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Research Article

Stand-Level Bird Response to Experimental Forest Management in the Missouri Ozarks

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ABSTRACT Long-term landscape-scale experiments allow for the detection of effects of silviculture on bird abundance. Manipulative studies allow for strong inference on effects and confirmation of patterns from observational studies. We estimated bird-territory density within forest stands (2.89–62 ha) for 19 years of the Missouri Ozark Forest Ecosystem Project (MOFEP), a 100-year experiment designed to study the effects of even-age and uneven-age management on wildlife. We spot-mapped territories of 15 species in 228 stands for 5 years before treatment and 14 years after treatment to assess the effects of stand-level silvicultural treatments (clearcut, select cut, thin, and no-harvest) applied within even-age, uneven-age, or no-harvest (control) management sites and year on avian territory density. We used 2 a priori contrasts to compare pre-treatment bird densities with densities during early (3–5 yr) and late (12–14 yr) post-treatment periods. The interaction of silvicultural treatment and year had significant effects on the densities of all 15 species. Densities of hooded warbler (*Setophaga citrina*), indigo bunting (*Passerina cyanea*), prairie warbler (*Setophaga discolor*), and yellow-breasted chat (*Icteria virens*) increased significantly 3–5 years post-treatment with the greatest changes in clearcuts, but densities 12–14 years post-treatment did not differ from pre-treatment densities. Densities of Acadian flycatcher (*Empidonax virescens*), wood thrush (*Hylocichla mustelina*), and especially ovenbird (*Seiurus aurocapilla*) had significant decreases in clearcut stands after treatment and lesser decreases in select cut or thin stands post-treatment. Densities of black-and-white warbler (*Mniotilta varia*), eastern wood-pewee (*Contopus virens*), and Kentucky warbler (*Geothlypis formosa*) increased in clearcut, thin, and select cut stands, but these increases were short-lived and sporadic by year after treatment. Densities of Acadian flycatcher and ovenbird remained lower in clearcut stands than no-harvest stands 13 years post-treatment. The results of this manipulative experiment were mostly consistent with our predictions of bird response to common silvicultural treatments in these forests. Managers can use these species-specific responses to silvicultural treatment to guide management decisions for target species or to balance management practices in a landscape to meet the needs of multiple species. © 2014 The Wildlife Society.

KEY WORDS breeding birds, density, experimental study, forest management, Missouri Ozark Forest Ecosystem Project, MOFEP, spot-mapping.

Timber harvest affects the structure and composition of forests and therefore has short- and long-term effects on wildlife. Many studies have addressed the effects of forest management on songbirds in eastern deciduous forests (Conner et al. 1979, Nichols and Wood 1995, Annand and Thompson 1997, Costello et al. 2000). Bird responses to forest management are generally species-specific and depend on the degree of overstory removal, the spatial extent of the treatment, the landscape context, and time since disturbance (reviewed by Thompson et al. 1995). Even though substantial research has occurred on these topics, there is still uncertainty on the effects of timber harvest on birds because of limited research on some management practices, species, or regions, and the difficulty of conducting manipulative experiments at large spatial and temporal scales that allow strong inference (Thompson et al. 2000).

Ecological research has been criticized because it often is observational rather than based on hypotheses evaluated by manipulative experiments. Statistical inferences about cause and effect are strongest when based on manipulative experiments that randomize treatments because the researcher can be relatively confident the experiment is unbiased and can design the experiment to control temporal

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and procedural effects (Romesburg 1981). The Missouri Ozark Forest Ecosystem Project (MOFEP) was initiated in 1989 by the Missouri Department of Conservation as a 100-year experiment designed to provide reliable knowledge on the effects of even- and uneven-aged forest management on wildlife, plants, and other ecosystem attributes at a landscape scale (Brookshire and Dey 2000). Previous MOFEP analyses of birds tested hypotheses concerning effects of even- and uneven-aged forest management systems at a site (e.g., landscape) scale in which sites consisted of a mix of treated and untreated stands typical of a managed, regulated forest (Gram et al. 2003, Wallendorf et al. 2007, Morris et al. 2013). Analyses at this site scale, however, do not provide information on bird response to stand-level silvicultural treatments because densities are averaged across both harvested and non-harvested stands within a site. Thus, we investigated the effects of silvicultural treatment and year on bird density at the stand scale to gain a more detailed understanding of the mechanisms that cause changes in density in the years following tree harvest. The stand-level scale is the scale at which silvicultural practices (i.e., treatments) are implemented and individual bird territories are affected.

Our objective was to determine the effects of clearcut, select cut, thin, and no-harvest silvicultural treatments over 14 years on stand-level territory density of 15 bird species within the original MOFEP design. We predicted that densities of a species would be similar among stands before silvicultural treatment regardless of the planned treatment because stands were similar in composition and structure before treatment. We predicted there would be an effect of stand treatment × year because densities of birds that tend to use early-successional habitat (e.g., indigo bunting [*Passerina cyanea*], prairie warbler [*Setophaga discolor*], and yellow-breasted chat [*Icteria virens*]) or forest gaps (e.g., hooded warbler [*Setophaga citrina*]) would increase for several years after treatment and thereafter decline, and that these increases would be greater in stands treated by clearcut than in stands select cut or thinned. We predicted that densities of Acadian flycatcher (*Empidonax virescens*), black-and-white warbler (*Mniotilta varia*), eastern wood-pewee (*Contopus virens*), Kentucky warbler (*Geothlypis formosa*), northern parula (*Setophaga americana*), ovenbird (*Seiurus aurocapilla*), scarlet tanager (*Piranga olivacea*), summer tanager (*Piranga rubra*), wood thrush (*Hylocichla mustelina*), worm-eating warbler (*Helmitheros vermivorum*), and yellow-billed cuckoo (*Coccyzus americanus*) would decrease after treatment and these decreases would be greater in stands treated by clearcut than in stands select cut or thinned, because these species are known to use mature forest and may abandon treated stands or areas near treated stands. We predicted that densities of these species may differ among no-harvest stands in sites with even-aged or uneven-aged management versus sites with no-harvest management because individuals might move from treated stands into nearby no-harvest stands or species might prefer or avoid edges created by harvest in an adjoining treated stand. For example, ovenbird density might decrease in no-harvest stands in sites managed by even-aged or uneven-aged management, because previous research suggests they avoid edges (Van Horn et al. 1995, Wallendorf et al. 2007), whereas Kentucky warblers may increase because they nest in dense understory vegetation (McDonald 2013), which may increase near edges created by harvest.

STUDY AREA

The 9 MOFEP sites ranged in size from 312 ha to 514 ha and were located in Carter, Reynolds, and Shannon Counties in southeastern Missouri (Fig. 1A). The MOFEP sites were in the Current River Hills subsection of the Ozark Highlands, characterized by moderate to steeply dissected hills and oak (*Quercus* spp.)-hickory (*Carya* spp.) and oak-pine (*Pinus* spp.) forests and woodlands, oak savanna, bluestem (*Andropogon* spp.) prairie, and glades (Meinert et al. 1997). This region was approximately 84% forested and at the beginning of the study, forest was generally even-aged and 60–80 years old (Brookshire et al. 1997).

METHODS

Experimental Design

The Missouri Ozark Forest Ecosystem Project was designed as a randomized block design consisting of 3 blocks of 3 sites. Within each block, sites were assigned to 1 of 3 management systems: even-aged, uneven-aged, and no-harvest. Each site was divided into 36–74 stands, which were delineated based on common slope, aspect, and ecological land type and ranged in size from 0.16 ha to 62 ha (Brookshire et al. 1997; Fig. 1 and Table 1). Even-aged management sites were managed on a 100-year rotation and a 15-year re-entry period; on the first entry in 1996, 6–8 stands per site 0.6–14.1 ha in size and totaling 10–12% of a site were clearcut. Clearcutting occurred by commercial harvest followed by non-commercial treatments to fell all residual stems except those left to meet state guidelines for cavity trees and snags. Additional stands on even-aged sites composed of small saw and pole timber that were overstocked and could yield enough timber for a commercial sale were treated by commercial thinning to reduce stocking and concentrate growth of desirable trees for clearcut harvest in the future (Brookshire and Dey 2000). The remaining stands received no treatment. Forty-one to 69% of each uneven-aged management site was treated by a combination of single-tree and group-selection cuts in 1996 and the remainder of the site received no treatment. Each site had 84–97 group openings 35–70 m in diameter within the treated stands. No stands on the no-harvest management sites received treatments.

We assigned all stands to the silvicultural treatment they received in 1996: clearcut, select cut, thin, or no-harvest. We further considered no-harvest treatments within each site-level management system as different practices because we hypothesized bird densities might differ among no-harvest stands in sites assigned to even-aged (no-harvest even-aged), uneven-aged (no-harvest uneven-aged), or no-harvest (no-harvest control) management. Therefore, the combination of years and 4 silvicultural treatments in sites assigned to 3

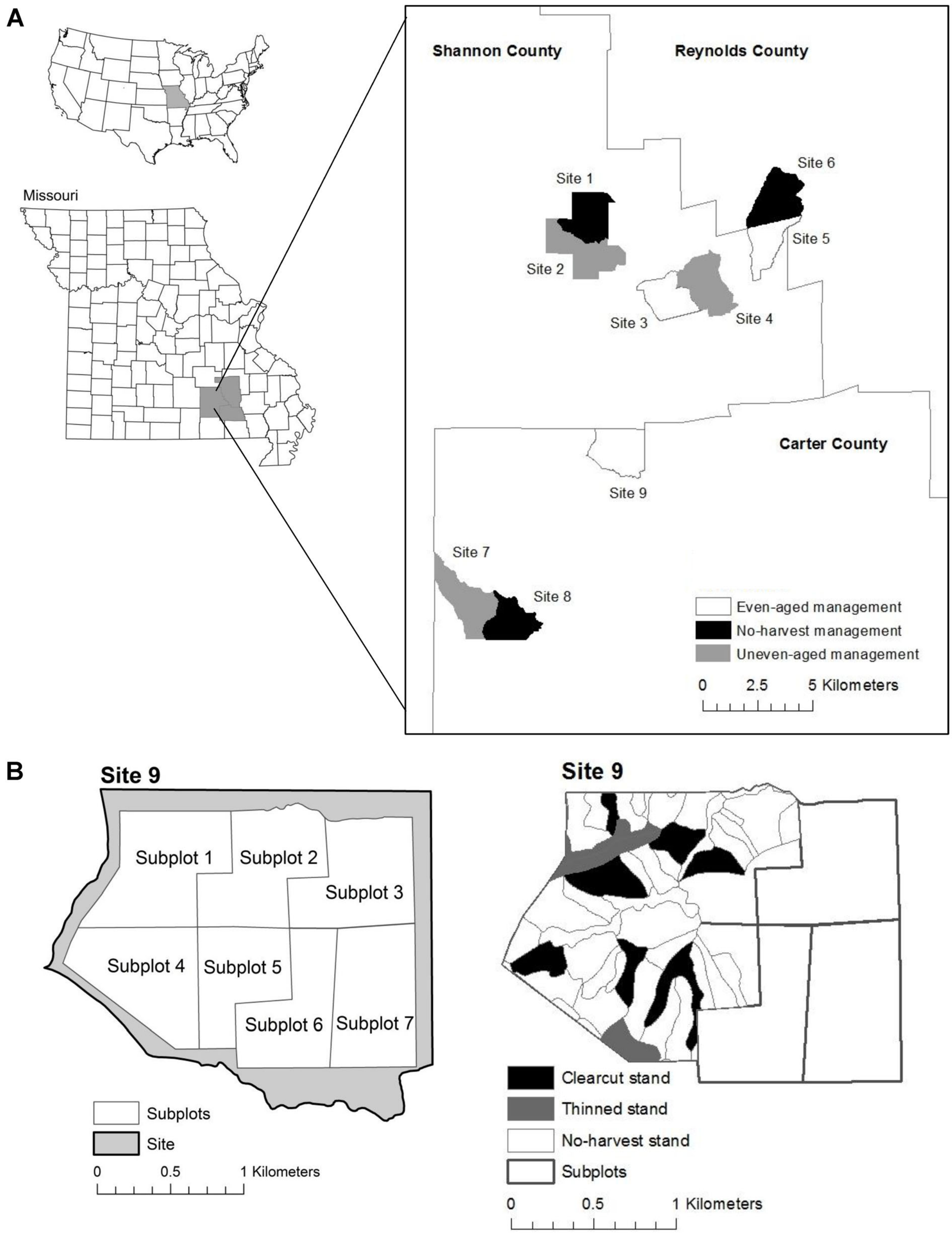

Figure 1. Study sites, management, and treatment types of the Missouri Ozark Forest Ecosystem Project in southeastern Missouri (A), including an example of the layout of 9 census subplots in a site (B), and an example of stand delineations and silvicultural treatment types in the 4 subplots on a site.

management systems represented a before-after-control design in which stands were monitored but not treated 1991–1995; clearcut, select cut, and thin treatments occurred in 1996; and stands were monitored post-treatment for selected years from 1997–2010.

Bird Census

We used the spot-mapping method (Svensson et al. 1970) to estimate bird densities in each year before harvest (1991–1995) and after (1997–2010). We divided each site into 7 subplots that averaged 45 ha in size (Fig. 1B). We censused

Table 1. Number of stands ($n = 228$) assigned to silvicutural treatments within sites assigned to even-aged, uneven-aged, or no-harvest management systems as part of the Missouri Ozark Forest Ecosystem Project, 1991–2010. Management systems were randomly assigned within blocks. Stands were selected for silvicultural treatments based on standard forest management guidelines and stand inventory data.

			Uneven-aged		Even-aged		
Site	**Block**	**No-harvest**	**Select cut**	**No-harvest**	**Clearcut**	**Thin**	**No-harvest**
1	1	25					
2	1		10	4			
3	1				4	7	13
4	2		24	5			
5	2				6	8	13
6	2	28					
7	3		13	16			
8	3	19					
9	3				7	3	23
Total		72	47	25	17	18	49

all 7 subplots on each site 1991–1995 and 1997–2000 but only 4 subplots per site during 2001–2003 and 2008–2010 to reduce effort while still sampling some stands in all treatments. We did not include data from 2004 to 2007 because we censused only clearcut stands during these years.

One technician censused each subplot for 3–4 hr 5 mornings per week starting at sunrise between mid-May and the end of June; we sampled each subplot 8–10 times at 2- to 3-day intervals and alternated observers daily to reduce observer bias. Each observer used slightly different routes across the subplot from the previous day's route. We recorded all observations on an enlarged topographic map of the subplot, and defined a territory as 3 or more clustered observations of a species observed on 3 separate dates. We entered the approximate centers of territories in ArcView GIS 3.2 (ESRI, Redlands, CA, USA) or ArcMap 9.3 (ESRI).

We mapped territories of 15 species (Acadian flycatcher, black-and-white warbler, eastern wood-pewee, hooded warbler, indigo bunting, Kentucky warbler, ovenbird, northern parula, prairie warbler, scarlet tanager, summer tanager, wood thrush, worm-eating warbler, yellow-billed cuckoo, and yellow-breasted chat). We chose species that were abundant enough to survey and that we hypothesized would respond to treatments. We did not include the very abundant red-eyed vireo (*Vireo olivaceus*) because territories were small, numerous, and too difficult to delineate by spot-mapping unmarked birds.

Analysis

We summed the number of territory centroids of each species in each stand and divided the sum by stand area to estimate density. We recognize that basing density estimates on territory centroids could lead to errors if territories overlapped multiple stands but we assumed errors were random, averaged out across stands, and therefore did not bias our results. We excluded partial stands that were split by plot boundaries or entire stands <2.89 ha because we considered them too small to contain an average-sized territory for the ovenbird, which had the largest territory among our focal species (Porneluzi and Faaborg 1999).

We evaluated the effects of silvicultural treatment × year on the density of 15 species with generalized linear mixed models (PROC GLIMMIX, SAS 9.3, SAS Institute, Cary, NC). We evaluated the use of gamma and normal distributions for the response variable and selected gamma because it resulted in values of overdispersion close to 1 and Pearson residuals with a mean and variance of 0 and 1, respectively. We used a randomized block, repeated measures design in which we treated block as a random effect to acknowledge the original MOFEP experimental design in which sites were grouped and treatments randomized within groups (Sheriff 2000). We included year as a second random effect to account for repeated (annual) measures of bird density in each stand and selected a first-order autoregressive covariance structure over homogenous covariance based on Akaike's Information Criterion (AIC). Our model included fixed effects for the silvicultural treatment × year interaction and the constituent effects of year and treatment; however, we only evaluated the silvicultural treatment × year effect because we hypothesized the effects of treatment varied by year. In addition, we specified 2 a priori contrasts for each species to test if density in stands assigned to each treatment changed from the 5 pre-treatment years (1991–1995) to 3–5 years (1999–2001) post-treatment and 12–14 years (2008–2010) post-treatment and refer to tests with $P < 0.05$ as significant; the contrasts were linear combinations of model parameters designed to test the hypothesis of no difference between 2 means. We selected 3–5 years post-treatment to give vegetation and birds time to respond and because it corresponds with the time that early-successional species are expected to be at the greatest abundance (Thompson and DeGraaf 2001). We also plotted least squares means for each species by silvicultural treatment from 1991 to 2010.

RESULTS

We used 26,396 total territories of 15 species in 228 stands >2.89 ha from 5 years pre-harvest (1991–1995) and up to 14 years post-harvest (1997–2004 and 2008–2010) in our analyses. The number of territories for a species ranged from 267 to 5,126 for prairie warbler and Acadian flycatcher, respectively. Our randomized-block repeated measures analysis of variance (ANOVA) was based on 3,420 observations per species (15 years × 228 stands) but accounted for 15 repeated measures (years) for 228 stands.

We found the silvicultural treatment × year interaction affected densities of all 15 species ($F_{70,\ 3,328} = 1.6–43.9$, $P \leq 0.001$) even considering a familywise error rate across all 15 species using a conservative Bonferonni adjustment ($P \leq 0.02$; Dunn 1961). Most contrasts comparing pre-treatment densities to early post-treatment (3–5 years after treatment) and late post-treatment (12–14 years after harvest) densities for each treatment were significant ($P < 0.05$), including many for no-harvest treatments, even in control sites (Table 2). The fact that densities often changed even in the no-harvest treatment stands in sites under no-harvest management indicated multiple factors affected densities, nevertheless, comparisons of the magnitude of changes in densities over time demonstrated response to treatments (Fig. 2 and Table 2).

Densities of all 15 species in clearcut stands were significantly different in the pre-treatment period from both early and late post-treatment periods, except for prairie warbler, whose density was no longer significantly different by the late post-treatment period (Table 2). Densities of black-and-white warbler, hooded warbler, indigo bunting, and yellow-breasted chat significantly increased in clearcuts in both early and late post-treatment periods, whereas densities of Acadian flycatcher, eastern wood-pewee, ovenbird, scarlet and summer tanager, wood thrush, worm-eating warbler, and yellow-billed cuckoo significantly decreased in both of these periods compared to pre-treatment (Fig. 2 and Table 2). Densities of Kentucky warbler significantly increased in clearcuts early post-treatment and significantly declined in clearcuts late post-treatment, whereas northern parula density significantly decreased early post-treatment and significantly increased late post-treatment compared to pre-treatment (Fig. 2 and Table 2).

Densities in select cut stands were significantly different from pre-treatment for 12 species in the early and late post-treatment periods (Table 2). Densities of Acadian flycatcher, eastern wood-pewee, ovenbird, scarlet tanager, and yellow-billed cuckoo significantly decreased in select cut stands early and late post-treatment, whereas summer tanager and worm-eating warbler decreased only in the late post-treatment period. Densities of black-and-white warbler, hooded warbler, and indigo bunting significantly increased in both of these periods in select cut stands. Kentucky warbler and prairie warbler significantly increased only in the early post-treatment period, however, these small increases were not likely biologically significant (Fig. 2 and Table 2). Wood thrush density estimates in select cut stands were not significantly different from the pre-treatment period in either the early or late post-treatment periods (Fig. 2 and Table 2).

Densities in thinned stands were significantly different from early post-treatment period and late post-treatment for 13 and 8 species, respectively (Table 2). Densities of black-and-white warbler and hooded warbler significantly increased in both the early and late post-treatment periods compared to the pre-treatment period (Fig. 2 and Table 2). Acadian flycatcher, yellow-billed cuckoo, and scarlet tanager densities significantly decreased in thinned stands in the early post-treatment period and changes were not significantly different in the late post-treatment period. Eastern wood-pewee, prairie warbler, and yellow-breasted chat densities significantly increased in the early post-treatment period and changes were not significantly different in the late post-treatment period (Fig. 2 and Table 2). Indigo bunting and Kentucky warbler densities significantly increased in thinned stands in the early post-treatment period and then significantly decreased in the late post-treatment period compared to the pre-treatment period, whereas the opposite trend was true for northern parula (Fig. 2 and Table 2). Ovenbird and summer tanager densities significantly decreased in both the early and late post-treatment periods in thinned stands compared to the pre-treatment period (Fig. 2 and Table 2).

Densities in no-harvest even-aged stands were significantly different in either or both the early or late post-treatment period from pre-treatment densities for all 15 species (Table 2). Densities of ovenbird, scarlet and summer tanagers, worm-eating warbler, and yellow-billed cuckoo decreased significantly in both the early and late post-treatment period compared to pre-treatment; conversely, hooded warbler density increased significantly in both of these periods (Fig. 2 and Table 2). Prairie warbler and yellow-breasted chat increased in the early post-treatment period and then decreased to near zero with no significant change in density in the late post-treatment period from pre-treatment (Fig. 2 and Table 2).

No-harvest uneven-aged stands had significantly different densities for 12 species in the early post-treatment period and 9 species in the late post-treatment period (Table 2). Densities of Kentucky warbler, ovenbird, scarlet and summer tanagers, wood thrush, and yellow-billed cuckoo decreased significantly in both the early and late post-treatment period compared to pre-treatment; conversely, hooded warbler density increased significantly in both periods (Fig. 2 and Table 2). Acadian flycatcher, prairie warbler, and worm-eating warbler densities did not significantly change in either period compared to pre-treatment (Fig. 2 and Table 2). The remaining species had short-lived changes in density (both increases and decreases) in the early post-treatment period only (Fig. 2 and Table 2).

No-harvest stands in the control sites had significantly different densities for 13 species in the early or late post-treatment periods, or both (Fig. 2 and Table 2). Densities of Acadian flycatcher, Kentucky warbler, ovenbird, scarlet and summer tanager, wood thrush, and yellow-billed cuckoo significantly decreased in both the early and late post-treatment periods compared to pre-treatment (Fig. 2 and Table 2). Prairie warbler and yellow-breasted chat densities were near zero in these stands throughout the study, and no significant density changes occurred in any period (Fig. 2 and Table 2). Remaining species experienced significant increases and decreases in both or just 1 post-treatment period compared to pre-treatment (Fig. 2 and Table 2).

Table 2. Changes in territory density (territories/100 ha) between 5 pre-treatment years and 3–5 years and 12–14 years post-treatment for 4 silvicultural treatments in the Missouri Ozark Forest Ecosystem Project, 1991–2010. *P*-Values are for a priori contrasts between pre-treatment and 2 post-treatment periods (*F* tests, df = 1, 3,328); we did not make corrections for experiment-wide error rates. Means are means of least-square means for each year in the time period and standard errors reflect variation among years in a period. Clearcut, select cut, and thin were tree harvest silvicultural treatments, whereas no-harvest treatments were stands with no tree harvest within sites subjected to even-aged (EAM), uneven-aged (UAM), or no-harvest (control) management.

Species and period	Clearcut			Select cut			Thin			No harvest EAM			No harvest UAM			No harvest control		
	Mean	SE	*P*	Mean	SE	*P*	Mean	SE	*P*	Mean	SE	*P*	Mean	SE	*P*	Mean	SE	*P*
Yellow-billed cuckoo																		
Pre	7.4	2.3		3.7	1.7		7.3	3.9		3.8	1.5		4.8	1.5		6.1	1.7	
Post 3–5	0.3	0.3	<0.01	2.2	1.5	<0.01	1.8	1.5	<0.01	3.5	2.7	0.01	2.7	1.4	<0.01	4.9	3.4	<0.01
Post 13–15	0.7	0.7	<0.01	0.5	0.2	<0.01	1.9	0.3	0.91	1.7	1.7	<0.01	0.5	0.5	<0.01	1.0	0.6	<0.01
Acadian flycatcher																		
Pre	28.3	1.2		24.4	2.1		27.4	3.4		32.0	2.1		27.1	1.5		28.4	1.1	
Post 3–5	1.6	0.9	<0.01	14.6	1.5	<0.01	14.3	3.2	0.01	26.8	2.7	0.22	26.2	2.4	0.87	19.3	1.5	<0.01
Post 13–15	3.9	0.6	<0.01	14.7	2.5	<0.01	18.9	4.2	0.11	23.4	3.7	0.02	25.9	6.2	0.66	18.8	2.3	<0.01
Eastern wood-pewee																		
Pre	13.2	3.1		14.0	2.5		6.6	2.3		10.6	1.5		10.9	1.7		12.1	2.0	
Post 3–5	5.3	3.4	<0.01	10.0	6.2	<0.01	8.7	5.8	0.04	5.9	3.0	<0.01	5.6	3.2	<0.01	7.1	4.3	<0.01
Post 13–15	3.2	0.4	<0.01	8.8	0.6	0.03	3.9	2.5	0.46	8.7	0.3	0.43	9.5	1.7	0.63	9.1	1.1	0.15
Wood thrush																		
Pre	7.2	1.1		2.6	0.5		9.3	1.9		8.7	0.7		7.7	1.5		8.5	0.5	
Post 3–5	0.7	0.4	<0.01	1.7	0.3	0.33	6.5	2.0	0.47	7.5	2.5	0.46	3.1	0.9	0.04	1.5	0.7	<0.01
Post 13–15	2.1	1.4	<0.01	2.8	0.7	0.70	0.5	0.3	<0.01	0.9	0.5	<0.01	2.1	0.6	0.01	2.5	1.0	<0.01
Ovenbird																		
Pre	20.9	3.9		19.0	0.8		30.8	3.2		30.3	2.1		39.5	2.8		23.7	0.8	
Post 3–5	0.3	0.2	<0.01	6.5	2.0	<0.01	5.9	1.1	<0.01	5.7	0.3	<0.01	18.7	2.1	0.01	15.9	2.7	0.01
Post 13–15	2.3	1.9	<0.01	13.8	4.4	0.04	16.4	4.8	0.03	11.9	3.9	<0.01	15.4	2.9	<0.01	15.4	3.0	<0.01
Worm-eating warbler																		
Pre	20.2	1.6		16.1	1.0		17.7	0.9		24.0	1.1		14.8	1.1		20.1	0.6	
Post 3–5	3.9	1.5	<0.01	14.7	3.1	0.36	16.0	4.2	0.42	17.5	3.4	0.02	15.1	1.6	0.92	16.9	3.2	0.07
Post 13–15	10.5	3.4	<0.01	10.3	1.1	<0.01	15.3	1.2	0.54	15.1	2.8	<0.01	12.8	1.5	0.46	13.4	1.5	<0.01
Black and white warbler																		
Pre	6.8	1.2		5.6	1.2		4.8	2.2		8.1	1.5		3.6	1.1		3.4	0.6	
Post 3–5	8.0	4.0	<0.01	7.5	5.1	<0.01	6.3	4.6	<0.01	5.4	3.0	<0.01	2.9	2.8	<0.01	1.6	1.2	<0.01
Post 13–15	14.6	2.3	0.05	13.0	2.6	<0.01	14.1	1.0	<0.01	9.1	2.8	0.69	9.6	1.8	<0.01	7.7	2.4	<0.01
Kentucky warbler																		
Pre	1.2	0.8		0.3	0.1		0.4	0.2		0.2	0.0		1.5	0.8		0.7	0.5	
Post 3–5	4.5	3.0	<0.01	1.0	0.7	<0.01	2.5	1.2	<0.01	0.1	0.0	0.01	0.0	0.0	<0.01	0.0	0.0	<0.01
Post 13–15	0.1	0.0	<0.01	0.1	0.0	0.26	0.1	0.0	<0.01	0.1	0.0	0.55	0.1	0.0	<0.01	0.0	0.0	<0.01
Hooded warbler																		
Pre	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Post 3–5	24.0	6.7	<0.01	5.7	2.3	<0.01	9.3	1.7	<0.01	3.4	1.0	<0.01	0.8	0.1	<0.01	0.0	0.0	1.00
Post 13–15	10.7	2.6	<0.01	9.4	0.5	<0.01	4.5	0.3	<0.01	4.3	0.4	<0.01	3.7	0.7	<0.01	1.9	0.5	<0.01
Northern parula																		
Pre	2.4	1.3		4.2	1.9		4.7	1.6		5.0	1.6		5.5	1.7		3.7	1.2	
Post 3–5	2.3	2.3	<0.01	2.0	1.5	<0.01	1.7	1.7	<0.01	2.5	2.5	<0.01	2.1	2.1	<0.01	2.5	1.3	<0.01
Post 13–15	4.9	0.9	0.01	12.0	1.2	<0.01	10.9	1.7	<0.01	12.5	1.5	<0.01	11.8	1.8	0.01	9.3	0.8	<0.01
Prairie warbler																		
Pre	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.7	0.7		0.0	0.0	
Post 3–5	335.5	113.6	<0.01	0.1	0.1	<0.01	0.9	0.6	<0.01	0.6	0.6	<0.01	0.1	0.0	0.56	0.0	0.0	0.23
Post 13–15	1.2	0.6	0.99	0.0	0.0	0.16	0.1	0.0	0.97	0.1	0.0	0.98	0.1	0.0	0.49	0.1	0.0	0.72
Yellow-breasted chat																		
Pre	0.0	0.0		0.1	0.1		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
Post 3–5	62.7	14.2	<0.01	9.7	2.8	<0.01	5.7	1.4	<0.01	1.4	0.7	<0.01	0.7	0.7	<0.01	0.0	0.0	0.08
Post 13–15	0.1	0.1	0.01	0.0	0.0	<0.01	0.0	0.0	0.98	0.0	0.0	0.10	0.0	0.0	0.48	0.0	0.0	0.08
Summer tanager																		
Pre	1.7	0.2		2.6	0.7		2.9	1.2		2.4	0.5		1.1	0.4		3.1	1.2	
Post 3–5	0.1	0.1	<0.01	3.6	3.2	0.20	2.8	2.8	<0.01	1.3	1.2	<0.01	0.9	0.8	<0.01	2.9	2.7	<0.01
Post 13–15	0.0	0.0	<0.01	0.1	0.0	<0.01	0.1	0.1	<0.01	0.0	0.0	<0.01	0.1	0.0	<0.01	0.1	0.0	<0.01
Scarlet tanager																		
Pre	14.0	3.1		9.3	2.0		9.2	2.0		11.1	1.3		12.4	2.6		10.4	2.0	
Post 3–5	1.2	1.0	<0.01	3.6	2.5	<0.01	6.8	4.2	<0.01	5.5	4.0	<0.01	3.6	1.8	<0.01	6.7	4.4	<0.01
Post 13–15	3.0	1.8	<0.01	4.7	1.5	<0.01	5.8	1.3	0.21	5.0	1.8	<0.01	4.7	1.0	<0.01	6.8	1.9	0.01
Indigo bunting																		
Pre	1.0	0.8		1.9	0.7		1.4	0.6		3.0	1.5		1.9	0.6		1.9	0.7	
Post 3–5	60.4	17.6	<0.01	28.3	2.1	<0.01	21.3	1.5	<0.01	9.6	1.1	<0.01	14.3	0.7	<0.01	5.5	1.5	<0.01
Post 13–15	3.6	2.8	<0.01	3.1	0.5	<0.01	0.0	0.0	<0.01	1.9	0.4	<0.01	3.1	1.2	0.42	1.5	0.4	0.95

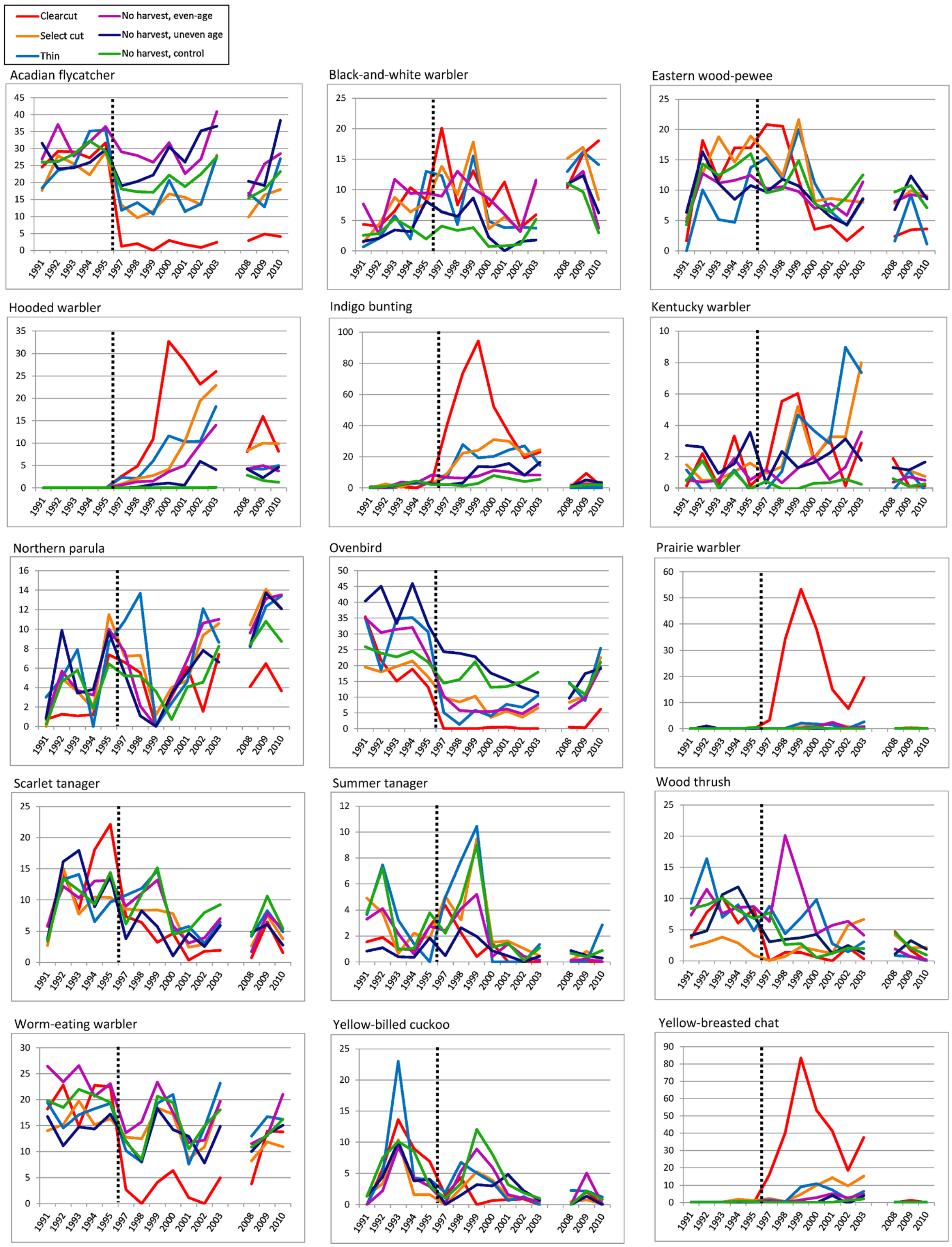

Figure 2. Densities (territories/100 ha) of 15 bird species in stands in 1 of 4 silvicultural treatments (clearcut, select cut, thin, no-harvest) within 3 management systems (even-aged, uneven-aged, or no-harvest) over 19 years of the Missouri Ozark Forest Ecosystem Project in southeastern Missouri, USA. Silvicultural treatments (clearcut, select cut, and thin) occurred in 1996 indicated by the dotted black line.

DISCUSSION

Our stand-level density analysis of 15 species over 19 years of MOFEP allowed a finer and more detailed look at breeding bird density response to silvicultural treatments within even-aged, uneven-aged, and no-harvest stands in Missouri than the site-level responses previously reported (Clawson et al. 1997, 2000; Gram et al. 2003; Wallendorf et al. 2007; Morris et al. 2013). Species changed in density over the duration of the study, even in the no-harvest control treatment. Given that this was a manipulative experiment with randomized assignment of management systems to sites, we suggest other factors outside our study also affected bird density in the region. These results further demonstrate the importance of validating observational studies with manipulative studies involving before-after-control designs to allow strong inference (Thompson et al. 2000). Even though densities of some species changed in the no-harvest stands, the magnitude of change was often greater in stands with harvest and followed a priori predictions. With a few exceptions discussed below, we generally confirmed our hypotheses and results of previous research for bird response to clearcut, select cut, thin, and no-harvest treatments with our experimental approach.

As predicted, hooded warbler, indigo bunting, prairie warbler, and yellow-breasted chat increased to their greatest densities in clearcut stands for several years post-harvest and then declined by late post-treatment. This pattern is consistent with other studies indicating early-successional species dependent on forest disturbance generally respond within 1–3 years of timber harvest and begin declining within 10 years, except hooded warblers initially declined for 3 years following harvest in bottomland hardwoods but then increased to densities exceeding untreated controls by 8 years (Conner et al. 1979, Thompson and DeGraaf 2001, Twedt and Somershoe 2010). Contrary to our expectation, Kentucky warbler also increased early post-treatment in clearcuts, but this is consistent with increases in densities seen by Thompson and Fritzell (1990) in 3-year-old clearcuts. Densities of Acadian flycatcher, ovenbird, scarlet tanager, summer tanager, worm-eating warbler, wood thrush, and yellow-billed cuckoo decreased post-treatment in clearcuts and were generally lower than in any other treatment, which confirms findings by others that these species are much less abundant in clearcuts than mature forest (Conner et al. 1979, Thompson et al. 1992, Annand and Thompson 1997). Densities of Acadian flycatcher, eastern wood-pewee, ovenbird, scarlet tanager, worm-eating warbler, and yellow-billed cuckoo were still lower in the late post-treatment period and less than other treatments in this period, indicating densities had not recovered 14 years post-clearcut harvest.

Changes in density in the select cut and thin treatments were similar for most species and supported our prediction that these treatments have a less severe effect on density than clearcutting. Prairie warbler and yellow-breasted chat had small increases in response to select cut and thin treatments, whereas hooded warbler and indigo bunting had more substantial increases in response to select cut treatment. Prairie warbler and yellow-breasted chat generally require large disturbances such as clearcuts to create successional habitat, whereas hooded warbler and indigo bunting are gap-using species that are common in selectively cut forests (Annand and Thompson 1997, Robinson and Robinson 1999, Costello et al. 2000, Alterman et al. 2005). Increases in these species were relatively brief (3–4 years) and decreases in density corresponded to the time at which the canopies of regenerating trees began to close and shade out understory and ground cover vegetation. Densities of other species that are commonly considered mature-forest species like black-and-white warbler, eastern wood-pewee, and Kentucky warbler increased to some of their greatest densities post-treatment in select cut and thinned stands, though density increases were short-lived. For example, Kentucky warbler density in all treatments declined to levels lower than pre-treatment by late post-treatment. Other studies have reported greater densities of Kentucky warbler, black-and-white warbler, and eastern wood-pewee in landscapes managed by even-age and uneven-age management (Gram et al. 2003) or in select cut or clearcut stands (Thompson and Fritzell 1990, Thompson et al. 1992, Annand and Thompson 1997, Twedt and Somershoe 2010). Other studies have also found smaller declines in mature forest species under partial-harvest (select cut treatment) compared to clearcuts (Annand and Thompson 1997, Robinson and Robinson 1999, Costello et al. 2000).

We hypothesized some birds might decline or increase in density in no-harvest stands within even-aged or uneven-aged management areas because of changes to the study area, even though stands under consideration were untreated. However, all species that declined in the no-harvest even-aged or no-harvest uneven-aged stands had similar declines in the no-harvest control stands and late post-treatment densities were mostly similar across all no-harvest stands (Table 2). This indicates that landscape-wide factors were affecting densities over time across all stands; however, we have no knowledge of what these were. Furthermore, examination of density trends over time (Fig. 2) suggests declines were under way before timber harvest occurred in 1996 for ovenbird, scarlet tanager, summer tanager, wood thrush, worm-eating warbler, and yellow-billed cuckoo. Ovenbirds were perhaps an exception to this; they declined less in the no-harvest control stands than no-harvest even-aged and no-harvest uneven-aged. Ovenbirds may be highly sensitive to harvest in the surrounding area because they may require larger patches of non-harvested forest (Burke and Nol 1998, Wallendorf et al. 2007) to accommodate larger territories (Porneluzi and Faaborg 1999), avoid harvest in the immediate area (Wallendorf et al. 2007), or avoid edges, which may influence pairing success (Van Horn et al. 1995). Wood thrush also declined in all no-harvest treatments, but densities were over 5 times greater in early post-treatment in no-harvest even-aged stands than in the no-harvest control stands, possibly so these birds could be near food and cover in clearcuts for fledglings (Anders et al. 1998, Vega Rivera et al. 1998). We believe that the small but significant increases of prairie warbler and yellow-breasted chat in no-harvest even-aged and no-harvest uneven-aged stands, respectively, occurred because birds with territories in adjacent clearcut or select cuts were occasionally observed in the forest or because of map errors.

Ovenbird stand densities slowly rebounded to reach the lowest pre-harvest densities in all stand treatments except clearcut by 2010; however, no-harvest stands (even in control sites) maintained low densities for the duration of our study, indicating lasting declines in density after harvest in the region, similar to the effects of select cuts on ovenbird abundance 12 years after harvest in northern Ontario (Holmes et al. 2012). Long-term density declines were also maintained across the study for eastern wood-pewee, scarlet and summer tanagers, wood thrush, and yellow-billed cuckoo.

MANAGEMENT IMPLICATIONS

Regulated, sustainable tree harvest in the predominantly contiguous forest of the Missouri Ozarks appears generally compatible with maintaining habitat for the mature-forest and early-successional bird species included in our study. Among the species we studied, wood thrush, worm-eating warbler, Kentucky warbler, yellow-billed cuckoo, eastern wood-pewee, prairie warbler, and yellow breasted chat are all considered priority species for conservation (Central Hardwoods Joint Venture 2012). Managers can use species-specific responses to silvicultural treatments we described to select appropriate management practices for individual species. For example, the clearcut treatment increased densities of prairie warbler and yellow-breasted chat and select cut or thin treatments increased densities of eastern wood-pewee, northern parula, Kentucky warbler, and black-and-white warbler. Also, concentrating or grouping harvest activities minimizes edge and potential edge effects for mature-forest species like ovenbirds (King et al. 1998, Manolis et al. 2002), while creating larger disturbance patches for early-successional species, which may also be area- or edge-sensitive (Annand and Thompson 1997, Burhans and Thompson 1999, Woodward et al. 2001). Therefore, managers need to be cognizant of the spatial and temporal tradeoffs among management systems in the distribution of bird habitats. Recent emphasis on restoration management in these landscapes further complicates planning, because there are similar tradeoffs for these bird species across a gradient of savanna, woodland, and forest (Reidy et al. 2014); thus, land managers and planners should consider the mix of these communities in addition to silvicultural systems in the landscape. Continued research on bird densities in the MOFEP study will further clarify bird responses over multiple entry periods, on longer-term temporal changes in density post-harvest, and help to distinguish landscape-wide and long-term changes in bird density in response to management. We suggest simple models be constructed that enable managers to evaluate trade-offs in species density and landscape diversity based on the mix of silvicultural treatment and restoration management in central hardwood landscapes.

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