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Small mammal responses to forest management for oak regeneration in southern Indiana

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ABSTRACT

We used a 5-decade chronosequence of harvest openings to characterize population and community-level responses of small mammals to forest management targeting oak regeneration in southern Indiana. Live-trapping at 42 different sites allowed modeling of occupancy and relative abundance using environmental covariates while incorporating imperfect detection. Species richness was higher in smaller openings on southwest-facing aspects. Similarity between species richness of different age classes decreased with increasing site age. Eastern chipmunk (*Tamias striatus*) relative abundance was greater in early seral stages, i.e., at young sites with low basal areas. Relative abundance of white-footed mice (*Peromyscus leucopus*) exhibited different responses to coarse woody debris on sites versus microsites. Pine voles (*Microtus pinetorum*) and short-tailed shrews (*Blarina brevicauda*) were more likely to occupy older sites. We observed a greater relative abundance of short-tailed shrews at sites with steep and northeast-facing slopes. Northeast-facing slopes also resulted in higher short-tailed shrew occupancy rates. Incorporating detection probability enabled us to derive more accurate estimates of relative abundance and, when coupled with a Bayesian framework, permitted the estimation of occupancy for uncommon species. Our estimated responses can be used by forest managers to determine the potential impacts of even-aged and uneven-aged oak management on small mammals, and the statistical methodology we used can be applied even more broadly to improve understanding of wildlife responses to forest management.

1. Introduction

Oak-hickory (*Quercus-Carya*) hardwood stands influence biodiversity, energy flow, nutrient dynamics, and hydrology of landscapes (Ellison et al., 2005; Johnson et al., 2002; McShea and Healy, 2002). Oak and hickory are important in regulating wildlife through mast, which supplies a critical energy source during winter months and positively influences small mammal abundance (Clotfelter et al., 2007; Jones et al., 1998; McShea et al., 2007; Smith and Scarlett, 1987; Wolff, 1996). Oak-hickory mast has increased in importance due to the disappearance of American chestnut (*Castanea dentata*) during the first half of the 20th century and the current decline of American beech (*Fagus grandifolia*) (Healy et al., 1997; McShea et al., 2007).

Over the past several decades, suppression of fire regimes has produced conditions favoring late successional, shade tolerant species such as maple (*Acer* spp.) in the understory instead of disturbance-dependent, shade-intolerant oak (Abrams, 1992, 2003; Cho and Boerner, 1991; Fralish, 1988, 1997; Fralish and McArdie, 2009). Considerable research has focused on forest management strategies to reverse declines in oak regeneration (Albrecht and McCarthy, 2006; Brudvig, 2008; Povak et al., 2008). An important corollary of this work is to develop a greater understanding of wildlife responses to these management strategies.

Small mammals are important components of forest ecosystems, where they function as primary and secondary consumers, dispersers of seeds and mycorrhizal fungi (Maser et al., 1978; Moore et al., 2007), staple items of prey for numerous vertebrate predators (Whitaker and Hamilton, 1998) and agents of soil aeration and enrichment (Abaturov, 1972; Bakker et al., 2004; Hole, 1981). As primary consumers, they are also important for managers to monitor due to their potentially negative impact on tree regeneration. Studies examining responses of small mammals to clearcuts, an approach commonly applied to regenerate oak (Hannah, 1987), have produced mixed results. In eastern deciduous forests, white-footed mice, *Peromyscus leucopus*, appear to respond in a neutral or positive manner shortly following clearcutting, although negative responses were reported in two studies (Fantz and Renken, 2005; Healy and Brooks, 1998; Schmid-Holmes and Drickamer,

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2001, review by Kirkland, 1990). Eastern chipmunks, *Tamias striatus*, exhibited both negative and positive numerical responses at latitudes slightly north of southcentral Indiana, the area in which we conducted our study (Kirkland, 1990). Measured short-term effects of harvest on short-tailed shrews, *Blarina brevicauda*, generally have been neutral or negative (Ford et al., 1997; Healy and Brooks, 1998; Kirkland, 1977a,b, but see Mitchell et al., 1997). Responses of various species of *Sorex* have tended toward neutral or positive, with exceptions (Kirkland, 1990). Fewer studies have examined the effects of uneven-aged management on small mammal populations. Soricid abundance did not change with partial over-story removal (Ford and Rodrigue, 2001). *Peromyscus* spp. exhibited positive responses shortly after uneven-aged harvests (Fantz and Renken, 2005).

The inability to infer general patterns of small mammal responses to even- and uneven-aged management of hardwood stands in prior studies may reflect temporal or spatial variation in factors regulating demography. Alternatively, general patterns in mammalian responses may have been masked in part by methodological shortcomings of these studies. Specifically, the studies cited in the previous paragraph used number of individuals captured, or captures per unit of effort, as population and community response variables. Because trapping yields a count of individuals detected, C, a canonical estimate of population size, N, can be expressed as $N = C/\beta$, where β is the probability of detecting an individual in the population (Williams et al., 2002, p. 244). Likewise, trapping yields a count of species detected, K, resulting in a canonical estimator of species richness, $S = K/p$, where p is the probability of detecting a species, given its occurrence in the community (Williams et al., 2002, p. 556). By failing to incorporate explicitly β and p, prior analyses of small mammal responses to timber harvest have assumed that probability of detection does not vary among sites or species. Unfortunately assuming perfect or homogeneous detection can lead to substantial bias (e.g., MacKenzie et al., 2006; Nichols, 1992). In addition, prior studies often have focused on common species because sample sizes associated with rarer species were too small to warrant conventional analyses (e.g., Fantz and Renken, 2005; Schmid-Holmes and Drickamer, 2001). We addressed each of these issues, thereby overcoming potential deficiencies associated with prior studies.

For analysis of species occupancy patterns and community-level responses to harvest and environmental covariates, we used a hierarchical Bayesian (HB) multi-species site occupancy model that also accounts explicitly for imperfect detection of species (Russell et al., 2009). The model allows for estimation of occupancy and detection rates for each individual species, incorporation of site- and species-level covariates, and approximation of the uncertainty associated with parameter estimates. An important advantage of the multi-species model of Russell et al. (2009) is its hierarchical structure, because it affords increased precision of estimators due to the sharing of information across species; i.e., the structure provides a composite estimate that applies to the community of observed species versus only those species that meet some arbitrary sample size threshold (Sauer and Link, 2002). For comparison of population responses, we incorporated detection probability using the abundance model of Royle and Nichols (2003) and bootstrapped encounter histories to obtain site-specific estimates of precision (Buckland et al., 2009).

Our objective is to characterize population and community responses of small mammals to forest stands managed for oak regeneration in southern Indiana. By using improved occupancy and abundance estimation methods that incorporate probability of detection, we derived more accurate estimates for a larger number of species than in prior studies. We hypothesize that when using these methods rodent populations will have higher abundances and shrew populations will have lower abundances in recently harvested openings. Also, we hypothesize that species richness will be greatest in older openings.

2. Materials and methods

2.1. Study area

Long-term studies can capture the large fluctuations in population dynamics of small mammals often missed by shorter-term research, but their cost can be prohibitive (Swihart and Slade, 1990). Chronosequences offer an alternative to longitudinal studies and can lead to working hypotheses regarding wildlife responses to forest management. A chronosequence involves sampling sites of similar habitat types that have had similar forest management treatments applied to them at varying times. Thus, sites of varying ages after treatment are selected for study and are representative of different seral stages (Fernandez et al., 1994; Ford et al., 2002; Homyack et al., 2005; Stuart-Smith et al., 2006). Chronosequences allow insights into responses developing over decades by taking a "snapshot" of conditions for sites of varying ages over a short period of time.

We sampled small mammals along a harvest chronosequence at Crane Naval Surface Warfare Center (NSWC) located in Martin County, IN (38°52′00″N/86°50′00″W). NSWC was first established in 1935 as a state forest and was later expanded to its current size (255 km^2) by the U.S. Navy in 1941. Before NSWC establishment, the land had been cleared by farmers using fire to permit agriculture and grazing. From 1940 to 1950, most of NSWC was allowed to succeed to forest. During this time, contracts for crop tree releases, such as cleanings and improvement cuttings, were used to reduce oak competitors at NSWC. These contract incentives, along with the previous human disturbances, encouraged high amounts of oak regeneration (T. Osmon, NSWC forester, pers. commun.). Currently, 82.5% of the base is forested, and harvest rates have not changed much since the 1950s. Approximately 1300–1500 ha per year are harvested, with about 180–200 ha in openings. As the NSWC forest matured, management practices before the 1990s had limited success in maintaining the high oak density due to a high proliferation of yellow poplar, *Liriodendron tulipifera*, and lack of human disturbance. Current harvest practices focus on clearcuts >2 ha and single-tree or group selection cuts ≤2 ha on south- or west-facing slopes to encourage oak regeneration. Occasional post-harvest timber stand improvement includes releasing oak seedlings 10 and 20 years after the initial cut, creating snags out of competing tree species and leaving all downed woody debris (T. Osmon, pers. commun.).

We selected six post-harvest age classes for sampling across the chronosequence: 1–2, 4–6, 8–10, 12–16, 27–33, and >40 years. The stands >40 years old have not been harvested since NSWC inception. Eight sample sites of each age class were chosen randomly from a larger set of possible sites using a GIS data layer. Within each age class, selected sites were constrained further to fall into two area classes (0.8–1.6 ha and 1.7–8.1 ha) and two aspects (northeast-facing slope, 5–85° azimuth, and southwest-facing slope, 185–265° azimuth). The small area class was comprised of group selection stands within a larger mature stand with an uneven-aged management regime. The larger area class was comprised of even-aged clearcuts created to replace an entire stand. The sampling design thus consisted of 6 age classes × 2 size classes × 2 aspects. Not all 48 age × size × aspect combinations were found within NSWC. Consequently, a total of 42 sample sites were chosen, with 22 sites sampled in 2007 and 20 in 2008 (Fig. 1). Additionally, one sample site from each of the six age classes was chosen for sampling in both years to assess inter-annual variation.