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Fuelwood collection depresses the seed-dispersal service provided by rodents

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ABSTRACT

Understanding the interaction between plants and their animal seed dispersers is essential for predicting the effects of disturbances on ecosystems. Timber harvests, including fuelwood collection, cause changes in both biotic and abiotic environments and could substantially reduce the total amount of forestland worldwide, thereby having multiple impacts on wildlife. Fluctuations and behavioral alterations of some species have been observed within fuelwood-collection forests, but the implications for forest recruitment processes are unknown. Here, using the acorn–rodent system, we quantified the impacts of fuelwood collection on the process of seed dispersal in two types of fuelwood-collection forests (i.e., active and abandoned) and an unharvested control forest in the non-mast and mast seeding year. Fewer seeds were dispersed at shorter distances in the active fuelwood-collection forest relative to the control forest, indicating depressed seed dispersal. Although seed dispersal effectiveness (SDE) in the active fuelwood-collection forest was similar to that in the control forest in a non-mast seeding year (0.029 vs. 0.031), we detected a 54.6% reduction in the active fuelwood-collection forest (0.017 vs 0.038) in the mast seeding year. The number and distance of seeds dispersed in a fuelwood-collection forest that had been abandoned for over 15 years, was intermediate between the low values observed in the active fuelwood-collection forest and the higher values found in the unharvested control. This suggests some recovery of seed dispersal after fuelwood-collection ceases; however, the SDE in this forest type was the lowest in both non-mast and mast seeding years (0.016 and 0.010). These patterns in the seed dispersal process (apart from SDE in fuelwood-collection forests) were stronger in the mast seeding year than in the non-mast seeding year. Variations in food availability, habitat structure, environmental pressure, and the size and composition of the disperser community following the removal of canopy trees for fuelwood induced these depressed seed dispersal processes. Given wildlife's key roles in plant recruitment as seed dispersers, depressed animal-mediated seed dispersal as observed in this study may affect tree recruitment success and thus has wider implications for the spatial structure of plant communities in diverse forest ecosystems in which fuelwood is collected.

1. Introduction

Humans rely on forests to supply energy, food, and building materials, and also to provide ecosystem services such as carbon storage, biodiversity maintenance, and climate regulation (Trumbore et al., 2015). However, forest loss has been one of the most pervasive land surface transformations on Earth. Agroindustrial timber harvest constitutes a strong driver in the decline of forested landcover (Tyukavina et al., 2017). Although there are various types of timber harvests, one of the most significant types in the world today is fuelwood collection (Bearer et al., 2008). In developing countries, fuelwood collection accounts for 75% of wood harvesting and has been documented to cause forest degradation and biodiversity loss (Specht et al., 2015). Yet, despite the widespread recognition of the negative impacts of fuelwood collection on ecosystems, surprisingly little is known about how fuelwood collection affects forest regeneration.

The regeneration of woody plants is necessary to promote the resilience of forests, and further ensures the long-term stability of forest ecosystems and its services to human beings (Trumbore et al., 2015). Plant regeneration comprises a cycle of life stages from seeds to adult plants, and includes many key processes such as pollination, seed dispersal and seedling establishment (Wang and Smith, 2002). Among these, seed dispersal plays a central and critical role in shaping plant recruitment (Nathan and Muller-Landau, 2000). Dispersal of seeds away from parent trees potentially contributes to recruitment success, as it allows offspring to escape attacks by distance- and density-

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responsive natural enemies concentrated around parents (Connell, 1971; Janzen, 1970) and colonize favorable sites (Caughlin et al., 2015; Peres et al., 2016). Seed dispersal effectiveness (SDE) is the best parameter to quantify the contribution of seed dispersal to plant recruitment and is estimated by multiplying the quantity component by quality component of seed dispersal (Schupp et al., 2017).

However, the process of seed dispersal is being disrupted worldwide (McConkey et al., 2012; McConkey and O'Farrill, 2016). Although forest disturbance, including fragmentation, defaunation, and selective logging, has been documented to negatively affect seed dispersal and further reduce plant regeneration (Zhang et al., 2016; Zhou et al., 2013), the mechanisms whereby fuelwood collection influences this process remain poorly understood. Disturbance due to fuelwood collection induces changes in the behavior of remnant wildlife, potentially altering ecological functions like seed dispersal (McConkey and O'Farrill, 2016). This in turn leads to changes in forest structure, as seed dispersal determines the potential area of plant recruitment and shapes subsequent processes (Nathan and Muller-Landau, 2000), imposing a challenge for the conservation of biodiversity and ecosystem services (Bearer et al., 2008). Therefore, addressing this knowledge gap is vital for informing forest management strategies.

Here, we quantify how fuelwood collection potentially influences tree recruitment by altering seed dispersal processes. We focus on the interaction between rodents and oak acorns, the former of which act as conditional mutualists in this system because they both predate upon and disperse acorns. Some acorns encountered by rodents are eaten immediately, whereas others are dispersed and hoarded, which potentially promotes germination and survival compared with undispersed acorns, if the cached acorns are not recovered (Perea et al., 2011b). This interaction is highly context-dependent, and susceptible to changes in food availability and the abundance and composition of rodents (Kellner et al., 2016). Mast seeding (i.e. the synchronous intermittent production of large seed) is a very common phenomenon in many oak species that depend on scatter-hoarding animals for seed dispersal, which has been proved to increase animal dispersal and reduce predation, thereby facilitating the success of oak recruitment (Kelly and Sork, 2002; Vander Wall, 2002).

Disturbance caused by fuelwood collection influences forest structure, which has two possibly counteracting effects on the interaction between rodents and oaks (Kellner et al., 2016): (1) canopy tree removal due to fuelwood collection reduces the canopy cover, which may increase the predation risk perceived by rodents and thus influences acorn fate (Manson and Stiles, 1998) and (2) more light reaching the forest floor following canopy tree removal results in an increase in the density of understory vegetation (Kellner et al., 2016), which may provide improved ground-level cover for rodents and thus alters acorn removal. If, overall, the vegetation cover following fuelwood collection is of better quality and/or more abundant for rodents, then more acorns may be removed (Perea et al., 2011a), although cache recovery may also be enhanced (Perea et al., 2011b). In contrast, if overall cover is reduced and the risks perceived by rodents are high, they trade vigilance for shorter and fewer foraging bouts (Sunyer et al., 2013), and the probability of acorns being dispersed would be decreased. Both cases may influence oak regeneration.

Timber harvests alter soil, leaf litter, and canopy and understory composition, and thus affect food availability and shelter for small mammals (Kellner et al., 2013). The responses of these mammals typically depend on species and harvesting methods (Scott et al., 2006). Some species show a significant decline following clear-felling, whereas in contrast, many species successfully exploit the altered environments created by clear-cutting (Zwolak, 2009). This should come as no surprise because small mammals have largely evolved in an environment characterized by natural periodic disturbances (e.g., fires), and were influenced by serious climatic and vegetation changes during Pleistocene glaciations (Krojerová-Prokešová et al., 2016). Clear-cuts have both positive (Kellner et al., 2013; Urban and Swihart, 2010) and negative (Kellner et al., 2013) effects on the eastern chipmunk (*Tamias striatus*) and white-footed mouse (*Peromyscus leucopus*), whereas midstory removal has been found to have no significant effects on small mammal abundance (Kellner et al., 2016). Canopy trees removal by fuelwood collection may alter food abundance and shelter for granivores due to a decrease in seed production and an increase in the density of understory vegetation, which could influence their behavior and population size, and by extension, potentially influences their role in the seed dispersal process. However, little information is available on the responses of small-mammals to fuelwood harvest in terms of population size and seed-dispersal service.

To better understand how fuelwood collection affects the plant regeneration process via its influence on seed dispersal and fate, four metrics were measured by tracking the fate of *Quercus aliena* var. *acuteserrata* seeds in three different forest types (i.e., active fuelwood-collection forest, abandoned fuelwood-collection forest, and control forest) in the non-mast and mast seeding year: (1) seed predation and survival, (2) number of seeds dispersed, (3) seed dispersal effectiveness (SDE, a more ecologically relevant metric that evaluates the contribution of rodent to oak recruitment, which is calculated as the product of the probability of acorn removal and acorn survival given removal; Kellner et al., 2016; Schupp et al., 2017), and (4) seed dispersal distance. After the completion of the seed dispersal experiment, rodent abundances were also surveyed in our sampling units to identify changes that may affect acorn predation and dispersal. Considering the critical role of rodents in seed dispersal (Lichti et al., 2017), we predicted that disturbance attributed to fuelwood collection would cause (i) a decline in the number of seeds dispersed and SDE due to canopy tree removal by fuelwood collection, and (ii) a decrease in seed dispersal distance and an increase in seed predation as a consequence of the response of animal seed dispersers to disturbance.

2. Materials and methods

2.1. Study site and species

Fieldwork was conducted on the southern slope of the Shennongjia region (31°19′N, 110°29′E), in central China. This area is characterized by a typical subtropical monsoon climate, with an annual precipitation of 1350 mm and annual mean temperature of 10.6 °C (Xie, 2012). The climax vegetation is montane evergreen and deciduous broad-leaved mixed forest, including *Quercus* spp., *Fagus* spp., and *Cyclobalanopsis* spp. (Zhu, 2011; Xie, 2012).

The study species, *Quercus aliena* var. *acuteserrata*, is a widespread deciduous broad-leaved tree within our study area. It is a mast seeding species, which produces wind-pollinated catkins from March to April, and bears mature fruits (i.e., acorns) from October to November. At the study site, rodents, mainly *Niviventer confucianus* and *Leopoldamys edwardsi*, remove and hoard its seeds (Chen, 2004). Oaks, like *Q. aliena* here, are major tree species used for fuelwood collection by residents in the montane subtropical and temperate forests in Asia.

2.2. Quantifying forests characteristics

To assess the effects of fuelwood collection on seed dispersal by rodents, three forest sites with canopies dominated by *Q. aliena* (up to 90%, Chen, 2004) were selected: one characterized by active fuelwood collection (i.e., active fuelwood-collection forest site), one that had fuelwood collected in the past (before 1995) but is currently abandoned (i.e., abandoned fuelwood-collection forest site), and one control forest, in which there has been no collection. The active fuelwood-collection forest site is being disturbed by the collection of dry wood on the forest floor and the felling of entire live trees (diameter at breast height > 10 cm). Other lesser disturbances include the occasional stocking of chickens, collection of mushrooms by residents, and barking of dogs. The abandoned fuelwood-collection forest site has recovered over