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Midstory removal reduces effectiveness of oak (*Quercus*) acorn dispersal by small mammals in the Central Hardwood Forest region

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ABSTRACT

Timber harvests that aim to promote oak (*Quercus*) regeneration may have indirect impacts on seedling recruitment by altering trophic interactions between oak and animals. For example, changes in habitat structure following harvest may alter the conditionally mutualistic relationship between oak and small mammal granivores like the gray squirrel (*Sciurus carolinensis*), eastern chipmunk (*Tamias striatus*) and white-footed mouse (*Peromyscus leucopus*) that act both as acorn predators and as dispersers. Over 4 years (2010–2013), we tracked the fate of a total of 8000 tagged acorns placed beneath black (*Quercus velutina*) and white oaks (*Quercus alba*) at 5 control (unharvested) sites and 5 sites where the midstory was removed as part of a three-phase shelterwood harvest in an oak-dominated forest in southern Indiana, USA. We found that acorns in harvested sites were more likely to be taken by granivores and were less likely to survive the winter, resulting in an overall 67% reduction in seed dispersal effectiveness (SDE). Harvested sites had more vegetative cover and coarse woody debris in the understory, providing increased cover from aerial predators and potentially facilitating greater acorn removal and a higher probability of cache recovery. Reduced seed dispersal effectiveness following midstory removal has potential to slow accumulation of oak regeneration prior to overstory removal and therefore to reduce the effectiveness of shelterwood treatments in promoting future oak dominance in harvested stands. Augmentation of shelterwoods with prescribed fire or other treatments to reduce understory density may counter this effect.

1. Introduction

Oak (*Quercus*) is an important genus of overstory trees in hardwood forests throughout the eastern deciduous forests of the United States (Ellison et al., 2005; Fralish, 2004), providing a crucial food resource (acorns) to nearly 100 animal species (Martin et al., 1961). Over the past century, changes in forest disturbance regimes highlighted by widespread fire suppression have contributed to an oak regeneration failure (Brose et al., 2001). As a result, overstory oaks are being replaced by other, more shade-tolerant species throughout the eastern forest (Abrams, 1992; Aldrich et al., 2005; Crow, 1988; Nowacki and Abrams, 2008). Loss of oak in the hardwood forest overstory could be catastrophic for the many wildlife species that rely on acorns as a food source (McShea et al., 2007).

Timber harvest can be used to create artificial disturbance (via overstory removal) favoring maintenance of oak as a canopy dominant (Johnson et al., 2009). Shelterwood harvesting, in which the overstory is removed in a series of partial harvests, appears particularly well-suited to promote oak regeneration (Johnson et al., 2009). The primary goal of the shelterwood approach is to generate enough competitive advanced oak regeneration underneath the partial canopy to ensure continued dominance of oak after removal of the remaining canopy (Johnson et al., 2009; Loftis, 1990; Schlesinger et al., 1993). While harvesting can create favorable light regimes for oak regeneration, it also alters habitat structure for animals (Hunter, 1990). The oak regeneration process will be impacted indirectly by harvest if trophic interactions between animals and oak (e.g. herbivory, seed predation, or seed dispersal) are also altered by these changes in habitat (Alverson et al., 1988; McConkey et al., 2012).

One key trophic interaction for oak in eastern deciduous forests involves granivorous small mammals which can serve both as acorn predators and dispersal agents. The eastern chipmunk (*Tamias striatus*), white-footed mouse (*Peromyscus leucopus*) and eastern gray squirrel (*Sciurus carolinensis*) rely on acorns as a primary food source. Some acorns encountered by these granivores are eaten immediately, while others are dispersed and cached for later use (Steele and Smallwood, 2002). If cached acorns are not

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recovered, they are usually in a better position to germinate than undispersed acorns remaining on the surface under the parent tree (Haas and Heske, 2005; Steele and Smallwood, 2002; Vander Wall, 2001). Thus, the overall effect of granivorous rodents on oak is conditionally mutualistic and falls somewhere on the spectrum from seed predator (negative) to dispersal agent (positive) (Theimer, 2005; Xiao and Krebs, 2015; Zwolak and Crone, 2012). A community's position on this spectrum can shift as a function of multiple environmental variables influencing granivore foraging behavior. For example, when ambient food availability is high relative to the size of the granivore population, granivores are less dependent on stored food and so many cached seeds will escape predation (Bergeron et al., 2011; Jansen et al., 2004; Janzen, 1971; Lichti et al., 2014; Schnurr et al., 2002; Vander Wall, 2010).

Habitat structure can also impact granivore foraging behavior, and thus influence seed fate. In forested habitat, for example, canopy cover mediates predation risk for small mammals (Bowers et al., 1993; Manson and Stiles, 1998), and small mammals adjust their behavior in response to varying levels of risk. For example, eastern chipmunks gather and carry smaller seed loads under more open canopies (Bowers and Ellis, 1993) and are more vigilant when adjacent to clearcut canopy openings relative to continuous forest (Mahan and Yahner, 1999). Similarly, gray squirrels consume food more quickly when further from cover and under higher predation risk (Newman et al., 1988). In the forest understory, vegetative cover allows small mammals to devote more attention to foraging, resulting in higher seed removal rates (Perea et al., 2011a; Pérez-Ramos and Marañón, 2008; Royo and Carson, 2008) and a greater probability of cache retrieval (Perea et al., 2011b).

Disturbance caused by shelterwood harvest impacts forest structure and, by extension, potentially impacts the trophic interaction between granivores and oak. For example, the initial phase of a 3-stage shelterwood harvest typically involves removal of midstory and some small overstory trees (hereafter "midstory removal") (Kalb and Mycroft, 2013). This removal has two important and possibly counteracting effects at different forest strata. First, there is a modest reduction in canopy cover, which may increase the predation risk perceived by granivores (Bowers et al., 1993; Manson and Stiles, 1998). Second, more light reaching the forest floor following midstory removal results in an increase in the density of understory vegetation (Kellner et al., 2014; Paquette et al., 2006; Quinby, 2000), which may provide improved ground-level cover for granivores. Depending on the relative strength of these two effects, perceived predation risk may change. If, overall, there is better quality and/or more abundant cover for granivores following midstory removal, then rates of acorn removal may increase (Perea et al., 2011a; Pérez-Ramos and Marañón, 2008; Royo and Carson, 2008) but cache recovery may as well (Perea et al., 2011b). If cover is reduced overall following midstory removal, fewer acorns may be dispersed. In either case, there are implications for oak regeneration success.

Because it is important to accumulate oak advanced regeneration in the early stages of a shelterwood harvest system (Johnson et al., 2009), understanding how harvest disturbance impacts seed predation and dispersal is a key research goal. Previous studies showed that seed removal by granivores appears initially to be unaffected by shelterwood harvest (Bellocq et al., 2005; Kellner et al., 2014). Measuring removal is attractive because it is easy to estimate: seeds are monitored and the rate at which they disappear is noted. However, equating removal with seed mortality is problematic; many seeds removed by predators may ultimately be cached and survive to germination (Moore and Swihart, 2008; Vander Wall et al., 2005), and these cached seeds may in fact be more likely to recruit successfully than seeds left under the parent tree (García et al., 2002; Gómez et al., 2008; Haas and Heske, 2005). Further, solely estimating removal provides no information about dispersal distance.

Seed dispersal effectiveness (SDE) is a more ecologically relevant metric to evaluate seed predation and dispersal, where SDE is calculated as the product of the probability of seed removal and seed survival given removal (Schupp et al., 2010). Increasing SDE for a given tree implies greater seedling recruitment (Schupp et al., 2010) working under the assumption that seeds left undispersed under the parent tree are unlikely to recruit successfully (Theimer, 2005). This is a reasonable assumption for oak acorns for several reasons: (1) there are numerous other acorn predators in eastern forests besides granivorous small mammals that do not also disperse acorns (Martin et al., 1961), (2) acorns left on the soil surface have much lower germination probabilities than when cached (García et al., 2002; Gómez et al., 2008; Haas and Heske, 2005), and (3) the relative shade intolerance of oak means seedlings that did recruit underneath the parent tree canopy would likely suffer low growth and high mortality (Beckage and Clark, 2003; Crow, 1992).

To better understand how midstory removal may indirectly affect the oak regeneration process via impacts on acorn dispersal and fate, we measured removal, SDE, and median dispersal distance for acorns of two oak species (black oak *Quercus velutina* and white oak *Quercus alba*) in midstory removal and unharvested control treatments over 4 years and for multiple components of the granivore community. Concurrently, we measured forest structure in the two treatments to identify changes that may affect acorn predation and dispersal. To account for variability in ambient food availability, we also measured acorn production and granivore abundance. We hypothesized that increased cover for granivores in the understory would outweigh the effects of lower canopy cover following midstory removal, facilitate higher rates of removal and cache recovery, and thus reduce SDE relative to the unharvested control.

2. Material and methods

2.1. Location

The study was conducted in Morgan-Monroe and Yellowwood State Forests in south-central Indiana, U.S.A., part of the Central Hardwood Forest region (Fralish, 2003) (Fig. 1). The two forests together comprise >19,000 ha and are composed predominantly of upland areas with steep slopes (25–35%) and silt-loam soils (Jenkins and Parker, 1998). The forest overstory is dominated by oaks (*Q. alba*, *Q. velutina*, *Quercus rubra*, and *Quercus prinus*) and hickories (*Carya* spp.) whereas the midstory and understory is composed mainly of shade tolerant species including sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*). Tree density ranges from 923 to 1527 trees/ha and basal area from 21.7 to 29.9 m^2/ha (Saunders and Arseneault, 2013). The predominant acorn consumers include white-tailed deer (*Odocoileus virginianus*), wild turkey (*Meleagris gallopavo*), gray squirrel, eastern chipmunk, white-footed mouse, blue jay (*Cyanocitta cristata*), tufted titmouse (*Baeolophus bicolor*), and various woodpeckers (*Picadae*) (Kellner et al., 2013; McShea and Healy, 2002; Richardson et al., 2013). Of these, the gray squirrel and blue jay, and to a lesser extent the eastern chipmunk and white-footed mouse, also serve as important dispersal agents for oaks (Moore and Swihart, 2006; Moore et al., 2007; Sork, 1984; Steele et al., 2006).

The forests in this study are managed for multiple uses including recreation and timber production. Historically, forest management in the area consisted of group and single-tree selection (Carman, 2013; Jenkins and Parker, 1998). In 2006, the Hardwood Ecosystem Experiment (HEE) was established in the state forests to