Avian community response to experimental forest management

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Abstract. 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) with harvest occurring on a different portion of trees every 15 yr over a 100-yr rotation. We used non-metric multidimensional scaling and linear mixed models to investigate the effects of silvicultural treatment and year-since-harvest on bird communities over a 24-yr period, before and after two harvests (1996 and 2011). Bird community compositions diverged among treatments immediately post-harvest, but the differences in community composition and structure began to diminish by 8 yr post-harvest. Species richness was higher in treated stands than no-harvest controls and lowest approximately 10 yr post-harvest regardless of treatment. Species diversity showed a linear decrease with year-since-harvest. Our findings demonstrate that even-aged and uneven-aged forest management can affect bird community composition and structure within the early post-harvest period, but differences may diminish relatively quickly as harvested stands regenerate. We recommend using a variety of silvicultural methods to provide the diversity of habitats needed for the conservation of diverse forest bird communities.

Key words: breeding birds; forest management; mature forest bird communities; Missouri Ozark Forest Ecosystem Project; shrubland bird communities.

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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, Duncker et al. 2012). 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 the organisms that rely on forests (Putz et al. 2008, Semlitsch et al. 2009, Chaudhary et al. 2016). For example, many bird species that are facing long-term population declines breed in forests that are routinely managed for timber (Thompson et al. 1995, Sauer et al. 2017). Thus, understanding the effects that different types of forest management have on bird communities is paramount for conservation planning.

Past studies have assessed bird response to forest management at the species and community level. However, most of these studies were not conducted 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 and Thompson 1997, Lindenmayer et al. 2002, Newell and Rodewald 2012). Long-term, broad-scale manipulative experiments with randomized treatments are critical for strong statistical inferences from forest management studies (Thompson et al. 2000, Faaborg et al. 2010). Thus far, studies completed 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, Severinghaus 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 (Colwell and Coddington 1994, Mace et al. 2012).

To date, research assessing the long-term, large-scale effects of forest management on bird community composition is lacking. Findings from shorter-term studies have been inconsistent, potentially reflecting differences in scale or forest type. For example, both even-aged management practices (EAM), such as clearcutting, and uneven-aged practices (UAM), such as selection-logging, can result in lower species richness than unharvested forests. However, effects differ widely across latitude and forest types (Chaudhary et al. 2016, LaManna and Martin 2017). The overall loss in species richness resulting from logging may be mediated by creation of early-successional forests in the years immediately following harvest. In the temperate zone, clearcutting may create habitat for distinct communities of shrubland bird species that may offset the potential loss of species that are sensitive to disturbance (Keller et al. 2003, George et al. 2019). Selection cutting may not achieve the same effect because many shrubland bird species avoid canopy openings that are <2 ha (Costello et al. 2000, Roberts and King 2017). Potential benefits of clearcutting for shrubland bird communities may begin to dissipate within 10 yr of harvest as clearcuts regenerate, resulting in a longer-term decline in species richness until forest structure reaches sufficient complexity for mature forest species to recolonize (Keller et al. 2003, George et al. 2019). Whereas EAM may increase species richness initially, the more complex vegetation structure resulting from UAM should permit regenerating stands to produce habitat for a greater number of bird species faster than EAM. Limited selection-logging can produce similar bird assemblages to those in unlogged forests in both the tropics and temperate zone, although multiple rounds of harvest in the same area may lower diversity (Edwards et al. 2010, Edwards and Laurance 2013, Morris et al. 2013). Thus, the effects of timber harvest on bird diversity are a function of both intensity and frequency of logging. Yet, most past studies of bird communities in managed forests have been limited in spatial extent or time period and thus are unable to directly compare management systems. A better understanding of how forest management affects the long-term health and diversity of avian communities is essential for sustainable forestry (Thompson et al. 1995, Haulton 2008).

We analyzed a 24-yr (1991–2014) data set from a landscape-scale manipulative 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 and year-since-harvest. We predicted that community composition would be most unique in EAM sites because shrubland species would replace mature forest species in regenerating clearcuts (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 in the early period following harvest gradually declining (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 9 sites that range in size from 312 to 514 ha and are located in Carter, Reynolds, and Shannon counties in the Current River Hills sub-section of the Ozark Highlands of southeastern Missouri (91°01’–91°13’ W and 37°00’–37°12’ N; Fig. 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. cocinea) 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).

When the study began in 1990, the region was 84% forested and generally even-aged with most of the overstory trees being 50-70 yr 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 yr prior to data collection (Brookshire and Shifley 1997).

Experimental Design

The MOFEP experiment was established following a randomized complete block design comprised of 3 blocks of 3 sites. Within each block, each site was randomly assigned to 1 of 3 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 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 resource agencies such as the Missouri Department of Conservation. On EAM and UAM sites, harvests occurred in different stands every 15 yr over a 100-yr rotation. The stands on NH sites serve as indicators of natural processes as the forest matures over the 100 yr 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 7–9 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) were administered across 41–69% of each site. Group-selection cuts ranged from 21 to 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).

Bird Densities

To estimate bird densities, we mapped breeding bird territories each 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 7 subplots (~45 ha each). From 1991 to 1995 and 1997 to 2000, we censused all 7 subplots on each site, but in 2001–2003 and 2008–2014, we only surveyed 4 subplots per site 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-d intervals; observers were alternated each visit to reduce observer bias. On each visit, field assistants began at dawn 5 d per week and spent 3–4 h 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 3 or more clustered observations of a species detected on 3 separate dates, countersinging, 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 olivaceus*) territories were counted but not mapped in years prior to 2008 because they were ubiquitous across the study area and were not a focal species for previous MOFEP studies. We adjusted stand-level density estimates for these
years using a simple linear model of year-since-harvest based on spot-mapping data from 2008 to 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, California, USA).

Statistical analyses

We used linear mixed models within an information theoretic framework to evaluate the relationships between temporal and habitat variables and avian community metrics (species richness and Shannon diversity). To account for the likelihood of larger stands overlapping mapped territories of more species, species richness was estimated for each stand in each year using the Chao1 non-parametric species richness estimator (Chao 1984, Walther and Martin 2001). We fit 7 candidate models for each response variable that included combinations of stand treatment 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. Model sets 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 using Akaike’s information criterion (AIC) and model weights.

To visualize how community structure differed among treatments, we performed non-metric multidimensional scaling (NMDS) ordinations. This method of ordination is a non-parametric 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). Bird densities were included in a site \times 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 yr post-first harvest), Period 4 (2008–2010; 12–14 yr post-first harvest), and Period 5 (2012–2014; 1–3 yr post-second harvest). Time periods were selected to accommodate the planned MOFEP reentry interval, and for consistency with previous MOFEP studies (Gram et al. 2003, Morris et al. 2013). For each time period, we calculated the NMDS on Bray-Curtis distance matrices derived from square root transformed densities (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). 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 pairwise PERMANOVA for that period to determine which stand treatment types were responsible for the differences in community structure. We performed analyses in R with packages nlme and vegan (R version 3.5.1; www.r-project.org).

RESULTS

Over the first 24 yr of the study (1991–2014), 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%; Fig. 2A–C). In clearcut stands, rank abundance plots showed a distinct change in the dominant species with early years (1–8 yr post-harvest) being dominated by shrubland species such as indigo bunting (Passerina cyanea), yellow-breasted chat (Icteria virens), and prairie warbler (Setophaga discolor; Fig. 2D). By
12–18 yr 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 (Fig. 2E). 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 yr post-harvest in both group-selection cut and thinned stands, but by 12–18 yr 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; Fig. 2F–I).

For species richness, the best-supported model included the additive effects of year-since-harvest and stand treatment type and had an AIC model weight of 0.99 (Tables 1, 2). Other candidate models were not well supported. Species richness was highest in thinned stands and lowest in NH stands and showed a quadratic
Predicted species richness was lowest ~10 yr post-harvest. For Shannon H', the best-supported model was year-since-harvest and had an AIC model weight of 0.98 (Tables 1, 2). 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 (Fig. 3C).

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 (pre-harvest), the NMDS plot showed broad overlap among all treatment types (Fig. 4A). In period 2, there was separation along the first axis with clustering corresponding to stand treatment type (Fig. 4B). In period 3, the separation was predominantly on the second axis (Fig. 4C). In period 4, the separation was mostly along the second axis and clustering was less distinct than the previous two periods (Fig. 4D). 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. 4E).

The global PERMANOVA (Appendix S1: Table S1) revealed differences in the multivariate community structure among treatment types in all five time periods. Pairwise PERMANOVA (Appendix S1: Table S2) showed that during period 1 (pre-harvest), 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. 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. In period 4, community structure differed in all treatment types except thinned vs. no-harvest stands and thinned vs. group-selection cut stands. 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 1. Model-selection results from the best-ranked a priori candidate models of the effects of year-since-harvest and treatment type on bird species richness and Shannon H' in the Missouri Ozark Forest Ecosystem Project, 1991–2014.

| Response variable | Model            | ΔAIC | K | Weight |
|-------------------|------------------|------|---|--------|
| Species richness  | YSH^2 + treatment| 0.0  | 9 | 0.99   |
|                   | YSH + treatment  | 13.3 | 8 | <0.01  |
|                   | YSH × treatment  | 19.0 | 11| <0.01  |
|                   | Treatment        | 39.3 | 7 | <0.01  |
|                   | YSH^2            | 67.0 | 5 | <0.01  |
|                   | YSH              | 76.6 | 6 | <0.01  |
|                   | Null             | 538.7| 3 | <0.01  |
| Shannon H'        | YSH              | 0.0  | 5 | 0.98   |
|                   | YSH + treatment  | 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             | 377.4| 3 | <0.01  |

Notes: YSH is year-since-harvest; treatment is treatment type of stand (clearcut, thinned, uneven-aged, and no harvest).

Table 2. Estimated coefficients for the best supported models of the effects of year-since-harvest (YSH) 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 Ozark Forest Ecosystem Project, 1991–2014.

| Response variable | Parameter | Coefficient | Standard error | Lower 95% CI | Upper 95% CI |
|-------------------|-----------|-------------|---------------|--------------|--------------|
| Species richness  | Intercept | 12.20       | 0.82          | 10.59        | 13.82        |
|                   | YSH       | -0.94       | 0.15          | -1.24        | -0.64        |
|                   | YSH^2     | 0.04        | 0.01          | 0.02         | 0.06         |
|                   | GSC       | 0.70        | 0.80          | -0.87        | 2.26         |
|                   | THN       | 1.70        | 0.94          | -0.13        | 3.54         |
|                   | NH        | -3.79       | 0.82          | -5.40        | -2.17        |
| Shannon H'        | Intercept | 1.31        | 0.03          | 1.26         | 1.37         |
|                   | YSH       | -0.02       | <0.01         | -0.03        | -0.01        |

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Fig. 3. Predictions of the best supported model showing the effects of treatment type on bird species richness (A) and effects of year-since-harvest on bird species richness (B) and Shannon H’ (C) in the Missouri Ozark Forest Ecosystem Project. Abbreviations are CC, clearcut; GSC, group-selection cut; NH, no harvest; THN, thinned. For model predictions, variables are held constant at their means. Shaded areas and error bars represent 95 % confidence intervals.

Fig. 4. NMDS ordination plots showing bird community structure changes in each treatment type through time in the Missouri Ozark Forest Ecosystem Project. Ellipses represent the standard deviation of site scores showing the degree of overlap in community structure among management types. (A) 1991–1995 (pre-harvest; stress = 0.19); (B) 1997–2000 (1–4 yr post- first harvest; stress = 0.21); (C) 2001–2003 (5–7 yr post- first harvest; stress = 0.12); (D) 2008–2010 (12–14 yr post-first harvest; stress = 0.16); (E) 2012–2014 (1–3 yr post- second harvest, 16–18 yr post- first harvest; stress = 0.17).
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 yr of data is among the 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 with other treatment types. The shrubland species remained until approximately 10–12 yr post-harvest, but by 12–14 yr, 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 early period following harvest. The community began to shift back towards a composition more typical of a mature forest as habitat became less suitable for shrubland species. This pattern is consistent with the findings of species-level analyses from the temperate zone that found that shrubland species colonize clearcuts quickly, reach their peak densities within 10 yr post-harvest, and then gradually decline (Conner and Adkisson 1975, Keller et al. 2003, Morris et al. 2013, George et al. 2019).

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 yr post-harvest, the communities began to return to pretreatment compositions. Other studies from the temperate zone have also found that the silvicultural treatment effects on bird densities diminish by 12 yr, with species composition thereafter being similar to pretreatment compositions (DeGraaf and Chadwick 1987, Twedt and Wilson 2017, George et al. 2019).

Our top model predictions showed that all treatment types resulted in higher species richness compared with 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 at least 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 with no-harvest stands (Falk et al. 2008, von Oehim 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 (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 clearcutting yields a total leaf area similar to that of old-growth stands, but the leaf area is all within 5 m of the ground. The compression of leaf area closer 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 with 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 decline within the first 10 yr following harvest. A long-term reduction in species richness post-harvest has also been observed in other studies of birds and other taxa (Kirkland 1977, Buddle et al. 2006, Chaudhary et al. 2016). The loss 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 suitability for shrubland species. As succession continues, forest structure becomes more heterogeneous, eventually resulting in an increase in animal species diversity (Franklin and Van Pelt 2004). Whereas bird species richness began to increase slightly by 15 yr post-harvest, the duration of our study may have been too short to detect increases in bird species richness and diversity that can occur in later successional stages (e.g., >25 yr post-harvest; Keller et al. 2003). The decline in diversity that we observed may likewise be an artifact of the MOFEP site history. Whereas the study area was considered relatively undisturbed when MOFEP was initiated, the region was logged during the late 19th and early 20th centuries, and most trees on our study sites were <100 yr old. Thus, structural heterogeneity and species diversity on no-harvest sites likely had not reached levels comparable to old-growth forests (Franklin and Van Pelt 2004).

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 larger openings such as those created by clearcutting (Annand and Thompson 1997, Robinson and Robinson 1999, Costello et al. 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 (McCreedy et al. 2004, King and Schlossberg 2014). 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, 2006, Kellner et al. 2019). 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 (Crookston et al. 2010, Bellard et al. 2012). 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.

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