



Demographic strategies of a dominant tree species in response to logging in a degraded subtropical forest in Southeast China

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Abstract

• **Key message** The demography of pioneer tree species (*Pinus massoniana* Lamb.) is significantly affected by logging in Southeast China. Logging negatively affects the population growth rate of *P. massoniana*, which facilitates the growth of individual trees but has no effect on reproduction probability. The survival and growth of seedlings contribute the most to population growth.

• **Context** Subtropical forest degradation caused by unreasonable disturbances is closely related to anthropogenic activities in Southeast China, and the frequent small-scale logging activity by local people was the dominated disturbance regime in forests in this region over the past several decades.

• **Aims** The objective of this study is to evaluate the demographic consequences of logging on *Pinus massoniana*, a pioneer tree species, at individual level (survival, growth, and fecundity) and population level (the population growth rate and size distribution) over short-term period.

• **Methods** The size of tree individuals was combined with vital rates using various modeling approaches based on demographic data from three annual censuses. The integral projection model (IPM) was constructed and used to conduct comparative demographic analyses.

• **Results** Logging negatively affected the population growth rate: from a slight expansion before logging to a moderate decline after logging. This study found a significant reduction in seedling recruitment after logging, and plant growth and mortality were slightly enhanced. The survival of seedlings greatly contributes to population growth rate compared to other life stages for both periods (before and after logging) while its relative importance decreases after logging. Seedling growth is also important to population growth, and its relative importance increased after logging. Shrinkage and fecundity have a minimal contribution effect on the population growth rate.

• **Conclusion** Growing plants in a nursery with a similar demography to *P. massoniana* could be beneficial for pioneer species regeneration in that this will improve the survival rate and growth of small individuals after logging.

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Contributions of the co-authors Xianyu Yang: Carried out the field and laboratory work, run the data analysis, and wrote the manuscript.

Shouzhong Li: Designing the experiment, carried out the field and laboratory work, coordinating the research project and supervised the work.

Shou-Li Li: Supported the statistical analysis, run the data analysis, and commented on the manuscript.

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1 Introduction

Many plant species subsist in disturbed environments characterized by frequent anthropogenic activities or natural hazards (Benavides et al. 2013; Caswell 2000). Habitat disturbances, acting as a major selective force, may cause variation in vital rates (survival, growth, reproduction, and mortality) and, furthermore, influence the performance and persistence of plant populations (Easterling et al. 2000). While changes in vital rates before and after habitat disturbances have been well documented (Alyemini and Sher 2010; Grogan et al. 2014; Mandle and Ticktin 2012; Schmidt et al. 2011; Yang et al. 2012), little is known about the demographic consequences of such variations at a population level. Forests are typically under tremendous pressure from human development, especially in degraded land (Ma et al. 2016). The mortality, growth, and recruitment of tree species are key factors that influence the population and successional dynamics of forests (Smith and Nichols 2005; Winkler et al. 2015). Identifying and understanding changes in plant demography are critical to understanding the numerous ecological processes that exist and provide guidelines for the sustainable management of forests (Grogan et al. 2014; Primack and Lee 1991).

Logging is one of the most common human disturbances of trees and is a commonly used practice in forest exploitation. It is increasingly being embraced to protect the integrity of forests (Dekker and de Graaf 2003; Egnell and Valinger 2003). The response of tree populations is closely associated with logging patterns (logging intensity, logging cycles, logging mode, logging number), species characteristics, and stand density. Previous studies have shown that the structure of populations could significantly change in the presence of dead trees caused by logging over a short time period, which, furthermore, could have an impact on plant demography over a long time period under a decrease in reproductive trees and seedling recruits (Carvalho et al. 2013; Villela et al. 2006). The resultant effects of logging differ among different species groups. For light-demanding tree species, studies have indicated that logging could promote plant growth and recruitment due to an increase in light availability after logging (Figueira et al. 2008; Smith and Nichols 2005). Generally, moderate logging practices have been shown to have the highest positive effects on stem density and basal area (Behjou and Mollabashi 2017; Qi and Zhao 2015). On the other hand, the proportion of pioneer

species could increase in logged forests due to the creation of more suitable habitat conditions. It has been shown that the successful regeneration of pioneer species has a positive correlation to canopy gaps (Arets et al. 2003). However, for shade-tolerant species, logging could have a significant impact on population dynamics through a reduction in recruitment, which could even cause extinction if exposed to periodic regime (Yamada et al. 2016).

Subtropical evergreen broad-leaved forests are the most extensive forest type in China, especially in the southeast, which is largely deforested and fragmented due to human activities and economic development (Gong et al. 2013; Sun et al. 2006). In this region of China, vegetation degradation is closely related to the improper management practices associated with anthropogenic activities, including logging, fires, and severe reclamation (Hua et al. 2015; Jin et al. 2015). In combination with natural factors like fragmented topography, soil erodibility, and concentrated rainfall, the excessive exploitation of forests has further led to desertification over the last century (Dou et al. 2013; Xu et al. 2013; Vajpeyi and Ponomarenko 2001). To address these environmental problems, the Government of China instigated an extensive reforestation program, which has been widely adopted throughout the country over recent decades (He et al. 2011; Ma and Zha 2008). This has yielded some results, such as the restraint in large-scale irrational exploitation under the auspice of ecological protection policies.

Although forest cover has greatly increased after the implementation of these reforestation programs, most secondary forests are monoculture plantations, where a small variety of commercial species are selected, such as *Pinus* and *Cunninghamia* (Ren et al. 2007; Xu 2011). *Pinus massoniana*, a dominant pioneer tree species, occurs widely in southeast China at present due to its high tolerance of poor soil nutrient conditions, high sunlight demand, and longevity (Dou et al. 2013; Liu and Zeng 2017). The demography of *P. massoniana* and its population dynamics could signify the state of succession and forest restoration in degraded lands. However, frequent small-scale logging is still prevalent due to our demand for energy and economic well-being with increased human population (An-Ping et al. 2011; Zackey 2015). Previous studies have indicated that the performance of *P. massoniana* could be significantly influenced by logging intensity. The diameter growth increment and the canopy area in logged forests (where 60–80% individuals were removed) are higher than those in unlogged forests, but they decrease with an increase in logging intensity (Zeng et al. 2017). A 20–30% logging intensity had the

greatest positive effect on the diameter at breast height (DBH) and height (Huang et al. 2013; Ma et al. 2017). The regeneration of pine trees could also be improved by low-intensity logging under higher light availability (Qi and Zhao 2015). However, unlike studies conducted in forests long after logging has occurred, demographic studies conducted in forests immediately after logging are inadequate in many regions, particularly in degraded subtropical forests. To fill this knowledge gap, research on the demographic response of *P. massoniana* populations under logging activities is essential to gain a complete understanding of sustainable forest management.

In this study, we investigate the effects of forest logging in Changting County, Fujian Province, southeast China. We examine the population dynamics of a dominant tree species *P. massoniana* and investigate the effects of logging on tree mortality, growth and fecundity. We attempt to test whether the population remained stable throughout the study period, as well as to identify and explain vital rate changes. We used the integral projection model (IPM) to provide insight into the response of the entire life cycle of *P. massoniana* by answering three main questions: (i) Do the vital rates of *P. massoniana* differ during periods before and after logging? (ii) How does logging affect population growth? (iii) Which demographic components are essential for population growth before and after logging? Following this, we provide recommendations for degraded subtropical forests management based on the implications of our findings.

2 Materials and methods

2.1 Experimental site and study species

This study was conducted in Changting County (25° 18' 40"–26° 02' 05" N, 116° 00' 45"–116° 39' 20" E) located in the southern region of the Wuyi Mountains in Southeast China (Ning et al. 2016). As shown in Appendix Fig. 5, the inter-annual average temperature in July and January is 27 and 8 °C, respectively. Summer is long and hot, where the maximum air temperature can reach 35 °C. Annual rainfall is 1710 mm (± 150 mm SD) with the most rainfall occurring March and June (Xu et al. 2013). The site is characterized by red tinged acidic soil with a high quartz content that is poorly resistant to corrosion and is lacking in fertility (Dou et al. 2013). As a typical soil erosion region example in Southeast China, the Government of China has allocated much effort to vegetating and re-vegetation this region since early 1980s (Xie et al. 2002). After three decades of silvicultural practices, secondary forests dominated by *P. massoniana* are widely distributed within the study area, where vegetation

coverage has increased from 48% in 1985 to 86.5% in 2013 (Dou et al. 2013; Zhang et al. 2015).

Pinus massoniana (Pinaceae) is a coniferous tree species (Fan et al. 2008). Its height ranges from 15 to 45 m, and its DBH can reach 1.5 m, with a broad, rounded crown with long branches. The bark is thick and flakes higher up on the trunk. It grows in dry, poor, and acidic soils (Dong 1987). Annual DBH growth increases with age and reaches its peaks after approximately 15–20 years. It is a dominant species during the early succession stages of evergreen broad-leaved forests in the subtropical zone of Southeast China. It produces seeds at 5 to 6 years old. Pine cones ripen in October, and seeds germinate in the following March. The seeds have one wing and are readily dispersed by wind (Chen and Su 2001).

2.2 Data collection

In 2011, one permanent plot approximately 900 m² (30 × 30 m) in size was established, where *P. massoniana* was the main dominant tree species. The total vegetation cover was 65 ± 3% (mean ± SE). To ease data collection, the plot was subdivided into 36 subplots of 5 × 5 m each. Measurements were taken within the entire plot in July 2011, 2012, and 2013. For each individual *P. massoniana* tree, basal diameter and total height were measured and labeled during the first census we conducted. For those individuals with heights greater than 1.5 m, DBH was also measured and recorded. In subsequent years, all labeled individuals were checked and re-measured, and new recruits (seedlings that germinated and established themselves between census periods) within the plot were searched for, labeled, and measured. The number of pine cones produced throughout the study period was also recorded. A total of 522 individuals were identified and measured throughout the study period, where the minimum size of basal diameter and height was less than 1 mm and 5 cm, respectively. The reason for calculating seedling recruitments based on measured plant size, instead of using measured pine cones or the number of pine nuts, was because of the following: (1) pinecones could remain attached to the tree until the second year after pine nuts have fallen off in the first year, thereby potentially causing measuring errors, where the same pine cones are counted twice in different years; (2) pine cones of *P. massoniana* usually produce an enormous amount of pine nuts, which makes it impossible to quantifiably count the number of pine nuts of each individual tree. Therefore, we assumed that the fecundity of a reproductive individual is positively associated with plant size, which is described by the basal diameter and the number of seedling produced per individual ($f_e(x)$) and was calculated as $f_e(x) = x(n/\text{sum}(x))$, where n is the number of established seedlings and x is the basal diameter of established seedlings in the plot.

We collected soil in the 0–10 cm layer, the 10–20 cm layer, and the 20–40 cm layer in the plot during the

census period and measured the weight of wet soil and dry soil, which we dried at 105 °C for 8 h. The soil water content was calculated by the weight of water in soil divided by the weight of wet soil. The ground surface temperature was also collected by means of surface thermometer during the census period.

The sample plot was logged in October 2012 after the second census, and 81% of large individuals (basal diameter > 50 mm) were removed, where 84% of the total number of individuals remained (Appendix Figs. 6 and 7). The number of *P. massoniana* individuals decreased from 1700 trees/ha before logging to 611 trees/ha after logging (calculated using trees with a measured DBH).

2.3 Statistical analyses

To test the differences in the vital rates during the different logging periods, the current plant size (x , at t) was used in conjunction with the future size (y , at $t+1$), applying multiple regression models. We used basal diameter (BD) to characterize plant size and to construct the IPM, due to its higher R^2 values compared to other size measurements (DBH and height) for all regression models. Paired t tests were used to test changes in temporal size ($g(y, x)$) between current and future basal diameters ($\text{size}_{t+1} - \text{size}_t$), and linear models were used to examine the effects of logging on future basal diameter ($\mu(x)$) and variance of growth ($\sigma^2(x)$). At the same time, logistic regressions were used to fit the probability of survival $s(x)$ and reproduction $P_r(x)$ with the current basal diameter as explanatory variables.

The IPM describes the dynamics of a population structured by a continuous individual-level state variable as follows (Easterling et al. 2000; Ellner and Rees 2006):

$$n(y, t+1) = \int_{\Omega} [p(y, x) + f(y, x)] n(x, t) dx \quad (1) \\ = \int_{\Omega} k(y, x) n(x, t) dx$$

where Ω is the range of all plant sizes used in the calculation. The kernel $k(y, x)$ is a nonnegative surface and represents all possibilities of transitions from size x to size y throughout the range of time t to time $t+1$, which is composed of $p(y, x)$ and $f(y, x)$. $p(y, x) dx$ represents the probability of living individuals growing from size x to size y during the time interval $(t, t+1)$, which is calculated as $p(y, x) = s(x) g(y, x)$. $s(x)$ is the probability that a size x individual survives to the next time step. $g(y, x)$ is a normal probability density function with a mean future plant size ($\mu(x)$) and a growth variance ($\sigma^2(x)$). Subsequently, $f(y, x) dx$ represents the number of newborns at time $t+1$ per size x individuals alive at time t , which is calculated as $f(y, x) = P_r(x) f_e(x) f_d(y)$, where $P_r(x)$ is the reproducing probability that a size x plant will reproduce in one time step, $f_e(x)$ is the number of seedlings produced on average per plant of size x ,

and $f_d(y)$ is the normal distribution of offspring size.

We converted the kernel $k(y, x)$ into a large transition matrix $\mathbf{K}(y, x)$, using the midpoint rule (Ellner and Rees 2006). According to the midpoint rule, we divided the size range of individuals to m mesh points, which means the matrix also has m size classes. In theory, the fitting precision of the matrix increases with m . However, the category width could affect the population growth rate. For example, the population growth rate was considerably overestimated when using ≤ 10 classes and was slightly underestimated when using ≥ 1000 classes (Zuidema et al. 2010). Therefore, we used 100 size classes, which have also been commonly used in the literature. We constructed IPMs for the period before and after logging, separately. IPMs can yield outputs of population growth rates (λ), stable size distributions, sensitivity, and elasticity. Confidence intervals of λ were calculated by bootstrapping (Jongejans et al. 2010). We resampled with replacements from the dataset ($n = 522$ in our study), recalculated regression coefficients, and established the kernel and calculated. This was repeated 5000 times, and 95% confidence intervals were obtained from the frequency distribution of these values (Li et al. 2011).

The stable population distribution that derived from IPM was compared to the observed population structure (means of before logging in 2011–2012 and after logging in 2013) using the percentage similarity index (PS). $PS = \sum(\min[\text{obs}_i, \text{ssd}_i]) \times 100$, where obs_i and ssd_i are vectors of observed size distributions and stable population structures, respectively (both vectors scaled to sum to 1) (Zuidema et al. 2007; Li et al. 2015). High values of this index are indicative of a high level of similarity and also a more stable population state.

Elasticity analysis quantifies the proportional change in λ resulting from infinitesimal relative changes in the matrix elements (de Kroon et al. 2000; Li et al. 2015), which indicates the relative importance of individuals and vital rates (survival, growth, shrinkage, and fecundity) to the population growth rate.

The survival rate would decrease with basal diameter if logged trees were added to the calculation, and, furthermore, the output of the IPM model may deviate from the trajectories of population dynamics in the long term. To avoid such errors, we therefore removed it from the data in 2012 when we constructed the IPM 2012–2013 model. All analyses were conducted using R version 3.4.1 software (R development core Team 2017).

Data availability The datasets generated during and/or analyzed during the current study are available in the PANGAEA repository, <https://doi.pangaea.de/10.1594/PANGAEA.890755> (Yang et al. 2018). Datasets are not peer-reviewed.

3 Results

3.1 Vital rate variations

During the period before logging (2011–2012), the survival probability of *P. massoniana* seedlings (with a basal diameter of 0–10 mm) was very high (greater than 82%; Table 1; Fig. 1a). The probability of survival increased with stem size, which was above 99.9% for juvenile (with a basal diameter of 10–50 mm) and adult (with a basal diameter > 50 mm) plants. Survival probabilities were lower for seedlings and juveniles after logging (2012–2013). The survival of seedlings and juveniles was decreased by 20 and 7%, respectively.

Stem growth increased with basal diameter as indicated by the regressions with slopes > 1 both before and after logging (Table 1; Fig. 1c, d). Logging slightly stimulated the growth of the population: mean growth increments varied from 1.81 ± 0.12 mm/year before logging to 2.06 ± 0.13 mm/year after logging. The growth increment varied significantly between life stages. For example, adults grew fastest (6.46 ± 0.72 mm/year) after logging, which was higher than juveniles and seedlings (3.79 ± 0.33 and 1.12 ± 0.71 mm/year, respectively). At the same time, the proportion of steams with negative growth rates was 4.0% prior to logging and 4.5% following logging.

The reproductive probability increased with basal diameter, and it was not significantly affected by logging (Fig. 1e, f). The number of reproductive trees was 381 and 402 throughout the study period. Plants generally started to reproduce at a basal diameter greater than 70 mm (> 50% reproductive probability). The number of pine cones per basal area significantly decreased from 0.2280 before logging (a total of 1551 pine cones) to 0.1920 after logging (a total of 110 in total pine cones). Furthermore, new seedling recruits declined by 82% after logging (Table 1; Appendix Fig. 8), suggesting a strong logging influence on seedling recruitment.

3.2 Population growth rate and stable structures

In our study, the population growth rate (λ) of *P. massoniana* before logging was 1.065, which showed that the population was expanding. The number of individuals increased by 30%, where the maximum size changed from 153.66 to 164.5 mm (Table 2; Appendix Fig. 6). However, the *P. massoniana* population declined ($\lambda = 0.946$) after logging with numbers decreasing by 14% (Table 2; Appendix Fig. 6). Logging reduced the numbers of seedlings by 24%, where the maximum size changed to 127.9 mm (Appendix Fig. 6). While the number of seedlings decreased by 24% after logging, the proportion of seedlings in population increased from 59.7 to 65.9% throughout the study period.

The kernels showed a higher positive growth transition and a lower fecundity transition after logging (Fig. 2a, b). Before and after logging, both showed that the observed population structure

Table 1 Statistical models and parameter estimates used to construct the kernels for the integral projection models of *Pinus massoniana* in a degraded subtropical forest during 2011–2012 (period 1) and 2012–2013 (period 2)

Demographic parameters	Period	Model
Survival probability (s)	1	Logit (s) = $1.296(0.638) + 0.573(0.240)x$ $n = 381, P < 0.05$
	2	Logit (s) = $0.850(0.159) + 0.057(0.017)x$ $n = 402, P < 0.01$
Reproductive probability (P_r)	1	Logit (P_r) = $-4.220(0.399) + 0.058(0.006)x$ $n = 381, P < 0.001$
	2	Logit (P_r) = $-5.296(0.594) + 0.071(0.011)x$ $n = 402, P < 0.001$
Future size (μ)	1	$\mu = 1.046(0.186) + 1.040(0.003)x$ $n = 369, R^2 = 0.995, P < 0.001$
	2	$\mu = 1.064(0.120) + 1.066(0.005)x$ $n = 310, R^2 = 0.994, P < 0.001$
Variance of growth (σ^2)	1	$\sigma^2 = 2.907(3.415) + 0.148(0.070)x$ $n = 339, R^2 = 0.009, P < 0.05$
	2	$\sigma^2 = 1.247(0.494) + 0.140(0.020)x$ $n = 310, R^2 = 0.137, P < 0.001$
Size distribution of new seedlings	1	Gaussian with mean = 2.070 Variance = 1.739, $n = 119$
	2	Gaussian with mean = 2.974 Variance = 4.372, $n = 22$

The models are functions of plant basal diameter (x , mm), treatment (logging), and interactions between basal diameter and treatment, using the unlogged period as a reference. Values in parentheses are standard errors of the parameter estimates. $P < 0.01$ indicates that slope and intercept in the regression models are significantly different from zero

of *P. massoniana* was characterized by a high abundance of seedlings and a low abundance of adults (Fig. 3). The similarity between the stable size distribution and the observed size distribution was 69.4% after logging, lower than the similarity (71.4%) before logging (Fig. 3).

3.3 Elasticity analysis

The survival of seedlings and juveniles yielded highest elasticity values both before and after logging (Fig. 4), which implied that seedlings and juveniles are critically important for the population maintenance of *P. massoniana*. Fecundity and shrinkage yielded much lower elasticity values, which suggested that the population growth rate was less sensitive to changes in these vital rates. Vital rate elasticity changed between periods (Fig. 4): the survival elasticity of seedlings was lower after logging compared to before logging, and the growth elasticity of seedlings was higher. There were minimal contributions of shrinkage and fecundity to the population growth rate.

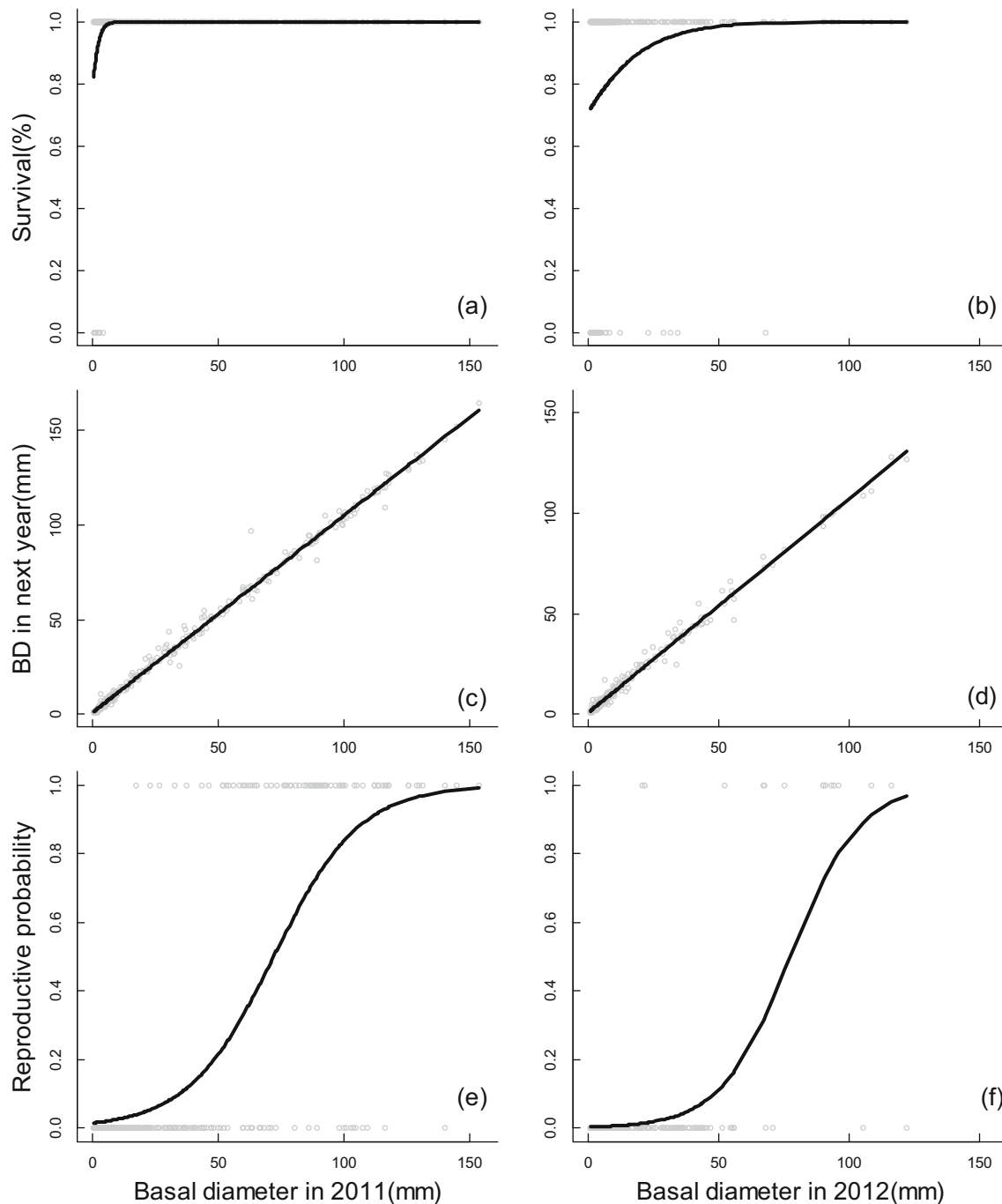


Fig. 1 Relationships between vital rates and plant the basal diameter for *Pinus massoniana* in a degraded subtropical forest during 2011–2012 (a, c, e) and 2012–2013 (b, d, f). Regression functions are described in Table 1. BD basal diameter

4 Discussion

4.1 Effects of logging on vital rates

The quality of plant survival is the result of both biotic and abiotic factors (Connell and Green 2000; Zhang et al. 2009). Logging could both have a direct and indirect effect on trees survival, through adjustment of relationships among

individuals and the change in habitat conditions in the forest (Carvalho et al. 2013). In our study, adult survival was not affected by logging, while there was a reduction in the survival rate of seedlings and juveniles after logging. In general, seedlings are highly sensitive to habitat variables and typically present nonrandom mortality during their immature development stage, and it is also the stage of the greatest change in numbers (Fangyuan et al. 2003; Han et al. 2012; Ma et al.

Table 2 Population growth rates of *Pinus massoniana* in a degraded subtropical forest during 2011–2013

Status	Period	Population growth rate
Before logging	2011–2012	1.065 [1.056, 1.074]
After logging	2012–2013	0.946 [0.943, 0.949]

Values in brackets refer to 95% confidence intervals

2016). After logging, when most large plants were removed, larger canopy gaps formed and higher temperature variations occurred in the forest. Soil water shortages could potentially be the principle factor that caused higher mortality of small sized individuals in the heat of the summer (Caspersen and Kobe 2001; Wang et al. 2001). On the other hand, due to poor

soil erodibility, small-sized plants could be buried and their roots could also be exposed after the frequent rainstorms that occur during the rainy period. In addition, trampling by humans and soil compaction during logging processes could also lead to an increase in mortality of small-sized individuals (Roovers et al. 2004; Schweitzer and Dey 2013; Waltert et al. 2002).

In general, ecosystems are subject to limited habitat resources (Donovan et al. 2000). Stem density can decrease resource competition. Tree growth can accelerate in more favorable habitats (Duclos et al. 2013; Huang et al. 2013; Yang 2004). In our study, the growth rate of *P. massoniana* was promoted by logging, but it differed across life stages. Being a light-demanding tree species, sunlight availability, compared to other resources, was the key factor for *P. massoniana*

Fig. 2 Fitted kernels of transitions for *Pinus massoniana* in a degraded subtropical forest during 2011–2012 (a) and 2012–2013 (b). Transition values are shown for transitions from present size (x -axis) to future size (y -axis). Gray tones indicate the magnitude of the transitions with values > 0.1 shown in white. Transitions along the diagonal represent survival-growth transitions, while those on the bottom correspond to recruitment

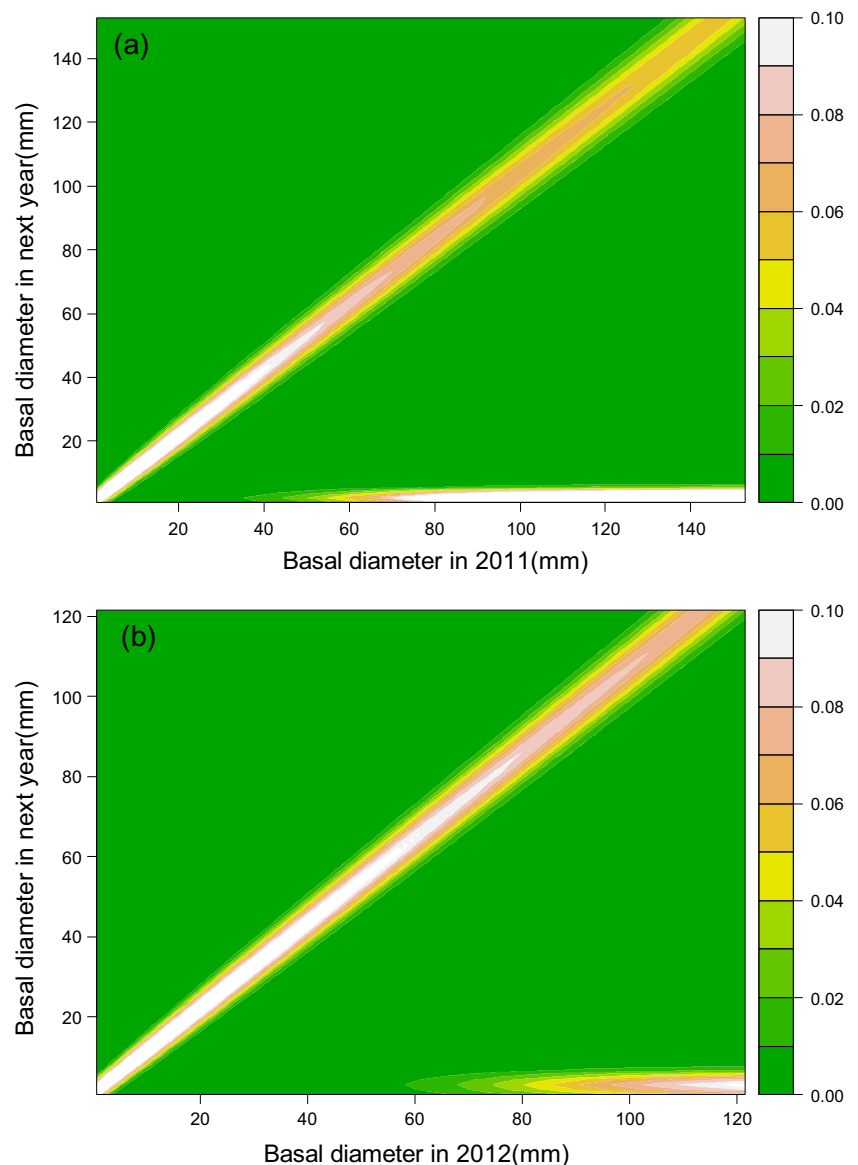
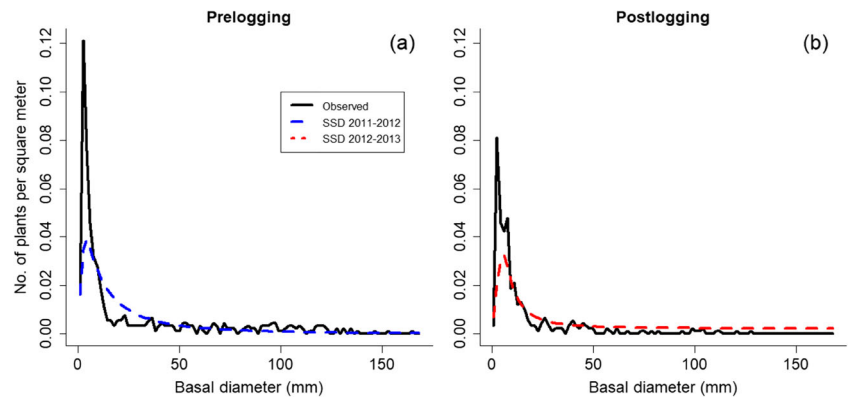


Fig. 3 Number of plants (*Pinus massoniana*) per square meter in degraded subtropical forest throughout the study period. The observed population structure (Observed) from study plot data in 2012 (prelogging) and 2013 (postlogging). Stable size structure (SSD) resulting from the integral projection model for 2011–2012 (prelogging) and 2012–2013 (postlogging)



growth (Zhang et al. 2005; Zhu 2015a, b). The fastest growth observed for larger sized individuals may have resulted from their larger crowns, where they were exposed to full sunlight and subsequently accumulated more photosynthetic products in the canopy layer (Win et al. 2012). On the other hand, being a common biological characteristic of pine trees, we frequently observed the exfoliation of rimose bark in our plots. We observed shrinkage in plant diameter when the growth rate was lower than bark exfoliation. Such shrinkage in plant size may help adult plants to maintain a high survival rate in degraded habitats (Salguero-Gómez and de Kroon 2010).

Recruitment limitations for tree species mainly include source limitations, dissemination limitations, and establishment limitations (Ning et al. 2011; Ma et al. 2016; Swamy et al. 2011). The seeds of *P. massoniana* are equipped with a wing and can be readily dispersed by wind; therefore, the

reproduction rate of *P. massoniana* is mainly influenced by source limitations and establishment limitations. In our plot, the reproductive probability of *P. massoniana* was less affected by logging, but seedling recruits significantly decreased. When logging was not taking place, we calculated a total of 575 pine cones (data not shown) and 119 seedling recruits (Table 1). The average pine cone and seedling recruit of individuals was 7.7 and 1.6, respectively. Establishment limitations could be a main factor that influenced plant recruitment during this period. However, the number of pine cones and new seedlings were calculated at 195 (data not shown) and 22 (Table 1) during the postlogging period, and the average pinecone and seedling recruits of individuals were 4.1 and 0.5, respectively. Taking into account the changes in pinecones and seedling recruits during the census period, the significant decline in the number of pine cones could be one of the main reasons for a decrease in seedling recruits after logging.

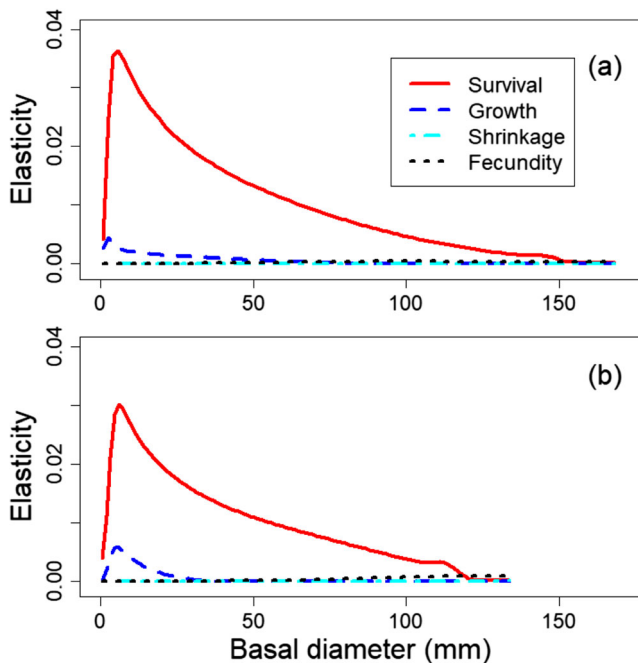


Fig. 4 Vital rate elasticity for *Pinus massoniana* in a degraded subtropical forest before logging (a) and after logging (b)

4.2 Effects of logging on population dynamics

According to our results, unlogged populations showed a slight growth rate ($\lambda = 1.065$), while logged populations showed a moderate decline ($\lambda = 0.956$), both being composed of highly abundant seedlings and a small proportion of adults. The effect of logging on population dynamics depends on the sensitivity of population growth rates to vital rates, which change under logging. The elasticity analysis revealed that population growth before and after logging exhibited similar patterns. However, the relative importance of the survival of small-sized individuals was suppressed after logging while their growth increased slightly.

Generally, pine species take a long time to reach maturity and experience a loss during this process (Franco and Silvertown 2004; Sánchez-Velásquez and Pineda-López 2009). In our study, the survival rate of large adults was less affected by logging but, on individual survival rates, was positively associated with size, and the individual survival rate is closely associated with the population growth of *P. massoniana*. The

importance of survival for population growth demonstrates the necessity of maintaining the survival of all individuals after logging, especially for seedlings and juveniles, which dominate the population structure. The higher mortality rates of seedlings and juveniles after logging could be a critical reason for the importance of the decline in the survival rate of small-sized plants during population development. Moreover, the increased importance of growth after logging also demonstrates the necessity in promoting the growth of seedlings and juveniles.

On the other hand, pioneer tree species generally achieve regeneration by means of massive seed production and low seedling establishment (Melo and Tabarelli 2003). Seed dispersal and seedling establishment of *P. massoniana* are typically significantly affected by habitat fluctuations in degraded subtropical regions (Peng et al. 2004; Tan et al. 2017). In order to reduce the influence of disturbance, the population growth rate of perennial trees are typically not sensitive to changes in the vital rates that are vulnerable to habitat fluctuations (Kolb et al. 2010; Winkler et al. 2015). Due to the low proportion of annual seedling recruitment and high mortality rates, fecundity has only a limited contribution to population growth both before and after logging.

4.3 Management implications

Although its long life span allows *P. massoniana* population to continue for a certain period after logging, this impediment to regeneration could result in a higher extinction risk to the remnant population over the long term (Vieira and Scariot 2008). Therefore, it is necessary to take some measures to promote the recovery of the population, especially after logging. Our study found that logging had different effects on vital rates, where survival and recruitment evidently decreased and growth was stimulated after logging. Management recommendations should be based on vital rates that are mostly affected by logging and those that are most important for population growth (Li et al. 2013).

An increase in vegetation cover is being increasingly recognized as an effective means of restoring ecosystem functions in degraded areas, especially in Southeast China (Zhu 2015a, b). Early successional species such as *P. massoniana* are typically selected for restoration due to their high survival rates and rapid growth, which can reduce the cost of restoration and provide forest products within a short period of time (Yang et al. 2017). Since *P. massoniana* population growth is highly sensitive to survival, especially for small-sized individuals, a slight decrease in seedling survival would result in a significant impact to the general population. Thus,

the reduction in the number of small sized individuals by logging and trampling should be prevented. On the other hand, tending treatments are considered an efficient way in which to restore forests. For example, digging holes at the base of small plants could improve water condition by collecting available rainwater, which is in alleviating drought injuries caused by summer heat conditions. Regular fertilization could also have a positive effect on the survival and growth of plants (Hu et al. 2000; Li et al. 2014; Zhang et al. 2013). The light-demanding early successional species typically performed well with high survival rates and rapid growth in a degraded site, while some mid-successional and late-successional species also can be incorporated into restoration plantings (Yang et al. 2017). As it pertains to the restoration of degraded forest ecosystems, it is important to carefully choose native species (including *Schima superba*, *Lespedeza bicolor*, and *Castanopsis sclerophylla*) that are adapted to local conditions (Chen et al. 2005; Pan et al. 2016). Mixed planting could improve species richness, accelerate forest succession, and elevate the ecological services in degraded forests ecosystems (Lin 2005; Yang et al. 2017). On the other hand, the regeneration of *P. massoniana* was driven by the massive production of seeds and low seedling establishment. Previous studies showed that demographic shifts in some species populations, which, caused by low number of recruits, have trouble surviving in the community (Ma et al. 2016). While seedling recruits had a low contribution to population growth, they could also cause a reduction in the population growth rate, especially after logging. Protecting these individuals would potentially be favorable to population growth while promoting viable population restoration measures. Field planting of larger seedlings increased postplanting care, and planting in less degraded sites can be an effective way to improve the restoration of forests (Yang et al. 2017).

Being a pioneer tree species with high fecundity, *P. massoniana* could highly effective in reestablishing forests after disturbances (Dong 1987; Primack and Lee 1991). However, we observed a population declined during the study period. That is to say, if forests are exposed to under continuous logging management practices, pioneer species with a similar demography to *P. massoniana* may experience a population decline and even disappear altogether due to low seedling recruitment (Hastings 2001; Yamada et al. 2016). On the other hand, previous studies have shown that it can take years or even decades for the influence of logging to be seen on long-lived tree populations (Bonnell et al. 2011; Egnell and Valinger 2003). Since our study is based solely on 3-year demographic data taken from a single

plot, it can only capture a part of the consequences of logging. Therefore, long-term monitoring studies at multiple sites are necessary to obtain a more comprehensive understanding of the effects of logging on pioneer species.

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Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

Appendix

Fig. 5 Average monthly temperature and precipitation in Changting County from 1960 to 2016

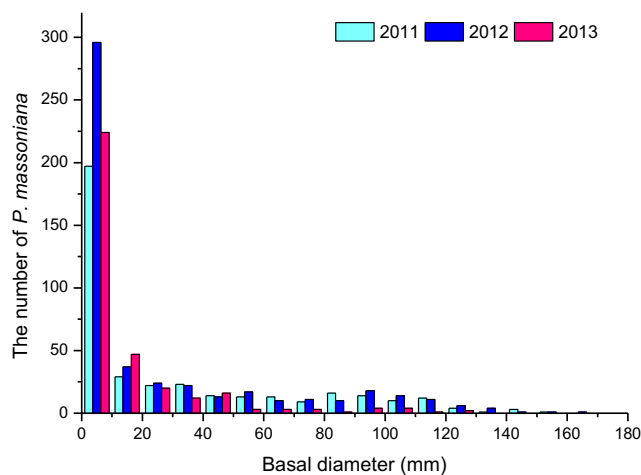
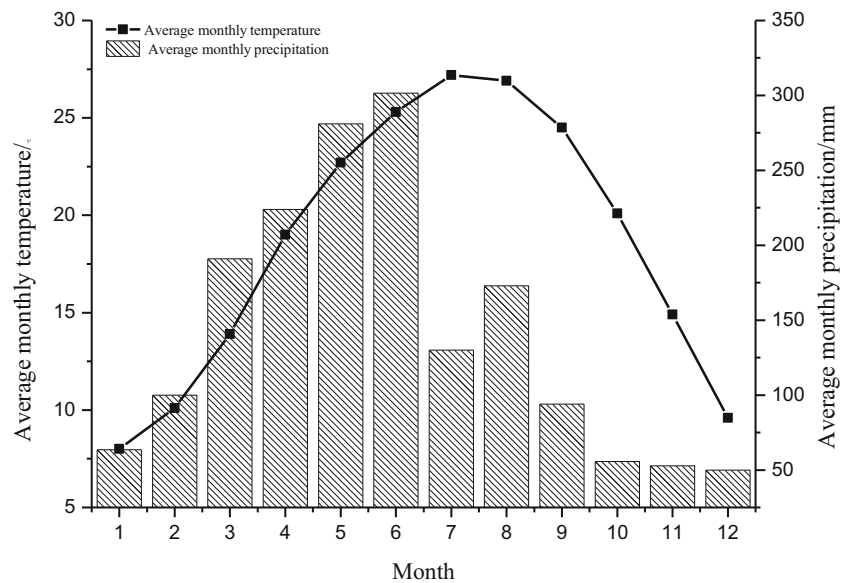


Fig. 6 The diameter class distribution of the *Pinus massoniana* population in a degraded subtropical forest from 2011 to 2013

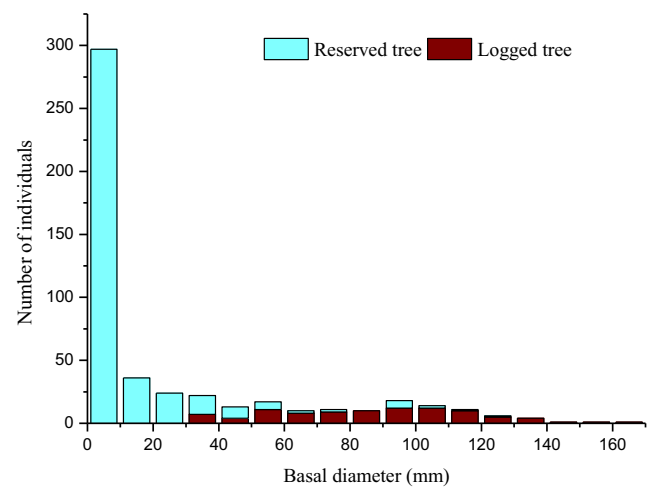


Fig. 7 Distribution of logged *Pinus massoniana* individuals in a degraded subtropical forest throughout the study period

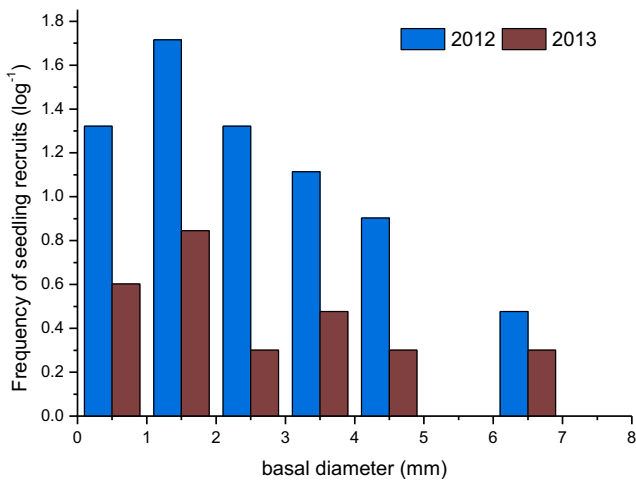


Fig. 8 The observed size distribution of seedling recruits in a degraded subtropical forest throughout the study period

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