Size-related seed use by rodents on early recruitment of *Quercus serrata* in a subtropical island forest

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A B S T R A C T

Rodents are ubiquitous seed predators in nature and their size-related seed choice plays an important role in the plant's community structure. However, to understand how size-related seed predation by rodents affects plant recruitment, it is fundamental to predict seed and seedling response to rodent predation. We assessed the interactive effects between seed size and rodent exclusion on seed germination and early seedling survival of *Quercus serrata* in 10 subtropical forested islands in Thousand Island Lake, China. We found that rodent exclusion significantly improved the proportion of seed germination but not for early seedling survival. The proportion of seed germination in rodent-accessed plots was lower than rodent-exclosure plots and such reduction was strengthened by seed size. The proportion of early seedling survival was similar in both treatments and both increased with seed size. Our study found a significant size-related seed choice by rodents at the seed germination stage and showed that seeds would experience conflicting selective pressures across life stages in the early recruitment. Our findings highlight that size-dependent seed use by rodents is a key biotic factor to limit the oak early recruitment.

1. Introduction

Seed size is an important trait in plant life history and influences several components of plant performance, such as dispersal, fecundity, seedling growth as well as predation risk to natural enemies (Vander Wall, 2010; Cao et al., 2016; Fricke et al., 2019; Dylewski et al., 2020). Plants are faced with a trade-off of producing small or large seeds. Small seeds are energetically "cheaper" to produce and are dispersed by myriad diversity of agents (e.g., small animals, wind), but they have a lower ability to tolerate drought and other stressful situations. Large seeds could tolerate stressful conditions and provide more benefits in competition and extreme environments (Moles and Westoby, 2004). However, large seeds have a higher predation risk and a lower probability of being dispersed to proper sites due to few fecundities or relatively fewer proper dispersers (Tilman, 1994; Muller-Landau, 2010).

Seed predation by rodents is a particularly strong biotic filter capable of determining plant distribution and recruitment (Maron et al., 2018, 2019; Dylewski et al., 2020). Notably, seed predation by rodents is closely linked to seed size (Cao et al., 2016; Dylewski et al., 2020; Fricke and Wright, 2016). Such size-related seed predation could have important consequences on seed predation patterns among ecosystems and habitats with the variation of seed size distribution. A recent global *meta*-analysis demonstrated that small mammals (e.g., rodents) would prefer larger seeds in grasslands dominated by small-seeded species and prefer smaller seeds in tropical forests dominated by large-seeded species (Dylewski et al., 2020).

Furthermore, size-dependent seed predation by rodents could also affect plant recruitment and structure the plant communities (Howe et al., 2006; Maron et al., 2018, 2019). For example, the large-seeded preference of rodents would greatly limit the recruitment of large-seeded species (Maron et al., 2012), which might shift plant community composition in favor of small-seeded species (Allington et al., 2013). More importantly, seed size could link other plant life-history trade-offs that affect the plant-plant and plant-environment interactions (Moles and Westoby, 2004; Adler et al., 2014; Maron et al., 2018, 2019), consequently altering the coexistence of plant species. For

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instance, large-seeded predation by rodents could exacerbate discrepancies in the relative abundance of small- versus large-seeded species. This leads to a destabilizing effect on plant coexistence in the Chihuahua Desert of the southwestern USA, where small-seeded species are favored because of environmental variability (Chen and Valone, 2017). However, Maron et al. (2018) found a stable coexistence of small- and large-seeded species because of the large-seeded preference of rodents in perennial grasslands of Montana, USA. Hence, linking the effects of rodent predation on recruitment to seed size could shed light on the mechanism underlying plant coexistence and community assembly. Although a recent *meta*-analysis showed that the size-dependent seed predation by small mammals could have strong and directional effects on plant recruitment at global scales, the empirical study is still rare, especially needing for seed-sowing experiments (Dylewski et al., 2020).

Seed and seedling are considered critical stages in plant early recruitment (Zhang et al., 2017; Yi et al., 2019). Many studies have demonstrated that the high mortality caused by abiotic and biotic factors at these two stages is a bottleneck for plant early regeneration (Moles and Westoby, 2004; Collet and Le Moguedec, 2007; Fricke et al., 2014). Moreover, previous studies indicated that the effects of mortality factors might be different across life stages, which might cause ontogenetic conflicts (Schupp, 1995; Pérez-Ramos et al., 2012). For example, Fricke et al. (2014) demonstrated that rodent predation would cause higher distance-dependent mortality on plants at germination stage than seedling survival stage. Therefore, from a demographic perspective, the

conclusion that derived from a single life stage may yield misleading results if the outcome of abiotic and biotic factors is not consistent at other life stages (Fricke et al., 2014). Yet, many relevant studies on the consequence of seed predation by rodents only focused on one stage of plant life history, mainly targeting the seedling stage alone (but see Wotton and Kelly, 2011; Fricke et al., 2014; Gripenberg et al., 2014). Thus, we still need more empirical studies to assess how the consequences of size-related seed predation by rodents change across different stages in plant recruitment.

In this study, we conducted a seed-sowing experiment and investigated the consequences of size-dependent seed utilization by rodents on oak recruitment in a subtropical forest in China. We planted seeds of the *Quercus serrata* with different seed mass in plots with rodent exclosures and plots accessed by rodents on each study island. Our sampling design aimed to assess the interactive effects between seed size and rodent exclusion on seed germination and early seedling survival, which reflects the consequences of size-related seed selection by rodents on oak recruitment. Specifically, we expect that (1) rodent exclusion would have greater effects on seed germination of large versus small seeds because rodents prefer large seeds (Galetti et al., 2015; Maron et al., 2019); (2) rodents would not have significant effects on early seedling survival. Because granivorous rodents are mainly seed predators (Fricke et al., 2014). In addition, the nutrient loss during seedling development would also reduce the attraction of seeds to rodents (Cao et al., 2016); (3) thus, at the seedling survival stage, we expect that large seeds would
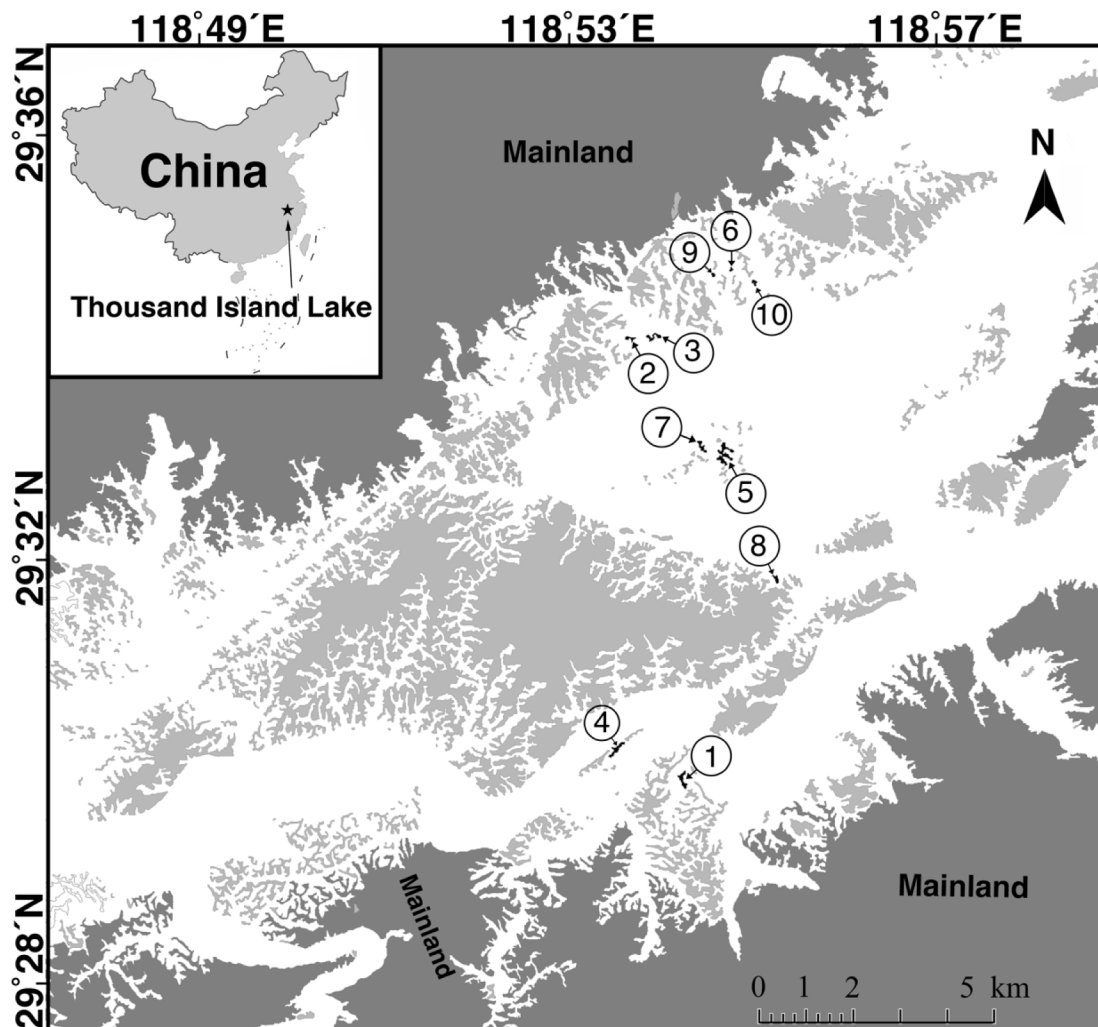

Fig. 1. The geographic distribution of 10 study islands in the Thousand Island Lake region, Zhejiang Province, eastern China.

positively determine the seedling survival. Because larger seeds could produce stronger root systems and large leaves (Leishman and Westoby, 1994) to resist light deficiency and insect herbivores in the understory.

2. Material and methods

2.1. Study site and species

Our experiments were conducted in the subtropical island forest in the Thousand Island Lake, China (2922′ – 2950′ N, 11834′ – 11915′ E; mean annual temperature 17 °C; mean annual precipitation 1430 mm, Fig. 1). It is a reservoir created by dam construction for hydroelectric production. The flooding transformed the previous continuous forest into fragmented forest islands, creating 1078 land-bridge islands with each area more than $> 2500 \, m^2$ at the highest elevation (108 m) of water (Si et al., 2018). The climate of the lake region is a typical subtropical monsoon. The forest on the islands was clear-cut and major vegetation now is secondary forest, dominated by *Pinus massoniana* (Hu et al., 2011; Liu et al., 2020). In the current study, we focused on the seed germination and early seedling survival of *Q. serrata* which is widespread in the lake region and mainly used by rodents in the fall. According to the previous rodent survey, *Niviventer confucianus* is the main predator of *Q. serrata* and the most abundant (84% of captured individuals) rodent species on islands (Zeng et al., 2019). Although the Eurasian jay, *Garrulus glandarius,* is also an important seed predator, we didn't consider this species because of its rare presence on our study islands.

2.2. Study islands and rodent survey

We conducted rodent surveys on 10 study islands (Fig. 1) from July to September in 2015 and 2016. Each study island had one transect with 10 steel-wired live traps (7.5 × 8.75 × 22.5 cm) spaced every 15 m. All traps were baited with fresh peanuts, and open for four consecutive nights. We rechecked all traps every morning and newly captured individuals were marked with uniquely coded ear tags. All captured individuals were identified to species and immediately released after body measurements. We used the number of new individuals per 100 trap-night to represent the relative abundance of rodents on each study island (Appendix A).

2.3. Seed addition and rodent exclusion experiments

At each study island, we established 16 plots (0.3 × 0.3 m) randomly across the rodent active section of the island but avoiding the edge of the islands. Half of the plots were fully accessed by rodents (thereafter control plots); the other half were closed to exclude rodent foraging. The rodent-exclusure plot had an exclosure (0.3 × 0.3 × 0.2 m) constructed by a metal-wired mesh with 1 cm holes. The bottom of rodent exclosures was buried 20 cm underground to avoid the access of rodents by digging holes. The top of rodent exclosure was topped by mesh to prevent rodents from climbing over.

The seed-sowing experiments were conducted on each study island in November 2015 and 2016. The ripe and sound seeds of *Q. serrata* were collected from the lake region during the seed fall peak in late October. Then, we planted 10 seeds into the rodent exclosure plots and control plots, respectively. The fresh mass of 10 seeds was averaged to represent the seed mass of each plot. We monitored all plots biweekly to record the number of seeds that germinated with a taproot ('germination' stage). The proportion of germination was calculated as the number of germinated seeds divided by 10 original experimental seeds. We checked all germinating seeds monthly until August next year (the end of the study period) to guarantee all the seedling's emergence after germination. For the proportion of early seedling survival ('seedling survival' stage), we defined it as the proportion of germinated seeds with seedlings that survived to the end of the study period. The proportion of early seedling survival used in the present study represents the probability of a

germinant becoming a survival seedling, which reflects the dynamic from the germination stage to the seedling survival stage (Fricke et al., 2014). For plots without seed germination, we could not calculate the proportion of seedling survival and thus these plots were excluded when we analyzed data at the seedling survival stage. In control plots, lost seeds would be hoarded by rodents and few of them might have a chance to germinate. Therefore, we made a conservative estimation on seed germination and early seedling survival in control plots. All seedlings that stemmed from experimental seeds were killed to ensure our experiments would not affect the dynamics of natural oak recruitment.

2.4. Statistical analysis

We analyzed our field data using generalized linear mixed-effects models with binomial error distribution weighted by the number of seeds initially planted inside each plot. The island mark was the random factor to account for the potential non-independence of the data across islands. To examine the effects of seed selection by rodents on the proportion of seed germination and early seedling survival, we ran generalized linear mixed-effects models with plot treatment, seed mass, and their interactive term as fixed factors. We particularly focused on assessing the seed mass by plot treatment interactions, since significant interactions could indicate that the significant effects of size-related seed selection by rodents on the proportion of seed germination and early seedling survival. The significance test of main factors and their interactions was performed by Wald Chi-square tests. All main factors were retained in the final models to facilitate showing their effects on predicted trends of seed germination rate and early seedling survival.

To reduce the effects of the different value range, we standardized the seed mass and defaunation by subtracting the mean value and divided by the standard deviation. The data analysis was conducted in R-4.0.0 develop environment (R Core Team, 2020) with packages of *lme4* (Bates et al., 2015) for generalized linear mixed-effects models, *car* (Fox and Weisberg, 2019) for Wald Chi-square tests.

3. Results

Overall, rodent-exclosure treatment enhanced the probability of seed germination significantly compared with control plots (Table 1, Appendix B), where we observed extensive evidence of rodents utilizing seeds (e.g., seed fragments, mouse feces) after seed addition. However, rodent-exclosure treatment had non-significant effects on the early seedling survival (Table 1, Appendix B). Of particular interest was how size-related seed utilization by rodents affected the proportion of seed germination and early seedling survival. Results showed that there was a significant seed mass × treatment interaction on the proportion of seed germination (Table 1, Appendix B) but not on early seedling survival (Table 1, Appendix B). At the seed germination stage, the germination rate was far lower in control plots than that in rodent-exclosure plots with increasing seed mass (Fig. 2a). At the seedling survival stage, early seedling survival was similar between both types of plots, and both increased with increasing seed mass of plots (Fig. 2b).

Table 1

Results of Wald Chi-square tests on the effects of seed mass, plot treatment (rodent exclosure vs. control), and their interaction on the proportion of seed germination and seedling survival in generalized linear mixed-effects model analysis. More details of parameters in models are in Appendix B.

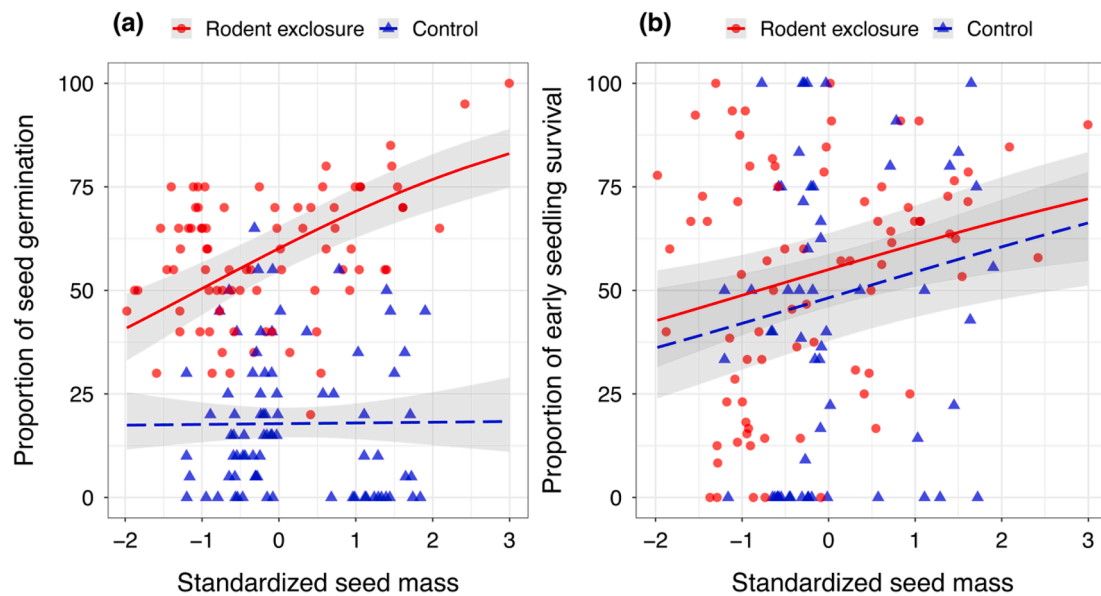|	Proportion of seed germination		Proportion of early seedling survival	
	χ^2	p	χ^2	p
seed mass	31.13	< 0.001	8.38	0.004
treatment	484.00	< 0.001	2.91	0.09
seed mass × treatment	15.45	< 0.001	0.72	0.40

Fig. 2. The interactive effects of plot treatment (rodent exclosure vs. control) and seed mass on the proportion of (a) seed germination and (b) early seedling survival. The colored circles and triangles are observed data. The lines are the predicted curve by the final generalized linear mixed-effects models. The red solid curve represents the predicted outcomes in rodent exclosures. The blue long dashed curve represents the predicted outcomes in control plots. The gray ribbon represents the standard errors estimated by models. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

We found that rodent-exclusion treatment improved the proportion of seed germination but not for the early seedling survival. Seed size had a switchable influence on how rodents operated the seeds from germination to seedling survival stage. At the germination stage, large seeds had a much lower proportion of seed germination in control plots, reflecting a large-seeded foraging preference of rodents. In contrast, such size-related seed preference of rodents had no significant effects on early seedling survival of different-sized seeds. Instead, seed size contributed more to determine the early seedling survival. Plots with larger seed mass had higher early seedling survival. These results indicate that there is an ontogenetic conflict between seed germination and early seedling survival.

Our results showed that the proportion of seed germination increased substantially after rodent exclusion, which is consistent with a previous study, where they found that rodents were a key factor to decrease seed germination (Fricke et al., 2014). However, the early seedling survival was not significantly changed after rodent exclusion. Hence, the impacts of rodents on seeds changes from germination to the seedling survival stage, a pattern not revealed by studies that only consider a single stage. One possible reason is that granivorous rodents are usually seed predators and might not consume much plant material. Therefore, rodent exclusion significantly improved the proportion of seed germination. The loss of nutrients in seeds due to seedling development might be another potential reason. With the development of seedlings, all the nutrients in cotyledon have been used to develop tissues, which will then be less attractive for rodents (Cao et al., 2016). Consequently, other mortality factors (e.g., insect, fungi, water, *etc.*) rather than rodents might determine the seedling survival at the seedling survival stage (Fricke et al., 2014). However, the proportion of seed germination and early seedling survival in our study is conservative. Because the final seed fates of lost seeds in control plots were not traced, there might be a chance to underestimate the seed germination. Hence, it might increase the differences of proportion of seed germination and early seedling survival between rodent-exclusion plots and control plots. Although our seed dispersal experiments in a previous study (Zeng et al., 2019; Zeng et al., 2021) showed that most rodent-hoarded seeds were finally predated and final probability of seedling survival was low

(4.37% on average), it is still necessary to trace the final seed fate of all lost seeds to more precisely assess the effects of rodents in further studies.

Seed size is considered an important trait to correlate with seed dispersal, seed germination, and seedling emergence (Vander Wall, 2010) because seed size is positively related to the ability to withstand several risks that seeds/seedlings may face in forests (Mendoza and Dirzo, 2007). Moreover, the seed size also affects the seed preferences of seed predators (Cao et al., 2016; Fricke and Wright, 2016; Moles et al., 2003). Our study showed that the seeds were more utilized by rodents in the control plots with larger seed mass at the seed germination stage (Fig. 2a), which reflected a potential large-seeded selection by rodents. A recent study focusing on the effects of conspecific seed size on seed and seedling survival also showed a similar pattern, i.e., that large seeds tended to be eaten after removal (Cao et al., 2016). Similarly, other studies focusing on seed size of single species also demonstrated that larger seeds were harvested by rodents preferentially (Gómez, 2004; Zhang et al., 2008). The simplest explanation could be that large seeds have more nutrients and energy, so they are valuable and more attractive to rodents compared with small seeds (Cao et al., 2016).

Besides that, some studies considering multiple plant species also showed similar results that the suppressive effects of seed predation by rodents on seed recruitment rate increased with increasing seed size (Reader, 1993; Vaz Ferreira et al., 2011; Maron et al., 2012; Maron et al., 2018, 2019). However, some other studies demonstrated the opposite results that small rodents would prefer small seeds and largely limit the recruitment of small-seeded plants (Dirzo et al., 2007; Mendoza and Dirzo, 2007). Contrasting results in effects of interspecific seed size demonstrated that not only seed size, but also other interspecific differences with regard to life history characteristics could determine the seed/seedling performance under a scenario of multiple plant species (Alcántara et al., 2000). As a result, interspecific tests for the relationship between seed size and seed predation by seed predators might show mixed results (Fricke and Wright, 2016). Thus, the experiments based on intraspecific comparisons are also needed to understand the effects of size on seed fitness (Alcántara et al., 2000; Fricke et al., 2019; Fricke and Wright, 2016).

Different from seed germination, we didn't detect the size-related preference of rodents at the seedling survival stage. But seed size had

positive effects on the proportion of early seedling survival in both types of plots (Fig. 2b). Rodents in our study are seed predators and consumer little plant materials of seedlings. Furthermore, nutrient loss with seedling development would also largely reduce the attraction of seedlings to rodents (Cao et al., 2016). Therefore, the abiotic factors (e.g., light and water) and other biotic factors (e.g., insects and fungi) would be the main determinants of seedling survival (Fricke et al., 2014; Gu et al., 2017; Sone et al., 2016). Large seed enables a seedling to allocate more energy to root development and thus produce an extensive and powerful root system to resist moisture deficiency (Leishman and Westoby, 1994). Such a powerful root system would help seedlings become well-established and produce more and larger leaves to resist light deficiency and insect herbivores in the understory. Hence, the increasing seed size improved the final proportion of seedling survival.

Our seed-sowing experiments in rodent-accessing plots versus rodent-excluded plots found a loss of size-related rodent choice from seed germination to seedling survival stages. It suggests a potential conflicting effect of rodents across different plant recruitment stages. Previous studies found that the seed preferences of rodents can be inconsistent across different life stages in plant early recruitment, causing conflicting selective pressures at different stages (Gómez, 2004; Muñoz and Bonal, 2008; Zhang et al., 2008; Cao et al., 2016). And such size-related selective pressure can even be offset by the opposite effect at another stage (Gómez, 2004; Zhang et al., 2008; Cao et al., 2016). Our study verified that rodent selection exerted more pressure on large seeds at the germination stage than that at the seedling survival stage. But higher early seedling survival of large seeds might offset the lower germination probability of larger seeds. The present results emphasized the importance of considering multiple life stages when assessing the effects of abiotic and biotic factors on seed/seedling performance (Fricke et al., 2014).

5. Conclusions

Rodent exclusion could enhance the proportion of seed germination but not for the early seedling survival. Rodents reduce oak recruitment with stronger effects on larger seeds due to size-dependent seed choice. Furthermore, our results indicate that seeds would experience conflicting selective pressures across life stages in the early recruitment. The present study highlights the importance of rodents as seed predators influencing plant recruitment through size-dependent seed utilization. Therefore, we appeal for treating seeds with repellants to protect seeds from rodent utilization, which might be a more effective method in oak management and restoration (Taylor et al., 2020).

CRediT authorship contribution statement

Di Zeng: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Software, Visualization, Writing – original draft, Writing – review & editing. **Mauro Galetti:** Conceptualization, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Juan Liu:** Investigation, Writing – review & editing. **Tinghao Jin:** Investigation, Writing – review & editing. **Yuhao Zhao:** Investigation, Writing – review & editing. **Ping Ding:** Conceptualization, Methodology, Supervision, Project administration, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119752.

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