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EFFECTS OF EXPERIMENTAL FOREST MANAGEMENT ON AVIAN COMMUNITIES IN THE MISSOURI OZARKS

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EFFECTS OF EXPERIMENTAL FOREST MANAGEMENT ON AVIAN COMMUNITIES IN THE MISSOURI OZARKS

A Thesis Submitted to the Graduate School in Partial Fulfillment of the Requirements for the Degree of Master of Science

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EFFECTS OF EXPERIMENTAL FOREST MANAGEMENT ON AVIAN COMMUNITIES IN THE MISSOURI OZARKS

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EFFECTS OF EXPERIMENTAL FOREST MANAGEMENT ON AVIAN COMMUNITIES IN THE MISSOURI OZARKS

An Abstract of the Thesis by
David Hollie

In recent decades, concern for migratory birds has stimulated research assessing the relationships between forest management and bird populations. The Missouri Ozark Forest Ecosystem Project (MOFEP) is a long-term, landscape-scale experiment designed to examine the effects of even-aged (i.e. clearcutting), uneven-aged (i.e. selection cutting), and no harvest forest management on ecosystem level processes. The management systems were randomly assigned to three sites each (mean area = 400 ha) under a 100-year rotation with a 15-year re-entry period.

In the first chapter, we used non-metric multidimensional scaling and linear mixed effects models to investigate the effects of silvicultural treatment and year-since-harvest on bird communities from 1991 to 2014 before and after two harvests (1996 and 2011). Bird communities diverged among treatments immediately post-harvest, but the differences in community composition and structure began to diminish by 8 years post-harvest. Species richness was higher in treated stands compared to no-harvest controls. Both species richness and diversity showed a linear decrease with year-since-harvest. Our findings demonstrate that even-aged and uneven-aged forest management can affect the bird community composition and structure within 3 years post-harvest, but differences may not be apparent by 12 years post-harvest. We recommend using a variety of silvicultural methods to provide the diversity of habitats needed for the conservation of diverse forest bird communities.

In the second chapter, we used six years (three years before and after harvest) of concurrent point count and spot mapping data from the nine MOFEP sites to assess the ability of 50 m fixed-radius point counts to estimate bird abundance and management effects for 11 focal species. Additionally, we used species richness estimates to examine how similar the two survey methods are for community-level comparisons. Point count densities were generally correlated with spot map densities, but the strength of the relationship varied among species. Point counts also showed similar treatment effects as spot mapping, but the confidence intervals were much wider in point counts. The species richness estimates were only weakly correlated between the two surveying methods. Our results show that 50 m fixed-radius point counts reflect general population trends for the 11 species examined. Therefore, if broad-scale trends are adequate, point counts provide reasonable proxies for the more labor-intensive spot mapping.

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CHAPTER I

AVIAN COMMUNITY RESPONSE TO EXPERIMENTAL FOREST MANAGEMENT IN THE MISSOURI OZARKS

Introduction

Managing forests in an ecologically sustainable way has become a priority for the conservation of biodiversity and overall health of the planet (Bettencourt and Kaur, 2011). An important aspect of forestry is the economic yield from timber production, but the harvest of timber inevitably affects forest structure and composition and thus can have long- and short-term effects on forest ecosystems (Putz et al., 2008; Semlitsch et al., 2009). Increased demand for wood and pulp products has resulted in more intense harvest of timber which has led to a proportional increase in concern for how forest management is affecting biological diversity (Berlik et al., 2002). The challenge is to find a balance between the ecological needs of forest species and the economic need for timber. Sustainable forest management aims to use strategies that provide for present-day needs through the goods and services derived from forests while still maintaining the forests' continued viability and the conservation of biological diversity (Flader, 2004; Duncker et al., 2012).

Concern for migratory bird populations has stimulated research into the population dynamics and conservation of forest songbirds (Holmes et al., 1986; Carter et al., 2000; Sillett et al., 2000; Martin et al., 2007; Ahlering et al., 2010). Some of the early concern was driven by the results of long-term population studies in small parks and woodlots that indicated sharp declines in the populations of forest-dwelling songbirds (Askins et al., 1990). Many decades of Breeding Bird Surveys now suggest that the significant declines in the populations of breeding songbirds are widespread across the forests of the eastern United States (Sauer et al., 2017). Although eastern forests have recovered from widespread historic deforestation, many current practices such as fire suppression and increased herbivory have resulted in a loss of understory and increased homogenization of forest structure which limits the habitat availability for forest-dwelling species (McShea et al. 2007). Many species that are facing population declines depend on forest ecosystems that are routinely managed for timber (Thompson et al. 1992, 1995). Thus, understanding the effects that different types of forest management have on bird communities is paramount when considering what management approach to use.

Past studies have assessed bird response to forest management at the species and community level. However, most of these studies were not done in an experimental framework and the data were collected over relatively small spatial scales (Holmes et al., 1986; Costello et al., 2000) or short time periods (Annand & Thompson, 1997; Lindenmayer et al., 2002; Newell & Rodewald, 2012). Long-term, broad-scale manipulative experiments with randomized treatments are critical for strong statistical inferences from forest management studies (Thomspon et al., 2000; Faaborg et al., 2010). Thus far, studies done in such a framework have focused on species-specific responses

(Gram et al. 2003; Morris et al. 2013; Kendrick et al., 2015). Results from these studies provide insight into how the reproductive success and densities of individual species change following harvest. This information is vital for management plans targeting an individual or group of species.

However, conclusions from species-level studies may fundamentally differ from community-level studies. While individual species may serve as indicators of a restricted component of the community (e.g. guild theory; Root, 1967; Servinghaus, 1981), co-occurring species can have disparate responses to environmental changes (James et al., 1984; Lindenmayer et al., 2006). Although biodiversity may not always be a priority (e.g. if a target species favors conditions that do not support a diverse community), a focus on community structure is crucial if conservation of biodiversity is the goal (May, 1988; Colwell & Coddington, 1994; Mace et al., 2011).

To date, research assessing the long-term, large-scale effects of forest management on bird community composition is lacking. A better understanding of how forest management affects the long-term health and diversity of avian communities is essential for sustainable forestry (Haulton, 2008). We analyzed a 24-year (1991-2014) data set from the MOFEP experiment to evaluate the long-term responses of bird communities to three forest management systems. Our goal was to investigate the changes in community composition, species richness, and diversity in response to treatment type, year-since-harvest, and stand area. We predicted that community composition would be most unique in clearcut stands (on even-aged sites) because shrubland species would replace mature forest species (Conner and Adkisson, 1975; Kendrick et al., 2015). Additionally, we predicted that treated stands would have higher species richness and diversity than no harvest stands (Chaudhary et al., 2016) and that species richness and diversity would be highest immediately post-harvest and decline with year-since-harvest (Keller et al., 2003).

Methods

Study Area

The Missouri Ozark Forest Ecosystem Project (MOFEP) is a long-term, landscape-scale study designed to examine the effects of three different forest management practices (even-aged management, uneven-aged management, and no harvest management) on the flora, fauna, and other ecosystem features of the landscape (Brookshire and Dey, 2000; Knapp et al., 2014). The study area includes nine sites that range in size from 312 ha to 514 ha and are located in Carter, Reynolds, and Shannon counties in the Current River Hills subsection of the Ozark Highlands of southeastern Missouri (91°01' – 91° 13'W and 37°00'–37°12'N; Figure 1). At least 50% of the relative density of tree species is made up of oak (*Quercus spp.*), with white oak (*Q. alba*), black oak (*Q. velutina*) and scarlet oak (*Q. coccines*) being the dominant oak species. Other species comprising a large proportion of the woody vegetation include shortleaf pine (*P. echinata*), post oak (*Q. stellata*), mockernut hickory (*C. tomentosa*), black hickory (*C. texana*), and pignut hickory (*C. glabra*; Shifley and Kabrick, 2000).

At the beginning of the study in 1990, the region was 84% forested and generally even-aged with most of the overstory trees being 50-70 years old. The sites were on land managed for timber prior to being purchased by the Missouri Department of Conservation in the early part of the 20th century but had remained unmanipulated for at least 40 years prior to data collection (Brookshire and Shifley, 1997).

Experimental Design

The Missouri Ozark Forest Ecosystem Project is composed of nine sites, randomly assigned to one of three management strategies: even-aged (EAM), uneven-aged (UAM), and no harvest (NH). Each site was further subdivided into 36–74 stands ranging in size from 0.16 ha to 62 ha; common aspect, slope, and ecological land type were the main features used to determine the boundaries of each stand (Brookshire et al., 1997). Treatments were applied at the stand level and designed to resemble common forest management practices implemented by the Missouri Department of Conservation. The stands on NH sites were not harvested, allowing these sites to serve as indicators of natural processes as the forest matures over the 100 years of the study. In May 1996 and 2011, the Missouri Department of Conservation supervised the harvest of timber from the sites in accordance with the following procedures:

In the EAM treatment, approximately 10-15% of the total forest area was clearcut in patches 3–13 ha, yielding seven to nine clearcut stands within each site (Brookshire and Shifley, 1997). Additional thinned stands were harvested on 5-24% of each site at the same time as the clearcutting to create growing space for residual trees of select sizes. In the UAM treatment, a combination of small-group and single-tree selection cuts (hereafter referred to as group-selection cuts for simplicity) were administered across 41-69% of each site. Group-selection cuts ranged from 21–43 m in diameter, depending on aspect; 5% of the harvested area per UAM site was treated with group-selection cuts (153-267 small-group cuts per site). In both EAM and UAM sites, a reserve of approximately 10% of each site was assigned to be left unharvested for the duration of the study (Morris et al., 2013). In this analysis, we examined 4 stand-level treatments: clearcut, thinned, group-selection cuts, and no-harvest.

Bird Densities

To estimate bird densities, we mapped breeding bird territories in every year from mid-May through June in all sites prior to harvest (1991–1995) and after harvest (1997–2003; 2008–2014) using the spot-mapping method (Svensson et al. 1970). Each site was divided into seven subplots (~45 ha each); subplots sometimes contained multiple stands which allows for the possibility of a mixture of treated and untreated stands within the same subplot. From 1991–1995 and 1997–2000, we censused all seven subplots on each site, but in 2001–2003 and 2008–2014, we only surveyed four subplots per site to reduce effort while still surveying some stands in all treatment types. Each subplot was visited eight to ten times per season at two- to three-day intervals; observers were alternated each visit to reduce observer bias. On each visit, field assistants began at dawn five days per week and spent three to four hours spot mapping one entire subplot. Individual detections of singing males were recorded on enlarged topographic maps of the subplot (map scale 1:3330 m). Territory centroids were defined based on three or more clustered observations of a species detected on three separate dates, counter-singing, and presence of nests. We estimated the density of each species by summing the total number of territories in a stand and dividing it by the area of the stand. Red-eyed vireo (*Vireo olivaceous*) territories were not spot-mapped pre-2008; however, red-eyed vireo densities for these years were interpolated from linear models from red-eyed vireo spot-mapping data collected 2008–2014. Some stands were too small to contain the territories of many of the species included in our analysis, so we chose to eliminate stands that were <2.89 ha to maintain consistency with the analyses done by Kendrick et al. (2015). This resulted in a total of 374 stands used in our analysis. Spatial analyses were performed using ArcMap 10.6 (ESRI, Redlands, CA, USA).

Statistical Analyses

To evaluate the relationships between temporal and habitat variables and avian community metrics (species richness and Shannon diversity), we used linear mixed effects models (lme function: nlme package) with a Gaussian distribution within an information theoretic framework. To account for stands with unequal area, species richness was calculated as total number of species/sampled stand area. The set of 12 candidate models for each response variable included combinations of stand treatment, stand area, and year-since-harvest as additive fixed effects, year-since-harvest and stand treatment as interactive effects, and year-since-harvest as a quadratic effect. In addition, we included a global model that contained all variables as well as a null model with only the intercept. To reduce multicollinearity, we eliminated variables with a VIF <2.3. We used an autoregressive error structure with stand as a random effect to account for the lack of independence for samples taken through time. Candidate models were fit and evaluated within an Akaike's Information Criterion (AIC) framework.

To describe changes in species composition following harvest, bird densities were used in a site x species matrix (with stands as sites) and divided into the five periods: Period 1 (1991–1995; pre-harvest), Period 2 (1997–2000; 1-4 years post-first harvest), Period 3 (2001–2003; 5-7 years post-first harvest), Period 4 (2008–2010; 12-14 years post-first harvest), and Period 5 (2012–2014; 1–3 years post-second harvest).

To determine if multivariate community structure differed among stand treatments within each period, we performed a permutational analysis of variance (PERMANOVA; adonis function: vegan package) using 999 permutations with Bray-Curtis distance matrices of square root transformed species densities. If differences were found during the global PERMANOVA for a period, we performed a pair-wise PERMANOVA for that period to determine which stand treatment types were responsible for the differences in community structure.

To visualize how community structure differed among treatments, we performed a non-metric multidimensional scaling (NMDS) ordination. This method of ordination is a nonparametric technique that benefits from having no assumptions about linear or unimodal response and reduces distortions that may result from eigenvector techniques (McCune et al., 2002). NMDS is especially useful for graphically simplifying complex communities by arranging the information in lower-dimensional space that can be related to the ecological dissimilarity among samples (Kenkel and Oroloci, 1986). We calculated the NMDS on a Bray-Curtis distance matrix derived from square root transformed relative abundances (metaMDS function: vegan package). We specified two axes for the NMDS and consulted a stress evaluation table to verify that the stress values observed were not the result of randomly arranged data (Sturrock and Rocha, 2000). Finally, we drew ellipses according to the standard deviation of site scores to assess degree of overlap in community structure among management types.

To evaluate the relationships between temporal and habitat variables and avian community metrics (species richness and diversity), we used linear mixed effect models within an information theoretic framework. To account for stands with unequal area, species richness was calculated as total number of species/sampled stand area. The set of 12 candidate models for each response variable included combinations of stand treatment, stand area, and year-since-harvest as additive fixed effects, year-since-harvest and stand treatment as interactive effects, and year-since-harvest as a quadratic effect. In addition, we included a global model that contained all variables as well as a null model with only the intercept. To reduce multicollinearity, we eliminated variables with a VIF <2.3. We used an autoregressive error structure with random effects to account for the lack of independence for samples taken through time. Candidate models were based on plausible hypotheses and models were fit and evaluated within an Akaike's Information Criterion (AIC) framework. All analyses were performed using R version 3.4.3 (R Development Core Team, 2017). Linear mixed effects models were done using *nlme* package (Pinheiro et al., 2018); all other analyses were performed using functions provided with the *vegan* package (Oksanen et al., 2018).

Results

Between 1991 and 2014, we recorded 49 bird species with territories in the 374 stands included in this analysis. The mean species richness for the stands was 5.48 (standard error = 0.12; range = 0.67 – 15.28). The mean Shannon H' for the stands was 1.34 (standard error = 0.02; range = 0 – 2.41; theoretical maximum = 3.89). Red-eyed vireo was the most abundant species across all sites pre-harvest (accounting for 19% of the total species present pre-harvest). Across all years, three species accounted for >10% of the species recorded in NH stands: red-eyed vireo (20%), acadian flycatcher (*Empidonax virescens;* 15%), and ovenbird (*Seiurus* aurocapilla; 11%; Figure 2A). In clearcut stands, rank abundance plots showed a distinct change in the dominant species with early years

(1-8 years post-harvest) being dominated by shrubland species, such as indigo bunting (*Passerina cyanea*), yellow-breasted chat (*Icteria virens*), and prairie warbler (*Setophaga discolor*; Figure 2B). By 12-18 years post-harvest, indigo bunting made up <3% of the recorded birds while yellow-breasted chat and prairie warbler accounted for <1%. Instead, clearcut stands in the late period were dominated by species more typical of mature forests, such as red-eyed vireo, which made up >25% of all species present (Figure 2B). Stands treated with group-selection cuts and thinning showed similar species composition between the two treatment types in both early and late post-harvest time periods, being dominated mostly by mature forest species, including red-eyed vireo, acadian flycatcher, and worm-eating warbler (*Helmitheros vermivorum*). Indigo bunting was the second most abundant species 1-8 years post-harvest in both group-selection cut and thinned stands, but by 12-18 years post-harvest its abundance had noticeably dropped in both group-selection cut and thinned stands (accounting for 3% and 2% of the recorded birds, respectively; Figure 2C-D).

The global PERMANOVA revealed differences in the multivariate community structure among treatment types in all five time periods (Table 1). Pairwise-PERMANOVA showed that during period 1 (preharvest), multivariate community structure only differed between no harvest and stands designated to be group-selection cut in the coming harvest, but stand treatment type only accounted for 1% of the statistical variance (Table 2). In periods 2 and 3, community structure differed among all treatment types, with the greatest statistical variance being between clearcut stands and all other treatment types (Table 2). In period 4, community structure differed in all treatment types except thinned vs no harvest stands and thinned vs group-selection cut stands (Table 2). In period 5 (post-second harvest), community structure differed in all treatment types except thinned 2011 vs group-selection cut and thinned 1996 vs no harvest (Table 2).

The first two dimensions of the NMDS ordination resulted in stress values ≤0.21 in all five periods which suggested a <1% chance of the ordinations having random structure (Sturrock and Rocha, 2000). In Period 1 (preharvest), the NMDS plot showed broad overlap among all treatment types (Fig 3A). In period 2, there was separation along the first axis with clustering corresponding to stand treatment type (Fig 3B). In period 3, the separation was predominantly on the second axis, indicating that the greatest amount of variance among the sites was not explained by treatment (Fig 3C). In period 4, the separation was mostly along the second axis and clustering was less distinct than the previous two periods (Fig 3D). Likewise, in period 5, the separation was along the second axis, and CC11 was the only treatment type that had a distinct clustering of points (Fig 3E).

For species richness, the best supported model was the global model, which included the additive effects of year-since-harvest, stand area, and stand treatment type and had an AIC model weight of 0.99 (Table 3, 4). Models containing interactive and quadratic effects were not well supported. Species richness was highest in thinned stands, lowest in NH stands, and showed a linear decrease with both year since harvest and stand area (Figure 4A-C). For Shannon H’, the best supported model included the variables year-since-harvest and stand area and had an AIC model weight of 0.93 (Table 3, 4). Models including the treatment variable as well as interactive and quadratic effects were not well supported. Shannon H’ showed a linear decrease with year since harvest and a linear increase with stand area (Figure 5A-B).

Discussion

Understanding how forest management affects bird communities across long time periods and at broad spatial scales remains an important goal for informed management decisions (Mitchell et al., 2008; Faaborg et al., 2010). Our stand-level analysis of over 24 years of data is the among first to look at the long-term large-scale bird community-level changes in response to forest management within an experimental framework. The most obvious community changes were in the clearcut stands where shrubland species responded quickly and formed a distinct community compared to other treatment types. The shrubland species remained until approximately 10-12 years post-harvest, but by 12-14 years, the clearcut stands showed broad overlap with no harvest stands. Shrubland species (e.g., indigo bunting, yellow-breasted chat, and prairie warbler) were the key drivers of the community changes in clearcut stands within the first 1-8 years following harvest. By 12 years post-harvest, the community began to shift back towards a composition more typical of a mature forest. This pattern is consistent with the findings of species-level analyses that found that shrubland species colonize clearcuts quickly, reach their peak densities within 10 years post-harvest, and begin to decline by 12 years post-harvest (Conner and Adkisson, 1975; Keller et al., 2003; Morris et al., 2013; Kendrick et al., 2015).

The stands treated with thinning and group-selection cuts resulted in similar bird communities. However, it should be noted that thinned stands were on EAM sites; the closer proximity to clearcut stands could affect thinned stands in ways that were not accounted for in this analysis. The post-harvest community changes in group-selection cut and thinned stands were less distinct than in clearcut stands when compared to no harvest stands, but community structure did show separation from no harvest stands in the ordination plots. The bird community response in group-selection cut and thinned stands was similar to clearcut stands in that within 10 years post-harvest the communities began to return to pretreatment compositions. Other studies have also found that the silvicultural treatment effects on bird densities diminish by 12 years, with species composition thereafter being similar to pretreatment compositions (Conner et al., 1979, DeGraaf and Chadwick, 1987; Twedt and Somershoe, 2009; Porneluzi et al., 2014; Twedt and Wilson, 2017).

Our top model predictions showed that all treatment types resulted in higher species richness compared to no harvest stands. This contradicts the results of a global meta-analysis that found that group-selection cut and clearcut forest management resulted in a decrease in bird species richness (Chaudhary et al., 2016). However, a different meta-analysis that separated treatments by latitude found that in temperate regions, uneven-aged management (e.g. group-selection cuts) resulted in an increase in species richness if the basal area retention was <60% (LaManna and Martin, 2017). On our sites, both thinned and group-selection cut stands had a ~75% basal area retention (Kabrick et al., 2002). Group-selection cuts and thinning result in a more heterogenous stand structure compared to no harvest stands (Falk et al., 2008; von Oheimb and Härdtle, 2009) and thus can promote habitat connectivity and structural diversity which may result in increased species richness as observed in these stand treatment types.

Clearcutting, on the other hand, has been criticized for leading to homogenous forests and loss of biodiversity (Rosenvald and Lohmus, 2008; Kuuluvainen, 2009). However, regenerating clearcuts have been found to be important for the conservation of shrubland species (Hunter et al., 2001; Thompson and DeGraaf, 2001; King and Schlossberg, 2014) and are used extensively by mature-forest bird species during the post-fledging period (Vega Rivera et al., 1998; Marshall et al., 2003; Vitz and Rodewald, 2006; Stoleson, 2013). Immediately following harvest, clearcut stands are characterized by increased horizontal heterogeneity (e.g. grassy openings among saplings) which allows for both terrestrial gleaners and low-foliage gleaners to inhabit the regenerating stands (Keller et al., 2003). Additionally, the rapidly regenerating plant material following clear cutting yields a total leaf area similar to that of old growth stands, but the leaf area is all within 5m of the ground. The compression of leaf area nearer to ground level results in more densely distributed arthropod prey in young stands (Holmes et al., 1996; Keller et al., 2003). Increased horizontal heterogeneity in combination with higher prey density could explain the higher species richness compared to no harvest stands during the time span of our analysis.

Despite the higher species richness immediately after harvest, model predictions for both species richness and diversity showed a linear decline with year-since-harvest. The long-term reduction in species richness post-harvest has also been observed in other studies of birds and other taxa (Kirkland, 1977; Martell, 1983; Keller et al., 2003; Buddle et al., 2006; Chaudhary et al., 2016). The long-term decline in species richness and diversity is especially apparent in clearcut treatments and is at least partially explained by the simplification of forest structure that occurs as young trees begin to form a closed canopy that blocks sunlight that had previously reached the herbaceous and shrub layer, creating an open understory which results in the reduced suitably for shrubland species.

Uneven-aged management can help mediate the decline in species richness and diversity that occurs following harvest while providing suitable habitat for some shrubland species (King et al., 2001; Fedrowitz et al., 2014). However, other shrubland bird species may be absent from uneven-aged managed forests because they require large openings such as those created by clearcutting (Annand and Thompson, 1997; Robinson and Robinson, 1999; Costello, 2000; Rodewald and Vitz, 2005; Schlossberg and King, 2007). Many of the species found predominantly or exclusively in clearcuts are species of conservation concern in parts of their range (Hunter et al., 1993; Thompson et al., 1993; McCreedy et al., 2004). Therefore, managers should consider the size of forest openings when attempting to meet the needs of shrubland species.

Because of the diverse habitat requirements of bird communities in forested landscapes, the sole reliance on any single management practice may be ineffective in providing the heterogeneity of habitat needed for the conservation of biodiversity (Bergeron et al., 1999; Lindenmayer et al., 2000; Lindenmayer et al., 2006; Mönkkönen et al., 2014). The use of both EAM and UAM, as well as areas reserved from harvest, can provide the variety of habitats needed for the conservation of diverse forest bird communities. Biodiversity is threatened with the projected landscape changes in the coming decades (Neilson et al., 2005; Crookston et al., 2010; Bellard et al., 2014). Long-term, large-scale studies within an experimental framework are imperative for sound management recommendations (Faaborg et al., 2010). Our long-term, large-scale examination of forest management effects on bird communities can facilitate empirically-based management decisions that will better provide a biodiverse forest ecosystem.

Table 1.1. Results from the global PERMANOVA testing for differences in multivariate bird community structure among stand treatment types during each period in the Missouri Forest Ecosystem Project. Period 1: 1991-1995 (pre-harvest); Period 2: 1997-2000 (1-4 years post- first harvest); Period 3: 2001-2003 (5-7 years post- first harvest); Period 4: 2008-2010 (12-14 years post- first harvest); Period 5: (2012-2014; 1-3 years post- second harvest, 16-18 years post- first harvest).

	DF	F-value	R^2	p-value
Period 1	3	2.11	0.02	<0.01
Period 2	3	26.59	0.18	<0.01
Period 3	3	13.65	0.10	<0.01
Period 4	3	4.14	0.05	<0.01
Period 5	5	5.56	0.11	<0.01

Table 1.2. Results from the pairwise PERMANOVA testing for differences in multivariate community structure between stand treatment types. Period 1: 1991-1995 (pre-harvest); Period 2: 1997-2000 (1-4 years post- first harvest); Period 3: 2001-2003 (5-7 years post- first harvest); Period 4: 2008-2010 (12-14 years post- first harvest); Period 5: (2012-2014; 1-3 years post- second harvest, 16-18 years post- first harvest).

	Pairs	F-value	R^2	p-value
Period 1	Clearcut'96 vs Thinned'96	1.07	0.03	0.37
	Clearcut'96 vs NoHarvest	0.70	<0.01	0.68
	Clearcut'96 vs Group-selection	1.02	0.01	0.37
	Thinned'96 vs NoHarvest	1.76	0.01	0.11
	Thinned'96 vs Group-selection	1.78	0.02	0.11
	NoHarvest vs Group-selection	4.05	0.01	<0.01
Period 2	Clearcut'96 vs Thinned'96	18.47	0.33	<0.01
	Clearcut'96 vs NoHarvest	49.91	0.15	<0.01
	Clearcut'96 vs Group-selection	28.73	0.25	<0.01
	Thinned'96 vs NoHarvest	13.44	0.05	<0.01
	Thinned'96 vs Group-selection	3.74	0.04	<0.01
	NoHarvest vs Group-selection	25.13	0.07	<0.01
Period 3	Clearcut'96 vs Thinned'96	8.59	0.19	<0.01
	Clearcut'96 vs NoHarvest	14.67	0.05	<0.01
	Clearcut'96 vs Group-selection	7.95	0.08	<0.01
	Thinned'96 vs NoHarvest	12.31	0.04	<0.01
	Thinned'96 vs Group-selection	3.57	0.04	0.01
	NoHarvest vs Group-selection	18.55	0.05	<0.01
Period 4	Clearcut'96 vs Thinned'96	4.85	0.14	<0.01
	Clearcut'96 vs NoHarvest	6.04	0.03	<0.01
	Clearcut'96 vs Group-selection	5.27	0.08	<0.01
	Thinned'96 vs NoHarvest	1.71	0.01	0.10
	Thinned'96 vs Group-selection	1.64	0.03	0.11
	NoHarvest vs Group-selection	4.93	0.02	<0.01
Period 5	Clearcut'11 vs Clearcut'96	8.77	0.32	<0.01
	Clearcut'11 vs Thinned'11	7.10	0.24	<0.01
	Clearcut'11 vs Thinned'96	8.52	0.27	<0.01
	Clearcut'11 vs NoHarvest	14.65	0.10	<0.01
	Clearcut'11 vs Group-selection	11.31	0.14	<0.01
	Clearcut'96 vs Thinned'11	2.29	0.08	0.01
	Clearcut'96 vs Thinned'96	3.01	0.10	<0.01
	Clearcut'96 vs NoHarvest	4.45	0.03	<0.01
	Clearcut'96 vs Group-selection	2.55	0.03	0.02
	Thinned'11 vs Thinned'96	2.84	0.08	<0.01
	Thinned'11 vs NoHarvest	3.94	0.03	<0.01
	Thinned'11 vs Group-selection	1.25	0.02	0.20
	Thinned'96 vs NoHarvest	1.80	0.01	0.07

	Thinned’96 vs Uneven-aged	2.22	0.03	0.03
	NoHarvest vs Uneven-aged	6.06	0.03	<0.01

Table 1.3. Model-selection results from the best-ranked a priori candidate models of the effects of year-since-harvest, total stand area, and treatment type on bird species richness and Shannon H' in the Missouri Ozarks, 1991-2014. YSH = year-since-harvest; Area = total stand area; treatment = treatment type of stand (clearcut, thinned, uneven-aged, and no harvest)

Response Variable	Model	ΔAIC	K	Weight
Species richness	YSH + Treatment	0.0	8	0.99
	YSH	9.3	5	<0.01
	YSH + YSH^2 + Treatment	12.1	9	<0.01
	YSH*Treatment	21.0	11	<0.01
	YSH + YSH^2	24.1	6	<0.01
	Treatment	26.9	7	<0.01
	null	2157.3	3	<0.01
Shannon H'				
	YSH	0.0	5	0.98
	global	7.6	8	0.02
	YSH + YSH^2	13.4	6	<0.01
	YSH + YSH^2 + Treatment	17.8	9	<0.01
	Treatment	22.7	7	<0.01
	YSH*Treatment	29.2	11	<0.01
	null	3774.4	3	<0.01

Table 1.4. Estimated coefficients for the best supported models of the effects of year-since-harvest (YSH), total stand area (Area), and stand treatment type (clearcut, thinned, group-selection cuts [GSC], and no harvest [NH]) on the species richness and Shannon H' of bird species in the Missouri Ozarks, 1991-2014

Response Variable	Parameter	Coefficient	Standard error	Lower 95 % CI	Upper 95 % CI
Species Richness	Intercept	1.16	0.08	1.00	1.32
	YSH	-0.02	<0.01	-0.03	-0.01
	Treatment-Thin	0.21	0.09	0.03	0.39
	Treatment-NH	-0.11	0.07	-0.25	0.03
	Treatment-GSC	<0.01	0.08	-0.16	0.16
	Area	-0.02	<0.01	-0.03	-0.01
Shannon H'					
	Intercept	1.09	0.05	0.99	1.19
	YSH	-0.02	<0.01	-0.03	-0.01
	Area	0.03	0.01	0.02	0.04

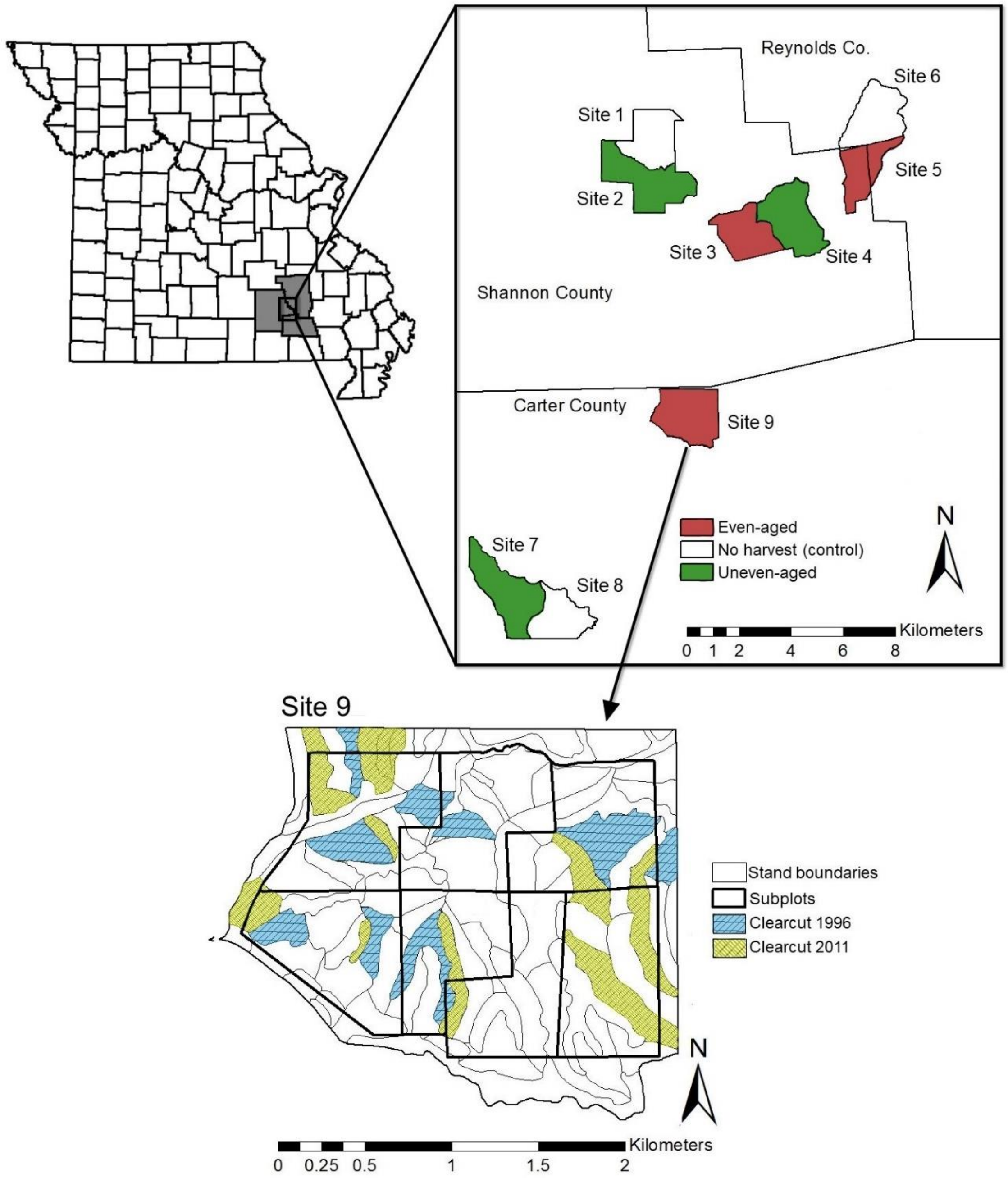

Figure 1.1. A: Map of the study sites in the Missouri Ozark Forest Ecosystem Project in southeastern Missouri. Nine sites, grouped into 3 blocks, were randomly assigned to even-aged, uneven-aged, or no harvest management systems. B: An example of census subplots and stand delineations and silvicultural treatments on a site.

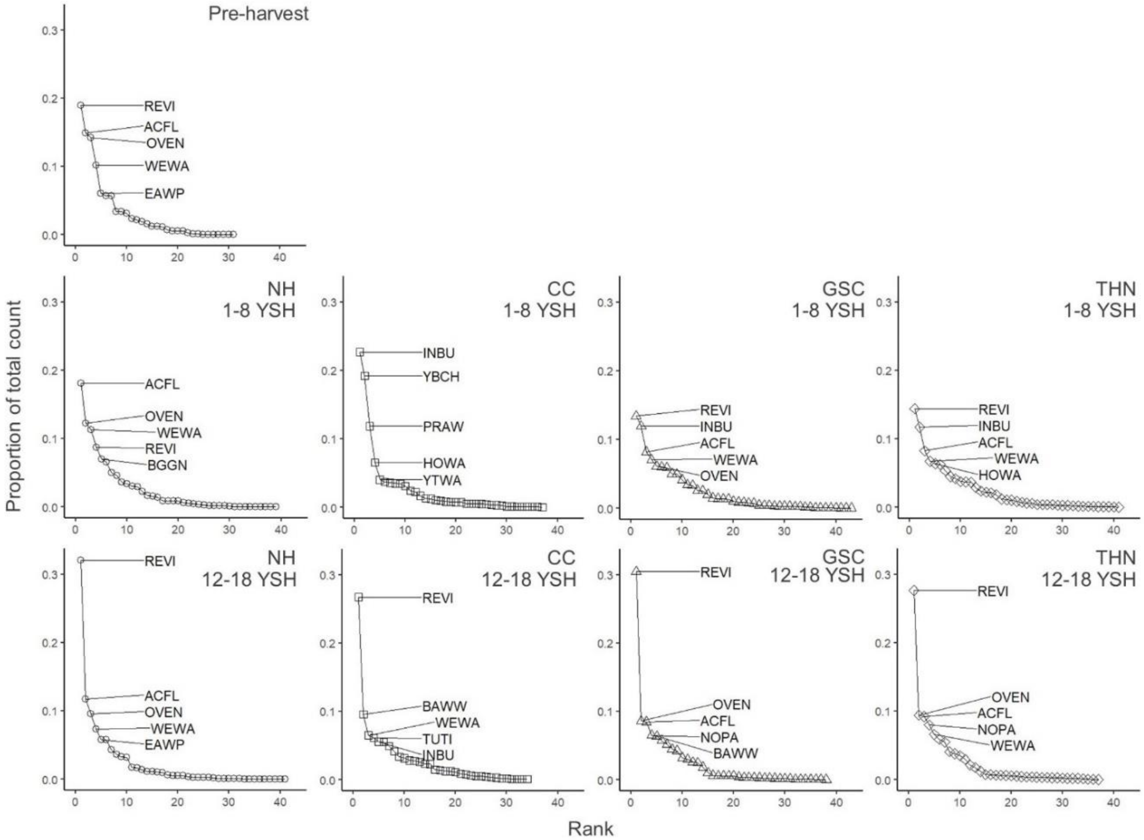

Figure 1.2. Rank abundance of bird species in the Missouri Ozarks across four stand treatment types (NH = no-harvest; CC = clearcut; GSC = group-selection cut; THN = thinned) within three management systems (no-harvest, even-aged, and uneven-aged) in early (1-8 years-since-harvest) and late (12-18 years-since-harvest) time periods. Four letter species codes (indicated for the top five most abundant species) can be found in Appendix I.

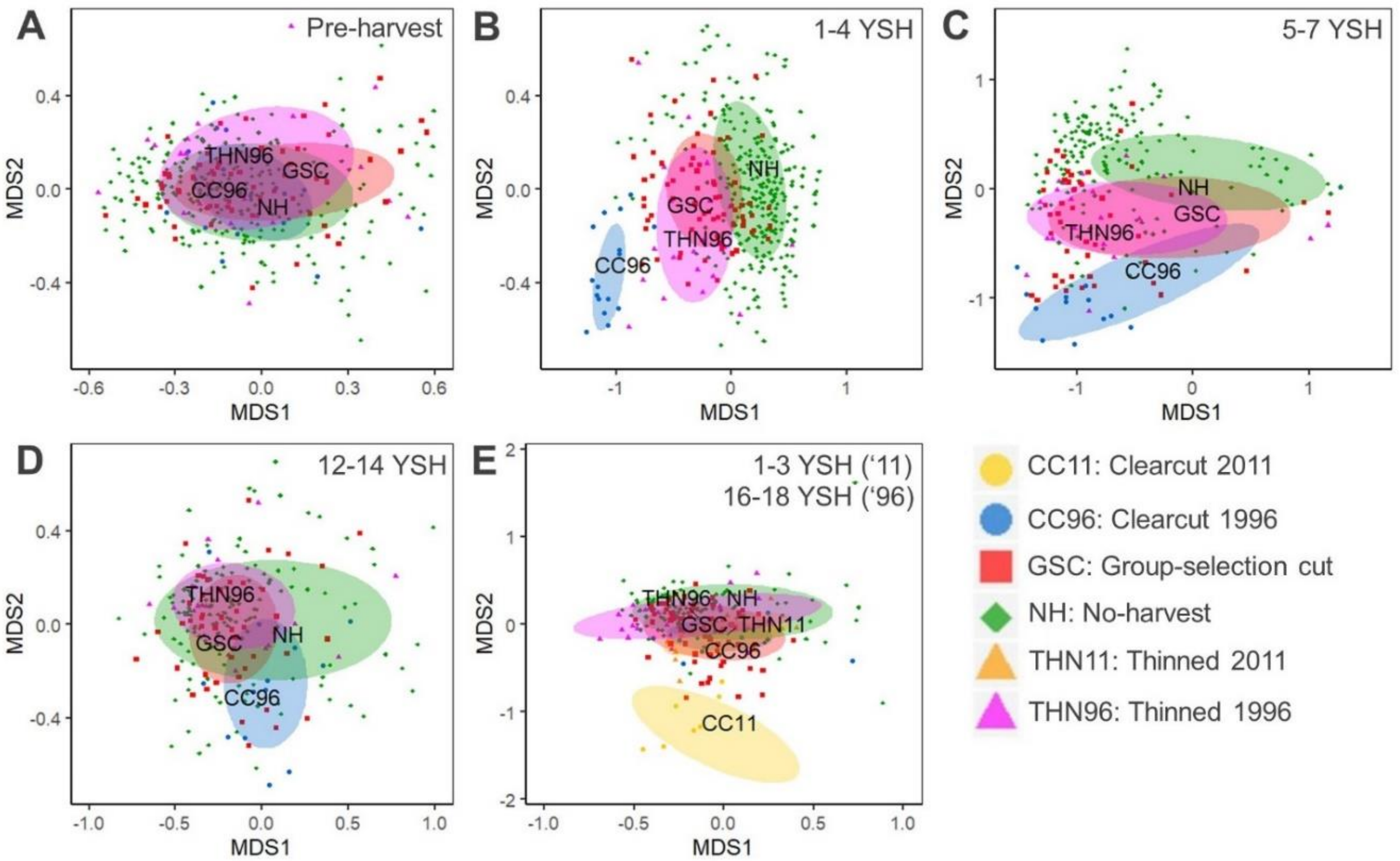

Figure 1.3 NMDS ordination plots showing bird community structure changes in each treatment type through time. A: 1991-1995 (pre-harvest; stress = 0.19); B: 1997-2000 (1-4 years post- first harvest; stress = 0.21); C: 2001-2003 (5-7 years post- first harvest; stress = 0.12); D: 2008-2010 (12-14 years post- first harvest; stress = 0.16); E (2012-2014; 1-3 years post- second harvest, 16-18 years post- first harvest; stress = 0.17).

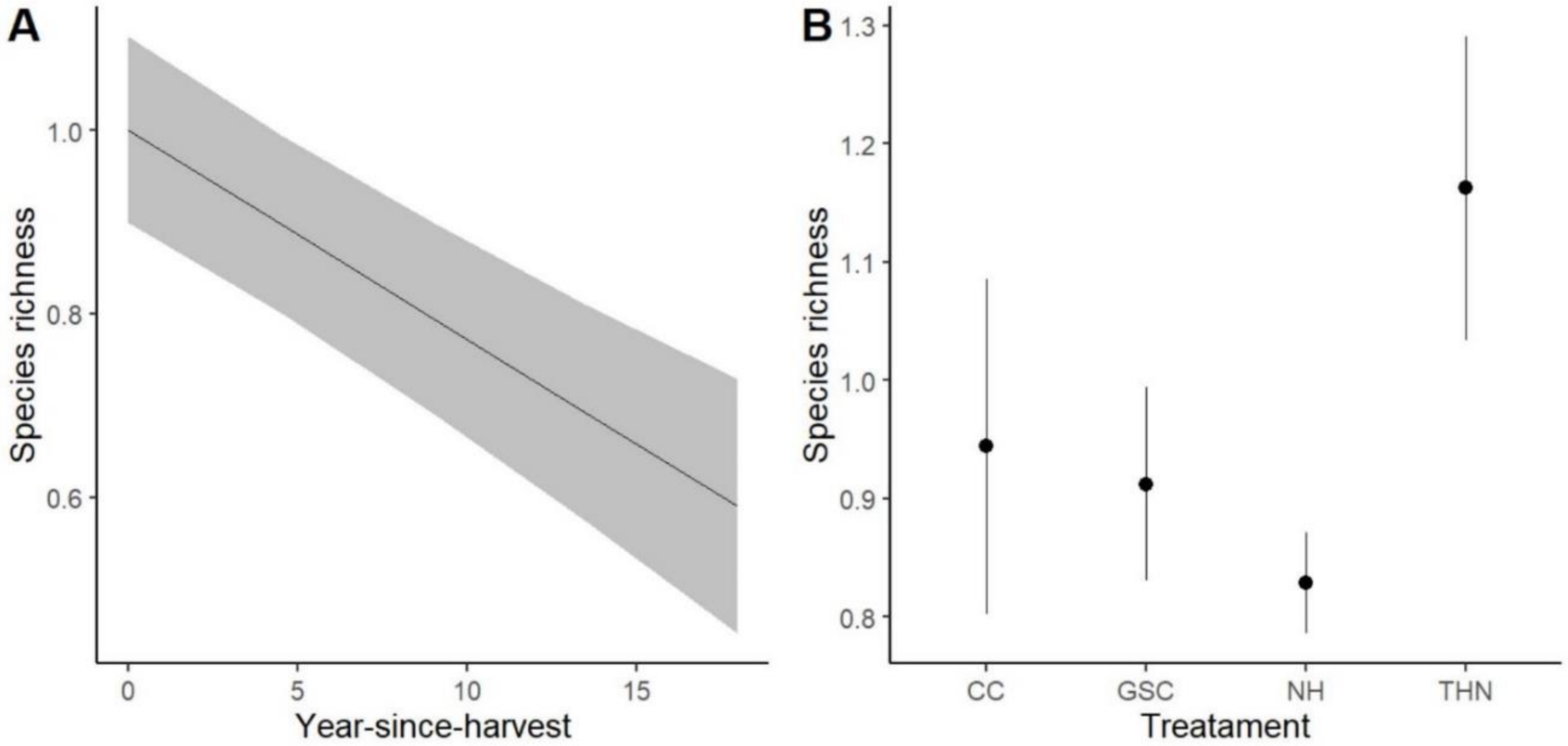

Figure 1.4. Predictions of the best supported model showing the effects year-since-harvest (A) and treatment type (B) on bird species richness (calculated as total number of species/sampled stand area) in the Missouri Ozarks (CC = clearcut; GSC = group-selection cut; NH = no-harvest; THN = thinned). For model predictions, variables are held constant at their means. Shaded areas represent 95 % confidence intervals.

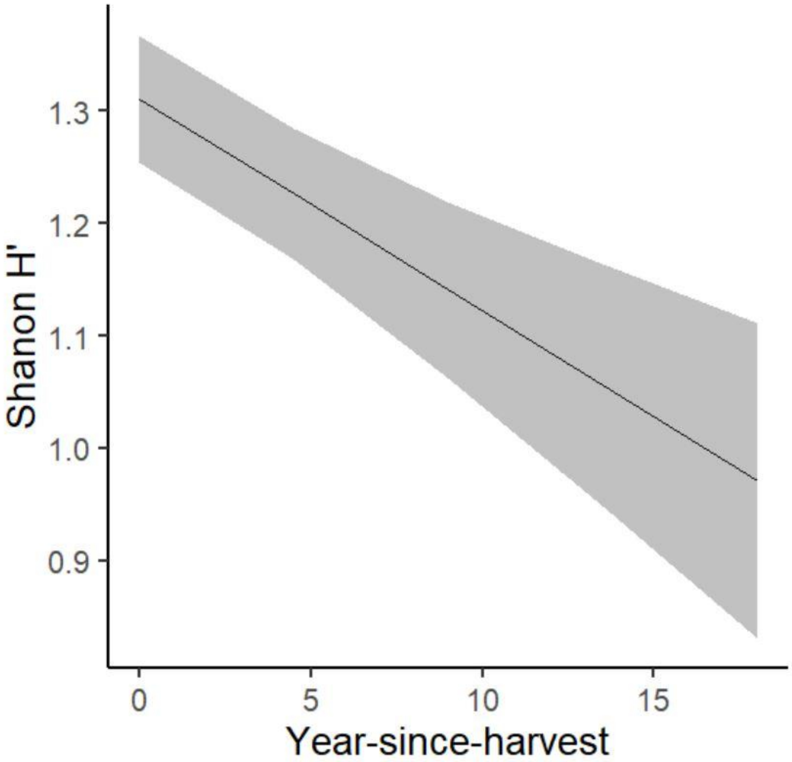

Figure 1.5. Predictions of the best supported model showing the effects of year-since-harvest on Shannon H’ of birds in the Missouri Ozarks. For model predictions, variables are held constant at their means. Shaded areas represent 95 % confidence intervals.

CHAPTER II

Comparison of Point Counts and Spot Mapping in Mature Forest and Shrubland Habitats

Introduction

Monitoring bird abundance is a foundation for the study and conservation of bird populations. The long-term assessment of bird populations can aid in identifying species at risk and help evaluate management approaches. Spot mapping (territory mapping) and point count surveys are widely-used methods for estimating breeding bird abundances (Bibby et al., 2000; Gregory et al., 2004) and are regularly used to help make informed conservation plans (e.g. Petit et al., 2003; Peh et al., 2006; Grüebler et al., 2012; Edwards et al., 2014). Each surveying method has strengths and drawbacks and requires a different level of temporal and financial resources.

Spot mapping is a technique used to census all bird territories in a defined area as thoroughly as possible and usually requires eight or more visits to a site. Thus, the amount of labor needed for spot mapping is high. Nevertheless, because of the completeness of the method, spot mapping is often considered among the best bird surveying methods and is frequently used as the standard against which to measure the accuracy of other methods (e.g., Dobkin and Rich, 1998; Howell et al, 2004; Toms et al., 2006; Newell et al., 2013).

Point counts are surveys recording all species detected from a set location for a set duration (usually 3 to 10 minutes; Ralph et al., 1995; Thompson et al., 2002) and usually entail one to three visits per survey point. Consequently, point counts require a fraction of the person-hours needed for spot mapping. However, point counts are generally considered less accurate than spot mapping because the limited time spent surveying at each point can result in species that are present but not detected during the short duration of a point count survey (Thompson et al., 2002; Simons et al., 2009; Schmidt et al., 2013). Additionally, the limited area surveyed by a fixed-radius point count is smaller than the territories of many songbirds. Accordingly, species with larger territories are likely to be under counted in point counts because the probability of detecting a species is reduced when only a small fraction of its territory is sampled (Toms et al., 2006). These concerns have led to increased scrutiny of the viability of point counts as an accurate method to monitor population trends (Thompson et al., 2002; Schmidt et al., 2013). However, the simple protocol and reduced time and cost of fixed-radius point counts has resulted in the method remaining a staple among bird surveying techniques used by both agencies and independent studies globally (e.g. Molaei et al., 2016; Barré 2018; Chawaka et al., 2018; Hallett and O'Connell, 2018; O'Donnell et al., 2019). For researchers currently using or considering using fixed-radius point counts to estimate breeding bird abundances, it is important to consider the strengths and limitations of the method when assessing whether the data derived from this technique are sufficient for the research goals.

In this study, we evaluate the bird densities and species richness derived from point count and spot map surveys in the context of the Missouri Ozark Forest Ecosystem

Project, a long-term experimental forest management project on public lands. The project is designed to examine the effects of three different forest management practices (even-aged management, uneven-aged management, and no harvest management) a variety of ecosystem features of the landscape (Brookshire and Shifley, 1997). While other studies have compared bird surveying methods (Dobkin and Rich, 1998; Howell et al., 2004; Gottschalk and Huettmann, 2011), few have compared methods within a forest management context (Newell et al., 2013). Our objective was to examine the difference between the two survey methods in estimating the densities of 11 focal species (five mature forest species and six shrubland species) across three different management systems (no-harvest, uneven-aged management, and even-aged management) in pre- and post-harvest time periods. Specific objectives were to (1) determine whether point counts tend to systematically over- or under-estimate bird densities compared to spot mapping, (2) examine how strong the relationship is between point count and spot map densities of our focal species, (3) evaluate the difference in treatment effects detected by the two survey methods, and (4) compare the species richness estimates derived from point count and spot map data. Understanding the cost and benefits of using each method can help agencies, managers, and independent researchers make better decisions based on the research goals of a project.

Methods

Study Area

The Missouri Ozark Forest Ecosystem Project (MOFEP) is a long-term, landscape-scale study designed to examine the effects of forest management on the flora, fauna, and other ecosystem features of the landscape (Brookshire and Dey, 2000; Knapp et al., 2014). The nine study sites (averaging ~400 ha each) are located in Carter, Reynolds, and Shannon counties in the Current River Hills subsection of the Ozark Highlands of southeastern Missouri (91°01' – 91° 13'W and 37°00'–37°12'N). Due to the clearing of nearly all forests in the region in the 19th and early 20th centuries, the forest landscape is relatively homogenous. The species composition of the forest is predominantly oak-hickory, with white oak (*Quercus alba*), black oak (*Q. velutina*) and scarlet oak (*Q. coccines*) being the dominant oak species. Other species comprising a large portion of the woody vegetation include post oak (*Q. stellata*), mockernut hickory (*Carya tomentosa*), black hickory (*C. texana*), pignut hickory (*C. glabra*), and shortleaf pine (*Pinus echinata*; Shifley and Kabrick, 2000). At the beginning of the study in 1990, the region was 84% forested and generally even-aged with most of the overstory trees being 50-70 years old. The sites were managed for timber in the early part of the 20th century, but the forests had remained unharvested for at least 40 years before the start of the study (Brookshire and Shifley, 1997).

Experimental Design

The Missouri Ozark Forest Ecosystem Project is comprised of nine sites that were randomly assigned to one of three management systems: even-aged (EAM), uneven-aged (UAM), and no harvest (NH). Each site was further subdivided into 36–74 stands ranging in size from 0.16 ha to 62 ha; stands were defined by features such as common aspect, slope, and ecological land type (Brookshire et al., 1997). Treatments were applied at the stand level and were designed to resemble common forest management practices implemented by the Missouri Department of Conservation. In May 1996 and 2011, the Missouri Department of Conservation applied treatments to the sites in accordance with the following procedures: In the EAM treatment, 10−15% of the total forest area was harvested in patches 3−13 ha, yielding seven to nine clearcut stands within each site (Brookshire and Shifley, 1997). Additional thinned stands were harvested on 5−24% of each EAM site to encourage the growth of residual trees of select sizes. In the UAM treatment, a combination of small-group and single-tree selection cuts were administered across 41−69% of each site. Group-selection cuts ranged from 21−43 m in diameter, yielding 153−267 small-group cuts per site. Approximately the same amount of timber was removed from both EAM and UAM sites. A reserve of approximately 10% of each site (both EAM and UAM) was assigned to be left unharvested for the duration of the study (Morris et al., 2013). No treatments were applied to the stands in the NH sites for the duration of the study, allowing these sites to serve as indicators of natural processes as the forest matures over the 100 years of the project.

Data collection

Breeding bird data collection started in 1991 using the spot-mapping method (Svensson et al. 1970; Bibby et al., 2000) which continued each breeding season on all sites through 2003. From 2003−2007, only clearcut stands were spot mapped, but in 2008 spot mapping resumed in all sites and continued through 2014. In 2004, 50 m fixed-radius point counts (Ralph et al., 1995) were initiated and continued until 2014. For this methods comparison analysis, we used data from 2008−2014 (3 years before and after the 2011 harvest) when both data collection methods were used on all sites concurrently. Both surveying methods seek to inventory the breeding bird communities

Spot mapping: Spot map surveys were conducted during the breeding season from mid-May through June. Each site was divided into seven subplots (~45 ha each) which served as the surveying units for spot mapping. During 2008-2014, only four subplots per site were surveyed to reduce effort while still surveying some stands in all treatment types. Each subplot was visited 8−10 times per season at 2- to 3-day intervals and observers were alternated to reduce observer bias. Field assistants started at dawn and took 3−4 hours to map an entire subplot. Subplots were surveyed with variable routes each day. Singing males were recorded on enlarged topographic maps of the subplot (map scale 1:3330 m). Territory centroids were defined based on three or more clustered observations of a species detected on three separate dates, counter-singing, and presence of nests. Birds that were recorded fewer than three times were not included in the dataset. We estimated the density of each species by summing the total number of territories detected in the four surveyed subplots and dividing it by the sampled area. Spatial analyses were performed using ArcMap 10.6 (ESRI, Redlands, CA, USA).

Point counts: In 2004, we started point counts which have continued every year from mid-May through June, except for 2011 when the second round of treatment was applied. Each point count route consisted of a grid of ten points in a five by two array, each point averaging 250 m apart. There were two point count routes on each of the nine sites, for a total of 180 points. Each point count route was visited three times in a season. To reduce the effects of observer bias, different observers surveyed a given route each of the three times, when possible. Birds recorded at the beginning of the season that were known to be migrants were removed from the dataset. We estimated the density for each species by taking the mean number of singing males detected per point count and dividing by the total area of a 50 m circle (~0.79 ha).

For analysis, we selected five mature forest species [Acadian Flycatcher (*Empidonax virescens*), Kentucky Warbler (*Geothlypis formosa*), Ovenbird (*Seiurus aurocapilla*), Worm-eating Warbler (*Helmitheros vermivorus*) and Wood Thrush (*Hylocichla mustelina*)] and six shrubland species [Blue-winged Warbler (*Vermivora cyanoptera*), Hooded Warbler (*Setophaga citrina*), Indigo Bunting (*Passerina cyanea*), Prairie Warbler (*Setophaga discolor*), White-eyed Vireo (*Vireo griseus*) and Yellow-breasted Chat (*Icteria virens*)]. Focal species were chosen based on their abundance and reliability of detection within the two major habitat types.

Statistical analyses

We pooled data from each of the nine MOFEP sites within each year for a total of 54 samples. To visualize the difference in density estimates from point counts compared to the density estimates of spot mapping, we plotted error (calculated as point count density minus spot map density) against spot map density (Figure 1). To evaluate the relationship between density estimates from spot mapping and point counts, we used linear models with point count densities as the predictor variable and spot map densities as the response variable. Because many shrubland species were absent from all sites pre-harvest, any site × year × species combination that had zero for a species density in both spot mapping and point counts was removed from the data set to avoid artificially inflating the strength of the relationship between spot map and point count density estimates.

The detection of treatment affects was examined using linear models for both spot mapping and point counts. We used the three site-level management systems (EAM, UAM, and NH) as our treatment variable and divided the time into two periods: before treatment (2008−2010) and after treatment (2012−2014). We used spot map and point count density estimates of our 11 focal species as the response variable and treatment × period interaction as the predictor variable. The estimated coefficients for EAM and UAM were used to visualize the 11 focal species' density change following harvest compared to NH densities.

We used linear models to compare species richness estimates between the two methods. Species richness from each site was estimated using the Chao1, a non-parametric, abundance-based species richness estimator that adds a correction factor to the observed species richness (Chao, 1984). Chao1 and other non-parametric species richness estimators have been shown to generally perform better than accumulation curve models (Colwell and Coddington, 1994; Walther and Martin, 2001; Brose and Martinez, 2004). Because of the difficulty of delineating the territories of Red-eyed Vireos (*Vireo olivaceous*), spot mapping data for this species were recorded as mean number of detections per visit. The Chao1 index of species richness is calculated from a matrix requiring integers, therefore, we rounded the mean number of Red-eyed Vireo detections to the nearest integer. All analyses were performed using R version 3.4.3 (R Development Core Team, 2017).

Results

During the breeding seasons of 2008 through 2014 (except the 2011 harvest year), we recorded 55 bird species with point counts and 45 bird species with spot mapping. The error plot showing the difference between point count and spot map density estimates revealed that point counts generally estimate higher densities compared to spot map density estimates (Figure 1).

The linear models of our 11 focal species (Figure 2) indicated that the relationship between spot map and point count density estimates was positive across all species (slope range: 0.01 – 0.31), but the strength of the relationship varied considerably among species (r^2 range: <0.01 – 0.82). In general, the five mature forest species, Acadian Flycatcher ($F_{1,52} = 12.79$; $p = <0.01$; $r^2 = 0.18$), Kentucky Warbler ($F_{1,45} = 10.04$; $p = <0.01$; $r^2 = 0.16$), Ovenbird ($F_{1,52} = 53.10$; $p = <0.01$; $r^2 = 0.50$), Worm-eating Warbler ($F_{1,52} = 8.79$; $p = <0.01$; $r^2 = 0.13$), and Wood Thrush ($F_{1,50} = 9.68$; $p = <0.01$; $r^2 = 0.14$), showed a relatively weak relationship between point count and spot map density estimates. The six shrubland species, Blue-winged Warbler ($F_{1,20} = 1.10$; $p = 0.31$; $r^2 = <0.01$), Hooded Warbler ($F_{1,47} = 72.34$; $p = <0.01$; $r^2 = 0.60$), Indigo Bunting ($F_{1,50} = 62.17$; $p = <0.01$; $r^2 = 0.55$;), Prairie Warbler ($F_{1,27} = 62.79$; $p = <0.01$; $r^2 = 0.69$), White-eyed Vireo ($F_{1,37} = 6.05$; $p = 0.02$; $r^2 = 0.12$), and Yellow-breasted Chat ($F_{1,31} = 151.02$; $p = <0.01$; $r^2 = 0.82$) showed higher r^2 values compared to the mature forest species, but the sample size for shrubland species was generally smaller than for mature forest species since a majority of the shrubland species were only present in the post-harvest years. Blue-winged Warbler was the only species that showed no relationship, but the sample size was the smallest of any species examined (fewer than half of the site × year combinations had a non-zero value for both spot map and point count) and the spot mapping densities for this species were lower than any other species examined. Across all species, the relationship was strongest at low- and mid-density estimates with the largest confidence intervals at high densities (Figure 2).

The linear models used to compare the two methods’ ability to detect treatment effects indicated that most species had similar treatment response results with both surveying techniques, but the confidence intervals from point count data were much wider compared to spot map data. In EAM sites, the confidence intervals overlapped zero with both survey methods in all species except for Acadian Flycatcher, Indigo Bunting, and Prairie Warbler. For Acadian Flycatcher, only spot map confidence intervals overlapped zero, whereas point count confidence intervals did not and showed a negative EAM treatment effect (Figure 3A). For Indigo Bunting and Prairie Warbler, both survey methods showed a positive treatment effect and confidence intervals did not overlap zero. In UAM sites, all species had confidence intervals overlapping zero with both survey methods (Figure 3B).

Estimated species richness was higher with point counts (mean observed: 32.98, range observed: 17−43; mean Chao1: 37.70, range Chao1: 17.33−60) compared to spot mapping (mean observed: 24.96, range observed: 17−34; mean Chao1: 27.80, range Chao1: 18−40). The linear models showed a weak relationship between Chao1 species richness estimated from both survey methods (pre-harvest: $F_{1,25} = 4.288$; $p < 0.05$; $r^2 = 0.11$; Figure 4; post-harvest: $F_{1,25} = 3.61$; $p = 0.07$; $r^2 = 0.09$).

Discussion

For our analyses, we considered spot mapping to provide accurate indices of breeding bird densities. While spot mapping has limitations (Best, 1975; Paul and Roth, 1983; Verner and Milne, 1990; Gottschalk and Huettmann, 2011), it is widely considered to be the best method for estimating breeding bird densities (Howell et al., 2004; Toms et al., 2006; Newell et al., 2013). Our results show that the two methods are positively correlated. Thus, we suggest that point counts are a good proxy for spot mapping in situations where low-resolution data is adequate for management plans.

Whereas point count densities are positively correlated with spot map densities, point counts consistently over-estimated densities compared to spot mapping. There was no apparent pattern in overestimation error among the management systems—all three showed systematic over-estimation of density from point count data. Other studies comparing spot map and 50 m fixed-radius point counts have found mixed results. In the four mature forest species examined by Howell et al. (2004), there was significant over-estimation in two species, significant under-estimation in one species, and slight under-estimation in the other species. Another study found that over- and under-estimation from 50 m fixed-radius point counts is affected by the point count duration. Ten-minute point counts showed higher density estimates compared to 5-minute point counts. Among the five mature forest species evaluated, half were over-estimated by 10-minute point counts while only one was over-estimated by 5-minute point counts (Newell et al., 2013). The point counts in our study were 10-minute surveys which could play a part in our systematic over-estimation of densities compared to spot mapping.

As with others (Cyr et al., 1995; Dobkin and Rich, 1998; Howell et al., 2004; Newell et al., 2013), we found that the density estimates from the two methods are positively correlated. The strength of the relationship varied with the species; among our 11 focal species, the shrubland species tended to have a stronger relationship compared to the mature forest species. The higher r^2 values of most of the shrubland species compared to mature forest species could result from the shrubland birds being primarily contained to the 3-13 ha clearcut patches on EAM sites, allowing for a more comprehensive census because the shrubland species are restricted to the small area. The mature forest species have much larger areas of habitat and thus more chances for error since mature forest species are detected from more point count stations and spot mapping subplots. The larger confidence intervals at higher densities is consistent with the findings of other studies that found a positive correlation with spot map density indices and point count bias (Jones et al., 2000; Howell et al., 2004).

The models examining the treatment effect predictions from the two survey methods resulted in very similar predictions from both point counts and spot mapping. Except for Acadian Flycatcher in EAM sites, all species showed the same treatment effect with both methods, though the confidence of the predicted treatment effect was variable. Point counts had much broader confidence intervals than spot maps, likely at least partly because point counts only require single detection on any of the three visits for a territory to be recorded, while spot mapping requires a minimum of three repeated observations out of ten visits for a territory to be recorded, thus increasing the accuracy of spot mapping. If the goal of a monitoring project is to determine broad-scale treatment effects, our results indicate that point counts are a reasonable substitution for more time- and resource-intensive methods such as spot mapping.

The weak relationship between the estimated species richness from the two survey methods may result from the fact that Chao1 estimates are largely influenced by the number of rare species that are only detected once or twice. As noted above, there is no detection threshold for a species to be recorded in point count data, whereas spot mapping requires at least three detections out of ten visits before being recorded in spot map data. Thus, a rare species detected once by each method would result in an increase in species richness for point counts but no change in spot mapping. Therefore, spot mapping is more likely to provide a consistent estimate of species richness while point counts are more prone to swings in estimated species richness depending on how many rare species were detected on a given site in a given year. Of the studies evaluating species richness estimates from the two surveying methods, we were unable to find any that tested the relationship of estimated species richness between the two methods. Instead, raw species richness numbers were compared and spot mapping generally reported higher species richness compared to point counts (Cyr et al., 1995; Dobkin and Rich, 1998).

The importance of accurately estimating the abundance of wildlife is a fundamental component of wildlife science and decision making in conservation plans (Engeman, 2003; Bart, 2005; Gregory and van Strein, 2010; Schmeller et al., 2015). Our results highlight the need for managers to evaluate which surveying method to use in order to best fulfill management goals, allowing for trade-offs among cost, effort, accuracy, and the ability to detect treatment effects. For broad-scale monitoring projects, point counts are sufficient since point count densities are generally correlated with actual densities, though the strength of the correlation varied for our focal species. Furthermore, if detecting treatment effects is an objective, point counts can detect relatively large changes. Nevertheless, for conservation of rare or endangered species where subtle population changes need to be detected or precise territory locations assessed, more intensive methods such as spot mapping may be necessary.

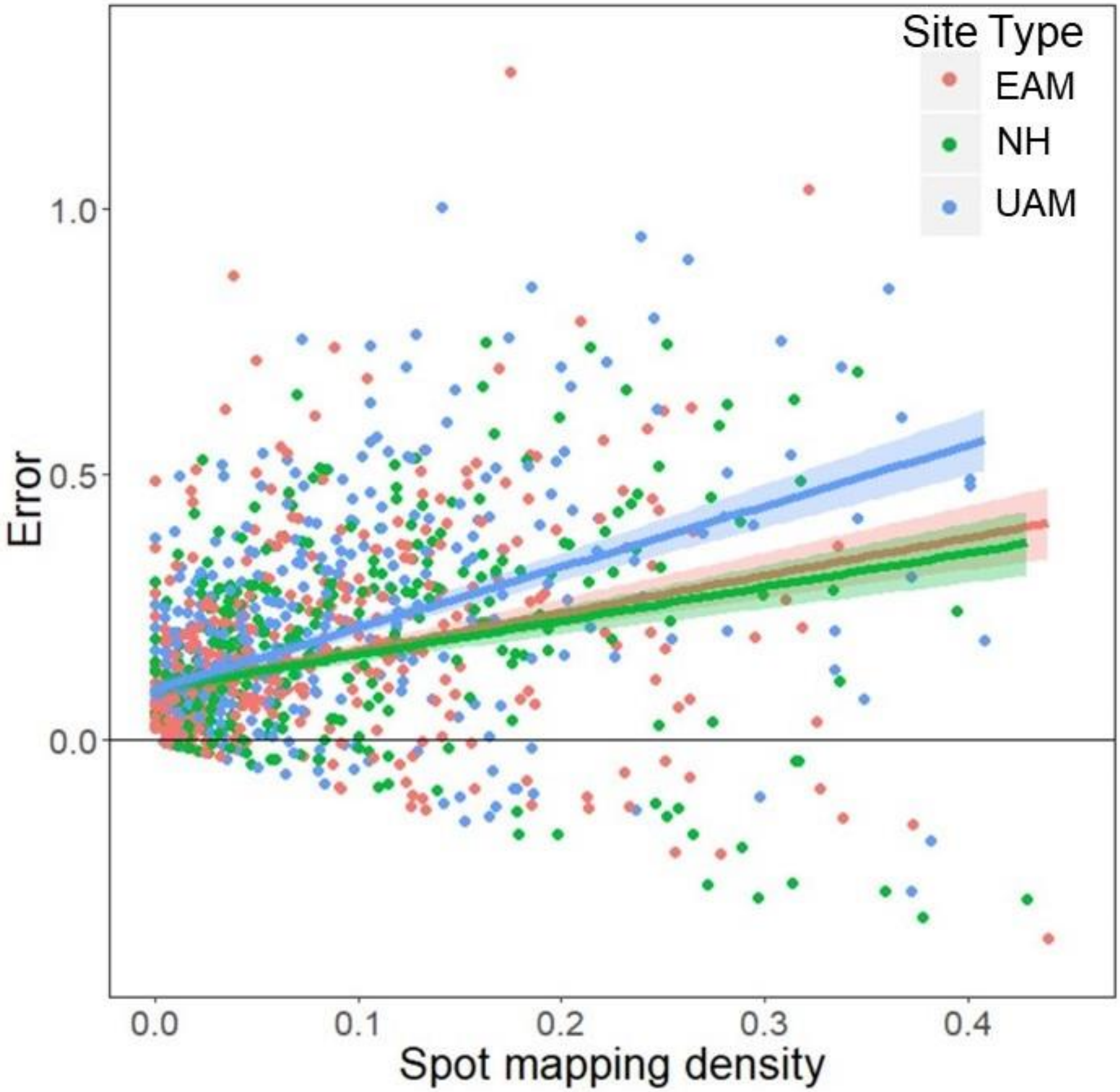

Figure 2.1. Relationship between spot mapping density indices and direction of error associated with point count density estimates for all species across all sites and years. Error is calculated as point count density estimate minus spot mapping density index. Overestimates are above the zero-line, underestimates are below the zero-line. Points and regression lines are colored according to site management type. Site types: even-aged management (EAM); no-harvest (NH); uneven-aged management (UAM).

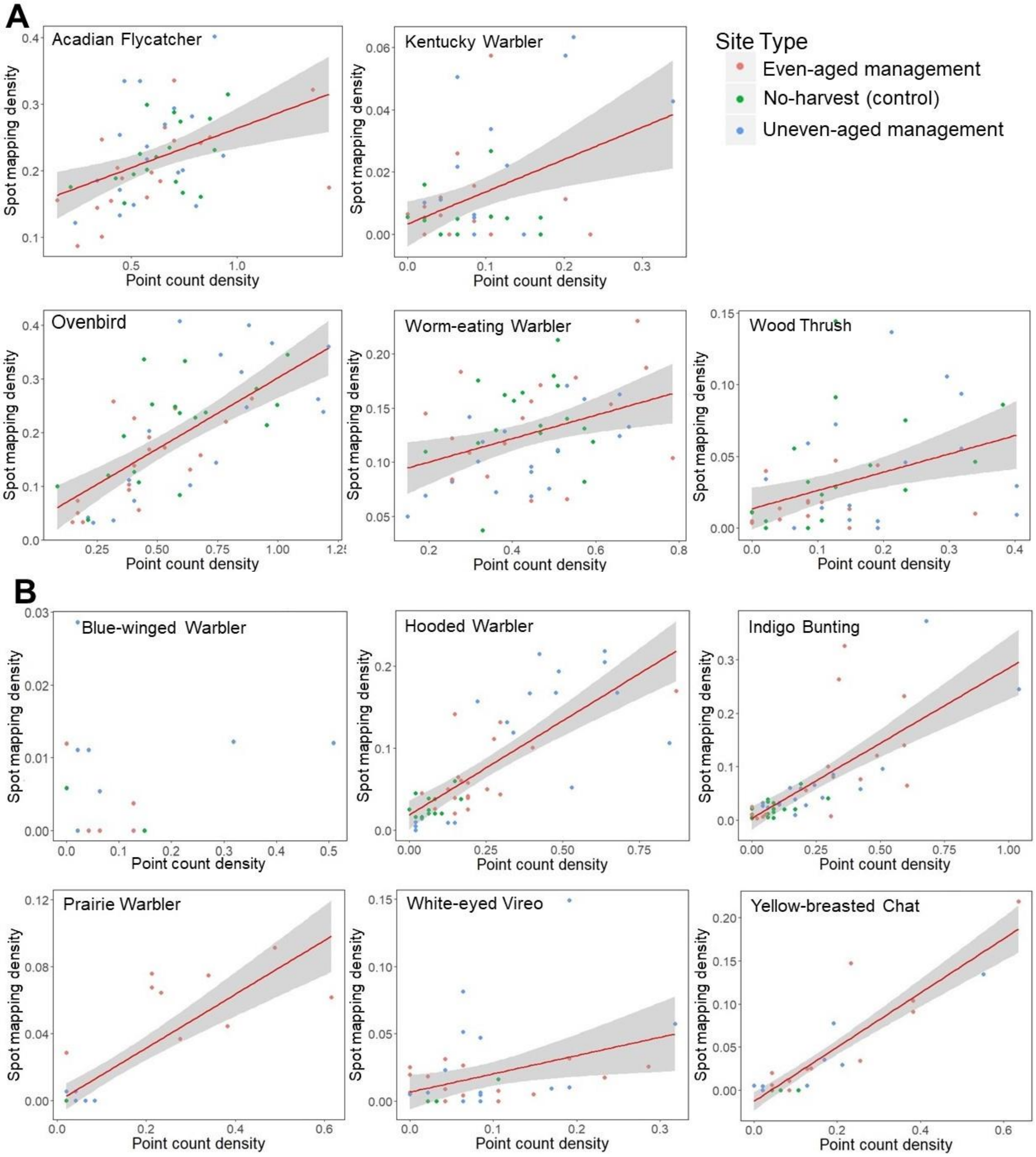

Figure 2.2. Linear models of spot map density predicted by point count densities of (A) mature forest and (B) shrubland species. Points are site × year combinations and are colored according to site management type.

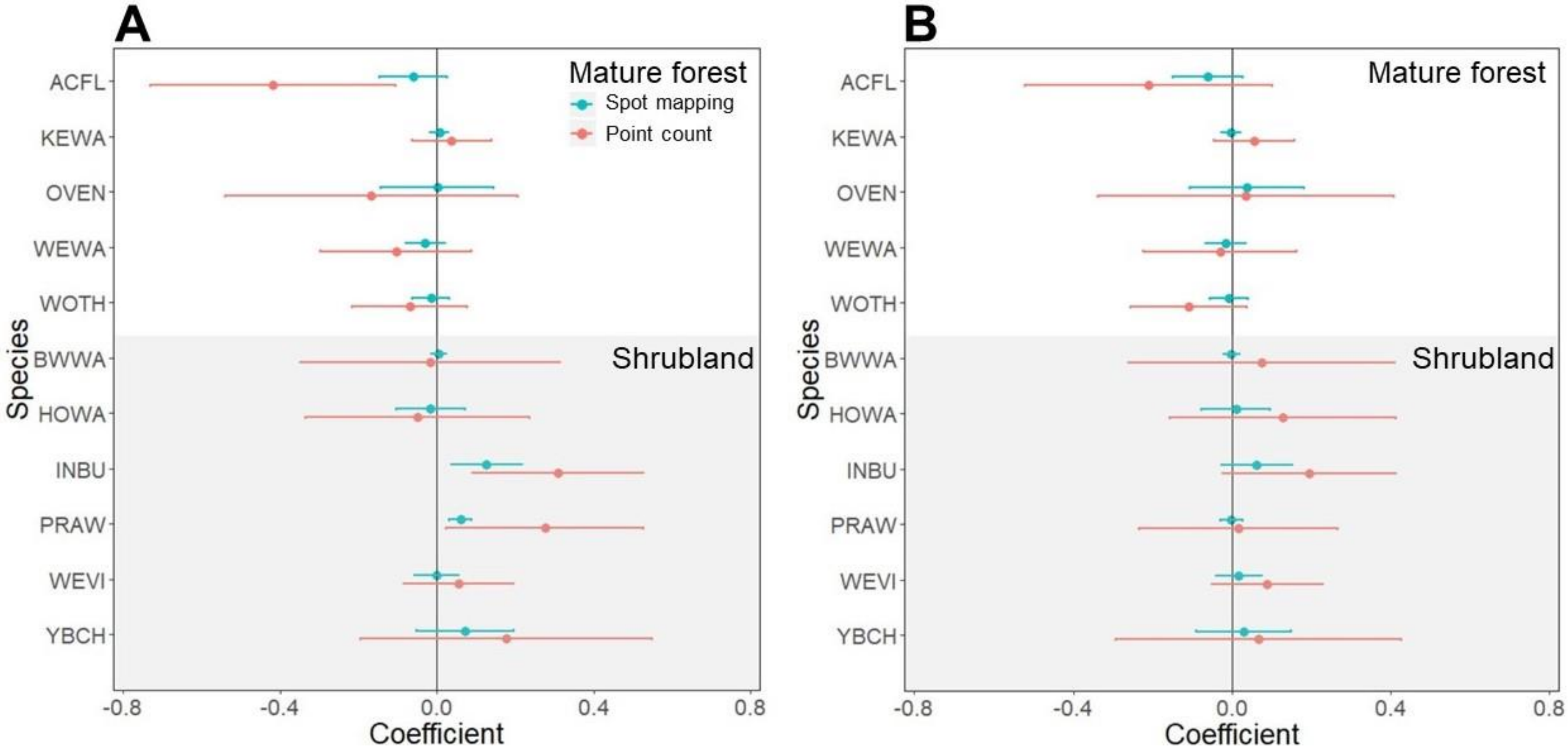

Figure 2.3. Coefficients from linear models predicting treatment effects on 11 focal species. (A) Treatment effects of even-aged management; (B) treatment effects of uneven-aged management. Species codes: Acadian Flycatcher (ACFL); Kentucky Warbler (KEWA); Ovenbird (OVEN); Worm-eating Warbler (WEWA); Wood Thrush (WOTH); Blue-winged Warbler (BWWA); Hooded Warbler (HOWA); Indigo Bunting (INBU); Prairie Warbler (PRAW); White-eyed Vireo (WEVI); Yellow-breasted Chat (YBCH).

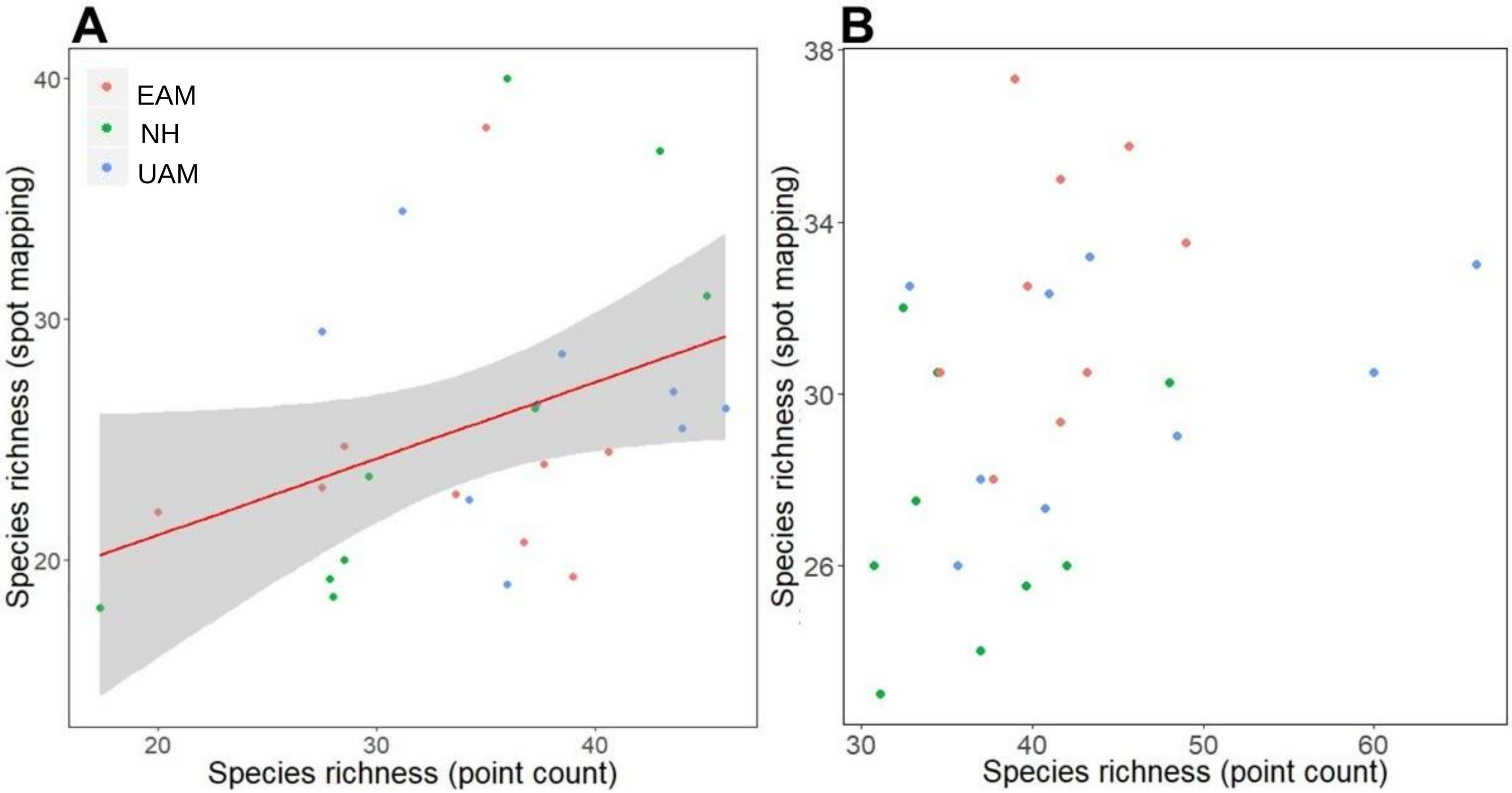

Figure 2.4. Linear model of Chao1 species richness estimates from point count and spot map data before harvest (A) and after harvest (B). Points are site × year combinations and are colored according to site management type.

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APPENDIX

Appendix I. English and taxonomic species names and habitat classification for species recorded at study sites

Code	English name	Taxonomic name	Habitat
ACFL	Acadian Flycatcher	Empidonax virescens	Mature forest
AMCR	American Crow	Corvus brachyrhynchos	Mature forest
AMRE	American Redstart	Setophaga ruticilla	Mature forest
BAWW	Black-and-white Warbler	Mniotilta varia	Mature forest
BGGN	Blue-gray Gnatcatcher	Polioptila caerulea	Mature forest
BHCO	Brown-headed Cowbird	Molothrus ater	Both
BLJA	Blue Jay	Cyanocitta cristata	Mature forest
BTNW	Black-throated Green Warbler	Setophaga virens	Mature forest
BWHA	Broad-winged Hawk	Buteo platypterus	Mature forest
BWWA	Blue-winged Warbler	Vermivora cyanoptera	Shrubland
CACH	Carolina Chickadee	Poecile caroloinensis	Mature forest
CARW	Carolina Wren	Thryothorus ludovicianus	Both
CERW	Cerulean Warbler	Setophaga cerulea	Mature forest
CEDW	Cedar Waxwing	Bombycilla cedrorum	Both
CHSP	Chipping Sparrow	Spizella passerina	Shrubland
COYE	Common Yellowthroat	Geothylpis trichas	Shrubland
DOWO	Downy Woodpecker	Dryobates pubescens	Mature forest
EABL	Eastern Bluebird	Sialia sialis	Shrubland
EAPH	Eastern Phoebe	Sayornis phoebe	Both
EATO	Eastern Towhee	Piplio erythrophthalmus	Shrubland
EAWP	Eastern Wood-Pewee	Contopus virens	Mature forest
GCFL	Great Crested Flycatcher	Myiarchus crinitus	Mature forest
HAWO	Hairy Woodpecker	Dryobates villosus	Mature forest
HOWA	Hooded Warbler	Setophaga citrina	Shrubland
INBU	Indigo Bunting	Passerina cyanea	Shrubland
KEWA	Kentucky Warbler	Geothylpis formosa	Mature forest
LOWA	Louisianna Waterthrush	Parkesia motacilla	Mature forest
MODO	Mourning Dove	Zenaida macroura	Both
NOCA	Northern Cardinal	Cardinalis cardinalis	Both
NOPA	Northern Parula	Setophaga americana	Mature forest
OVEN	Ovenbird	Seiurus aurocapilla	Mature forest
PIWA	Pine Warbler	Setophaga pinus	Mature forest
PIWO	Pileated Woodpecker	Dryocopus pileatus	Mature forest
PRAW	Prairie Warbler	Setophaga discolor	Shrubland
RBWO	Red-bellied Woodpecker	Melanerpes carolinus	Mature forest
REVI	Red-eyed Vireo	Vireo olivaceous	Mature forest
RHWO	Red-headed Woodpecker	Melanerpes erythrocephalus	Both
RSHA	Red-shouldered Hawk	Buteo lineatus	Mature forest
SCTA	Scartlet Tanager	Piranga olivacea	Mature forest

SUTA	Summer Tanager	Piranga rubra	Mature forest
TUTI	Tufted Titmouse	Baeolophus bicolor	Mature forest
WBNU	White-breasted Nuthatch	Sitta carolinensis	Mature forest
WEVI	White-eyed Vireo	Vireo griseus	Shrubland
WEWA	Worm-eating Warbler	Helmitheros vermivorum	Mature forest
WOTH	Wood Thrush	Hylocichla mustelina	Mature forest
YBCH	Yellow-breasted Chat	Icteria virens	Shrubland
YBCU	Yellow-billed Cuckoo	Coccyzus americanus	Mature forest
YTVI	Yellow-throated Vireo	Vireo flavifrons	Mature forest
YTWA	Yellow throated Warbler	Setophaga dominica	Mature forest