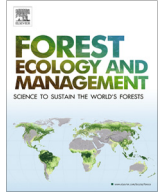




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Comparing the responses of larval and adult lepidopteran communities to timber harvest using long-term, landscape-scale studies in oak-hickory forests

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ABSTRACT

Lepidoptera (moths and butterflies) are important components of forest ecosystems; they affect tree growth and influence nutrient cycling as caterpillars, provide food for higher trophic levels as caterpillars and adults, and are pollinators as adults. Here, we report on and compare the results of two long-term studies of the effects of logging on Lepidoptera in oak hickory forests. In one study, the Missouri Ozark Forest Ecosystem Project (MOFEP), caterpillars were used as response taxa. Sampling via observation without removal focused on larvae found on leaves of two dominant tree species, *Quercus alba* and *Q. velutina*, in alternative harvest regimes. In a second, the Hardwood Ecosystem Experiment of Indiana (HEE), we examined the response of adults to alternative harvest levels by sampling with blacklighting. Caterpillar sampling in MOFEP and in an associated chronosequence revealed that clearcutting decreases numbers and diversity of Lepidoptera, year effects were as important in influencing caterpillar assemblages as the harvest *per se*, and that species richness of caterpillars continued to increase each year post-harvest. When using adult moths as response taxa, species composition was resilient to timber harvest under shelterwood management, recovering to the near original condition three years post treatment. Communities in patch cut or clear cut stands were slower to recover, and appeared to develop novel communities relative to their pre-harvest condition. A late spring frost decreased abundance and species richness of caterpillars, while a severe drought impacted adult lepidopterans, depressing species richness in patch cut stands to a greater degree than in control or shelterwood cut stands. Together, these results demonstrate that Lepidoptera communities in oak-hickory forests respond immediately to logging due to changes in host plant availability, but may also be impacted many years subsequent due to stochastic year effects and seral changes in forest structure and composition.

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1. Introduction

Timber harvest in the eastern deciduous forest association of North America is linked to changes in biodiversity for a range of taxa (Lousier, 2000). The magnitude of species population increase or decline, and the degree to which community composition shifts in response to logging differs depending on the harvest regime used, the spatial scale which is harvested, and the functional traits of the species being studied (Summerville, 2011; Slade et al., 2013). Recovery pathways for species and ecological communities are less well known, in part because testing hypotheses regarding alternative stable states, community re-assembly, and forest regeneration

require multi-year (or multi-decadal) commitments. In the eastern deciduous forest, three such studies exist: The Hubbard Brook Ecosystem Study, the Hardwood Ecosystem Experiment (HEE), and the Missouri Ozark Forest Ecosystem Project (MOFEP). While the precise goals of each large-scale, multi-year project differ, they each focus on assessing how timber harvest affects ecosystem structure and function across multiple scales and for multiple taxa. The goal of this paper is to compare and synthesize the results from two of these studies (HEE, MOFEP) for lepidopteran communities. The forests of HEE and MOFEP are both dominated by *Quercus* and *Carya*, less so by *Acer*, and in contrast to the Hubbard Brook site, there is very little representation by conifers at HEE and MOFEP study sites.

The Lepidoptera are critical components of forest ecosystems. First and foremost, the larval stages eat plant material (leaves, buds, stems, flowers, seeds, and less often, wood) and, in so doing,

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decrease growth of individual trees (Marquis and Whelan, 1994; Man and Rice, 2010; Bashir and MacLean, 2015). This growth impact is the summed result of feeding by species whose populations remain relatively low in abundance from year to year, but also by a few species that go through population eruptions, causing widespread defoliation (Hunter, 1991). Importantly, phytophagous Lepidoptera are critical for nutrient cycling in forest systems; herbivory is well-known to change distribution of carbon and nitrogen between the canopy and the soil compartments (e.g., see Lovett et al., 2002). Population control is, in part, imposed by a vast array of predators of both adult and larval Lepidoptera including bats, birds, rodents, and invertebrates (arthropod predators and parasitic insects). At the same time, these moths and caterpillars serve as the food base for those natural enemies (Holmes et al., 1986; Marquis and Whelan, 1994). Finally, a large percentage of the adult moths and butterflies are important pollinators, contributing to the successful seed production of herbs, shrubs, and trees that would otherwise go locally extinct without them (MacGregor et al., 2015).

Logging affects lepidopteran communities at different spatial scales. Within a managed stand, species should respond to loss of the host species, with specialists being more adversely impacted than generalists, especially when harvest regimes target the removal of their host trees (Summerville, 2013). Across a forested landscape, timber harvest creates spatial heterogeneity in forest structure and stand composition (Franklin et al., 2003; Povak et al., 2008). Heterogeneity in forest composition at larger spatial scales is driven, in part, by regeneration dynamics and whether a few trees are left or sprouting stumps are available to encourage recruitment (Stapanian and Cassell, 1999). The spatial heterogeneity of lepidopteran communities in forested landscapes is poorly known, but species are likely to respond to patchiness based on dispersal dynamics, host species presence and quality (Forkner and Marquis, 2004), and regional population size (Summerville, 2011). The spatial distribution of predation and parasitism (Le Corff et al., 2000) may also contribute to heterogeneity (Rodenhouse and Holmes, 1992; Burford et al., 1999). Processes structuring communities at the landscape scale are likely critical to predicting the relative resilience of a lepidopteran community. Resilience of lepidopteran communities within managed forest stands, that is, the time required for a community property to return to a level within a natural range of variability occurring prior to harvest (see Cumming, 2011), is also likely under strong influence of these aforementioned landscape-level processes (Summerville, 2013).

In this paper, we use two multi-year data sets to synthesize our current understanding of the resilience of forest lepidopteran communities to contrasting levels of timber harvest at both local and landscape scales. Assessing the resilience of lepidopteran communities to logging presents some unique challenges. First, Lepidoptera are holometabolous insects, possessing a larval stage that tends to be restricted to feeding on its host plant and a winged

adult that can move across larger spatial scales. Second, the sampling methodologies used to assess each life stages carry their own biases and constrain inference in different ways. For example, cryptic coloration larvae can make some species easily overlooked. In turn, adults of different species are not equally attracted to light traps. Both are likely to lead to different levels of sampling bias from species to species.

In general, we find that the short-term consequences of timber harvest are significant, with species loss of woody-plant feeders proportional to the level of timber removed from a stand and a more minimal gain in species which require ephemeral, disturbed habitat (see Summerville and Crist, 2002; Jeffries et al., 2006). Estimates of lepidopteran recovery transients may differ considerably based on whether data from larvae or adults are used. Insights from both larval and adult Lepidoptera illustrate that community reassembly following disturbance is spatially heterogeneous and driven by both direct and indirect impacts of harvest.

2. Methods

2.1. Experimental systems

2.1.1. MOFEP

The Missouri Ozark Forest Ecosystem Project is a long-term research project designed to estimate the impact of two alternative means of forest extraction (even-aged versus uneven-aged management) on forest productivity and biodiversity. Originally established to measure the effect of forest management on North American songbird populations, sampling was soon expanded to include additional components of forest biodiversity, including leaf-feeding insects of *Quercus alba* L. (white oak) and *Q. velutina* L. (black oak). There are nine replicate plots, each 350–525 ha in area, located in the Current River watershed of Shannon and Reynolds Counties of southeastern Missouri (37°14'30"N, 90°58'7"W). Approximately 10% of the land surface is harvested every 10–15 years. Harvests have taken place in 1996 and 2011. See Brookshire et al. (1997) and Sherrif (2002) for more information on timber extraction procedures and the experimental design (see also Table 1). Data presented here are for the years 1993–2004.

2.1.2. HEE

The Hardwood Ecosystem Experiment is a long term research project designed to test how differing levels of timber removal interact with stochastic disturbances to influence biodiversity changes across a wide range of taxa (summarized in Kalb and Mycroft, 2012). Research focusing on the response of adult Lepidoptera was performed within Morgan-Monroe State Forest, a ≈ 9725 ha system in south central Indiana (39°31'28"N, 86°44'13"W). In unfragmented landscapes, canopy cover tends to

Table 1
Comparison of harvest treatments and sampling effort used in the Hardwood Ecosystem Experiment (HEE) and the Missouri Ozark Forest Ecosystem Project (MOFEP). The patch cut treatment in the HEE is equivalent to uneven-aged management in the MOFEP, and the clear cut treatment in HEE is equivalent to even-aged management in the MOFEP. The MOFEP sites were harvested in 1996; the HEE sites were harvested in 2008.

Treatment	Hardwood ecosystem experiment			Missouri ozark forest ecosystem project		
	Mean basal area harvested (m ² /ha)	Number of stands	Number of samples per year	Mean basal area harvested (m ² /ha)	Number of stands	Number of samples per year
Unlogged	0.0	4	20	0.0	18	4
Shelterwood	2.7	3	15	N/A	NA	NA
Shelterwood matrix	0.0	3	15	N/A	NA	4
Patch cut	27.4	4	20	16.1	Not sampled	NA
Patch cut matrix	5.2	4	20	0.0	18	4
Clear cut	34.1	2	10	39.0	6	4
Clear cut matrix	N/A	N/A	N/A	N/A	18	4

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