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Peromyscus responses to alternative forest management systems in the Missouri Ozarks, USA

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ABSTRACT

Operational-scale forest management experiments are long-term investments because harvest treatment effects may be dynamic throughout one or more rotation lengths. We examined deermouse (*Peromyscus* spp.) abundance over the first 20 years of the Missouri Ozark Forest Ecosystem Project (MOFEP), which assesses ecological responses to even-aged, uneven-aged, and no-harvest forest management systems applied at landscape scales in the Missouri Ozarks. In the spring of each of 11 sampling years, we sampled *Peromyscus* populations on two permanent trap grids on each of nine study sites ($n = 3$ sites per management system). Management entries occurred in 1996 and 2011, with small mammal sampling conducted during two pre-treatment years (1994–1995), and Years 2–5 (1998–2001), Years 13–14 (2009–2010), and Years 16–18 (2012–2014) after the first entry. We estimated abundance for each grid in each sampling year with Bayesian closed-population mark-recapture models, and modeled variation in abundance with negative binomial log-linear mixed effects models. Uneven- and even-aged management systems caused similar increases in *Peromyscus* abundance that were detectable shortly after the first management entry [proportional effect of even-aged management on *Peromyscus* abundance vs. no-harvest management: posterior median = 1.8, 95% credible interval 1.0–3.2; proportional effect of uneven-aged vs. no harvest management = 1.7 (1.0, 2.8)]. These effects were not surprising given positive effects of harvest treatments on understory cover and food resources. However, the consistency of this increase was less expected, as we observed no conclusive dissipation of harvest effects even in Years 13–14 after the first entry or amplification of harvest effects after the second entry. Observing extremely high system-wide yearly variation in *Peromyscus* abundance, we did not detect evidence of increasing divergence in effects of these three management systems or of any area-wide trends in abundance during 1994–2014. However, over subsequent decades, we expect higher potential for divergence in *Peromyscus* abundance as the three management systems differentially shape forest structure and tree species composition. Thus, the MOFEP study offers a unique framework for building and testing hypotheses about patterns and mechanisms of long-term changes in Ozark forests and effects on vertebrate communities.

1. Introduction

Controlled experiments at operational scales allow direct statistical inference about effects of forest management treatments, using randomization and pre-treatment measures to reduce effects of potential confounding factors that may be impossible to address adequately in non-experimental studies (Ganio, 2006; Monserud, 2002; Sheriff and He, 1997). However, when experimental treatments involve harvesting

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mature forests, such studies face the challenge that the full responses to forest disturbances can unfold over temporal scales ranging from short-term immediate effects and year-to-year early successional dynamics, to decadal- and century-scale changes (Franklin et al., 2002; Gill et al., 2017; Lindenmayer and Laurance, 2012; Oliver, 1980; Olson and Saunders, 2017). This challenge is especially relevant for understanding responses by forest-floor small mammals, which are a frequent research component of multidisciplinary operational experiments (Converse et al., 2006; Fantz and Renken, 2005; Kellner et al., 2013; Lehmkuhl et al., 1999). Although small mammal populations can show especially strong changes in the first few years after canopy-removing disturbances (Gashwiler, 1970b; Kirkland, 1990; Sullivan et al., 2008), responses r1emain dynamic over subsequent stages of stand development (Ecke et al., 2002; Fisher and Wilkinson, 2005; Sullivan et al., 1999; Zwolak, 2009). Decades after a disturbance, small mammal populations may continue to be shaped by the disturbance's long-term effects on key habitat characteristics such as abundance of large down logs (Carey and Johnson, 1995) and abundance and species composition of mast-producing trees (Ostfeld et al., 1996; Wang et al., 2009). Even in the absence of physical disturbances, populations of small mammal taxa such as deermice (*Peromyscus* spp.) can show enormous temporal variation in abundance due to extrinsic variability in food resources and weather along with intrinsic effects of density dependence at intra- to interannual time scales (e.g. Lewellen and Vessey, 1998; Luis et al., 2010; Wang et al., 2009). Such variation creates the potential for corresponding temporally heterogeneous population responses to manipulative treatments (sensu, for example, Seamon and Adler, 1996; Wheatley et al., 2002). Conversely, examining treatment effects in the context of background spatial and temporal variation may provide a better understanding of the relative importance of forest management as an agent of population change.

One of the longest-active multidisciplinary forestry experiments using large-scale operational treatments is the Missouri Ozark Forest Ecosystem Project (MOFEP) in southeastern Missouri, USA (Knapp et al., 2014). This Missouri Department of Conservation (MDC) study was initiated in the early 1990s to help managers better understand the impacts of harvest practices in state-owned forests of the region. Intended to be a multi-century study, MOFEP compares long-term application of three operational management systems (i.e. three experimental treatments: no-harvest management, uneven-aged management, and even-aged management) applied on a 100-year rotation length to several-hundred ha experimental sites (Brookshire and Shifley, 1997; Shifley and Kabrick, 2002). Individual management entries occur periodically, with each entry affecting a subset of the stands within each site. Compared to stand-level studies, a long-term perspective is especially critical in MOFEP given that experimental treatments are long-term applications of management systems at the scale of local landscapes. After two decades of data collection in core research areas (Knapp et al., 2014), the experiment has reached a uniquely valuable stage in which researchers and managers can begin comparing long-term effects of the three management systems (e.g. Morris et al., 2013; Olson et al., 2015; Olson et al., 2017; Rota et al., 2017).

During the first five years post-treatment in MOFEP, uneven- and even-aged management had similar positive effects on relative abundance of *Peromyscus* spp., the primary taxa captured in the study's small mammal component (Fantz and Renken, 2005). Specifically, harvest treatments appeared to buffer populations from an apparent regional multi-year decline in abundance documented on no-harvest sites. It was unknown whether this multi-year decline was part of a longer term trend, but this possibility highlights an additional temporal complexity that can be assessed with long-term studies. Operational experiments such as MOFEP take place in forest ecosystems that may be undergoing broader directional changes due to factors such as climate change, introduced diseases, and altered disturbance patterns (Gillen and Hellgren, 2013; Hanberry et al., 2014; Olson et al., 2014; Zenner et al., 2006). Thus, there is potential for interactions between experimental treatments and larger scale agents of change (Olson et al., 2017).

Building on previous work by Fantz and Renken (2005), we examined patterns of change in *Peromyscus* abundance for 11 years of sampling during the first 20 years of the MOFEP small mammal study. Timing of sampling was tied to the first (1996) and second (2011) management entries. Sampling occurred in four groups of years: pre-treatment (1994–1995), and Years 2–5 (1998–2001), Years 13–14 (2009–2010), and Years 16–18 (2012–2014) after the first management entry, with the last group covering the first three years after the second management entry. We focused on several questions about comparative effects of MOFEP treatments on *Peromyscus* abundance. First, we examined whether the positive initial effects of uneven- and even-aged harvest treatments noted by Fantz and Renken (2005) persisted over a decade (13–14 years) after the first management entry. Second, we assessed whether short-term population changes after the second management entry showed similar patterns as those observed after the first entry. Third, to give context for the relative importance of harvest treatments as drivers of *Peromyscus* population abundance, we compared treatment effects to the range of background variation among years and sites in this study system. Finally, we assessed whether there were detectable system-wide trends in *Peromyscus* abundance during the first 20 years of the MOFEP study, particularly treatment-specific trends that would indicate divergence among management approaches.

2. Materials and methods

2.1. MOFEP design

We provide a brief description of MOFEP's experimental design, study sites, and small mammal sampling protocol; other publications provide more extensive details (Brookshire and Shifley, 1997; Knapp et al., 2014; Shifley and Kabrick, 2002). The study occurs in the south-central Missouri Ozark Highlands, in mature, second-growth forests dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.), other hardwoods, and shortleaf pine (*Pinus echinata*). Any prior timber harvesting on study sites occurred before 1950. The experiment uses a complete randomized block design, with three blocks each consisting of three, 312–514-ha sites (Sheriff and He, 1997). Each of three experimental treatments [no harvest (NH), uneven-aged (UA), or even-aged (EA) management] was randomly assigned to one site per block. Uneven-aged and even-aged management systems follow MDC management guidelines current at the time of each entry (e.g. MDC, 2014), with management entries planned every 15 years such that sites are managed on a 100-year rotation for uneven- and even-aged systems.

Each study site comprises a local landscape of 44–82 individual forest stands. Manipulations applied at the stand level are components of each management system (e.g. clearcut harvests in even-aged management), but are not applied to all stands within a site at each entry. Rather, decisions about whether and how to treat each stand during each entry are based on stand and site characteristics as in standard operational management, albeit within the bounds of the randomly assigned site-level management approach (Sheriff, 2002). Thus, the primary focus of MOFEP is the comparative landscape-scale effects of long-term application of these management systems rather than stand-level effects of individual entries.

To date, treatment entries have occurred in 1996 and 2011. In even-aged treatments, during each of the two entries 10–15% of each site was regeneration harvested (clearcut) in openings 3–12 ha in size, with up to 2.3 m^2 ha^{-1} residual basal area retained in clearcut areas (Knapp et al., 2014). In 2011, 11% of one even-aged treatment site was shelterwood harvested. In both entries, other stands on even-aged sites received intermediate thinning (average of 15.7% of site area per entry, Knapp et al., 2014) or were not treated. In sites assigned to uneven-aged management, during the first entry, single-tree and small group selection harvests occurred on much of each site (average area harvested = 57%, Kabrick et al., 2002). Group selection harvests were