Functional diversity response to hardwood forest management varies across taxa and spatial scales

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Abstract. Contemporary forest management offers a trade-off between the potential positive effects of habitat heterogeneity on biodiversity, and the potential harm to mature forest communities caused by habitat loss and perforation of the forest canopy. While the response of taxonomic diversity to forest management has received a great deal of scrutiny, the response of functional diversity is largely unexplored. However, functional diversity may represent a more direct link between biodiversity and ecosystem function. To examine how forest management affects diversity at multiple spatial scales, we analyzed a long-term data set that captured changes in taxonomic and functional diversity of moths (Lepidoptera), longhorned beetles (Coleoptera: Cerambycidae), and breeding birds in response to contemporary silvicultural systems in oak–hickory hardwood forests. We used these data sets to address the following questions: how do even- and uneven-aged silvicultural systems affect taxonomic and functional diversity at the scale of managed landscapes compared to the individual harvested and unharvested forest patches that comprise the landscapes, and how do these silvicultural systems affect the functional similarity of assemblages at the scale of managed landscapes and patches? Due to increased heterogeneity within landscapes, we expected even-aged silviculture to increase and uneven-aged silviculture to decrease functional diversity at the landscape level regardless of impacts at the patch level. Functional diversity responses were taxon-specific with respect to the direction of change and time since harvest. Responses were also consistent across patch and landscape levels within each taxon. Moth assemblage species richness, functional richness, and functional divergence were negatively affected by harvesting, with stronger effects resulting from uneven-aged than even-aged management. Longhorned beetle assemblages exhibited a peak in species richness two years after harvesting, while functional diversity metrics did not differ between harvested and unharvested patches and managed landscapes. The species and functional richness of breeding bird assemblages increased in response to harvesting with more persistent effects in uneven- than in even-aged managed landscapes. For moth and bird assemblages, species turnover was driven by species with more extreme trait combinations. Our study highlights the variability of multi-taxon functional diversity in response to forest management across multiple spatial scales.

Key words: biodiversity; birds; Cerambycidae; disturbance; ecosystem function; functional diversity; habitat loss; Lepidoptera; oak–hickory forests; resilience; spatial heterogeneity; timber harvesting.

INTRODUCTION

Functional diversity metrics hold great promise for understanding the effects of disturbance on community-level processes and corresponding changes in ecosystem function (Villéger et al. 2008, Laliberté and Legendre 2010, Mouillot et al. 2013). Ecologists have long postulated that disturbance can influence ecosystem function by altering species composition and species interactions (e.g., MacArthur 1955, Hutchinson 1959, Loucks 1970, Attiwill 1994, McCann 2000). Early theory predicted

that species diversity stabilizes ecosystem function (Elton 1958), and that disturbance destabilizes function when species are lost (Loucks 1970). Empirical testing and refinement of this theory revealed the importance of species' functional traits (Tilman et al. 1996). Greater species richness tends to foster higher levels of functioning through the sampling effect and niche differentiation (Tilman 1999). This refinement led to the prediction that the functional diversity of a community should represent a more direct link between the environment and emergent ecosystem functions (Díaz and Cabido 2001, Violle et al. 2007). Furthermore, functional diversity cannot be assumed to have positive covariance with species richness due to functional redundancy, where multiple species perform similar roles in an ecosystem (Díaz and Cabido 2001, Hooper et al. 2005, Violle et al. 2007,

Flynn et al. 2009). Standardized methods for measuring functional diversity (e.g., Pla et al. 2011, Mouillot et al. 2013) have recently driven research on functional diversity responses to disturbance in a variety of ecosystems and taxonomic groups.

The overall objective of our study was to determine how widely used even-aged and uneven-aged silvicultural systems influence the species and functional diversities of moths, longhorned beetles, and birds. This objective is broadly applicable to forest ecosystems worldwide, but is currently of high importance in the northern United States where deciduous forests are decreasing in age-class diversity, a trend that began following a sequence of land clearing, farming, and farm abandonment in the 19th–mid-20th centuries (Whitney 1994, Jenkins 2013). For example, half of forests within the Central Hardwood Region, which covers portions of 18 states in the eastern United States (Braun 1950), are between 40 and 80 yr in age (Shifley and Thompson 2011, Shifley et al. 2014). Maintaining diverse forested landscapes that include a mix of early-, mid-, and late-successional forests tends to enhance the diversity of plant and animal species (Greenberg et al. 2011, Hunter and Schmiegelow 2011). In the pre-settlement eastern forest, age-class diversity and spatial heterogeneity were regulated by the combined effects of abiotic (e.g., wind, ice storms, wildfire), biotic (e.g., herbivory), and anthropogenic (e.g., fire, swidden agriculture) disturbances (Whitney 1994, Greenberg et al. 2016). Depressed timber markets, fire suppression, and expansion of exurban populations wary of harvesting have all contributed to low disturbance frequency and intensity during recent decades (Shifley et al. 2014).

Forest management is a form of anthropogenic disturbance that influences rates of ecosystem functions, such as carbon cycling, nutrient cycling, pollination, and trophic interactions, which are critical to ecosystem service flows that benefit humanity (Bonan 2008, Food and Agriculture Organization of the United Nations and European Commission Joint Research Centre 2012, Agrawal et al. 2013, Haddad et al. 2015). Forest ecosystems may be conceptualized as complex adaptive systems where interactions generate emergence, feedback, and cross-scale linkages (Puettmann et al. 2009, Messier et al. 2013, Parrott and Lange 2013). The inability to predict aggregate behavior by studying isolated components is a hallmark of complex adaptive systems (Parrott and Lange 2013). When viewed through the lens of complexity theory, functional diversity is an emergent property of forests that is influenced by forest management when management actions alter ecosystem heterogeneity and results in the loss of mature forest habitats and their associated ecological niches. Such habitat loss impairs spatial resilience, the ability to handle small- to intermediate-size disturbances without crossing a threshold to an alternative state, through the disappearance of key system components and connections at larger spatial scales (i.e., ecological memory, sensu Nyström and Folke 2001, Parrott and Lange 2013). However, even-aged and uneven-aged

silvicultural systems, embedded within a continuously forested landscape, would be expected to increase functional diversity across the landscape by increasing the spatial heterogeneity of forest types (Greenberg et al. 2011). This outcome would occur regardless of how harvesting affected functional diversity at the smaller scale of harvested forest patches (Bengtsson et al. 2000). Compared to even-aged silvicultural systems, uneven-aged systems would result in a more diffusely perforated forest canopy at the landscape level because harvested patches are smaller in area, there is less distance between them, and reentry occurs more frequently. Such silvicultural systems are associated with the loss of mature forest species and ecological processes (Franklin and Forman 1987). When a forest's structural properties of heterogeneity and ecological memory interact to drive dynamic emergent properties at the landscape scale (Parrott and Lange 2013), then forest managers face a trade-off between these structural properties.

Moths (Lepidoptera), longhorned beetles (Coleoptera: Cerambycidae), and birds are functionally important taxa whose communities are known to be impacted by silviculture. However, much of what is known about their responses to silvicultural systems is based on species or functional group diversity from taxon-specific studies. In forest food webs, primary consumers (moths and longhorns) are abundant and have traits that suggest they may respond differently to disturbance compared to secondary consumers (birds). Adult moths function as pollinators while moth larvae are herbivores and detritivores. In forests, moth species diversity is linked to the diversity of available host plants, which can be negatively affected by harvesting (Summerville and Crist 2002, 2004, 2008). Larval moth functional group diversity can be negatively affected by more intense harvest regimes (Forkner et al. 2006). This trend may not be the case for longhorns, a family of wood-boring beetles that primarily decompose deadwood, but include some pest species that damage or kill live trees. The total abundance and species diversity of beneficial, decomposer longhorns increases after harvesting (Thibault and Moreau 2016), but harvesting may also increase the access of pest species to adjacent unharvested patches, as has been noted for other wood-boring beetles (Drooz 1985). Likewise, birds also perform important ecological functions in forest ecosystems including insect predation and seed dispersal. Bird species richness is affected by forest management, and tends to increase in response to partial harvesting within otherwise forested landscapes (Annand and Thompson 1997, DeGraaf et al. 1998, Gram et al. 2003, Morris et al. 2013).

We tested the effects of silviculture on functional diversity with a long-term data set that included forest moth, longhorned beetle, and breeding bird assemblages sampled across a landscape-scale silvicultural experiment in south-central Indiana, USA. Based on this data set and experimental framework, we investigated two questions focused on multi-taxon diversity in managed

forest ecosystems: (1) how do even-aged and uneven-aged silvicultural systems affect species and functional diversity at the landscape level relative to individual harvested and unharvested forest patches and (2) how do the silvicultural systems affect the functional similarity of assemblages at the landscape level compared to individual harvested and unharvested patches? By addressing these questions, we applied ecological concepts to identify functional trade-offs among even-aged, uneven-aged, and preservation management regimes across multiple forest animal taxa. With respect to our first question, we predicted that functional diversity would increase in managed forest landscapes after harvest due to the habitat heterogeneity that is created. We expected this to occur regardless of changes in functional diversity within individual harvest patches. We also expected even-aged silviculture to foster the greatest levels of diversity due to the positive effects of heterogeneity combined with lower levels of mature forest habitat loss. With respect to our second question, we expected harvesting to increase the patch-level functional similarity of assemblages while reducing functional similarity within managed landscapes. Our findings will illuminate how silvicultural techniques may be applied to achieve ecological goals in multi-use forested landscapes.

METHODS

Our study took place on the Hardwood Ecosystem Experiment (HEE), which is a landscape-scale, replicated, forest management experiment with silvicultural treatments planned for 100 yr (Kalb and Mycroft 2013). The HEE is located on nine forest management compartments in Morgan-Monroe and Yellowwood State Forests, two overlapping multi-parcel forests in south-central Indiana, USA. The Indiana Department of Natural Resources selected these nine compartments in 2006, and oversaw the first harvest cycle in the fall of 2008. The forests on all nine management compartments regenerated after widespread farm abandonment during the Great Depression of the 1930s (Jenkins 2013). At the time of our study, these forests were irregularly even aged, after several decades of single-tree and group selection management (Kalb and Mycroft 2013). There were no differences in structure and composition among the compartments prior to the 2008 harvest cycle, although some patch-level differences were noted (Saunders and Arsenault 2013). The silvicultural treatments included a set of even-aged and uneven-aged prescriptions that are commonly used to facilitate oak regeneration in the Central Hardwoods Region (Johnson et al. 2002) as well as no-harvest reference areas.

The HEE forest management compartments ranged in area from 83.5 ha to 110.4 ha (Table 1). The management compartments were surrounded by buffer areas universally managed by single-tree selection, which closely resembled extant management practices used by the Indiana Division of Forestry. In the fall of 2008, an even-aged or uneven-aged silvicultural system was applied to six of the nine management compartments, with three replicates of each system. The remaining three compartments served as no-harvest reference areas. In the even-aged compartments, two 4.1-ha forest patches were cleared of all woody stems >30 cm diameter at breast height by a contracted logger. After harvest, all remaining stems in these "clearcuts" were felled and left on site. Additionally, two 4.1-ha patches were thinned of midstory and understory layers of non-oak species

TABLE 1. Landscape attributes of the Hardwood Ecosystem Experiment silvicultural prescriptions by management compartment.

Compartment	No. harvests	Harvest area (ha)[†]	Area (ha)	Harvest area (ha)	Thinned area (ha)[‡]	Edge area (ha)[§]	Forest area (ha)[¶]	Buffer area (ha)
Even-aged silviculture								
3	2	4.39 ± 0.04	110.44	8.78	8.10	11.26	82.26	332.69
6	2	3.21 ± 0.49	87.15	6.42	8.10	10.31	62.37	383.34
9	2	4.15 ± 0.10	78.31	8.30	8.10	12.58	49.32	302.28
Uneven-aged silviculture								
1	8	1.19 ± 0.26	91.46	9.49	0	24.08	57.93	253.90
7	8	1.15 ± 0.31	92.42	9.16	0	23.11	60.13	269.11
8	8	1.11 ± 0.20	84.59	8.85	0	22.70	53.05	296.61
Reference compartments								
2	0	n.a.	83.52	0	0	0	83.52	350.83
4	0	n.a.	89.92	0	0	0	89.92	392.71
5	0	n.a.	84.74	0	0	0	84.74	219.24

Notes: Areas were determined using ArcMap 10.2 (Esri 2013). n.a., not applicable.

[†] Mean ± SE.

[‡] Shelterwood preparatory cuts, which were applied only in even-aged management compartments. The total area was divided approximately evenly between two treatment areas. Each treatment area was planned for 4.05 ha, and actual treatment boundaries were not yet mapped.

[§] Area within 50 m of a harvest boundary (excluding shelterwood preparatory cuts).

[¶] Forested area located >50 m from a harvest boundary (excluding shelterwood preparatory cuts) and within the management compartment. Note that each compartment was fully contained within a continuously forested buffer area.

≤25 cm diameter at breast height in a shelterwood preparatory cut. Timber harvest did not occur in the matrix of the even-aged compartments. In the uneven-aged compartments, all woody stems were cleared from eight forest patches in three size categories: two 2.0 ha, two 1.2 ha, and four 0.4 ha. These "patch-cuts" were akin to wildlife openings that are often used in selection forestry throughout the eastern United States. The matrix areas of the uneven-aged compartments were harvested with single-tree selection to a target residual basal area of 16.1–22.9 m^2/ha (Kalb and Mycroft 2013). The matrix areas are henceforth referred to as the "even-aged matrix" and "uneven-aged matrix." More detailed information on the experimental design and management plan can be found in Hardwood Ecosystem Experiment (2017).

Field sampling

Moths.—Forest moths were sampled in the three management compartments located in Morgan-Monroe State Forest, including one even-aged compartment, one uneven-aged compartment, and one reference compartment (Fig. 1). In the even-aged compartment, adult moths were sampled in two clearcut sites, three shelterwood preparatory cut sites, and three matrix sites. In the uneven-aged compartment, moth sampling included four patch-cuts and four matrix sites. Four sites were sampled in the no-harvest reference compartment. The same sites were sampled one year before harvest (2007) and annually for six years after harvest (2009–2014). In our study, a moth constitutes a member of the insect order Lepidoptera excluding the superfamily Papilonoidea (butterflies) and Hesperiioidea (skippers). We further truncated our definition of moth to only include the traditional macromoth families Apatelodidae,

Cossidae, Drepanidae, Erebidae, Euteliidae, Geometridae, Lasiocampidae, Limacodidae, Megalopygidae, Mimallonidae, Noctuidae, Nolidae, Notodontidae, Saturniidae, Sphingidae, Yponomeutidae, and Zygaenidae. Sampling occurred from 21:00 to 08:00 EDT on five nights each season, approximately every 14 d from late May through late August, for a total of 100 samples per season (20 sites × 5 nights). Adult moths were collected with a Universal black-light trap (12-watt; BioQuip Products, Rancho Dominguez, California, USA) powered by 12-V, 26 amp-hour batteries, placed near the center of the patch. Specimens were identified to species and stored at Drake University in Des Moines, Iowa, USA (Summerville et al. 2013).

Longhorned beetles.—Longhorned beetles were sampled at one site in four of the harvested patches of each treated compartment as well as at four sites in each reference compartment (Fig. 1) for two years before harvest (2006 and 2007) and for four of the first six years after harvest (2009, 2010, 2013, and 2014). A beetle trap array was placed in each of the two clearcuts and two shelterwood preparatory cuts in the even-aged compartments, and in four of the eight patch-cuts in the uneven-aged compartments. Four trap arrays were placed in each reference compartment by randomly selecting four bird survey points, which are described in *Birds*. Each trap array consisted of four traps, including a Lindgren multiple-funnel trap (12 funnel model; Pherotech, Delta, British Columbia, Canada), one panel trap for bark beetles (Alpha Scents, Portland, Oregon, USA), one intersecting pane window trap, and one linear purple sticky trap (Holland 2010). Sampling effort was therefore 144 trap-sessions each year. A bottle containing 60 mL of 99% ethanol was hung from the first three types of traps in
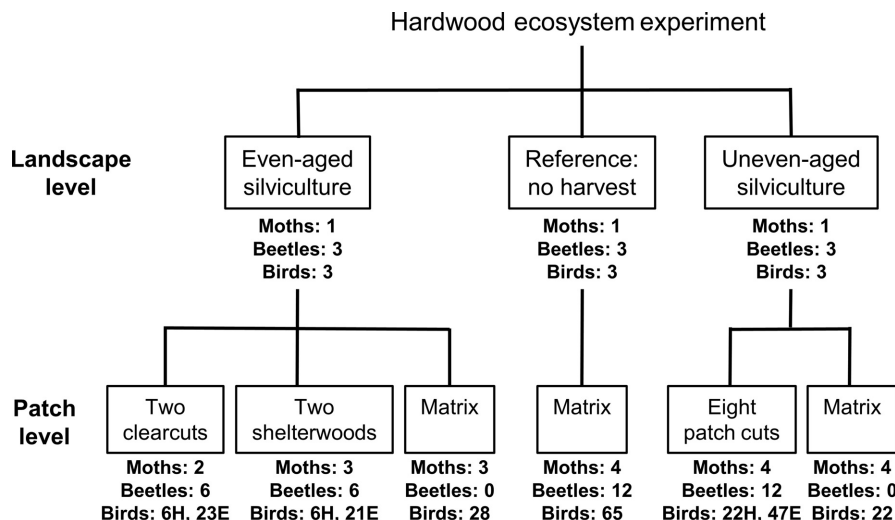

Fig. 1. Graphical schematic of the experimental design of the Hardwood Ecosystem Experiment, and annual sample sizes by taxon and level of focus. Note that there were two clearcuts and two shelterwoods per even-aged compartment, for a total of six across the entire experiment. Also, there were eight patch cuts per uneven-aged compartment for an experiment-wide total of 24. For bird samples at the patch level, H signifies harvest and E signifies edge.

order to lure beetles. A jar of ethylene glycol plus a few drops of liquid soap was hung underneath each of the traps to kill and preserve the beetles. Square plastic rain covers (0.67 × 0.67 m) were placed over these traps to reduce the dilution of trap fluid by rain. The purple sticky traps did not require ethanol, ethylene glycol, or a rain cover. The traps were placed in early May, and insects were collected from the traps every three weeks until late August. Specimens were identified to species and stored at Purdue University in West Lafayette, Indiana, USA (Holland et al. 2013).

Birds.— Breeding birds were sampled in both harvested and unharvested patches of all nine compartments (Fig. 1). Aural and visual point count surveys occurred annually for three years before harvest (2006–2008) and for five of the first six years after harvest (2009–2012 and 2014). One survey point was located near the center of each harvested patch ("harvest" points) and two to four points were placed within 50 m of the edge of each harvested patch ("edge" points). Survey points in the matrix areas and the reference compartments were arranged in a 150 × 150 m grid. Grid points were sampled if they were located >100 m from a harvest boundary, >100 m from the research core boundary, and >100 m from an existing survey point. Between 2006 and 2011, annual sampling included 28 points in the even-aged matrix, 22 points in the uneven-aged matrix, 21 points in the edges of the shelterwood preparatory cuts, six points within the shelterwood preparatory cuts, 47 points in the edges of the patch-cuts, 22 points within the patch-cuts, 23 points in the edges of the clearcuts, and 6 points within the clearcuts (Fig. 1). Total sample sizes over the even-aged, uneven-aged, and reference compartments were 84, 91, and 65, respectively, for a grand total of 240 points. As part of the long-term monitoring program, sample sizes in 2012 and 2014 were reduced to 36 points in the reference compartments, 10 points in the even-aged matrix, 13 points in the uneven-aged matrix, 6 points in the shelterwood preparatory cut edges, 37 points in the patch-cut edges, and 8 points in the clearcut edges. Surveys were conducted during 20 May–20 June between 06:00 and 11:00 EDT across the same network of survey points each season. Each survey point was visited twice per season by a different pair of field technicians each visit. During each survey, the technicians recorded the species of each bird seen or heard over a ten-minute period and estimated the distance from the point to the bird (Malloy and Dunning 2013). Birds estimated to be >100 m from the point were excluded from the current analyses. We transformed bird counts to species incidence per survey point to minimize detection bias among species.

Diversity

Taxon diversity was represented by species richness (the number of species, excluding rare species). Functional diversity was estimated based upon three metrics:

functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv; Villéger et al. 2008). First, a functional space was developed for each taxon separately, from a reduced set of axes obtained by principal coordinates analysis (Appendix S1: Table S1; Mason et al. 2005, Villéger et al. 2008). Each principal coordinates analysis was based on a species–species Gower dissimilarity matrix that was computed from a mix of continuous, ordinal, and categorical traits (Gower 1971). The quality of the reduced space was computed by dividing the sum of the eigenvalues of the retained axes by the sum of the eigenvalues of all of the axes (Legendre and Legendre 2012). FRic is the proportion of the total niche space that is occupied by the species in one assemblage. It is quantified as the convex hull volume of the assemblage divided by the convex hull volume of the experiment-wide species pool. FEve is analogous to species evenness, and is quantified as the sum of the minimum spanning tree among species in functional space, weighted by the number of captures. FDiv represents the level of niche differentiation and resource competition in an assemblage, and is quantified based on the distribution of species within functional space. Species richness and the functional diversity metrics were computed using the R package FD (Laliberté and Legendre 2010, Laliberté et al. 2014). We excluded rare species because they are likely to be incidental observations that mask niche assembly dynamics (Hamback et al. 2007, Summerville and Crist 2008). Moth and longhorned beetle species were considered to be rare if fewer than three total individuals were sampled across all years, and bird species if they were observed at fewer than three bird points, summed across all years.

We selected traits that influence resource capture, resource use, dispersal ability, and vital rates. We used these criteria because resource capture and use traits are likely to affect ecosystem function (Spehn et al. 2005), while dispersal ability and vital rates indicate the rate of recolonization after harvest (Spitzer et al. 1984). Moth traits included wingspan, voltinism, larval diet breadth, larval feeding guild, and overwintering stage; longhorned beetle traits included adult body length, larval diet breadth, larval host condition, plant parts and layers occupied (by larvae), larval host plant growth form, adult active season, active period of day (for adults), and mimicry; and bird traits included body mass, clutch size, nest location, foraging location, foraging behavior, and food type (Table 2). Species traits were obtained from the existing literature (Appendix S3: Tables S1–S3). This list includes continuous, ordinal, and categorical traits, which could be either nominal or binary. Nominal and binary categorical traits differed in how they were used to compute Gower's dissimilarity for a species pair (Table 2). Nominal traits were either the same (1) or different (0) among each pair. For each level of a binary trait, a species received a 1 if the level were true and a 0 if the level were false. The trait's contribution to Gower's dissimilarity was determined by the proportion

TABLE 2. Functional traits that were used to determine the functional diversity, including functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) of each taxon.

Trait	Description	Range or levels	Coverage[†]
Moths[‡]			
Wingspan (cm; ln-transformed)	continuous	0.095–2.6	99.7
Voltinism	continuous	1–4 flights/yr	100
Larval diet breadth	ordinal	monophagous (1); oligophagous (2); polyphagous (3)	99.4
Larval feeding guild	categorical (nominal)	herbaceous plants; detritus; fungi-lichens-mosses; woody plants; generalist	99.4
Overwintering stage	categorical (nominal)	egg; larva; pupa; colonize	100
Longhorned beetles[§]			
Adult body length (mm; ln-transformed)	continuous	1.23 – 3.62	100
Larval diet breadth	continuous	1–21 plant families eaten	95.6
Larval host condition	categorical (binary)	live; stressed; moribund; dead; decayed	87.8
Plant parts eaten (by larvae)	categorical (binary)	twigs; branches; trunk; roots	76.7
Plant parts and layers occupied (by larvae)	categorical (binary)	bark; cambium; sapwood; heartwood	74.4
Larval host plant growth form	categorical (binary)	coniferous tree; hardwood tree; herbaceous plant; shrub; vine	92.2
Active season (for adults)	categorical (binary)	March–November (by month)	95.6
Active period of day (for adults)	categorical (binary)	diurnal; nocturnal; crepuscular	70.0
Mimicry	categorical (binary)	ant; parasitoid; wasp	100
Birds[¶]			
Body mass (g; ln-transformed)	continuous	1.13 – 6.11	95.4
Clutch size	ordinal	2 eggs; 3; 4; 5; 6 (6 or more)	95.4
Nest location	categorical (nominal)	tree; shrub; ground; cavity; building	98.5
Foraging location	categorical (binary)	ground; understory; midstory; upper canopy; aerial	100
Foraging behavior	categorical (binary)	foliage-gleaner; sally-gleaner; bark-gleaner; hover; ground; driller; aerial	100
Food type	categorical (binary)	invertebrates; vertebrate endotherms; vertebrate ectotherms; carrion; fruit; nectar; seeds; plants	100

[†]The percentage of species for which trait information was available.

[‡]For a list of moth (Lepidoptera) functional trait sources, please see Appendix S3: Table S1. The reduced functional trait space was composed of six axes with a quality of 0.261. The species-species distance matrix was transformed according to Cailliez (1983) in order to be Euclidean.

[§]For a list of longhorned beetle (Coleoptera: Cerambycidae) functional trait sources, please see Appendix S3: Table S2. The reduced functional trait space was composed to two axes with a quality of 0.271. The species–species distance matrix was transformed according to Cailliez (1983) in order to be Euclidean.

[¶]For a list of breeding bird functional trait sources, please see Appendix S3: Table S3. The reduced functional trait space was composed of four axes with a quality of 0.775.

of overlap among trait levels that were true for at least one species in the pair. Gower's dissimilarity is compatible with missing trait data (Gower 1971), but trait data were available for most of the sampled species (Table 2).

Statistical analysis

We conducted the following analyses at two analytical foci, including the patch level and the landscape level (Forman and Godron 1981), to assess whether or not landscape-level effects are simply an aggregation of patch-level effects. In the patch-level analyses, we pooled captures (moths and longhorned beetles) or observations (birds) at the same sampling site within each sampling year, and regarded each site as an independent sample of a forest patch. We defined a landscape as a collection of patches, with each management compartment representing a landscape. The sampling units of the

landscape-level analyses differed by taxon according to sampling designs.

We used repeated-measures, mixed-effects ANOVA models to determine if species richness, FRic, FEve, and FDiv were affected by harvest type at the patch level and silvicultural system at the landscape level. We developed a separate model for each combination of diversity metric, taxon, and management period (before and after harvest) at each analytical focus. In the patch-level models, the sample units were the individual sites representing harvest patches or local areas within the forested matrix or reference areas. Harvest type, sample year, and their interaction were fixed effects and management compartment and site (nested within management compartment) were random effects (Appendix S2: Tables S1–S3). Moth diversity models differed from longhorned beetle and avian diversity models in that fixed-effect ANOVA models were used for the pre-harvest period

and site was the only random effect. These differences occurred because only one year of pre-harvest data was available and the sampling of silvicultural systems was not replicated (Fig. 1). The landscape-level models were as described above except that silvicultural system replaced harvest type as a fixed effect (Appendix S2: Table S3). Captures (longhorns) or observations (birds) were pooled by species within management compartments, and the sample units were the management compartments. Silvicultural system and year were fixed effects and management compartment was a random effect (Appendix S2: Table S4). Moths were not included in the landscape-level models due to the lack of replication at this level (Fig. 1). Each model was fit using maximum likelihood estimation using the R package lme4 (Bates et al. 2015, R Core Team 2015).

We used likelihood ratio tests on sets of nested models to assess how harvest type (or silvicultural system) affected each functional diversity metric. We also determined if the rate of change in a diversity metric differed by harvest type (or silvicultural system) by testing its interaction with sampling year (Appendix S2: Tables S1–S5). The test statistic for the likelihood ratio tests was χ^2 distributed with $A - 1$ degrees of freedom, where A was the number of factor levels of the main effect that was removed to create the reduced model. Where the interaction term was removed, the degrees of freedom were $(A - 1) \times (B - 1)$. We considered a main effect or interaction to have a statistically significant effect on a diversity metric response variable if its removal resulted in a significantly less informative model, where the P-value of the test statistic <0.05. However, we interpreted results cautiously where $0.01 < P < 0.05$, taking ΔAIC and plots of the data into consideration. We checked the assumptions of homoscedasticity and circularity with Levene's test and Mauchly's test, respectively, and also examined plots of the standardized residuals. In a few cases where the homoscedasticity assumption was not met, we square-root transformed the response variable. If the transformation failed to stabilize the variance, then we estimated P values using bootstrapping with 10000 iterations. Each model met the assumption of circularity. When a statistically significant effect was detected, we conducted post hoc pairwise comparisons using the R package multcomp (Hothorn et al. 2008). If the interaction term was significant, then we compared harvest types (or silvicultural systems) within the same year after applying a Bonferoni correction for all comparisons. If the pairwise comparison only included main effects, then we used Tukey's HSD test (von Ende 2001, Gotelli and Ellison 2004, Zuur et al. 2009). We created figures with the R package ggplot2 (Wickham 2009).

To assess whether timber harvest leads to the selection of more functionally similar species within assemblages, we compared expected and observed levels of functional diversity (FRic, FEve, and FDiv) after harvest using a standardized effect size (SES). We computed SES as [(observed − mean expected)/standard deviation of

expected]. We estimated expected functional diversity based on 1000 random communities that were created using the independent swap algorithm in R package picante (Kembel et al. 2010). This algorithm preserves species occurrence frequency and sample species richness (Gotelli 2000). We tested if the mean SES of each functional diversity metric in each year × harvest type (or silvicultural system) group differed from zero using one-sample t tests. We compared the P values without adjusting them for multiple comparisons because the large number of comparisons would have made the test very conservative (Gotelli and Ellison 2004). We conducted these analyses at both the patch and landscape levels for all three taxa. Within individual patches, we expected sampled assemblages to be more functionally similar to one another than predicted by randomly generated assemblages. Within landscapes, we predicted that sampled assemblages would be more functionally different than expected from random assemblages.

RESULTS

We recorded a total of 378 moth species (macromoths), 121 longhorned beetle species, and 73 breeding bird species over seven, six, and eight seasons of sampling, respectively. After removing rare species, defined as species with fewer than three records over the entire study period, total species richness was 324 moth species (Appendix S3: Table S1), 90 longhorned beetle species (Appendix S3: Table S2), and 65 bird species (Appendix S3: Table S3). All longhorned beetle species retained had larvae that develop within woody vegetation, i.e., no retained species developed in herbaceous plants.

Species richness

Timber harvesting affected the species richness of each taxon in some way. For moths, species richness was reduced by harvesting. Our models suggested that moth richness differed among harvest areas before they were harvested ($\chi^2 = 11.3$; df = 4; $P = 0.023$), but none of the pairwise comparisons were statistically significant (Fig. 2A, B). After harvest, the harvest type by year interaction was significant ($X^2 = 42.0$; df = 20; $P = 0.002$). Patch cuts contained fewer species than the reference compartment in 2009, and then fewer species than all other treatments each year thereafter (Fig. 2A, B). The matrix of the uneven-aged compartment contained fewer species than the reference in 2009, and all other treatments (except the shelterwood) in 2011. Although we cannot formally test whether the clearcuts differed from other treatments, it is notable that the difference in species richness between the clearcuts and reference was greater than or equal to that of the patch cuts each year except 2013 (Fig. 2A, B). The landscape-level pattern suggests that both even-aged and uneven-aged silviculture reduced moth species richness at this level (Fig. 2C).
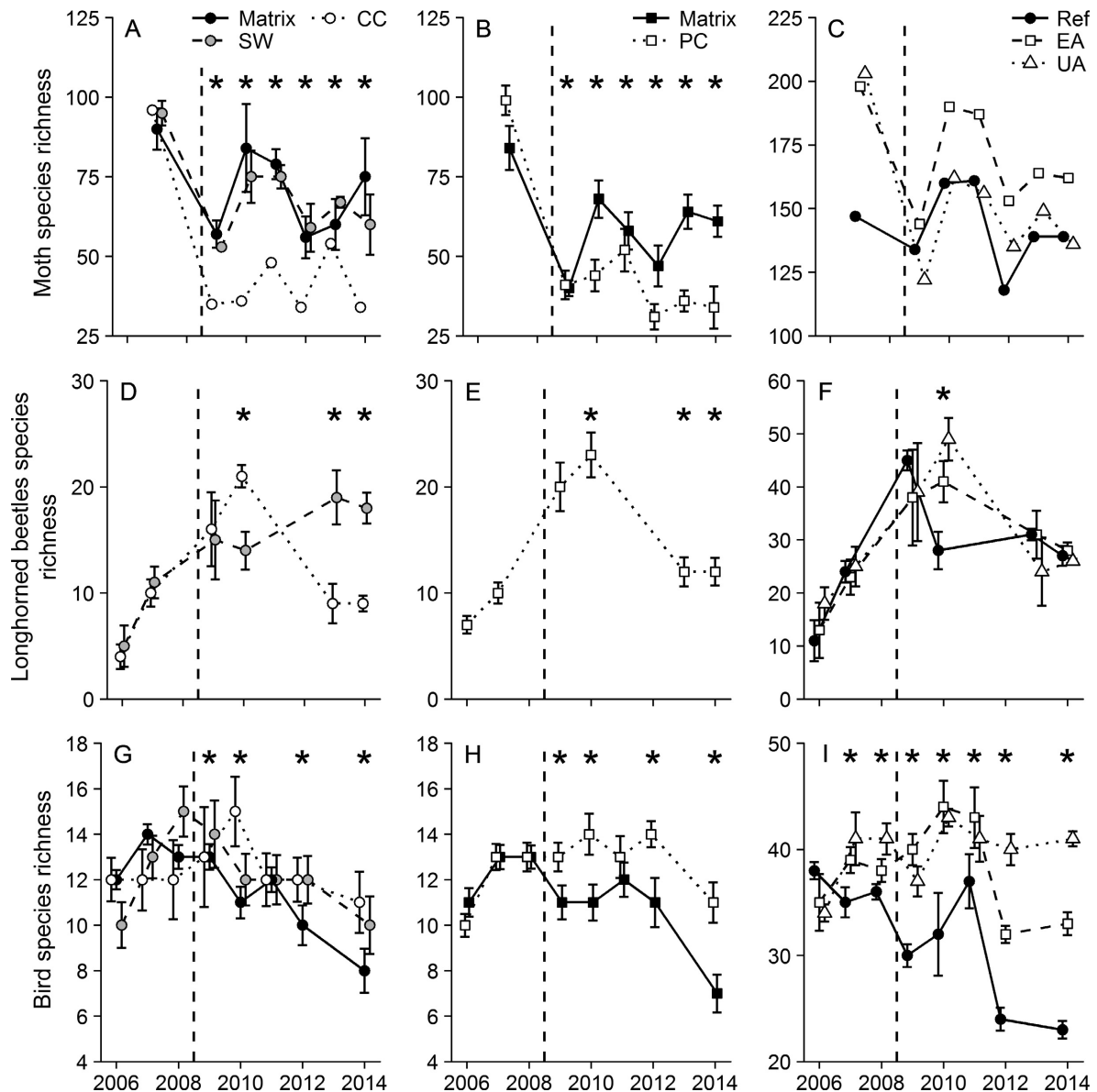
FIG. 2. Species richness of (A–C) moth, (D–F) longhorned beetle, and (G–I) breeding bird assemblages before and after timber harvesting in Morgan-Monroe and Yellowwood State Forests, in south-central Indiana, USA. Harvest occurred in the fall of 2008, which is indicated by the vertical dashed line. Patch-level effects of even-aged silviculture, including clearcuts (with a treatment area size of 4.05 ha), shelterwood preparatory thinnings (4.05 ha), and the forest matrix, are shown in the first column. Patch-level effects of uneven-aged silviculture, including patch cuts and the forest matrix, are shown in column two. Landscape-level effects of even-aged and uneven-aged silviculture are shown along with unharvested reference areas in column three. Symbols represent annual means and bars represent the standard error of the mean, except for panel C, where moth sampling was not replicated at the landscape level. Note that the patch-level data shown in columns one and two were analyzed together, but are shown separately for clarity. The breeding bird edge assemblages are not shown, but were included in statistical analyses. Treatment sample sizes vary by taxon and are reported in Methods, *Field sampling*. Legend abbreviations are CC, clearcut; SW, shelterwood; PC, patch cut; EA, even-aged; UA uneven-aged; and Ref, reference. Asterisks denote years in which at least one pair of treatments differed significantly ($P < 0.05$) in species richness based upon post hoc pairwise comparisons.

The species richness of longhorned beetles increased during pre-harvest sampling across the study area (Fig. 2D–F). The harvest type by year interaction was not significant ($\chi^2 = 2.32$; df = 3; $P = 0.508$). The main effect of harvest type was also not significant ($\chi^2 = 3.26$; df = 3; $P = 0.354$), but the main effect of year was significant ($\chi^2 = 44.0$; df = 1; $P < 0.001$). After harvest, the interaction of harvest and year was significant ($\chi^2 = 57.5$; df = 9; $P < 0.001$). Initially species richness increased across the study area, but there were no significant

differences among harvest types in 2009 (Fig. 2D, E). In 2010, clearcuts and patch cuts contained more species than the reference compartments and shelterwood areas. During the 2013 and 2014 sampling periods, species richness decreased across the study area but was greater in clearcuts than in shelterwoods (Fig. 2D, E). At the landscape level, the silvicultural system by year interaction was not significant before harvest ($\chi^2 = 1.42$; df = 2; $P = 0.491$). The main effect of silvicultural system was also not significant ($\chi^2 = 2.14$; df = 2; $P = 0.343$), but the main effect of year was significant ($\chi^2 = 14.8$; df = 1; $P < 0.001$). After harvest, the interaction between silvicultural system and year was significant ($\chi^2 = 20.2$; df = 6; $P = 0.003$). Even-aged and uneven-aged compartments contained more species than the reference compartments in 2010, but richness did not differ among the silvicultural systems during other years (Fig. 2F).

In breeding bird assemblages, the harvest type by year interaction was significant both before harvest ($\chi^2 = 45.6$; df = 16; $P < 0.001$) and after harvest ($\chi^2 = 61.6$; df = 32; $P = 0.001$). However, none of the pre-harvest pairwise comparisons were statistically significant (Fig. 2G, H). In the first year after harvest (2009), the clearcuts, the edges of clearcuts, the edges of shelterwoods, and the matrix of even-aged compartments each contained significantly more species than the reference compartments. In 2010, the clearcuts, patch cuts, and edges of patch cuts contained more species than the references. In 2011, no differences occurred between any of the harvest types. Then in 2012 and 2014, the patch cuts contained more species than the references. It is notable that the clearcut harvests regularly contained more species than the references, but only six clearcuts were available to sample (Fig. 2G, H). At the landscape level, the silvicultural system by year interaction was significant before harvest ($\chi^2 = 21.0$; df = 4; $P < 0.001$) and after harvest ($\chi^2 = 38.9$; df = 8; $P < 0.001$). The areas selected for uneven-aged silviculture contained significantly fewer species than the references in 2007 and 2008 (Fig. 2I). After harvest, the even-aged and uneven-aged compartments contained more species than the reference compartments in 2009 and 2010. In 2011, only the even-aged compartment was more species-rich than the references. In 2012 and 2014, the uneven-aged compartment contained more species than the even-aged compartment, which contained more species than the references (Fig. 2I).

Functional richness

For the moths, FRic differed among the planned harvest areas in 2007 before they were harvested ($\chi^2 = 20.3$; df = 4; $P = 0.027$), but none of the post-hoc pairwise comparisons were significantly different (Fig. 3A, B). After harvest, the main effects of harvest type ($\chi^2 = 27.3$; df = 4; $P < 0.001$) and year ($\chi^2 = 38.8$; df = 5; $P < 0.001$) significantly affected FRic, but the harvest type by year interaction was not significant ($\chi^2 = 27.1$; df = 20; $P = 0.134$). Patch cuts were significantly lower in FRic than all of the other harvest types (Fig. 3A, B). Clearcuts appeared to be lower in FRic than all of the other harvest types except for patch cuts, but statistical significance could not be determined due to the small sample size. With respect to year, FRic was greatest in 2010 than the other post-harvest sampling years (Fig. 3A, B). At the landscape level FRic tended to be lowest in the reference unit, but this pattern occurred both before and after harvest and could not be tested statistically (Fig. 3C).

In longhorned beetle assemblages, FRic differed among years both before harvest ($\chi^2 = 14.6$; df = 1; $P < 0.001$) and after harvest ($\chi^2 = 21.0$; df = 3; $P < 0.001$). Before harvest, FRic increased from 2006 to 2007. After harvest, FRic was greater in 2013 compared to all other post-harvest sampling years (Fig. 3D, E). The interaction between harvest type and year was not significant ($\chi^2 = 17.2$; df = 9; $P = 0.046$) and the main effect of harvest type was also not significant ($\chi^2 = 3.17$; df = 3; $P = 0.366$). At the landscape level, beetle FRic also differed among years before harvest ($\chi^2 = 6.98$; df = 1; $P = 0.008$) and after harvest ($\chi^2 = 15.6$; df = 3; $P = 0.001$). The silvicultural system by year interaction was not significant ($\chi^2 = 12.7$; df = 6, $P = 0.048$), and the main effect of silvicultural system was also not significant ($\chi^2 = 2.90$; df = 2, $P = 0.235$).

In breeding bird assemblages, the interaction between harvest type and year was significant before harvest ($\chi^2 = 34.0$; df = 16; $P = 0.005$). Post-hoc pairwise comparisons did not reveal any significant differences among planned harvest areas before treatment (Fig. 3G, H). After harvest, the main effects of harvest type ($\chi^2 = 39.4$; df = 8; $P < 0.001$) and year ($\chi^2 = 72.4$; df = 4; $P < 0.001$) were significant, while the interaction between harvest type and year was not significant ($\chi^2 = 38.2$; df = 32; $P = 0.208$). Specifically, the clearcuts and their edges, the patch cuts and their edges, and the shelterwood harvest areas contained more functional richness than the unharvested reference areas (Fig. 3G, H). Also, patch cut harvests were significantly greater in FRic than their edges, and significantly lower in FRic than the matrix of uneven-aged compartments and the edges of shelterwood harvests. With respect to year, FRic was significantly greater in 2014 compared to all other post-harvest sampling years (Fig. 3G, H). At the landscape level, FRic differed among years before harvest ($\chi^2 = 14.6$; df = 2; $P < 0.001$), but not among planned silvicultural systems ($\chi^2 = 3.91$; df = 2; $P = 0.142$) or in their interaction with year ($\chi^2 = 6.49$; df = 4; $P = 0.166$). After harvest, the interaction between silvicultural system and year was significant ($\chi^2 = 17.1$; df = 8; $P = 0.029$). The even-aged compartments were greater in FRic than the reference compartments in 2009 (Fig. 3I). The uneven-aged compartments were greater than the reference compartments in 2012. In 2014, both the even-aged and uneven-aged compartments were greater than the reference compartments in FRic.
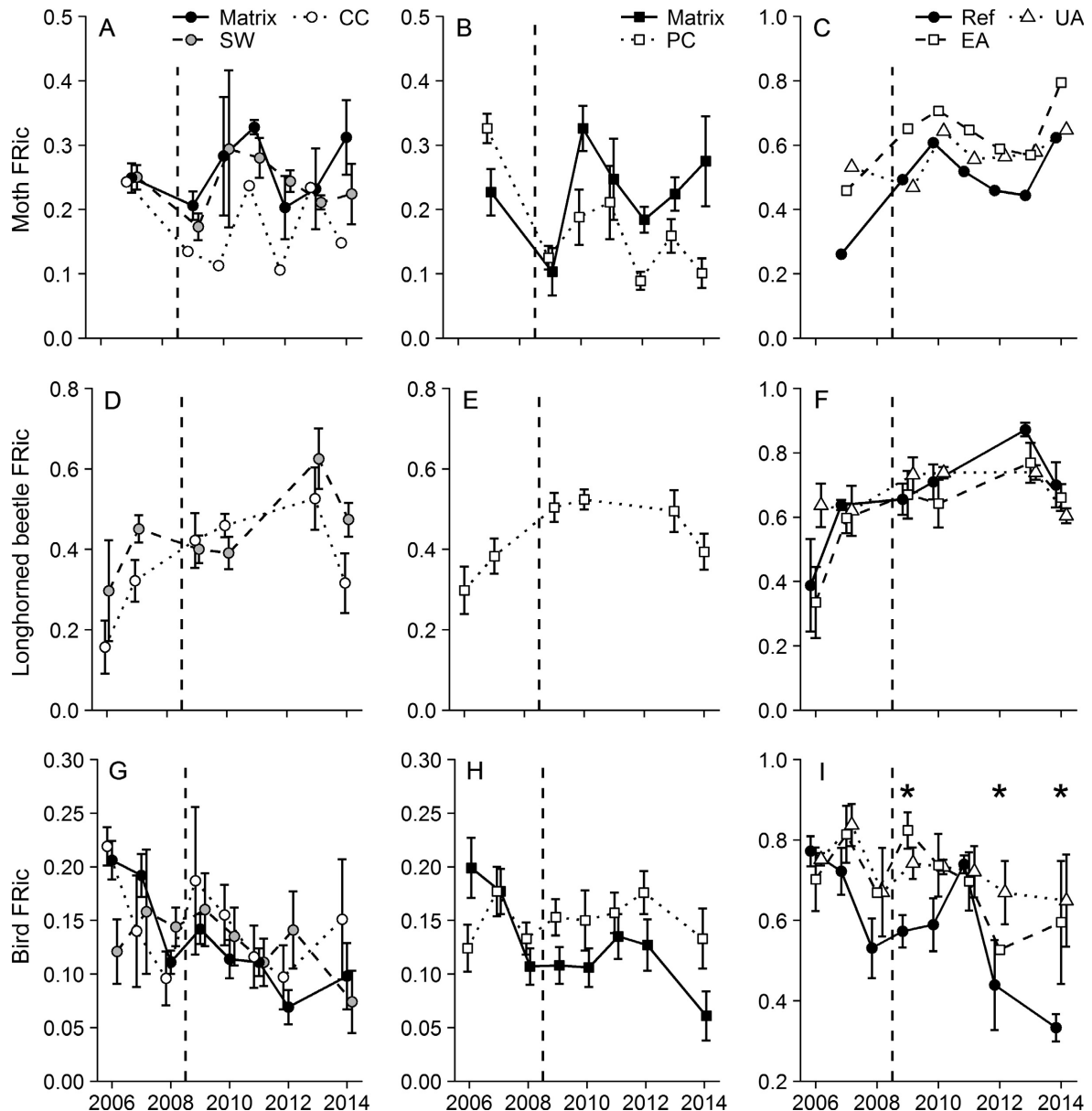
FIG. 3. Functional richness (FRic) of (A–C) moth, (D–F) longhorned beetle, and (G–I) breeding bird assemblages before and after timber harvesting in Morgan-Monroe and Yellowwood State Forests, in south-central Indiana, USA. Harvest occurred in the fall of 2008, which is indicated by the vertical dashed line. Patch-level effects of even-aged silviculture, including clearcuts (4.05 ha), shelterwood preparatory thinnings (4.05 ha), and the forest matrix, are shown in the first column. Patch-level effects of uneven-aged silviculture, including patch cuts and the forest matrix, are shown in column two. Landscape-level effects of even-aged and uneven-aged silviculture are shown along with unharvested reference areas in column three. Symbols represent annual means and bars represent the standard error of the mean, except for Fig. 2C where moth sampling was not replicated at the landscape level. Note that the patch-level data shown in columns one and two were analyzed together, but are shown separately for clarity. The breeding bird edge assemblages are not shown, but were included in statistical analyses. Treatment sample sizes vary by taxon and are reported in Methods, *Field sampling*. Legend abbreviations are as in Fig. 2. Asterisks denote years in which at least one pair of treatments differed significantly ($P < 0.05$) in FRic based upon post-hoc pairwise comparisons.

Functional evenness

    There were no differences in FEve among moth assemblages before harvest ($\chi^2 = 10.0$; df = 4; $P = 0.112$). After harvest, the harvest type by year interaction was not significant ($\chi^2 = 26.3$; df = 20; $P = 0.158$) while the main effects of harvest type ($\chi^2 = 34.5$; df = 4; $P < 0.001$) and year ($\chi^2 = 48.9$; df = 5; $P < 0.001$) were statistically significant. Patch-cuts were significantly greater in FEve than all other harvest types and the

matrix of the uneven-aged compartment was greater than the reference compartment (Fig. 4A, B). With respect to year, 2012 was greater in FEve compared to all other post-harvest sample years (Fig. 4A, B). Harvesting generally increased the FEve of moth assemblages at the landscape level (Fig. 4C).

For the longhorned beetles, FEve did not differ by the interaction between planned harvest type and year ($\chi^2 = 1.5$; df = 3, $P = 0.682$) or the main effects planned harvest type ($\chi^2 = 1.89$; df = 3; $P = 0.596$) and year ($X^2 = 0.11$; df = 1, $P = 0.737$). After harvest, the interaction between harvest type and year was significant ($\chi^2 = 26.0$; df = 9; $P = 0.002$). In 2010, clearcuts and patch cuts exhibited lower FEve compared to longhorn assemblages in the reference compartments (Fig. 4D, E). At the landscape level, FEve did not differ by the interaction between planned silvicultural system and year ($\chi^2 = 4.34$; df = 2, $P = 0.114$) or the main effects planned silvicultural system ($\chi^2 = 0.54$; df = 2; $P = 0.763$) and

year ($\chi^2 = 0.23$; df = 1, $P = 0.628$). After harvest, the interaction between silvicultural system and year was significant ($\chi^2 = 15.3$; df = 6; $P = 0.018$). This occurred because, in 2010, the uneven-aged compartments were lower in FEve compared to the reference compartments (Fig. 4F).

Functional divergence

Moth assemblages did not differ in FDiv across the planned harvests ($\chi^2 = 3.78$; df = 4; $P = 0.467$). After harvest, the harvest type by year interaction was significant ($\chi^2 = 40.4$; df = 20; $P = 0.004$). Patch cuts experienced reduced FDiv compared to the matrix of the even-aged compartment in 2009, the reference compartment and shelterwoods in 2011, the even-aged and uneven-aged matrix areas plus the shelterwoods in 2012, and the matrix in the uneven-aged compartment and shelterwoods in 2013 (Fig. 5A, B). At the landscape
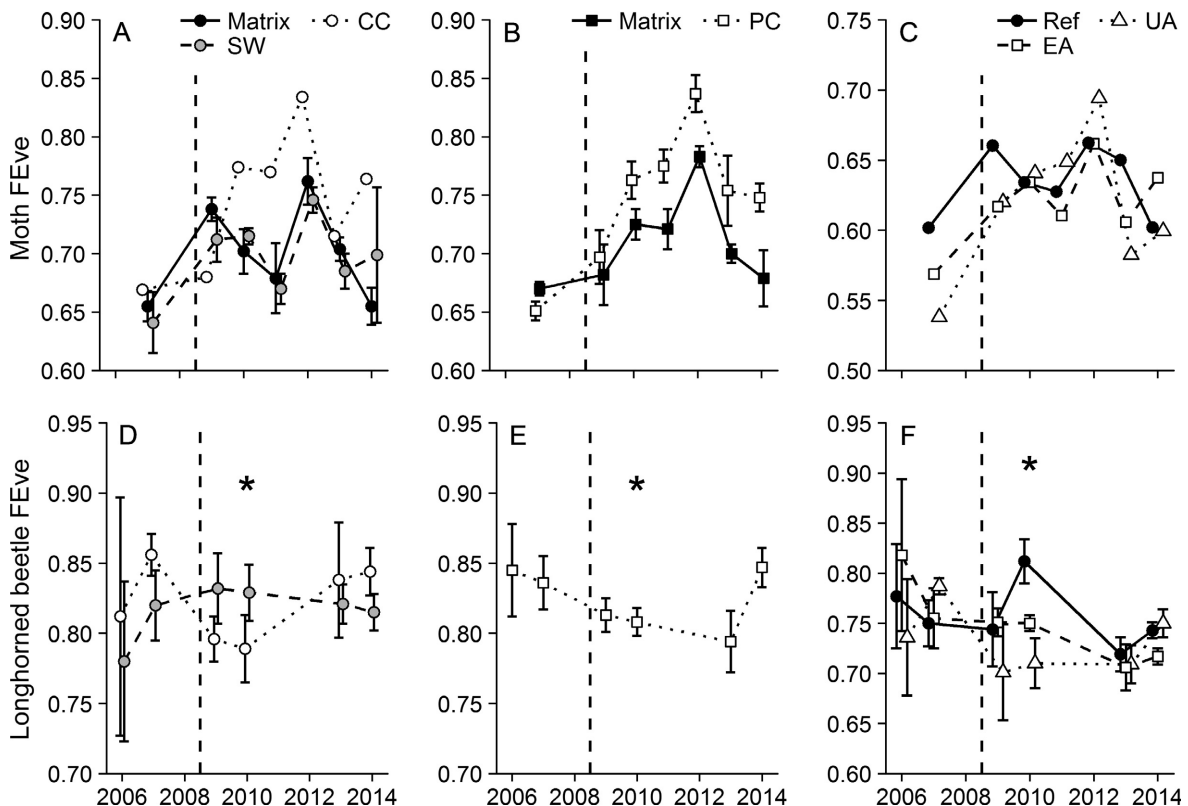

Fig. 4. Functional evenness (FEve) of (A–C) moth and (D–F) longhorned beetle assemblages before and after timber harvesting in Morgan-Monroe and Yellowwood State Forests, in south-central Indiana, USA. Harvest occurred in the fall of 2008, which is indicated by the vertical dashed line. Patch-level effects of even-aged silviculture, including clearcuts (4.05 ha), shelterwood preparatory thinnings (4.05 ha), and the forest matrix, are shown in the first column. Patch-level effects of uneven-aged silviculture, including patch cuts and the forest matrix, are shown in column two. Landscape-level effects of even-aged and uneven-aged silviculture are shown along with unharvested reference areas in column three. Symbols represent annual means and bars represent the standard error of the mean, except for panel C where moth sampling was not replicated at the landscape level. Note that the patch-level data shown in columns one and two were analyzed together, but are shown separately for clarity. The breeding bird edge assemblages are not shown, but were included in statistical analyses. Treatment sample sizes vary by taxon and are reported in Methods, *Field sampling*. Legend abbreviations areas in Fig. 2. Asterisks denote years in which at least one pair of treatments differed significantly ($P < 0.05$) in FEve based upon post-hoc pairwise comparisons.

level, FDiv in the uneven-aged compartment increased during 2013 and 2014, but otherwise the compartments were similar in FDiv (Fig. 5C).

The FDiv of longhorned beetle assemblages increased over time before harvest (χ^2 = 8.58, df = 1; P = 0.012), but the interaction between year and planned harvest type (χ^2 = 2.27; df = 3; P = 0.615) and the main effect of planned harvest type (χ^2 = 6.73; df = 3; P = 0.065) were not significant. After harvest, the interaction between harvest type and year was significant (χ^2 = 27.9; df = 9; P < 0.001). Patch cuts were greater in FDiv compared to reference areas in 2013 and shelterwoods in 2014 (Fig. 5D, E). At the landscape level, the interaction between silvicultural system and year was significant both before harvest (χ^2 = 6.41; df = 2; P = 0.041) and after harvest (χ^2 = 22.6; df = 6; P < 0.001). Before harvest, the planned uneven-aged compartments were greater in FDiv than the planned reference compartments in 2006 (Fig. 5F). After harvest, the uneven-aged compartments

contained greater FDiv than the reference compartments in 2013 and 2014 (Fig. 5F).

Functional similarity

Moths were the only taxon for which silviculture increased functional similarity within patches, but this only occurred during the first two years after harvest. During this time, moth assemblages were more similar than expected in FRic within the clearcuts, patch-cuts, and uneven-aged matrix, and in FDiv within patch-cuts (Appendix S4: Table S1). Moth FEve was also less similar than expected in patch-cuts. Overall, moth SES tended to be less than zero in harvested patches and near zero in all management compartments (Appendix S4: Table S1).

The prediction that timber harvest would affect functional similarity was not supported by longhorned beetle assemblages. Although some longhorn SES were
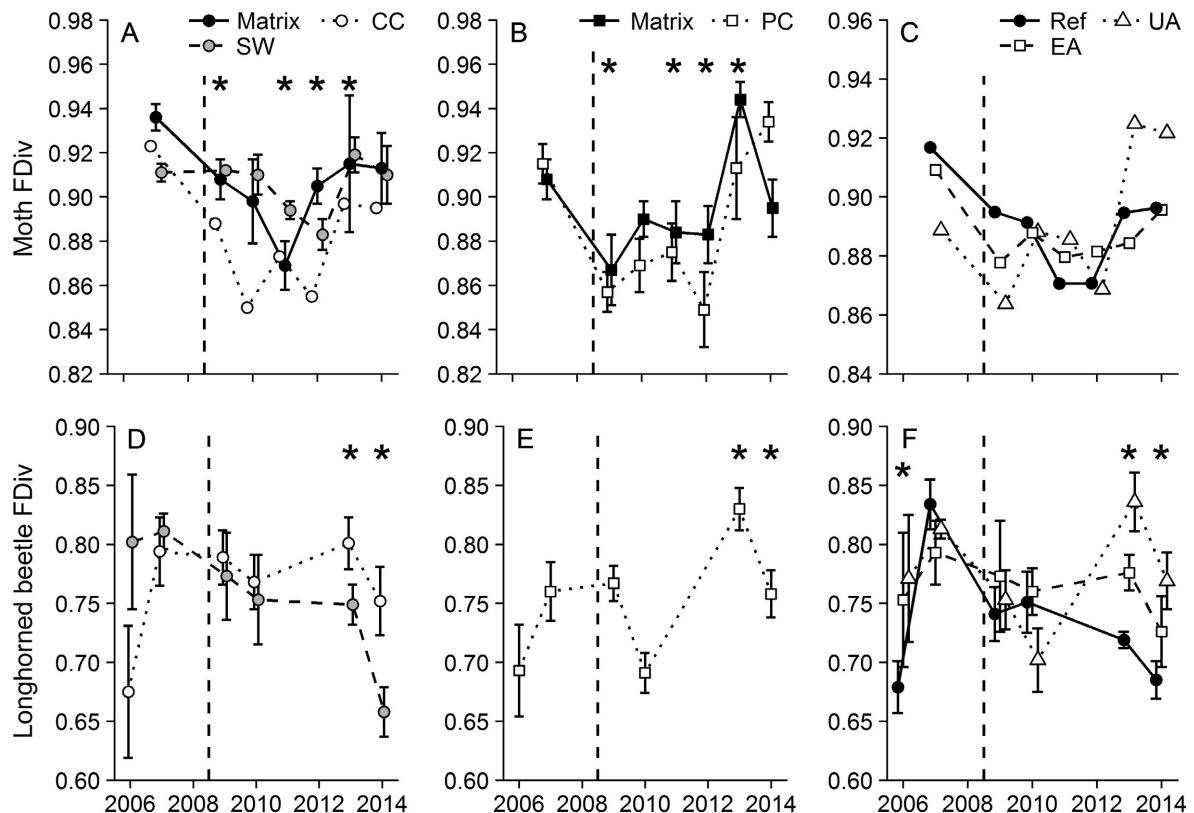

Fig. 5. Functional divergence (FDiv) of (A–C) moth and (D–F) longhorned beetle assemblages before and after timber harvesting in Morgan-Monroe and Yellowwood State Forests, south-central Indiana. Harvest occurred in the fall of 2008, which is indicated by the vertical dashed line. Patch-level effects of even-aged silviculture, including clearcuts (4.05 ha), shelterwood preparatory thinnings (4.05 ha), and the forest matrix, are shown in the first column. Patch-level effects of uneven-aged silviculture, including patch cuts and the forest matrix, are shown in column two. Landscape-level effects of even-aged and uneven-aged silviculture are shown along with unharvested reference areas in column three. Symbols represent annual means and bars represent the standard error of the mean, except for panel C where moth sampling was not replicated at the landscape level. Note that the patch-level data shown in columns one and two were analyzed together, but are shown separately for clarity. The breeding bird edge assemblages are not shown, but were included in statistical analyses. Treatment sample sizes vary by taxon and are reported in the text. Legend abbreviations are as in Fig. 2. Asterisks denote years in which at least one pair of treatments differed significantly (P < 0.05) in FDiv based upon post-hoc pairwise comparisons.

significantly different from zero, they occurred regardless of the time period (before and after harvest) and treatment (Appendix S4: Table S2). However, it was notable that longhorn FRic was consistently more similar (SES < 0) and FEve was consistently less similar (SES > 0) at the patch level. At the landscape level, longhorn SES did not differ from zero. While longhorn FRic tended to be more similar within even-aged and uneven-aged compartments and less similar within reference compartments, this pattern occurred both before and after harvest (Appendix S4: Table S2).

For breeding bird assemblages, timber harvest tended to reduce functional similarity. The SES of FRic was greater than expected in the clearcuts, patch-cuts, and shelterwood preparatory cuts, their edges, and in the uneven-aged matrix. However, few SES were significantly different from zero (Appendix S4: Table S3). In the references, the SES of avian FRic tended to be less than expected at the patch level and greater than expected at the landscape level. The even-aged matrix sites also tended to be lower in SES than expected.

DISCUSSION

Our study shows that whether silviculture fosters or erodes functional diversity is taxon-dependent. Uneven-aged silvicultural systems, which result in a more diffuse and persistent level of disturbance, are associated with greater overall changes in functional diversity that persist for a longer period of time, as compared to even-aged silvicultural systems. In our study, avian species richness and FRic increased from reference compartments, to even-aged management compartments, and to uneven-aged management compartments. In contrast, moth species richness and functional diversity decreased. Longhorned beetle species richness increased after treatment, but for a short period of time, and with little change in functional diversity. Such different responses among taxa suggest the existence of trade-offs among ecosystem functions that are driven by different taxa.

The stronger negative effect of uneven-aged silviculture on moth diversity indicates that moth assemblages are more negatively affected by silviculture through habitat loss and forest degradation, rather than benefitting from increased spatial heterogeneity. Uneven-aged managed forests are characterized by a higher density of smaller openings compared to even-aged managed forests, making them more susceptible to the negative effects of mature forest habitat loss and degradation. Moth diversity is closely tied to the diversity of available host plants for larvae (Summerville and Crist 2002, 2004, 2008). Silvicultural systems that create patches of forest openings increase foraging resources for moth species that feed on herbaceous plants while reducing resources available for species that feed on woody plants. In the current study, timber harvesting increased captures of herbaceous plant feeding moths, while oak feeding moths continued to be the dominant foraging guild

(see Summerville 2011, 2013). Declines in the species richness and total abundance of Lepidopteran assemblages are typically associated with timber harvesting (Kitching et al. 2000, Savilaakso et al. 2009, Summerville 2011, 2013). Previous research has shown that uneven-aged silviculture reduces caterpillar diversity to a greater extent than even-aged silviculture or preservation (no-harvest) management (Forkner et al. 2006). These effects can extend from harvested patches into the matrix, particularly for species whose larvae are host plant specialists (Summerville 2014).

The increase in longhorned beetle species richness with no change in functional diversity suggests that longhorn assemblages are primarily affected by the pulse of fresh coarse woody debris that follows harvesting operations. Such resource pulses temporarily increase the number of species that can utilize a habitat patch. Over time, species richness decreases due to mortality and emigration as the resource pulse subsides. For example, Thibault and Moreau (2016) reported up to 200% more longhorned beetle species in commercially thinned spruce plantations compared to unthinned plantations for up to three years after thinning. In our study, inter-annual variability was high before and after harvest for each of the diversity metrics, suggesting that environmental factors influenced longhorn diversity independently of timber harvest (Holland et al. 2013). Overall, our results indicate that longhorned beetle diversity is not influenced by the effects of spatial heterogeneity or forest habitat loss in the silvicultural systems that we studied, although longhorn diversity may change at higher levels of habitat loss and fragmentation (Holland 2010).

In our study, managed forest landscapes contained greater avian species richness and functional diversity compared to no-harvest reference areas, suggesting that avian diversity is increased by spatial habitat heterogeneity. The effect was stronger in uneven-aged than in even-aged compartments. The positive effect of habitat heterogeneity on the species diversity of breeding birds is well known (Greenberg et al. 2011, Hunter and Schmiegelow 2011). Silvicultural openings are used by a wide range of birds because they create habitat for early-successional species (Annand and Thompson 1997, King et al. 2001, Thompson and DeGraaf 2001, Gram et al. 2003) and enhance foraging conditions for species that breed in mature forest and forage in early-successional habitat (Anders et al. 1998, Pagen et al. 2000, Vitz and Rodewald 2006, McDermott and Wood 2010). Previous research has shown that uneven-aged silviculture has stronger positive effects on breeding bird species richness compared to even-aged silviculture and preservation management (Gram et al. 2003, Morris et al. 2013), although even-aged silviculture is also recommended for maintaining diversity of Neotropical migrants (Keller et al. 2003). In a similar experiment located in the Missouri Ozarks, Morris et al. (2013) observed a peak in the abundance of early-successional birds six to eight years after timber harvest, while mature-forest species

abundance was generally not affected. Finally, our results suggest that silvicultural openings may increase the resistance of avian diversity to regional dynamics. We found that avian species richness decreased in the reference compartments, but not in the managed compartments, around the time of harvest. Since harvesting would not have affected bird assemblages in the reference compartments, this pattern likely reflects interannual variation in bird populations across the region.

Theoretical implications

The patterns that we observed between species richness and FRic, and FRic and FEve, suggest that ecologically important relationships occur among these metrics. The three functional diversity metrics that we measured are not inherently correlated (Villéger et al. 2008). However, FRic is somewhat dependent on species richness because species must be added for FRic to increase, and removed for FRic to decrease. Changes in species richness with no effect on FRic occur when species added or removed from assemblages are functionally redundant with the existing or remaining species. Our results suggest a lack of redundancy among the moth and bird assemblages in our study system because decreases in moth species richness tended to coincide with decreases in FRic, and increases in bird species richness (relative to references) corresponded with increases in FRic. This pattern also suggests that timber harvest reduces the volume of niche space for moths while increasing niche space volume, or at least enhancing functional resilience, for birds. However, other studies have reported that moth assemblages can be highly structurally redundant, which suggests high functional redundancy (Truxa and Fiedler 2016). Also, insectivorous forest birds are well known to partition resource use across gradients of spatial and temporal variance in resource availability (e.g., MacArthur 1958), which can foster functional redundancy and resilience. The temporary increase in longhorned beetle species richness in year two was not matched by an increase in FRic, suggesting that the new species were functionally redundant with existing species. Resource pulses can increase species richness through aggregative effects that do not necessarily influence niche space volume. For example, Gerisch et al. (2012) found that the species richness of floodplain ground beetle assemblages was positively influenced by flood frequency, which increased resource availability. However, the additional species were functionally redundant with ground beetles found in more species-poor assemblages.

These conclusions are also supported by the negative relationship between FRic and FEve that we observed in moth and bird assemblages. FRic tended to increase when species were gained while FEve tended to decrease. The opposite occurred when species were lost. This relationship means that the changes in species composition that drove changes in FRic and FEve were due to species gain and loss from the edges of functional space. In comparison, if FEve were to vary positively with species richness, and FRic did not change, this would indicate changing species composition from the interior of the functional space polygon. Moth species lost tended to have generalist and woody plant-feeding larvae, while those that were gained tended to specialize on herbaceous plants. Bird species gained tended to be those that forage and nest in ground, shrub, and midstory habitats, while those that were lost tended to be canopy foragers and tree nesters. Future studies should seek to determine the generality of this relationship in forest communities.

In addition to the effects of spatial heterogeneity and mature forest habitat loss, the species richness and functional diversities of forest ecological communities are also influenced by factors operating at broader spatial and temporal scales. The ability of forest animal communities to absorb (resistance) or cope with (resilience) the effects of forest management is likely to be greater where the focal forested area is embedded within a broader forested landscape. For forest birds, our results are consistent with previous studies reporting little change in avian diversity in the unharvested portions of managed forests that are connected to more forests (Guénette and Villard 2005, Vanderwel et al. 2007, Morris et al. 2013). Although the moth assemblages in our study experienced reduced diversity, some functional groups recovered within a few years in the less intensely harvested patches (Summerville 2013). A second explanation for the generally high resistance and resilience that we observed is that historic land-use practices eliminated the most sensitive species several decades ago, and they have not returned (Olden et al. 2004). The forests in our study area, like others throughout the eastern United States, were certainly harvested and were also likely cleared, burned, and/or farmed for an extended time during the 19th and early 20th centuries (Whitney 1994, Jenkins 2013). The functional diversity of several taxa may have been compromised by such intensive and widespread land uses. For example, Flynn et al. (2009) found reduced functional diversity relative to species richness in birds and mammals in a regional-scale meta-analysis covering the eastern United States. Specifically, species with traits that increase sensitivity to widespread land clearing, such as specialization, few generations per year, and limited dispersal distances, may have been negatively impacted to the point of extirpation or extinction (McKinney and Lockwood 1999).

Management implications

Silvicultural systems were designed to enhance the growth and yield of targeted commercial tree species. In the 1980s, forest management began moving toward a paradigm of ecosystem-based management that includes other ecosystem services (Creed et al. 2016). This newer focus is inspiring research to examine how silvicultural systems affect the biodiversity of non-commercial plant and non-game animal species (Hunter and Schmiegelow

2011). Applying these concepts to on-the-ground forest management is critical due to the broad range of ecosystem services that are obtained from forests and the increasing risk and uncertainty of how forests may react to disturbances during an era of global change (Dale et al. 2001). Management decisions could either ameliorate or exacerbate the negative impacts of stochastic disturbances (Puettmann 2011, O'Hara and Ramage 2013, Keyes et al. 2014). Recently developed conceptual frameworks for forest management that account for rapid global change emphasize the importance of building resistance and resilience at the patch and landscape levels, but have thus far emphasized trees and the production of woody biomass (DeRose and Long 2014). There is a need to understand how diversity responds to forest management across taxa in order to enhance both ecological theory and on-the-ground management strategies.

Our findings support the notion that there are trade-offs when managing forests for multiple ecosystem services (Rodríguez et al. 2006, Brandt et al. 2014). When ecosystem services supported by pollination and decomposition are to be prioritized, even-aged silviculture would maintain a wider variety of moth functional groups across the landscape. Where forests are to be managed for bird habitat, uneven-aged silviculture would create greater levels of avian functional diversity compared to even-aged silviculture. Uneven-aged managed forests are also more resistant and resilient (in terms of wood production) to stochastic disturbances (O'Hara and Ramage 2013). However, uneven-aged silviculture may also increase the prevalence of pest species (those that damage or kill live trees) in the mature forest matrix (Muzika et al. 1998).

Conclusions

Sustainable silviculture within largely forested regions enhances the multi-functionality of forest ecosystems and landscapes. Forest managers should seek to create a landscape mosaic that includes both early-successional and mature forest habitats. Rather than optimize the rate of any one ecosystem function, the goal of such a multi-functional landscape is to balance important ecosystem services as diverse as biodiversity conservation, recreation, timber production, carbon sequestration, pollination, and nutrient cycling. If changes in species richness and composition are driven by species with more unique sets of traits, as our results suggest, then management will influence these ecosystem functions even when species-level changes are small. Information generated through studies like ours will help decision-makers select trade-offs between different services in specific contexts. Such a management paradigm is consistent with recent advances in resilience theory (Walker and Salt 2006), and begins to address the general question of how to achieve landscape multi-functionality in forest-lands. Finally, while information linking disturbance or management to functional diversity is growing, knowledge gaps remain in the linkage of functional traits among taxa and trophic levels within biotic communities, and the biotic community's effect on ecosystem function (i.e., effect diversity). In the absence of management that adds early-successional habitats, temperate deciduous forests can be expected to decline in functional diversity. This may require a paradigm shift as current trends in forest management will likely result in a deficit of early-successional habitat (Shifley and Thompson 2011).

Ecological theory that links species richness, functional group diversity, and ecosystem function was initially developed for plants at the scale of experimental plots (Hooper and Vitousek 1997, Tilman et al. 1997). Forest ecosystems contain critical ecosystem functions that are driven by multiple taxa interacting across scales. Such interactions generate emergent properties that can only be understood by studying the system and its multiple components (Messier et al. 2013). With respect to our study system, previous work has shown that moth species richness decreases when host plant diversity is reduced (Summerville and Crist 2004), longhorn species richness increases with the availability of course woody debris substrates at a variety of decomposition stages (Grove 2002), and breeding bird species richness increases with habitat structural complexity (James and Warner 1982). Our study shows how these effects of harvest disturbance have implications for landscape-level patterns in ecosystem function because they also affect the functional component of diversity at the landscape scale. By studying concurrent effects of disturbance on functional diversity at the spatial extent of both the patch and the landscape, we begin to move beyond predicting how numbers of species change to predicting how ecological communities function.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1532/full

Data Availability

Data associated with this paper have been deposited in the Purdue University Research Repository https://doi.org/10.4231/ R73F4MM3.