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Dense understory dwarf bamboo alters the retention of canopy tree seeds

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ABSTRACT

Tree seed retention is thought to be an important factor in the process of forest community regeneration. Although dense understory dwarf bamboo has been considered to have serious negative effects on the regeneration of forest community species, little attention has been paid to the relationship between dwarf bamboo and seed retention. In a field experiment we manipulated the density of *Fargesia decurvata*, a common understory dwarf bamboo, to investigate the retention of seeds from five canopy tree species in an evergreen and deciduous broad-leaved mixed forest in Jinfoshan National Nature Reserve, SW China. We found that the median survival time and retention ratio of seeds increased with the increase in bamboo density. Fauna discriminately altered seed retention in bamboo groves of different densities. Arthropods reduced seed survival the most, and seeds removed decreased with increasing bamboo density. Birds removed or ate more seeds in groves of medium bamboo density and consumed fewer seeds in dense or sparse bamboo habitats. Rodents removed a greater number of large and highly profitable seeds in dense bamboo groves but more small and thin-husked seeds in sparse bamboo groves. Seed characteristics, including seed size, seed mass and seed profitability, were important factors affecting seed retention. The results suggested that dense understory dwarf bamboo not only increased seeds concealment and reduced the probability and speed of seed removal but also influenced the trade-off between predation and risk of animal predatory strategies, thereby impacting the quantity and composition of surviving seeds. Our results also indicated that dense understory dwarf bamboo and various seed characteristics can provide good opportunities for seed storage and seed germination and has a potential positive effect on canopy tree regeneration.

1. Introduction

Dwarf bamboo, a perennial evergreen, is broadly distributed in the understory of subalpine forests and some subtropical mountain forests in southwest China, Japan, and South America (Kudo et al., 2011; Lima et al., 2012; Taylor et al., 1996; Wang et al., 2009). It can quickly colonize forest gaps and other types of secondary open land due to its clonal growth; it often becomes the dominant species in the shrub layer of forest communities (Iida, 2004; Kudo et al., 2011; Taylor et al., 2004, 1996; Wang et al., 2009) and easily forms shallow cover (Wang et al., 2012). It is generally believed that a layer of solely dwarf bamboo has a negative impact on forest regeneration because of its clumped stem growth, intertwined bamboo rhizomes, and dense foliage. However, this is based on the observation that dense dwarf bamboo alters the seed density and composition of seed rain (Rother et al., 2009), has considerable influence on the ground surface microenvironment (i.e., light, moisture, temperature) (Campanello et al., 2007) and has serious negative impact on the growth and survival of tree seedlings and saplings (Kudo et al., 2011). We know little about the effects of a dense cover of dwarf bamboo on seed removal, especially how it alters seed removal due to composition, abundance, and behavior of animals. Addressing these questions is important for understanding the role of dwarf bamboo in forest community regeneration.

Tree seeds, the potential population of forest trees, are an important biotic basis for forest regeneration (Harper, 1977). Seed dispersal is an integral part of forest ecosystem function that directly contributes to seed fate and community regeneration, thereby affecting community species composition (Ferreira et al.,

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2011; Janzen, 1988; Rey and Alcantara, 2000). Seed dispersers, such as frugivorous birds (Karubian et al., 2012; Predavec, 1997), mammals (Yi and Zhang, 2008), and arthropods (Savolainen et al., 1989), may consume and damage many seeds in the process of seed dispersal, and this would reduce the fitness of plant species (Gomez, 2004; Munzbergova and Herben, 2005). However, seed dispersal by animals also has several benefits, including (1) escaping mortality (i.e., enhanced seedling survival away from parent trees); (2) directing seed dispersal to suitable sites (i.e., enhanced probability of germination and establishment of new individuals); and (3) colonization (i.e., enhanced seed deposition at unoccupied sites) (Schupp et al., 2010). Moreover, seed dispersal by animals promotes the natural regeneration of communities and the recovery of degraded ecosystem function (Gomez, 2004; Perea et al., 2011; Xiao et al., 2006). Hence, identifying the factors that impact seed dispersal by animals is extremely important.

Previous studies have not comprehensively considered the effects of dwarf bamboo density, animal groups, seed species, and other factors on seed dispersal (Iida, 2004; Rother et al., 2013); especially in complex forest communities such as those where dwarf bamboo is the dominant species in the shrub layer and influences the microenvironment (Campanello et al., 2007). Different animals could be subject to a trade-off between benefits and risks during the seed foraging and may adjust their behavior accordingly. The goal of this study is to better understand the effects of three animal groups (arthropods, birds and rodents) on the retention of canopy tree seeds in dwarf bamboo groves of different densities. Specifically, we seek answers to the following two questions: Do the different densities of dwarf bamboo groves affect the removal behavior of animal groups? Do animal groups demonstrate a selective removal behavior to different tree seeds in different densities of dwarf bamboo groves? Because many bird species locate seeds on the forest floor by flying or perching above the understory, we predict that dense bamboo will obscure their vision and reduce their efficiency of seed detection and removal. In contrast, rodents and macro-arthropods (e.g. beetles, ants) that tend to forage on the forest floor are likely to be affected less by bamboo cover density. To help answer these questions, we conducted a field experiment to study the relationship between animal groups and the retention of canopy seeds in different densities of dwarf bamboo groves by controlling the dwarf bamboo density and animal groups artificially. We selected the seeds, which differed in size, mass, and husk thickness, from five dominant canopy tree species. We hypothesized that 1) the seed removal of animal groups, particularly birds versus ground-dwelling rodents and macro-arthropods, whose foraging habits and activity space are mainly above dwarf bamboo and on the ground surface in bamboo groves, respectively, is different in dense dwarf bamboo; 2) different animals could deal differentially with the trade-off between benefits and risks during the seed foraging in bamboo groves and adjust their behavior accordingly, and demonstrate a selective removal behavior to different tree seeds in different bamboo densities; 3) seed retention is also associated with seed characteristics in different densities of dwarf bamboo groves.

2. Methods

2.1. Study site

The study was carried out in the Jinfoshan National Nature Reserve (28°46′–29°38′ N, 106°54′–107°27′ E, about 1450 m above sea level), Chongqing, China. The reserve is a karst geomorphic unit on a plateau watershed. The area has a subtropical monsoon climate with high relative humidity, an annual average temperature of 14.5 °C, average annual precipitation of 1395.5 mm, and average annual sunshine of 1091.6 h.

The selected evergreen and deciduous broad-leaved mixed forest, which possesses great timber volume and has a wide distribution, is a typical forest type in the Jinfoshan National Nature Reserve. The forest canopy is dominated by *Castanea henryi* (Skan) Rehd. et Wils., *Rhododendron faberi* Hemsl., *Symplocos setchuensis* Brand, *Elaeocarpus japonicus* Sieb. & Zucc., *Acer davidii* Franch., *Elaeocarpus sylvestris* (Lour.) Poir. and *Carpinus viminea* Lindl.. The understory vegetation is dominated by *Viburnum chinshanense* Graebn., *Eleutherococcus sieboldianus* Makino, *Nothopanax davidii* (Franch.) Harms ex Diels, *Rhododendron simsii* Planch and a diversity of dwarf bamboo species. Clonal dwarf bamboo, consisting of *Fargesia decurvata* J. L. Lu (height approximately 0.52 m, crown size: 0.4 cm × 0.4 cm), *Chimonobabusa utilis* (Keng) Keng f. (height approximately 3.12 m), and *Qiongzhuea communis* Hsueh (height approximately 1.51 m), commonly form a dense stratum near the forest understory in this area. In our study sites, *F. decurvata* was the categorical dominant species in the forest understory (Yi and Huang, 2004).

The study area is used by various mammals and birds. The common rodent species are *Apodemus agrarius* Pallas, *A. draco* Barrett-Hamieton, *A. speciosus* Temminck and *A. argenteus* Temminck, while the most common seed-eating birds are *Passer rutilans* Temminck, *P. montanus* Linnaeus, *Parus major* Linnaeus, *Streptopelia orientalis* Latham, *Aegithalos concinnus* Gould, and *Alcippe nipalensis* Hodgson (Peng et al., 1996).

2.2. Experimental design

2.2.1. Seed collection

During the seed-fall season in 2012, seeds with no apparent damage were collected from four species of dominant canopy trees in the study area (*E. sylvestris*, *E. japonicus*, *A. davidii*, *S. setchuensis*) and *Castanea mollissima* BL.; because seeds of *C. henryi* had been almost completely removed by predators we chose to replace them with seeds of the congeneric *C. mollissima*. These five species of canopy tree have significant differences in seed traits. We collected at least 750 healthy-looking seeds of each species for a total of more than 3800 seeds. After the seeds had been air dried, we used the flotation method to discard those infected by moths or beetle larvae (Gribko and Jones, 1995; Perez-Ramos and Maranon, 2008). We then selected eight seeds from each species, put a small mark on them with green dye, stored them in a paper bag (5 species × 8 seeds = 40 seeds/bag), and repeated this 72 times. These 72 bags were then stored in a refrigerator at 2–4 °C until the beginning of the experiment. A subsample of seeds in each species was used to measure seed traits (Table 1).

2.2.2. Arrangement of experimental areas

After reconnaissance we selected six blocks for sampling. Our criteria for blocks selection was that (1) the stands should have a relative flat topography; (2) the stands should represent the range of forest structure and species composition observed in the study area; (3) the stands' habitat should have little evidence of human disturbance (i.e., cut stumps); (4) the shrub layer in the stands should be dominated by *F. decurvata*, which was very dense and uniformly distributed, and the species composition of the overstory should be similar among the selected stands.

We counted the original number of the most dense dwarf bamboo (1 m × 1 m, n = 30) and used this number to represent a relative density of 100% as our reference in study area. Implementing, where necessary, the method of experimental symmetrical removal of dwarf bamboo, we created four treatments of dwarf bamboo densities, each with one of the following relative densities: 100% (76.29 ± 6.51 culm/m^2), 50% (38.11 ± 3.52 culm/m^2), 25%