingley, M. Global mountain topography and the fate of montane species under climate change. *Nat. Clim. Change* **2015**, *5*, 772–776. [CrossRef]
7. Walck, J.L.; Hidayati, S.N.; Dixon, K.W.; Thompson, K.; Poschlod, P. Climate change and plant regeneration from seed. *Glob. Chang. Biol.* **2010**, *17*, 2145–2161. [CrossRef]
8. Bradford, K.J. Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. *Weed Sci.* **2002**, *50*, 248–260. [CrossRef]
9. Dürr, C.; Dickie, J.B.; Yang, X.Y.; Pritchard, H.W. Ranges of critical temperature and water potential values for the germination of species worldwide: Contribution to a seed trait database. *Agric. For. Meteorol.* **2015**, *200*, 222–232. [CrossRef]
10. Picciau, R.; Pritchard, H.W.; Mattana, E.; Bacchetta, G. Thermal thresholds for seed germination in Mediterranean species are higher in mountain compared with lowland areas. *Seed Sci. Res.* **2018**, *29*, 44–54. [CrossRef]
11. Maleki, K.; Soltani, E.; Seal, C.E.; Colville, L.; Pritchard, H.W.; Lamichhane, J.R. The seed germination spectrum of 486 plant species: A global meta-regression and phylogenetic pattern in relation to temperature and water potential. *Agric. For. Meteorol.* **2023**, *346*, 109865. [CrossRef]
12. Daibes, L.F.; Cardoso, V.J.M. Seed germination of a South American forest tree described by linear thermal time models. *J. Therm. Biol.* **2018**, *76*, 156–164. [CrossRef]
13. Filipe, J.C.; Ahrens, C.C.; Byrne, M.; Hardy, G.; Rymer, P.D. Germination temperature sensitivity differs between co-occurring tree species and climate origins resulting in contrasting vulnerability to global warming. *Plant Environ. Interact.* **2023**, *4*, 146–162. [CrossRef]
14. Zhang, H.; Yu, Q.; Huang, Y.; Zheng, W.; Tian, Y.; Song, Y.; Li, G.; Zhou, D. Germination shifts of C_3 and C_4 species under simulated global warming scenario. *PLoS ONE* **2014**, *9*, e105139. [CrossRef]

15. Cochrane, A. Can sensitivity to temperature during germination help predict global warming vulnerability? *Seed Sci. Res.* **2015**, *26*, 14–29. [CrossRef]
16. Finch, J.; Walck, J.L.; Hidayati, S.N.; Kramer, A.T.; Lason, V.; Havens, K. Germination niche breadth varies inconsistently among three *Asclepias congeners* along a latitudinal gradient. *Plant Biol.* **2019**, *21*, 425–438. [CrossRef]
17. Sentinella, A.T.; Warton, D.I.; Sherwin, W.B.; Offord, C.A.; Moles, A.T. Tropical plants do not have narrower temperature tolerances, but are more at risk from warming because they are close to their upper thermal limits. *Glob. Ecol. Biogeogr.* **2020**, *29*, 1387–1398. [CrossRef]
18. Solouki, H.; Kafi, M.; Nabati, J.; Ahmadi-Lahijani, M.J.; Nezami, A.; Ahmady, R.S. Quantifying cardinal temperatures of fenugreek (*Trigonella foenum-graecum* L.) ecotypes using non-linear regression models. *J. Appl. Res. Med. Aromat. Plants* **2022**, *31*, 100401. [CrossRef]
19. Luna, B.; Pérez, B.; Torres, I.; Moreno, J.M. Effects of incubation temperature on seed germination of Mediterranean plants with different geographical distribution ranges. *Folia Geobot.* **2012**, *47*, 17–27. [CrossRef]
20. Mondoni, A.; Rossi, G.; Orsenigo, S.; Probert, R.J. Climate warming could shift the timing of seed germination in alpine plants. *Ann. Bot.* **2012**, *110*, 155–164. [CrossRef]
21. Watt, M.S.; Xu, V.; Bloomberg, M. Development of a hydrothermal time seed germination model which uses the Weibull distribution to describe base water potential. *Ecol. Model.* **2010**, *221*, 1267–1272. [CrossRef]
22. Bewley, J.D.; Bradford, K.J.; Hilhorst, H.W.M.; Nonogaki, H. *Seeds: Physiology of Development, Germination and Dormancy*; Springer: New York, NY, USA, 2013. [CrossRef]
23. Xue, X.; Du, S.; Jiao, F.; Xi, M.; Wang, A.; Xu, H.; Jiao, Q.; Zhang, X.; Jiang, H.; Chen, J.; et al. The regulatory network behind maize seed germination: Effects of temperature, water, phytohormones, and nutrients. *Crop. J.* **2021**, *9*, 718–724. [CrossRef]
24. van Midden, K.P.; Mantz, M.; Fonovič, M.; Gazvoda, M.; Svete, J.; Huesgen, P.F.; van der Hoorn, R.A.; Klemenčič, M. Mechanistic insights into CrCEP1: A dual-function cysteine protease with endo- and transpeptidase activity. *Int. J. Biol. Macromol.* **2024**, *271*, 132505. [CrossRef]
25. Daniel, R.M.; Donson, M.J. Temperature and the catalytic activity of enzymes: A fresh understanding. *FEBS Lett.* **2013**, *587*, 2738–2743. [CrossRef]
26. Schlenker, W.; Roberts, M.J. Nonlinear temperature effects indicate severe damages to U.S. crop yields under climate change. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 15594–15598. [CrossRef]
27. Qin, F.; Xue, T.; Zhang, X.; Yu, J.; Gadagkar, S.R.; Yu, S. Past climate cooling and orogenesis of the Hengduan Mountains have influenced the evolution of *Impatiens* sect. *Impatiens* (Balsaminaceae) in the Northern Hemisphere. *BMC Plant Biol.* **2023**, *23*, 60. [CrossRef]
28. Liang, D.; Pan, X.; Luo, X.; Wenda, C.; Zhao, Y.; Hu, Y.; Robinson, S.K.; Liu, Y. Seasonal variation in community composition and distributional ranges of birds along a subtropical elevation gradient in China. *Divers. Distrib.* **2021**, *27*, 2527–2541. [CrossRef]
29. Chen, K.; Chen, Z.H.; Huang, Y.Y.; Jiang, Z.H. Elevation and phylogeny shape herbaceous seed dormancy in a biodiversity hotspot of southwest China. *Ecol. Evol.* **2023**, *13*, e09986. [CrossRef]
30. Aragón-Gastélum, J.L.; Flores, J.; Jurado, E.; Ramírez-Tobías, H.M.; Robles-Díaz, E.; Rodas-Ortiz, J.P.; Yáñez-Espinosa, L. Potential impact of global warming on seed bank, dormancy and germination of three succulent species from the Chihuahuan Desert. *Seed Sci. Res.* **2018**, *28*, 312–318. [CrossRef]
31. Burnham, K.P.; Anderson, D.R. *Model Selection and Inference: A Practical Information-Theoretic Approach*; Springer: New York, NY, USA, 2002. [CrossRef]
32. Dormann, C.F.; Elith, J.; Bacher, S.; Buchmann, C.; Carl, G.; Carré, G.; Marquéz, J.R.G.; Gruber, B.; Lafourcade, B.; Leitão, P.J.; et al. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **2013**, *36*, 27–46. [CrossRef]
33. Wang, J.; Qian, Q.; Zhang, F.; Jia, X.; He, J. The possible future changes in potential suitable habitats of *Tetrastigma hemsleyanum* (Vitaceae) in China predicted by an ensemble model. *Glob. Ecol. Conserv.* **2022**, *35*, e02083. [CrossRef]
34. R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. 2020. Available online: https://www.R-project.org/ (accessed on 9 October 2020).
35. Perglová, I.; Pergl, J.; Skálová, H.; Moravcová, L.; Jarošík, V.; Pyšek, P. Differences in germination and seedling establishment of alien and native *Impatiens* species. *Preslia* **2009**, *81*, 357–375. [CrossRef]
36. Liu, K.; Baskin, J.M.; Baskin, C.C.; Bu, H.; Liu, M.; Liu, W.; Du, G. Effect of storage conditions on germination of seeds of 489 species from high elevation grasslands of the eastern Tibet Plateau and some implications for climate change. *Am. J. Bot.* **2010**, *98*, 12–19. [CrossRef]
37. Cabrera-Santos, D.; Ordoñez-Salanueva, C.A.; Sampayo-Maldonado, S.; Campos, J.E.; Orozco-Segovia, A.; Flores-Ortiz, C.M. Quantifying cardinal temperatures of Chia (*Salvia hispanica* L.) using non-linear regression models. *Plants* **2022**, *11*, 1142. [CrossRef]
38. Rosbakh, S.; Poschlod, P. Initial temperature of seed germination as related to species occurrence along a temperature gradient. *Funct. Ecol.* **2014**, *29*, 5–14. [CrossRef]
39. Hopper, S.D.; Gioia, P. The southwest Australian floristic region: Evolution and conservation of a global hot spot of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **2004**, *35*, 623–650. [CrossRef]

40. Peng, D.; Sun, L.; Pritchard, H.W.; Yang, J.; Sun, H.; Li, Z. Species distribution modelling and seed germination of four threatened snow lotus (*Saussurea*) and their implication for conservation. *Glob. Ecol. Conserv.* **2019**, *17*, e00565. [CrossRef]
41. Wu, H.; Wang, S.; Wei, X.; Jiang, M. 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. *Trees* **2019**, *33*, 1435–1445. [CrossRef]
42. Peng, D.; Yang, L.; Yang, J.; Li, Z. Seed dormancy and soil seed bank of the two alpine *Primula* species in the Hengduan Mountains of Southwest China. *Front. Plant Sci.* **2021**, *12*, 582536. [CrossRef]
43. Zhou, R.; Yang, P.; Chen, X.; Song, M.; Sun, H.; Chen, J. Simulated climate warming strongly constrains the seedling establishment of alpine cushion *Arenaria oreophila*. *Plant Divers.* **2023**, in press. [CrossRef]