Luo *et al. Ecological Processes (2024) 13:47*
https://doi.org/10.1186/s13717-024-00526-4

Ecological Processes

RESEARCH

Open Access

Understory bamboo removal impacts on woody seedling regeneration in forest ecosystems: a meta-analysis

Weixue Luo[1,2†], Yuxuan Ma[1†], Jie Luo[1], Shunxin Han[1], Chengxiang Sun[1], Ziyi You[1], Haohan Du[1], Zongfeng Li[1,2], Jinchun Liu[1,2*] and Jianping Tao[1,2,3*]

Abstract

Background Tree seedling regeneration in forests is often hindered by the competitive influence of dense understory bamboo competition. While localized studies have investigated the ecological effects of understory bamboo removal on tree seedlings, a comprehensive analysis at a global scale is lacking. In this meta-analysis, we synthesized 497 observations from 32 experimental studies to assess the overall effects of understory bamboo removal on tree seedling regeneration.

Results The results showed that understory bamboo removal enhanced tree seedling survival, emergence, and height growth. However, the response of tree seedlings to bamboo removal varied depending on regeneration characteristics, forest types, and bamboo removal methods. Specifically, understory bamboo removal increased the survival rate of deciduous seedlings but had no significant effect on evergreen seedlings. For regeneration stages, bamboo removal had a significant positive effect on the survival rate of saplings but not on seedlings. Regarding differences across forest types, bamboo removal significantly increased the emergence density of seedlings in deciduous broadleaf forests but had a significant negative influence in evergreen and mixed evergreen-deciduous forests. Additionally, natural removal of bamboo showed a greater positive effect on seedlings than bamboo removal by artificial or animal gnawing methods. Furthermore, we found that the duration of bamboo removal, mean annual temperature, precipitation of seasonality, and soil pH strongly influenced the response ratios of tree seedling regeneration.

Conclusions Our meta-analysis demonstrates the significant effects of understory bamboo removal on multiple facets of tree seedling dynamics across different regeneration characteristics, forest types, and bamboo removal methods. In addition, our study emphasizes that the duration of bamboo removal, climate, and soil pH have a critical effect on tree seedling regeneration. Our findings elucidate the effects of understory bamboo removal on seedling regeneration, offering robust scientific insights for sustainable forest management.

Keywords Bamboo removal, Forest management, Meta-analysis, Regeneration characteristics, Tree seedling regeneration, Understory bamboo

†Weixue Luo and Yuxuan Ma Shared first authorship.

*Correspondence:
Jinchun Liu
jinchun@swu.edu.cn
Jianping Tao
taojp@swu.edu.cn
Full list of author information is available at the end of the article

© The Author(s) 2024. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

Introduction

Bamboo, a perennial flowering plant belonging to the subfamily Bambusoideae of the family Poaceae, predominantly thrives in tropical and semi-tropical habitats (Soderstrom and Calderon 1979). Its propagation relies primarily on asexual reproduction, specifically underground stems called bamboo whips, which contribute to its rapid growth, large biomass, and high litter production (Christanty et al. 1996). Previous studies have highlighted the negative effects of bamboo dominance in the understory on various aspects of forest ecosystems (Pearson et al. 1994; Itô and Hino 2004; Buziquia et al. 2019), including tree growth, tree seedling regeneration, and nutrient turnover in the understory (Taylor et al. 2004; Larpkern et al. 2011). In particular, understory bamboo has been posited as an ecological filter (Itô and Hino 2007), exerting robust competitive pressure on the emergence, establishment, and survival of tree seedlings in forests by effectively capturing light and vital resources (Takahashi et al. 2003; Doležal et al. 2009; Giordano et al. 2009; Montti et al. 2011a, b; Wijewickrama et al. 2022).

Tree regeneration plays a crucial role in forest succession, particularly during the seedling stage (Green et al. 2014; Marchin and Yuan 2023), as it directly and indirectly influences the composition, structure, and dynamics of forest communities (De Lombaerde et al. 2021). Nonetheless, the process of seedling regeneration within the forest understory is significantly influenced by the presence of dense bamboo, which alters light availability and soil nutrient dynamics (Narukawa and Yamamoto 2002; Qian et al. 2016). For instance, dense understory bamboo reduces seedling emergence by altering the microsite environment (Qian et al. 2019) and hindering the growth and establishment of tree seedlings in the forest (Itô and Hino 2007; Doležal et al. 2009). Conversely, areas without bamboo exhibit increased biomass, height, leaf count, and bud production in saplings (Marchesini et al. 2009). Consequently, effective management of dense understory bamboo is imperative to ensure the robust and sustainable development of forest communities.

However, the influence of understory bamboo on tree seedling regeneration and growth can be subject to alteration through bamboo die-off or removal. Firstly, most bamboo species exhibit a unique life history characterized by a singular reproductive event leading to massive flowering and subsequent bamboo die-off (Janzen 1976; Zheng et al. 2020), which has been shown to enhance tree seedling regeneration and growth (Montti et al. 2011a, b; Abe et al. 2005; André 2021). Secondly, understory bamboo may decline due to gnawing by wild animals (Yokoyama et al. 2000). In Japanese forests, the gnawing behavior of sika deer on dwarf bamboo promotes the survival of *Abies homolepis* seedlings (Itô and Hino 2004), and alters the emergence and growth of small coniferous seedlings (Kumar and Shibata 2007). Moreover, the artificial cutting of bamboo has a notable impact on tree seedling regeneration. Specifically, artificial bamboo harvesting can greatly enhance the survival rate of seedlings compared to uncut areas (Bitariho and McNeilage 2008; Doležal et al. 2009). In addition, the impact of bamboo removal on the understory environment is multifaceted, with direct consequences for tree seedling regeneration. Notably, bamboo removal leads to an increase in both the quantity of incident solar radiation and the red to far-red light ratio within the understory (Montti et al. 2011a, b; Giordano et al. 2009). These alterations in light availability can directly impact the photomorphogenic responses of seedlings, potentially influencing their survival and growth. Additionally, the removal of bamboo has been observed to mitigate the reduction rate of soil moisture following the rainfall events, potentially enhancing the water availability for seedling growth (Takahashi et al. 2003). Consequently, understanding how bamboo removal impacts the dynamics of tree seedlings through environmental changes is essential to formulating forest management strategies that balance ecological health and conservation objectives.

Over the past two decades, numerous single-site experimental studies have investigated the effects of bamboo removal on tree seedling regeneration, primarily in East Asia and South America (Takahashi et al. 2003; Taylor et al. 2004; Itô and Hino 2007; Giordano et al. 2009; Montti et al. 2011a, b). However, these studies are conducted across different climatic regions, influenced by diverse environmental factors and varying biomes (forest types, life form, regeneration characteristics), resulting in disparate conclusions. For instance, a study in the Patagonian mixed forest investigated the impact of bamboo die-off on tree seedling regeneration and uncovered both positive and negative effects on tree seedlings of different species within the gaps created by bamboo die-off (Caccia et al. 2015). Conversely, a study in Japan demonstrated that understory bamboo removal had a positive effect on seedling emergence (Itô and Hino 2007). Furthermore, the response of tree seedling regeneration to understory bamboo removal exhibits variability, which can be attributed to the diverse responses of different species to alterations in light and nutrient availability, particularly during the sensitive seedling stage (Hammond and Brown 1995; Ligot et al. 2014). Additionally, in contrast to the phenomenon of bamboo flowering and die-off, the underground stems of understory bamboo remain alive even after their aboveground parts are cut down or gnawed by animals. This leads to a competitive interaction between the underground bamboo stems and the roots of tree seedlings, thereby affecting the growth of tree seedlings (Mommer et al. 2016). In summary, although multiple case studies have examined the effects of bamboo removal on tree seedling regeneration (Itô and Hino 2007; Caccia et al. 2015), there is considerable variation among these studies. Furthermore, climatic conditions such as temperature and precipitation characteristics varied among study areas, particularly between Argentina, Chile, China, and Japan (Caccia et al. 2015; Itô and Hino 2007; Muñoz et al. 2012; Taylor et al. 2004). The effects of understory bamboo removal on seedling regeneration may vary among study areas depending on climatic conditions. Variations in temperature and precipitation lead to differences in seedling recruitment and height growth (Al-Hawija et al. 2015; Walbott et al. 2018). Consequently, it is crucial to synthesize and integrate the findings from these diverse studies in order to draw a comprehensive conclusion regarding the impact of understory bamboo removal on tree seedling regeneration at a global scale.

In this study, we conducted a meta-analysis to synthesize the differences observed in bamboo removal studies conducted across various climate regions and biomes. To achieve this, we performed a systematic literature search to identify studies investigating the effects of understory bamboo removal on various aspects of tree seedling regeneration, including emergence, survival, and growth in terms of height (De Lombaerde et al. 2021). We addressed the following research questions: (1) How do tree seedling regeneration processes, including emergence, survival, and growth, respond to understory bamboo removal? Our hypothesis posited that the removal of understory bamboo would benefit seedling establishment, survival, and growth of seedling by reducing competition. (2) What are the primary factors that significantly influence the effects of bamboo removal on tree seedling regeneration, and how do these key factors relate to the observed effects on seedling regeneration? We expected that regeneration characteristics, forest types, bamboo removal methods, and environmental factors (e.g., climate conditions, and soil factors) would play pivotal roles in shaping the response of seedling regeneration to bamboo removal. Moreover, we predicted that as the mean annual temperature increased, the response ratios of seedling emergence, survival, and height growth gradually decreased and eventually turn negative.

Materials and methods

Literature search

To investigate the relationship between understory bamboo removal and tree seedling regeneration, we conducted a comprehensive literature search until December 2023, using the Web of Science (https://www.webofscience.com/wos/alldb/basic-search) and the China National Knowledge Infrastructure Database (https://www.cnki.net). We employed the following keyword combinations: [(bamboo) AND (seedling* OR sapling* OR regeneration* OR recruitment*) AND (effect*)]. Our primary focus was on woody plant seedlings. Initially, we retrieved a total of 624 articles from many countries (Table A1), with each article subjected to careful screening to ensure it met our analysis criteria. These criteria were as follows: (1) involve removal methods of understory bamboo (e.g., cutting, gnawing, or flowering); (2) provide regeneration data, both with and without bamboo presence; (3) include seedlings or saplings with a height less than or equal to 100 cm; (4) report effects on seedling emergence, survival, height growth, diameter growth, or biomass growth, along with sample size and error estimates. Although we have collected numerous articles about understory bamboo die-off, being cutting or gnawing, most of them do not have data about bamboo before and after treatment. Finally, our meta-analysis incorporated a total of 32 selected articles, as detailed in Table A2. These articles collectively encompass data on six distinct regeneration indicators (Table 1), with each article contributing one or more of these indicators to our study.

Data extraction

We conducted data extraction by retrieving the means, standard deviations (SD), or standard errors (SE), along with their corresponding sample sizes, from figures using the software "GetData" or directly from the texts and tables of the original references. In cases where the SD

Table 1 Seedling regeneration indicators and calculation formulas

Regeneration indicators	Formula
Survival Rate	N_1/N_0 N_1 = seedling density at the sampling date N_0 = seedling density at the previous sampling date
Survival Density	N_1/Area N_1 = seedling density at the sampling date Area = the size of plot
Emergence Rate	E_1/S E_1 = density of new seedling S = number of living seeds
Emergence Density	E_1/Area E_1 = density of new seedling in plot Area = the size of plot
H.RGR	$\ln H_1 - \ln H_0$ H_0 = height in the previous year H_1 = current year height
H.Growth	$(H_1 - H_0)$/Time H_0 = height in the previous year H_1 = current year height Time = years of experiment

was not reported, we calculated it using SE and sample size. A total of 497 observations were extracted, mainly from South America and East Asia (Fig. 1). These observations comprised 205 survival data, 51 growth data, and 241 emergence data. Due to the limited sample size, data on diameter and biomass were not included in our analysis. The regeneration indicators encompassed emergence rate, emergence density, survival rate, survival density, height relative growth rate, and height annual growth of tree seedlings.

To assess the potential impacts of bamboo removal on tree seedling regeneration, we incorporated three key categories of potential variables (Table 2). The first category was regeneration characteristics, including the method of seedling regeneration, seedling life form, and regeneration stage (Gibert et al. 2016). The second category encompassed forest types, consisting of seven types such as coniferous, deciduous, and mixed coniferous-broadleaf forests. The third category comprised experimental factors, primarily focusing on the bamboo removal methods and duration of bamboo removal. Furthermore, we extracted relevant important environmental factors from articles, the WorldClim dataset (https://worldclim.org), and the SoilGrids database (https://soilgrids.org/) according to the geographic coordinates (latitude and longitude), including mean annual temperature (MAT), mean annual precipitation (MAP), precipitation of seasonality (Pre-season), and soil pH.

Quantifying effect size

To quantify the effect size of understory bamboo removal on tree seedling regeneration, we calculated the log response ratio (lnRR) for treatment group from each study (Hedges et al. 1999). The lnRR was calculated as follows:

$$lnRR = \log\left(\overline{X_t}/\overline{X_c}\right) \tag{1}$$

where $\overline{X_t}$ represents the mean of the seedling regeneration indicator without bamboo (cutting, gnawing, or flowering), and $\overline{X_c}$ represents the mean of the seedling regeneration indicator with bamboo.

Given the variability in data quality across studies, we evaluated data quality based on sample size and weighted the effect ratio accordingly:

$$Weighted = (n_t \times n_c)/(n_t + n_c) \tag{2}$$

where n_t is the sample size of treatment group, and n_c is the sample size of control group.

The relationship between standard deviation (SD), standard error (SE), and sample size is described as follows (Zhang et al. 2022):

$$SD = SE \times \sqrt{n} \tag{3}$$

Data analysis

To quantitatively assess the impact of bamboo removal on seedling regeneration indicators, we employed mixed-effects models, which incorporate random effects to account for non-independence in the data (Kisamore and Brannick 2008). These models were specifically chosen to allow for the exploration of heterogeneity across studies, enabling us to test the influence of potential covariates on the observed effects. The equation for our mixed-effects model is detailed as follows:

Table 2 Variables potentially influencing the effects of bamboo removal on tree seedling regeneration

Type	Sub-type	Factors
Regeneration characteristics	Regeneration methods	Natural regeneration (rege_colonization) Artificially sow (rege_seed) Artificially transplant (rege_plant)
	Life forms	Deciduous seedlings (leaf_d) Evergreen seedlings (leaf_e)
	Regeneration stage	Seedling (< 50 cm in height) Sapling (> 50 cm in height, but diameter < 10 cm)
Forest types		Evergreen forests (EF) Deciduous forests (DF) Coniferous forests (CF) Deciduous broadleaf forests (DBF) Mixed evergreen-deciduous forests (EDF_mixed) Mixed coniferous and broadleaf forests (CBF_mixed) Mixed coniferous-deciduous forests (CDF_mixed)
Experimental factors	Removal methods	Natural removal Unnatural removal
	Period	Duration of bamboo removal

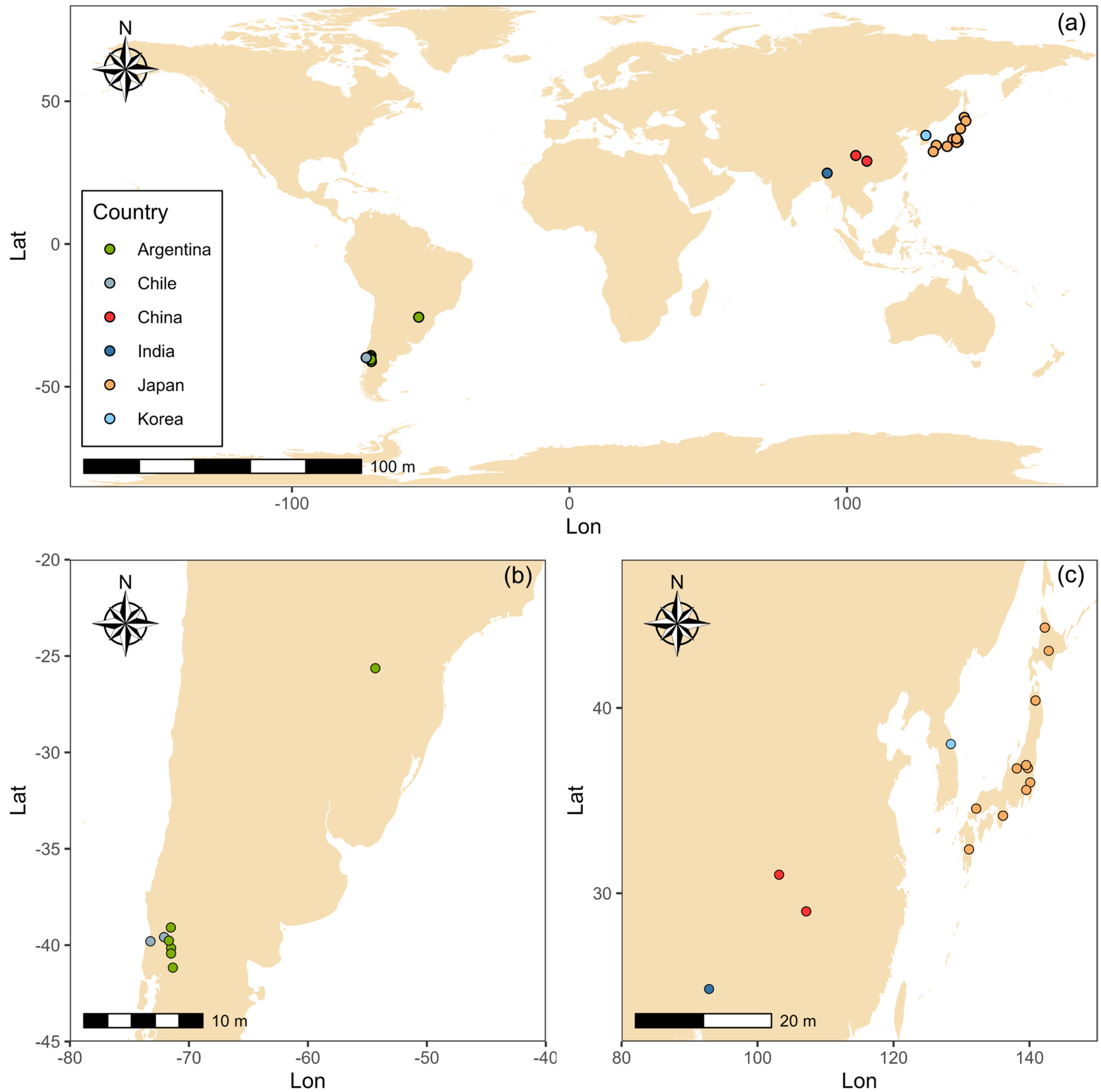

Fig. 1 Geographical distribution of the 32 studies identified through our systematic literature search. Panel **a** gives an overview of the studies on a global scale, whereas Panel **b** on the studies from South America and Panel **c** on those from East Asia

$$R_{ji} = \mu + \alpha_j + \beta \times X_{ji} + \mathcal{E}_{ji} \quad (4)$$

In this model, μ represents the fixed intercept, α_j represents the random effect for the j_{th} study, which is assumed to be normally distributed with a mean of zero and variance σ_{α}^2 (i.e., α_j ~N (0, σ_{α}^2), β is the fixed effect coefficient for the bamboo removal treatment X_{ji}, and $\mathcal{E}_{ji}$ represents the sampling error for the i_{th} observation within the j_{th} study, assumed to be normally distributed with a mean of zero and constant variance σ_{ϵ}^2.

Furthermore, we conducted subgroup analyses for categorical variables (regeneration characteristics, forest types, and bamboo removal methods), to estimate their mean effect sizes and to assess the significant differences among subgroups in the impact of understory bamboo removal on seedling regeneration indicators (seedling emergence, growth, and survival).

To determine the influence of covariates on the effect of bamboo removal, we performed model selection analysis using Akaike's information criterion (AIC) with the 'MuMIn' package in R (Bartoń 2018). For each possible model, we calculated the AICc values (corrected for small sample sizes), ΔAICc (difference in AICc compared to the top-ranked model), and Akaike weights (probability that a model is the best possible model). The relative contribution for a particular covariate was then calculated as the sum of Akaike weights (*W*) derived for all the models through model averaging (Anderson 2008). A threshold *W* value of 0.8 was set to distinguish important and non-important covariates (Terrer et al. 2016; Chen et al. 2020a, b). The relationship between the sum of Akaike weight (*W*) and ΔAIC is described as follows (Si et al. 2014):

$$W = \frac{e^{(-\frac{1}{2}\Delta AIC_i)}}{\sum e^{(-\frac{1}{2}\Delta AIC_i)}} \quad (5)$$

where $\Delta AIC_i = AIC_i - AIC_{min}$, AIC_i is the AIC value for model *i*, and AIC_{min} is minimum AIC value in the model set.

Additionally, a linear regression model was constructed to explore the relationship between the regeneration response ratio and covariates, including mean annual temperature (MAT), precipitation of seasonality (Pre-season), soil pH and duration of bamboo removal (period). The mixed-effect model was implemented using the R package 'lme4', and the linear regression was performed using the R package 'stats' (Collyer and Adams 2018), with a significance level set at $p < 0.05$. All figures were generated using the R packages 'ggplot2' and 'ggpmisc'.

Results

Overall effects of understory bamboo removal on tree seedling regeneration

The removal of understory bamboo had a positive effect on the survival, emergence, and growth of tree seedlings (Fig. 2). The highest increase was observed in the survival rate (mean: 1.399, 95% CI: 0.960–1.839), followed by survival density (mean: 0.565, 95% CI: 0.050–1.080), emergence rate (mean: 0.678, 95% CI: 0.175–1.181), emergence density (mean: 0.736, 95% CI: 0.175–1.298), annual height growth (H.Growth, mean: 0.693, 95% CI: 0.112–1.273), and relative growth rate of height (H.RGR, mean: 0.478, 95% CI: 0.215–0.742), all showing significant average increases.

The impacts of regeneration characteristics, forest types, and removal methods on tree seedling regeneration

To further clarify the response of seedling emergence, growth, and survival to bamboo removal under different conditions, we performed subgroup analysis. We observed significant disparities in seedling responses to understory bamboo removal across various regeneration characteristics (seedling life forms, regeneration stages, and regeneration methods). Specifically, we found that understory bamboo removal had a significant positive effect on the annual height growth of both deciduous and evergreen seedlings (Fig. 3B). Furthermore, understory bamboo removal led to an increase in the survival rate of deciduous seedlings (leaf_d), while no significant effect on survival rate of evergreen seedlings (leaf_e) was observed (Fig. 3C). In terms of regeneration stages (e.g., saplings and seedlings), bamboo removal increased the survival rate of saplings but not seedlings (Fig. 3C). Conversely, bamboo removal improved the annual height growth of seedlings but not saplings (Fig. 3B). In addition, we found that understory bamboo removal had a positive effect on emergence density under natural removal conditions, but it had no effect under unnatural removal conditions (Fig. 3A).

Furthermore, our results demonstrated that the response of tree seedling regeneration differs (Fig. 3). In terms of emergence density, bamboo removal increased seedling density in deciduous broadleaf forest (DBF), while it had a significant negative influence in evergreen forest (EF) and mixed evergreen-deciduous forest (EDF_mixed), with no significant effect observed in other forest types (Fig. 3A). Additionally, the survival rate exhibited a significant positive effect in deciduous forest (DF) and mixed coniferous broad-leaved forest (CBF_mixed), while a negative effect was observed in evergreen broad-leaved forest (EBF) (Fig. 3C).

Moreover, we found that the effect of unnatural removal group on emergence density was significantly positive, while no significant effect was observed in natural removal group (Fig. 3A). Furthermore, the natural removal method had a significant and positive effect on the annual height growth of tree seedlings, whereas the unnatural removal group exhibited the opposite trend (Fig. 3B). Bamboo removal had a positive effect on the survival rate under both natural and unnatural removal, with the effect being stronger in the natural removal group (Fig. 3C).

Relative importance covariates on tree seedling regenerations

Model-averaged relative importance of covariates regulating the effects of bamboo removal on tree seedling regenerations (Fig. 4). Specifically, we found the effects

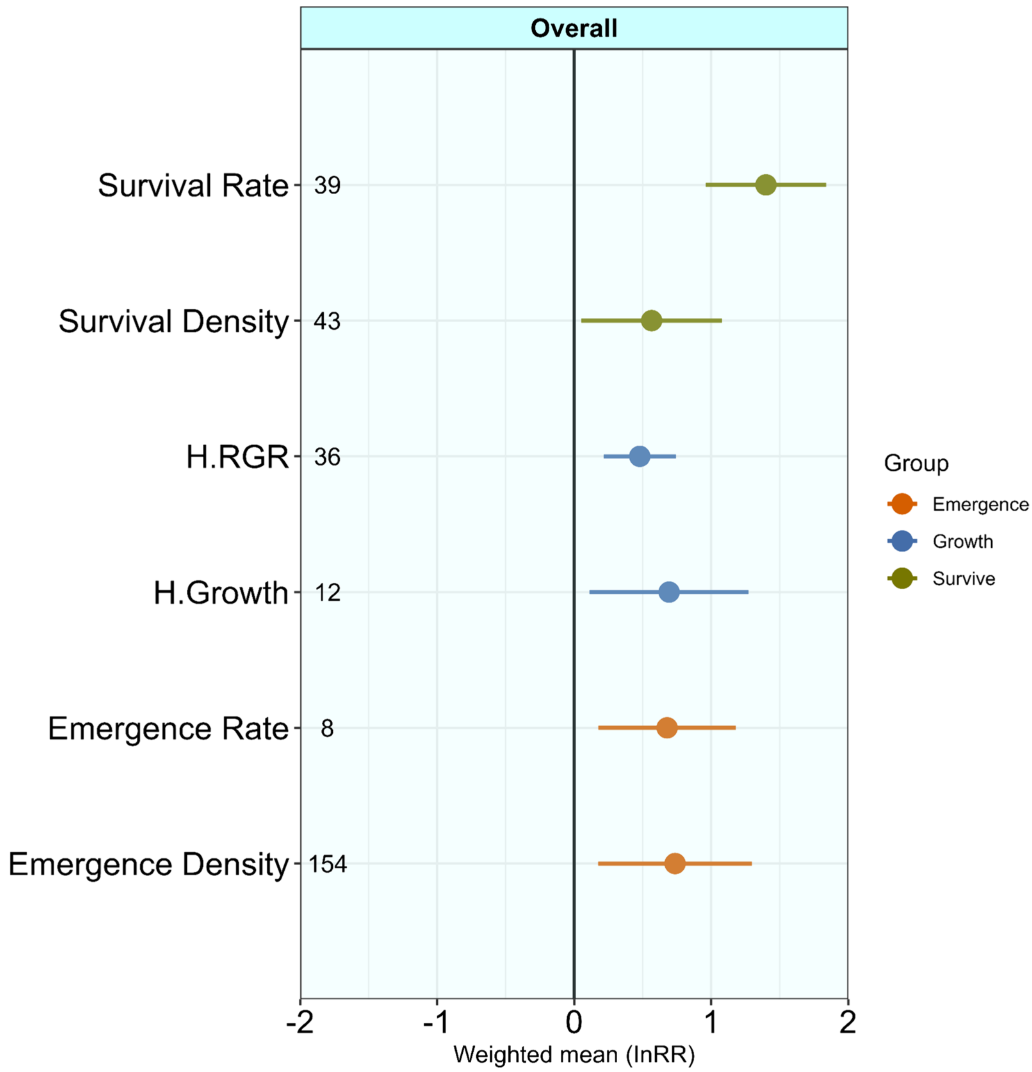

Fig. 2 Forest plot showing the mean weighted response ratios of bamboo removal on seedlings regeneration indicators. The horizontal lines on either side of the point represent 95% confidence intervals. Numbers on the left side are the observation sample size of each indicator. The black line in the middle indicates no effect. H.RGR: the relative growth rate of height. H.Growth: annual growth in height

of bamboo removal were mainly explained by changes in seedling emergency density across different soil pH (Sum of Akaike weights = 0.98), forest types (Sum of Akaike weights = 0.98), mean annual temperature (MAT, Sum of Akaike weights = 0.98), duration of bamboo removal (Period, Sum of Akaike weights = 0.92), bamboo removal method (Sum of Akaike weights = 0.85), and mean annual precipitation (MAP, Sum of Akaike weights = 0.81) (Fig. 4A). Moreover, for annual height growth, life forms (Sum of Akaike weights = 0.4) and bamboo removal methods (Sum of Akaike weights = 0.4) were identified as the primary factors, although their sum of Akaike weights did not exceed 0.8 (Fig. 4B). Furthermore, the analysis showed that the regeneration methods (Sum of Akaike weights = 0.95) and forest types (Sum of Akaike weights = 1.0) played crucial roles in explaining the effects of bamboo removal on survival density and survival rate, respectively (Fig. 4D, E).

Effects of period and environmental factors on tree seedling regeneration

Our results showed the influence of mean annual temperature (MAT), precipitation of seasonality (Pre-season), soil pH, and duration of bamboo removal (Period) on the natural logarithm of the response ratios (lnRR) of tree seedling regenerations (Table 3 and Figs. 5, 6). Specifically, the lnRR for emergence density (lnRR.ed) was negatively correlated with MAT and positively correlated

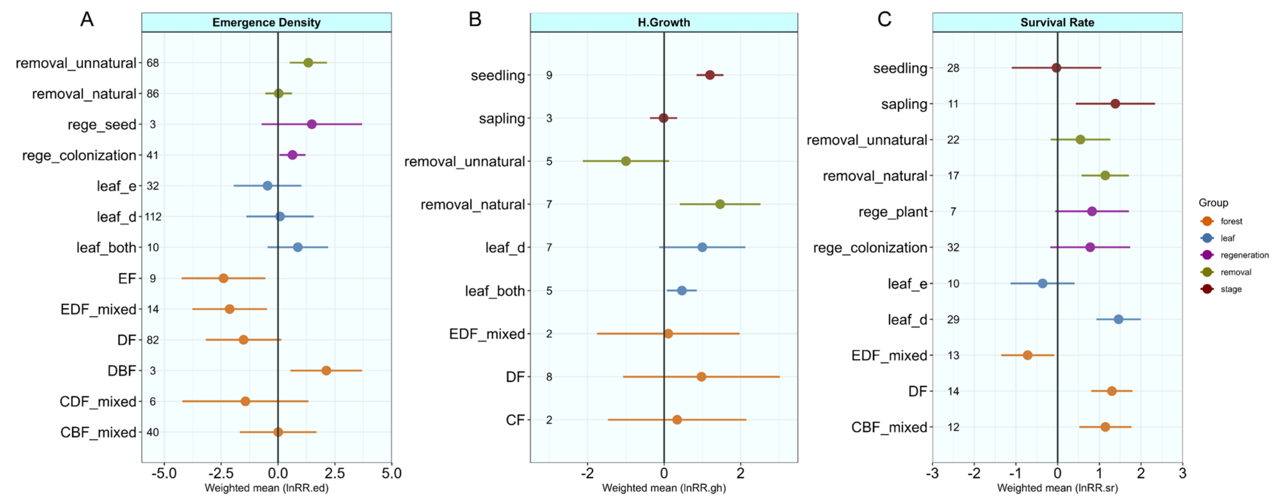

Fig. 3 Effects of bamboo removal on seedling emergence density (**A**), height growth (**B**), and survival rate (**C**) in different conditions. The horizontal lines on either side of the point represent 95% confidence intervals. Text on the left side is the sample size of each covariate. The black line in the middle indicates no effect. H.Growth: annual growth in height; rege_plant: artificially transplanted; rege_colonization: natural regeneration; rege_seed: artificially sow; leaf_e: evergreen seedling; leaf_d: deciduous seedling; leaf_both: both evergreen and deciduous seedlings; EF: evergreen forest; DF: deciduous forest; CF: coniferous forest; DBF: deciduous broadleaf forest; EDF_mixed: mixed evergreen-deciduous forest; CBF_mixed: mixed coniferous and broadleaf forest; CDF_mixed: mixed coniferous-deciduous forest

with soil pH (Table 3 and Fig. 5). In addition, the lnRR for height growth (lnRR.gh) showed a significant decline with both Per-season and soil pH, contrasting with a positive correlation with period (Table 3 and Fig. 5). Moreover, the lnRR for survival rate (lnRR.sr) was negatively correlated with MAT, showing no significant response to Pre-season and soil pH (Table 3 and Fig. 6).

Discussion

Understanding the impacts of understory bamboo removal on tree seedling regeneration in forests is crucial. In this study, we conducted a comprehensive meta-analysis of literature primarily sourced from Asia and South America. Specifically, we investigated the response of tree seedling regeneration to understory bamboo removal across various regeneration characteristics, forest types, bamboo removal methods, bamboo removal durations, and environmental factors. Our findings shed light on the importance and effects of understory bamboo removal on bamboo forest management.

Positive effects of bamboo removal on tree seedlings' emergence, survival, and growth

Our findings revealed that understory bamboo removal improved tree regeneration, likely attributed to the alleviation of competition for light, water, and nutrient resources between seedlings and bamboo, which is consistent with previous studies (Abe et al. 2002; González et al. 2002; Giordano et al. 2009; Montti et al. 2011a, b). The alteration of the microsite environment in the understory after bamboo removal affects tree seedling regeneration (Marchesini et al. 2009; Montti et al. 2011a, b). Specifically, the removal of understory bamboo would create a favorable environment for seedling height growth by alleviating resource competition, particularly for light (Gratzer et al. 1999; Colleta et al. 2001). Additionally, understory bamboo removal enhances tree seedling emergence by increasing understory openness and reducing leaf litter cover, which are likely the main factors promoting this process (Nakagawa et al. 2023; Sayer 2006). Moreover, fluctuations in soil temperature resulting from understory bamboo removal also play a role in facilitating the emergence of pioneer seedling species (Abe et al. 2002). Our findings align with the previous experiments demonstrating that understory bamboo removal promotes seedling survival (Larpkern et al. 2011).

Effects of regeneration characteristics, forest types, and removal methods on tree seedling regeneration

Our analysis indicated significant variations in seedling responses to understory bamboo removal across various regeneration characteristics (seedling life forms, regeneration stages, and regeneration methods), forest types, and removal methods. Regarding life forms, our findings revealed that the removal of understory bamboo had no effect on the survival rate of evergreen seedlings but showed a positive effect on deciduous seedlings. This effect on deciduous species may be attributed to their shade-tolerance and their ability to regenerate

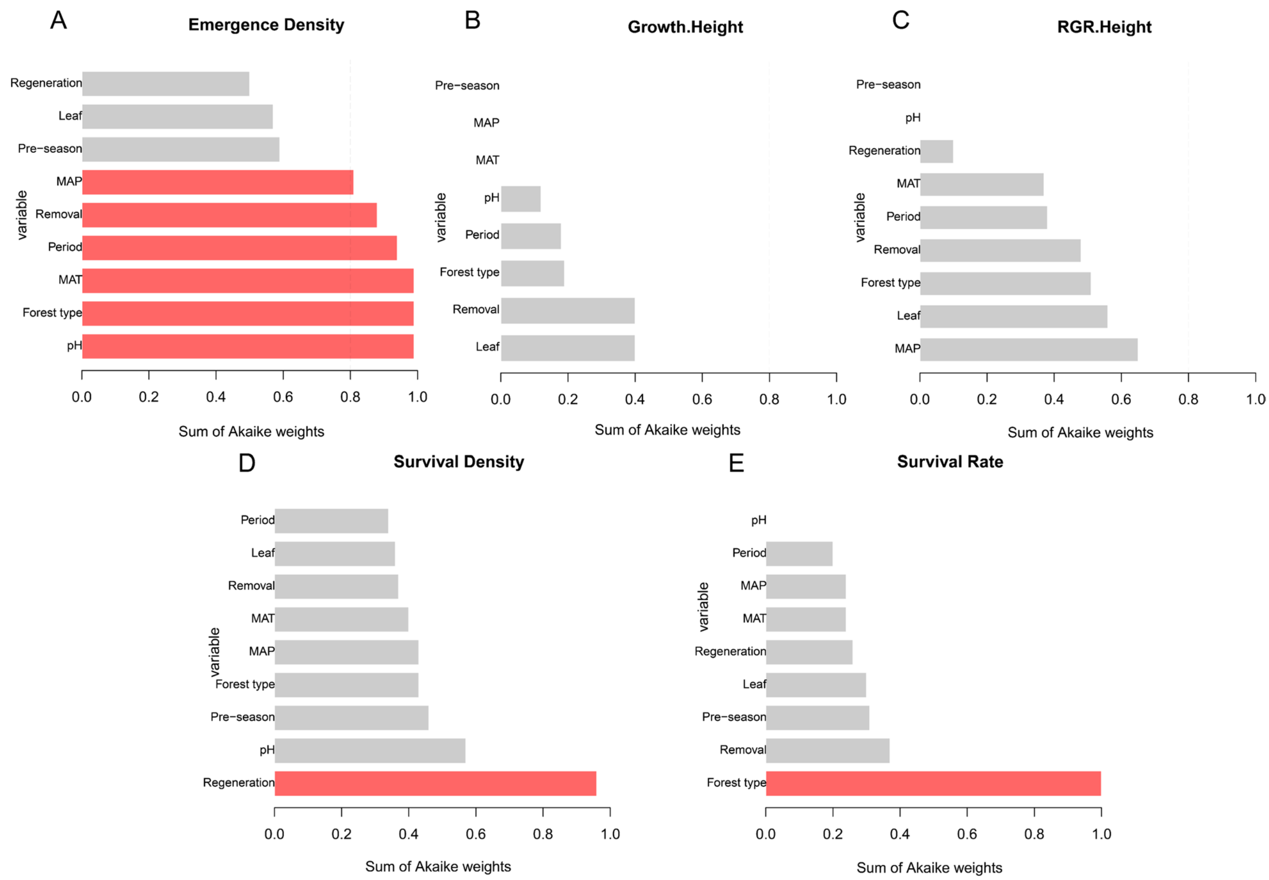

Fig. 4 The relative importance of covariates was assessed in their influence on various responses to bamboo removal, including seedling emergence density (**A**), height growth (**B**), relative growth rate of height (**C**), survival density (**D**), and survival rate (**E**). The variables include forest types, environmental factors (e.g., MAT and MAP), regeneration characteristics (e.g., life form and regeneration method), and experimental factors (e.g., method and duration of bamboo removal). The cutoff was set to 0.8 to differentiate between important and nonessential variables. Leaf: life form; Regeneration: regeneration method; Removal: removal method; Period: duration of bamboo removal; MAT: mean annual temperature; MAP: mean annual precipitation; Pre-season: precipitation of seasonality

Table 3 Parameters of linear regression of environmental factors and period with the natural logarithm of the response ratios (lnRR) for seedling regeneration indicators

Response ratio	MAT		Pre-season		pH		Period	
	k	*p*-value	*k*	*p*-value	*k*	*p*-value	*k*	*p*-value
lnRR.ed	− 0.152	0.004**	− 0.014	0.088	0.968	< 0.001***	0.147	0.097
lnRR.gh	− 0.232	0.341	− 0.063	0.049*	− 1.59	0.043*	0.231	0.033*
lnRR.sr	− 0.626	0.028*	− 0.011	0.325	0.413	0.567	− 0.186	0.379

MAT mean annual temperature, *Pre-season* precipitation of seasonality, *pH* soil pH, *Period* duration of bamboo removal. k: slope of the regression equation. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

aggressively in gaps, as they are typically shade-intolerant or intermediate (Zhu et al. 2014). For instance, a recent study conducted in secondary forests in northern China showed that the abundance and density of shade-intolerant species were higher than that of shade-tolerant species in forest gaps during natural regeneration (Lu et al. 2019). Conversely, evergreen species exhibit a more conservative resource-use strategy, resulting in less variability in their growth and survival across different habitats (Reich 1998; Jin et al. 2017). Moreover, deciduous seedlings exhibit greater morphological and physiological plasticity, enabling them to benefit more from bright light conditions compared to evergreen species (Ke and Werger 1999). These findings align with previous studies,

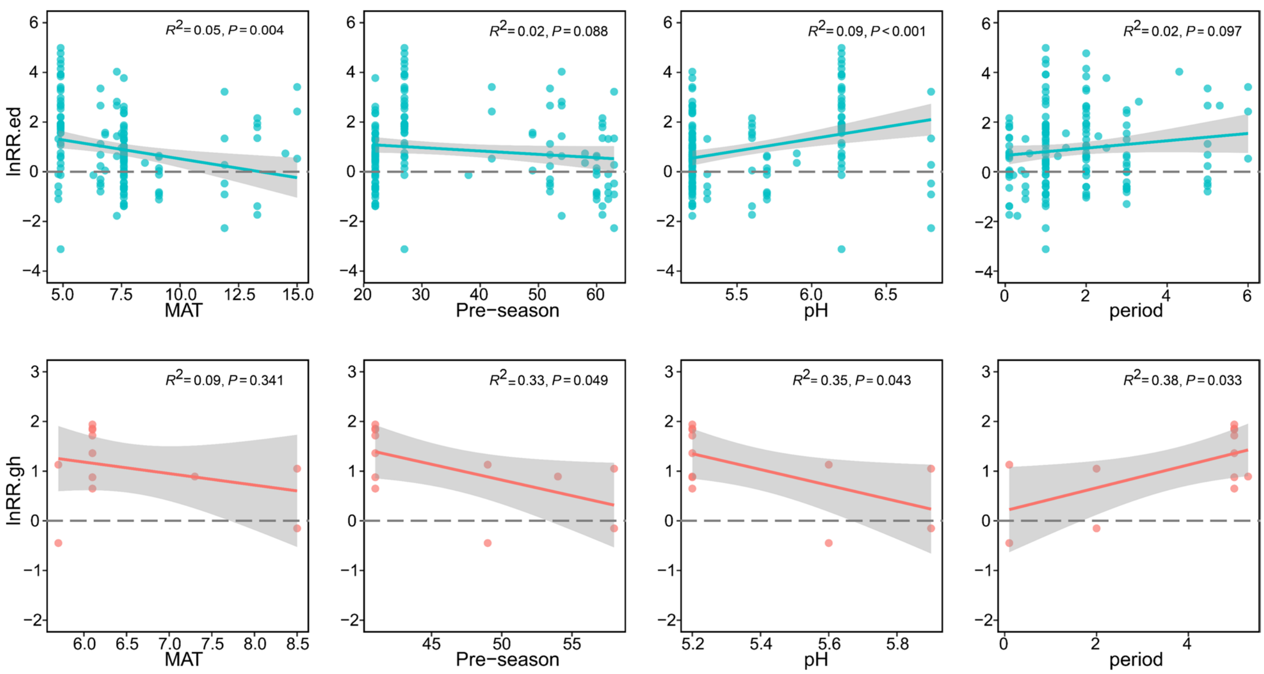

Fig. 5 Regression models of emergence density and annual height growth response ratio to key drivers. MAT: mean annual temperature; Pre-season: precipitation of seasonality; pH: soil pH; Period: duration of bamboo removal

suggesting that shade-tolerant species have limited sensitivity to strong light environment (Yoshida and Kamitani 2000; Lin et al. 2002). However, there was no significant difference in emergence density among different life forms. Studies have shown that seedling emergence is more influenced by soil conditions than life form (Iijima et al. 2007), especially soil temperature (Qian et al. 2019).

In addition, our findings revealed distinct responses among seedlings at different regeneration stages to understory bamboo removal. Specifically, we observed that understory bamboo removal increased the survival rate of saplings but had no effect on the seedling survival rate. We speculated that although the increased light conditions following understory bamboo removal enhanced seedling survival, for small individuals, the removal of large amounts of bamboo from the understory increases their vulnerability to herbivores, thereby offsetting the positive effects and potentially leading to negative outcomes (Nakashizuka 2001; Lusk 2004). However, we did not find a significant effect of understory bamboo removal on sapling height growth, but a significantly positive effect on height growth of seedlings. Height growth appears to be encouraged by bamboo removal only at a very early growth stage (Sumida et al. 1997).

Furthermore, previous studies have demonstrated notable variations in understory light conditions across various forest types (Kabakoff and Chazdon 1996; Van Der Meer et al. 1998; Montgomery and Chazdon 2001). Our study showed that bamboo removal promotes survival rates in deciduous forests and mixed coniferous-broad leaved forests, but inhibits survival in mixed evergreen-deciduous forests. This discrepancy can be attributed to the higher light availability in the former two forest types during the deciduous stages, which potentially enables more seedlings to survive (Tanouchi 1996; Zhou et al. 2020). Interestingly, our findings indicated negative responses in emergence density to bamboo removal in evergreen forests, mixed evergreen-deciduous forests, and deciduous forests, aligning with previous studies (Abe et al. 2002; González et al. 2002; Holz and Veblen 2006; Muñoz et al. 2012). A previous case study found that the emergence of *Aucuba japonica*, *Cercidiphyllum japonicum*, and *Sorbus commixta* was negatively affected by the removal of bamboo (Abe et al. 2002). However, another separate experiment in Chile has demonstrated that the establishment of *Araucaria araucana*, *Nothofagus dombeyi* and *Laureliopsis philippiana* understory was not promoted by bamboo removal (Muñoz et al. 2012). Additionally, a recent study has demonstrated that a strong and positive relationship between microsite light availability and seedling height and diameter (Sangsupan et al. 2021). However, our findings showed that forest type has no significant effect on annual height growth. We suspected that the increase in light resulting from understory bamboo removal in these forest types is not sufficient to significantly affect the

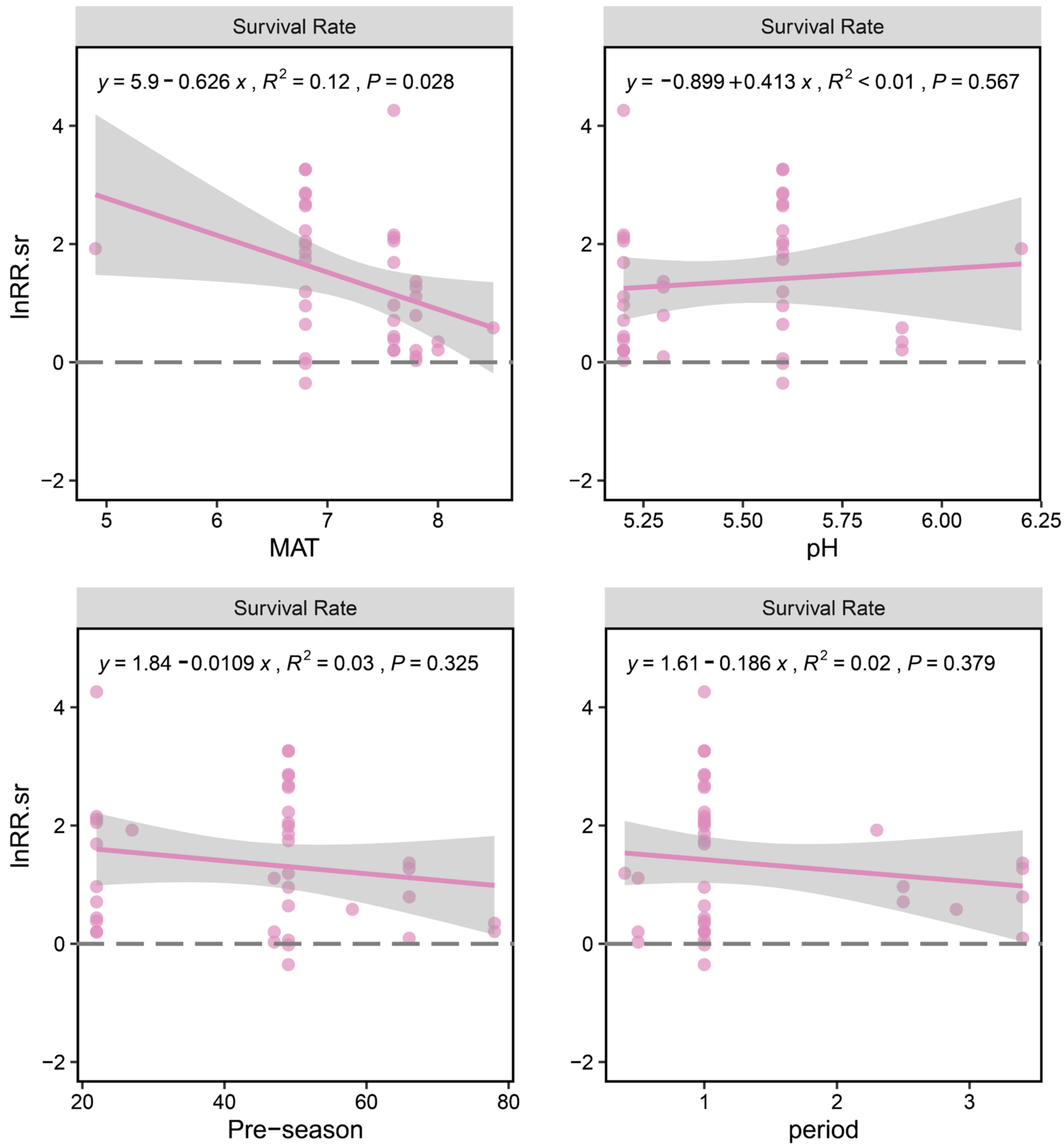

Fig. 6 Regression models of survival rate to drivers. MAT: mean annual temperature; Pre-season: precipitation of seasonality; pH: soil pH; Period: duration of bamboo removal

height growth of seedlings compared to the original light intensity (Liu et al. 2018).

Additionally, our findings showed that natural removal significantly enhanced the survival and height growth of seedlings, whereas unnatural removal had no such effect. Compared with natural removal, unnatural removal (artificial cutting and animal gnawing) bamboo will leave the underground parts (bamboo whips) and sometimes aboveground parts (Qian et al. 2019), which will compete with understory seedlings for resources, affecting their survival and growth of seedlings (Narukawa and Yamamoto 2002; Tripathi et al. 2005). Interestingly, natural removal had no impact on seedling emergence density, while unnatural removal significantly promoted it. The thick litter layer produced after bamboo flowering is a hindrance to seedling emergence (Cavieres and Arroyo 2000; Hastwell and Facelli 2000; Larpkern et al. 2011), and there is no litter production in unnatural removal.

Factors influencing the effect of bamboo removal

Seedling establishment and survival, representing the most climate-sensitive phase of tree development, are influenced by various environmental factors (Petrie et al. 2016; Bailey et al. 2021). Among these factors, temperature emerged as a crucial determinant. Notably, the effect of bamboo removal on emergence density and height growth shifted to negative when the mean annual temperature exceeds 12 °C. Our findings indicated that the removal of understory bamboo results in the creation of gaps and an increase in light intensity, which in turn can cause a rise in temperature (Giordano et al. 2009; Caccia et al. 2015). This can lead to elevated temperatures and reduced soil moisture content (Marchesini et al. 2009), particularly in areas with high mean annual temperatures, thereby impacting the growth of seedlings. In addition, the successful emergence of seedlings often requires low temperatures to break dormancy, making areas with lower average annual temperatures more favorable for seedling emergence (Junttila 1973; Chen et al. 2020a, b; Song et al. 2023). Moreover, water availability is another critical factor for seedling regeneration (Delerue et al. 2015; Verhoeven et al. 2018). The coefficient of variation of precipitation seasonality (Pre-season) reflects the extent of seasonal fluctuation in precipitation. High precipitation seasonality means heavy precipitation concentrates on multiple months (Liu et al. 2021). We observed that areas with more stable precipitation patterns were more conducive to seedling establishment and growth. This suggests that the greater the value of precipitation seasonality (Pre-season), the greater the possibility and frequency of drought and flooding events in the area, which are detrimental to seedling growth and survival (Galiano et al. 2013; Maxwell et al. 2016).

In addition, the chemical properties of the soil, which serves as the substrate for seedling regeneration, play a crucial role in the regeneration process (Martini et al. 2020; Puhlick et al. 2021). We observed a negative correlation between the response ratio of seedling height growth and soil pH. Forest soils in many regions are acidic (Gilliam 1991; Valentin et al. 2018), and the species living in them have adapted to acidic soil. Therefore, acidic soil is more suitable for survival and growth than neutral soil for seedlings of these species.

Moreover, the effects of understory bamboo removal on emergence density and annual height growth were found to be strengthened as the bamboo removal period increased. This delayed response can be attributed to the necessary time for the understory environment to adapt, primarily due to the slow decomposition of bamboo litter, leading to a prolonged release of nutrient resources that support seedling growth (Singh and Singh 1999; Marchesini et al. 2009). Over time, more nutrient resources are released for seedling growth. However, we found that long treatment times had a negative impact on seedling survival. We speculated that with a longer interval between bamboo removal and the start of the experiment, new bamboo seedlings may emerge in the bamboo flowering areas, influencing seedling survival of other species in the understory (Marchesini et al. 2009; Montti et al. 2011a, b; Montti et al. 2011a, b). These findings underscore the complexity of the interactions between understory bamboo removal and seedling responses, emphasizing the importance of considering environmental factors and temporal dynamics in bamboo forest management and conservation efforts.

While our study provides valuable insights into the impacts of bamboo removal on tree seedling regeneration across varying conditions, it is essential to acknowledge several limitations. Our dataset predominantly originates from East Asia and South America, potentially limiting the generalizability of our findings to other regions. In addition, due to constraints in sample size, we were unable to collect environmental data after bamboo removal, hindering our ability to elucidate direct influences on seedling regeneration dynamics. Moreover, while our study focused on tree seedling regeneration, the regeneration of herb and shrub communities after bamboo removal remains unclear. Therefore, future research should focus on extensive data collection across diverse ecosystems and environmental conditions to enhance our understanding of forest regeneration dynamics.

Conclusions

Our meta-analysis demonstrates the significant positive effects of understory bamboo removal on multiple facets of tree seedling dynamics, encompassing survival rate, density, emergence characteristics, and height growth indices. Notably, the influence of bamboo removal on tree seedling regeneration varied greatly across different regeneration characteristics, forest types, and bamboo removal methods. Furthermore, the duration of bamboo removal, mean annual temperature, precipitation of seasonality, and soil pH exerted strong impacts on the response ratios of tree seedling regeneration. These findings not only enhance our understanding of the ecological implications of bamboo removal across diverse forest ecosystems, but also provide valuable insights for seedling management and conservation of post-clearance.

Abbreviations

H.RGR	The relative growth rate of height
H.Growth	Annual growth in height
rege_plant	Artificially transplanted
rege_colonization	Natural regeneration
rege_seed	Artificially sow
leaf_e	Evergreen seedling
leaf_d	Deciduous seedling

leaf_both	Both evergreen and deciduous seedlings
EF	Evergreen forest
DF	Deciduous forest
CF	Coniferous forest
DBF	Deciduous broadleaf forest
EDF_mixed	Mixed evergreen-deciduous forest
CBF_mixed	Mixed coniferous and broadleaf forest
CDF_mixed	Mixed coniferous-deciduous forest
Leaf	Life form
Regeneration	Regeneration method
Removal	Removal method
Period	Duration of bamboo removal
MAT	Mean annual temperature
MAP	Mean annual precipitation
Pre-season	Precipitation of seasonality.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-024-00526-4.

Supplementary Material 1.

Acknowledgements
We like to thank authors who kindly provided the data for meta-analysis. We would like to thank all the students who participated in the data collection.

Author contributions
All authors conceived the ideas of study. LWX provided the methodology, analyzed the data and revised the manuscript. MYX collected and analyzed data, wrote the manuscript. LJ analyzed data and revised the manuscript. HSX, SCX, YZY, DHH and LZF proposed revisions to the manuscript. LJC supervised the completion of the manuscript and provided valuable revisions. TJP conceptualized the article and provided valuable revisions to the manuscript. All the authors reviewed and approved the manuscript.

Funding
This research was supported by the National Natural Science Foundation of China (grant number 32171766) and the Fundamental Research Funds for the Central Universities (grant number SWU-KQ22009).

Availability of data and materials
The datasets analyzed during the current study are available in the Figshare Dataset. https://doi.org/https://doi.org/10.6084/m9.figshare.23708337.v1.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1]Key Laboratory of Eco-Environments in Three Gorges Reservoir Region (Ministry of Education), Chongqing Key Laboratory of Plant Ecology and Resources Research in Three Gorges Reservoir Region, School of Life Sciences, Southwest University, Chongqing, China. [2]Chongqing Jinfo Mountain Karst Ecosystem National Observation and Research Station, Southwest University, Chongqing, China. [3]Present Address: Southwest University, No. 2 Tiansheng Road, Beibei District, Chongqing 400715, China.

Received: 27 January 2024 Accepted: 29 May 2024
Published: 7 June 2024

References

Abe M, Izaki J, Miguchi H, Masaki T, Makita A, Nakashizuka T (2002) The effects of *Sasa* and canopy gap formation on tree regeneration in an old beech forest. J Veg Sci 13:565–574. https://doi.org/10.1111/j.1654-1103.2002.tb02083.x

Abe M, Miguchi H, Honda A, Makita A, Nakashizuka T (2005) Short-term changes affecting regeneration of *Fagus crenata* after the simultaneous death of *Sasa kurilensis*. J Veg Sci 16:49–56. https://doi.org/10.1111/j.1654-1103.2005.tb02337.x

Al-Hawija BN, Lachmuth S, Welk E, Hensen I (2015) Seedling performance of cupressus sempervirens. Plant Species Biol 30:257–271. https://doi.org/10.1111/1442-1984.12060

Anderson DR (2008) Model based inference in the life sciences: a primer on evidence. Springer, New York, NY. https://doi.org/10.1007/978-0-387-74075-1

Bailey SN, Elliott GP, Schliep EM (2021) Seasonal temperature–moisture interactions limit seedling establishment at upper treeline in the Southern Rockies. Ecosphere 12(6):e03568. https://doi.org/10.1002/ecs2.3568

Bartón K (2018) MuMIn: multi-model inference. R Package Cran-R 1:289–290

Bitariho R, McNeilage A (2008) Population structure of montane bamboo and causes of its decline in Echuya Central Forest Reserve, South West Uganda. Afr J Ecol 46:325–332. https://doi.org/10.1111/j.1365-2028.2007.00840.x

Buziquia ST, Lopes PVF, Almeida AK, Almeida IK (2019) Impacts of bamboo spreading: a review. Biodivers Conserv 28:3695–3711. https://doi.org/10.1007/s10531-019-01875-9

Caccia FD, Kitzberger T, Chaneton EJ (2015) Episodic bamboo die-off, neighbourhood interactions and tree seedling performance in a Patagonian mixed forest. J Ecol 103:231–242. https://doi.org/10.1111/1365-2745.12349

Cavieres LA, Arroyo MTK (2000) Seed germination response to cold stratification period and thermal regime in *Phacelia secunda* (Hydrophyllaceae). Plant Ecol 149(1):1–8. https://doi.org/10.1023/A:1009802806674

Chen DL, Luo XP, Yuan Z, Bai MJ, Hu XW (2020a) Seed dormancy release of *Halenia elliptica* in response to stratification temperature, duration and soil moisture content. BMC Plant Biol 20:352. https://doi.org/10.1186/s12870-020-02560-8

Chen J, Elsgaard L, Groenigen KJ, Olesen JE, Liang Z, Jiang Y, Lærke PE, Zhang Y, Luo Y, Hungate BA, Sinsabaugh RL, Jørgensen U (2020b) Soil carbon loss with warming: new evidence from carbon-degrading enzymes. Global Change Biol 26:1944–1952. https://doi.org/10.1111/gcb.14986

Christanty L, Mailly D, Kimmins JP (1996) "Without bamboo, the land dies": biomass, litterfall, and soil organic matter dynamics of a Javanese bamboo talun-kebun system. For Ecol Manag 87:75–88. https://doi.org/10.1016/S0378-1127(96)03834-0

Colleta C, Lantera O, Pardosb M (2001) Effects of canopy opening on height and diameter growth in naturally regenerated beech seedlings. Ann Forest Sci 58:127–134. https://doi.org/10.1051/forest:2001112

Collyer ML, Adams DC (2018) RRPP: an R package for fitting linear models to high-dimensional data using residual randomization. Methods Ecol Evol 9:1772–1779. https://doi.org/10.1111/2041-210X.13029

De Lombaerde E, Baeten L, Verheyen K, Perring MP, Ma S, Landuyt D (2021) Understorey removal effects on tree regeneration in temperate forests: a meta-analysis. J Appl Ecol 58:9–20. https://doi.org/10.1111/1365-2664.13792

Delerue F, Gonzalez M, Michalet R, Pellerin S, Augusto L (2015) Weak evidence of regeneration habitat but strong evidence of regeneration niche for a leguminous shrub. PLoS ONE 10:e0130886. https://doi.org/10.1371/journal.pone.0130886

Doležal J, Matsuki S, Hara T (2009) Effects of dwarf-bamboo understory on tree seedling emergence and survival in a mixed-oak forest in northern Japan: a multi-site experimental study. Community Ecol 10:225–235. https://doi.org/10.1556/ComEc.10.2009.2.13

Galiano L, Martínez-Vilalta J, Eugenio M, Granzow-de La Cerda Í, Lloret F (2013) Seedling emergence and growth of *Quercus* spp. following severe

drought effects on a *Pinus sylvestris* canopy. J Veg Sci 24:580–588. https://doi.org/10.1111/j.1654-1103.2012.01485.x
Gibert A, Gray EF, Westoby M, Wright IJ, Falster DS (2016) On the link between functional traits and growth rate: meta-analysis shows effects change with plant size, as predicted. J Ecol 104:1488–1503. https://doi.org/10.1111/1365-2745.12594
Gilliam FS (1991) Ecosystem-level significance of acid forest soils. In: Wright, RJ, Baligar VC, Murrmann RP (eds) Plant-soil interactions at low pH, pp 187–195
Giordano CV, Sánchez R, Austin AT (2009) Gregarious bamboo flowering opens a window of opportunity for regeneration in a temperate forest of Patagonia. New Phytol 181:880–889. https://doi.org/10.1111/j.1469-8137.2008.02708.x
Gonzále ME, Veblen TT, Donoso C, Valeria L (2002) Tree regeneration responses in a lowland *Nothofagus*-dominated forest after bamboo dieback in South-Central Chile. Plant Ecol 161:59–73. https://doi.org/10.1023/A:1020378822847
Gratzer G, Rai PB, Glatzel G (1999) The influence of the bamboo *Yushania microphylla* on regeneration of *Abies densa* in central Bhutan. Can J For Res 29:1518–1527. https://doi.org/10.1139/x99-125
Green PT, Harms KE, Connell JH (2014) Nonrandom, diversifying processes are disproportionately strong in the smallest size classes of a tropical forest. Proc Natl Acad Sci USA 111(52):18649–18654. https://doi.org/10.1073/pnas.1321892112
Hammond DS, Brown VK (1995) Seed size of woody plants in relation to disturbance, dispersal, soil type in wet neotropical forests. Ecology 76:2544–2561. https://doi.org/10.2307/2265827
Hastwell GT, Facell JM (2000) Effects of leaf litter on woody seedlings in xeric successional communities. Plant Ecol 148:225–231. https://doi.org/10.1023/A:1009834425538
Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156. https://doi.org/10.2307/177062
Holz CA, Veblen TT (2006) Tree regeneration responses to *Chusquea montana* bamboo die-off in a subalpine *Nothofagus* forest in the southern Andes. J Veg Sci 17:19–28. https://doi.org/10.1111/j.1654-1103.2006.tb02419.x
Iijima H, Shibuya M, Saito H (2007) Effects of surface and light conditions of fallen logs on the emergence and survival of coniferous seedlings and saplings. J Forest Res 12:262–269. https://doi.org/10.1007/s10310-007-0012-1
Itô H, Hino T (2004) Effects of deer, mice and dwarf bamboo on the emergence, survival and growth of *Abies homolepis* (Piceaceae) seedlings. Ecol Res 19:217–223. https://doi.org/10.1111/j.1440-1703.2004.00626.x
Itô H, Hino T (2007) Dwarf bamboo as an ecological filter for forest regeneration. Ecol Res 22:706–711. https://doi.org/10.1007/s11284-006-0066-0
Janzen DH (1976) Why bamboos wait so long to flower. Annu Rev Ecol Syst 7:347–391. https://doi.org/10.1146/annurev.es.07.110176.002023
Jin Y, Russo SE, Yu M (2017) Effects of light and topography on regeneration and coexistence of evergreen and deciduous tree species in a Chinese subtropical forest. J Ecol 106:1634–1645. https://doi.org/10.1111/1365-2745.12911
Junttila O (1973) The mechanism of low temperature dormancy in mature seeds of syringa species. Physiol Plantarum 29:256–263. https://doi.org/10.1111/j.1399-3054.1973.tb03102.x
Kabakoff RP, Chazdon RL (1996) Effects of canopy species dominance on understorey light availability in low-elevation secondary forest stands in Costa Rica. J Trop Ecol 12(6):779–788. https://doi.org/10.1017/S0266467400010038
Ke G, Werger MJA (1999) Different responses to shade of evergreen and deciduous oak seedlings and the effect of acorn size. Acta Oecol 20:579–586. https://doi.org/10.1016/S1146-609X(99)00103-4
Kisamore JL, Brannick MT (2008) An illustration of the consequences of meta-analysis model choice. Orang Res Methods 11:35–53. https://doi.org/10.1177/1094428106287393
Kumar S, Shibata E (2007) Establishment and growth of coniferous seedlings in an altered forest floor after long-term exclusion of deer. J Forest Res 12(4):306–311. https://doi.org/10.1007/s10310-007-0014-z
Larpkern P, Moe SR, Totland Ø (2011) Bamboo dominance reduces tree regeneration in a disturbed tropical forest. Oecologia 165(1):161–168. https://doi.org/10.1007/s00442-010-1707-0
Ligot G, Balandier P, Courbaud B, Jonard M, Kneeshaw D, Claessens H (2014) Managing understory light to maintain a mixture of species with different shade tolerance. For Ecol Manag 327:189–200. https://doi.org/10.1016/j.foreco.2014.05.010
Lin J, Harcombe P, Fulton MR, Hall RW (2002) Sapling growth and survivorship as a function of light in a mesic forest of southeast Texas, USA. Oecologia 132(3):428–435. https://doi.org/10.1007/s00442-002-0986-5
Liu B, Liu Q, Daryanto S, Ma X, Guo S, Wang L, Wang Z (2018) Seedling emergence and early growth of Chinese fir under different light levels and seed positions: implications for natural regeneration. Can J For Res 48:1034–1041. https://doi.org/10.1139/cjfr-2017-0412
Liu H, Johnson DJ, Yang Q, Xu M, Ma Z, Fang X, Shang Y, Wang X (2021) The dynamics of conspecific tree and seedling neighbors on seedling survival in a subtropical forest. For Ecol Manag 483(2):118924. https://doi.org/10.1016/j.foreco.2021.118924
Lu D, Zhang G, Zhu J (2019) Early natural regeneration patterns of woody species within gaps in a temperate secondary forest. Eur J Forest Res 138:991–1003. https://doi.org/10.1007/s10342-019-01219-w
Lusk CH (2004) Leaf area and growth of juvenile temperate evergreens in low light: species of contrasting shade tolerance change rank during ontogeny. Funct Ecol 18(6):820–828. https://doi.org/10.1111/j.0269-8463.2004.00897.x
Marchesini VA, Sala OE, Austin AT (2009) Ecological consequences of a massive flowering event of bamboo (*Chusquea culeou*) in a temperate forest of Patagonia, Argentina. J Veg Sci 20(3):424–432. https://doi.org/10.1111/j.1654-1103.2009.05768.x
Marchin RM, Yuan Z (2023) Natural tree seedling establishment and forest regeneration under climate change. Front For Global Change 6:1256577. https://doi.org/10.3389/ffgc.2023.1256577
Martini F, Xia S, Zou C, Goodale UM (2020) Seedling growth and survival responses to multiple soil properties in subtropical forests of south China. For Ecol Manag 474(2):118382. https://doi.org/10.1016/j.foreco.2020.118382
Maxwell A, Capon SJ, James CS (2016) Effects of flooding on seedling establishment in two Australian riparian trees with contrasting distributions: *Acacia stenophylla* A. Cunn. ex Benth. and *Casuarina cunninghamiana* Miq. Ecohydrology 9:942–949. https://doi.org/10.1002/eco.1691
Mommer L, Kirkegaard J, van Ruijven J (2016) Root-root interactions: towards a rhizosphere framework. Trends Plant Sci 21(3):209–217. https://doi.org/10.1016/j.tplants.2016.01.009
Montgomery RA, Chazdon RL (2001) Forest structure, canopy architecture, and light transmittance in tropical wet forests. Ecology 82(10):2707–2718. https://doi.org/10.2307/2679955
Montti L, Campanell PI, Gatti MG, Blundo C, Austin AT, Sala OE, Goldstein G (2011a) Understory bamboo flowering provides a very narrow light window of opportunity for canopy-tree recruitment in a neotropical forest of Misiones, Argentina. For Ecol Manag 262(8):1360–1369. https://doi.org/10.1016/j.foreco.2011.06.029
Montti L, Campanello PI, Goldstein G (2011b) Flowering, die-back and recovery of a semelparous woody bamboo in the Atlantic Forest. Acta Oecol 37(4):361–368. https://doi.org/10.1016/j.actao.2011.04.004
Muñoz AA, González ME, Celedón C, Veblen TT (2012) Early response of tree regeneration after *Chusquea culeou* (Bambuceae) dieback in Andean old-growth forests of south-central Chile. Bosque 33(2):153–162. https://doi.org/10.4067/S0717-92002012000200005
Nakagawa M, Yoda K, Asahi K, Yumigeta Y, Watanabe A (2023) Reproductive characteristics in an understory bamboo and gradual environmental changes after its dieback provide an extended opportunity for overstory tree regeneration in a mixed cool-temperate forest in central Japan. Plant Biol 25:687–695. https://doi.org/10.1111/plb.13528
Nakashizuka T (2001) Species coexistence in temperate, mixed deciduous forests. Trends Ecol Evol 16(4):205–210. https://doi.org/10.1016/S0169-5347(01)02117-6
Narukawa Y, Yamamoto S (2002) Effects of dwarf bamboo (*Sasa* sp.) and forest floor microsites on conifer seedling recruitment in a subalpine forest, Japan. For Ecol Manag 163(1–3):61–70. https://doi.org/10.1016/S0378-1127(01)00527-8
Pearson AK, Pearson OP, Gomez IA (1994) Biology of the bamboo *Chusquea culeou* (Poaceae: Bambusoideae) in Southern Argentina. Vegetatio 111:93–126. https://doi.org/10.1007/BF00040331

Petrie MD, Wildeman AM, Bradford JB, Hubbard RM, Lauenroth WK (2016) A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. For Ecol Manag 361:328–338. https://doi.org/10.1016/j.foreco.2015.11.028

Puhlick JJ, Laughlin DC, Moore MM, Sieg CH, Overby ST, Shaw JD (2021) Soil properties and climate drive ponderosa pine seedling presence in the southwestern USA. For Ecol Manag 486:118972. https://doi.org/10.1016/j.foreco.2021.118972

Qian F, Song H, Chen M, Zeng J, Dang C, Tao J (2019) Multivariate path analysis of the relationships between seedling regeneration and environmental factors beneath a dwarf bamboo understory. Ecol Evol 9(3):10277–10290. https://doi.org/10.1002/ece3.5548

Qian F, Zhang T, Guo Q, Tao J (2016) Dense understory dwarf bamboo alters the retention of canopy tree seeds. Acta Oecol 73:38–44. https://doi.org/10.1016/j.actao.2016.02.004

Reich P (1998) Variation among plant species in leaf turnover rates and associated traits: implications for growth at all life stages. In: Lambers H, Porter H, Van Vuuren MMI (eds) Inherent variation in plant growth: Physiological mechanisms and ecological consequences. Backhuys Publishers, Leiden, pp 467–487

Sangsupan HA, Hibbs DE, Withrow-Robinson BA, Elliott S (2021) Effect of microsite light on survival and growth of understory natural regeneration during restoration of seasonally dry tropical forest in upland northern Thailand. For Ecol Manag 489(5):119061. https://doi.org/10.1016/j.foreco.2021.119061

Sayer EJ (2006) Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. Biol Rev 81(1):1–31. https://doi.org/10.1017/S1464793105006846

Si X, Pimm SL, Russell GJ, Ding P (2014) Turnover of breeding bird communities on islands in an inundated lake. J Biogeogr 41:2283–2292. https://doi.org/10.1111/jbi.12379

Singh AN, Singh JS (1999) Biomass, net primary production and impact of bamboo plantation on soil redevelopment in a dry tropical region. For Ecol Manag 119(1):195–207. https://doi.org/10.1016/S0378-1127(98)00523-4

Soderstrom TR, Calderon CE (1979) A commentary on the bamboos (Poaceae: Bambusoideae). Biotropica 11:161–172. https://doi.org/10.2307/2388036

Song Y, Li X, Zhang M, Xia G, Xiong C (2023) Effect of cold stratification on the temperature range for germination of *Pinus koraiensis*. J For Res 34:221–231. https://doi.org/10.1007/s11676-022-01540-y

Sumida A, Ito H, Isagi Y (1997) Trade-off between height growth and stem diameter growth for an evergreen oak, *Quercus glauca*, in a mixed hardwood forest. Funct Ecol 11:300–309. https://doi.org/10.1046/j.1365-2435.1997.00085.x

Takahashi K, Uemura S, Suzuki J, Hara T (2003) Effects of understory dwarf bamboo on soil water and growth of overstory trees in a dense secondary *Betula ermanii* forest, northern Japan. Ecol Res 18:767–774. https://doi.org/10.1111/j.1440-1703.2003.00594.x

Tanouchi HHRC (1996) Survival and growth of two coexisting evergreen oak species after germination under different light conditions. Int J Plant Sci 157(4):516–522. https://doi.org/10.1086/297370

Taylor AH, Huang J, Zhou S (2004) Canopy tree development and undergrowth bamboo dynamics in old-growth *Abies-Betula* forests in southwestern China: a 12-year study. For Ecol Manag 200(1):347–360. https://doi.org/10.1016/j.foreco.2004.07.007

Terrer C, Vicca S, Hungate BA, Phillips RP, Prentice IC (2016) Mycorrhizal association as a primary control of the CO_2 fertilization effect. Science 353(6294):72–74. https://doi.org/10.1126/science.aaf4610

Tripathi SK, Sumida A, Shibata H, Uemura S, Ono K, Hara T (2005) Growth and substrate quality of fine root and soil nitrogen availability in a young *Betula ermanii* forest of northern Japan: effects of the removal of understory dwarf bamboo (*Sasa kurilensis*). For Ecol Manag 212(1–3):278–290. https://doi.org/10.1016/j.foreco.2005.03.030

Van Der Meer PJ, Sterck FJ, Bongers F (1998) Tree seedling performance in canopy gaps in a tropical rain forest at Nouragues, French Guiana. J Trop Ecol 14:119–137. https://doi.org/10.1017/S026646749800011X

Verhoeven D, de Boer WF, Henkens RJHG, Sass-Klaassen UGW (2018) Water availability as driver of birch mortality in Hustai National Park, Mongolia. Dendrochronologia 49:127–133. https://doi.org/10.1016/j.dendro.2018.04.001

Walbott M, Gallet C, Corcket E (2018) Germination et croissance des plantules de hêtre (*Fagus sylvatica*) sous contraintes climatiques et allélopathiques. CR Biol 341:444–453. https://doi.org/10.1016/j.crvi.2018.09.003

Wijewickrama T, Karunaratne I, Wijesundara S, Madawala S (2022) Impacts of bambusa bambos spread on seedling recruitment, mortality and regeneration potential of native species in tropical moist evergreen forests of Sri Lanka. J Trop For Sci 34(1):48–62. https://doi.org/10.26525/jtfs2022.34.1.48

Yokoyama M, Kaji K, Suzuki M (2000) Food habits of sika deer and nutritional value of sika deer diets in eastern Hokkaido, Japan. Ecol Res 15(3):345–355. https://doi.org/10.1046/j.1440-1703.2000.00355.x

Yoshida T, Kamitani T (2000) Interspecific competition among three canopy-tree species in a mixed-species even-aged forest of central Japan. For Ecol Manag 137:221–230. https://doi.org/10.1016/S0378-1127(99)00330-8

Zhang K, Li Y, Wei H, Zhang L, Li F, Zhang F (2022) Conservation tillage or plastic film mulching? A comprehensive global meta-analysis based on maize yield and nitrogen use efficiency. Sci Total Environ 831:154869. https://doi.org/10.1016/j.scitotenv.2022.154869

Zheng X, Lin S, Fu H, Wan Y, Ding Y (2020) The bamboo flowering cycle sheds light on flowering diversity. Front Plant Sci 11:381. https://doi.org/10.3389/fpls.2020.00381

Zhou G, Liu Q, Xu Z, Du W, Yu J, Meng S, Zhou H, Qin L, Shah S (2020) How can the shade intolerant Korean pine survive under dense deciduous canopy? For Ecol Manag 457:117735. https://doi.org/10.1016/j.foreco.2019.117735

Zhu J, Lu D, Zhang W (2014) Effects of gaps on regeneration of woody plants: a meta-analysis. J For Res 25(3):501–510. https://doi.org/10.1007/s11676-014-0489-3

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.