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Response of Breeding Birds to Forest Disturbance in the Arkansas Ozarks: Impacts of Uneven-Aged Management, Ice Damage, and Woodland Restoration

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RESPONSE OF BREEDING BIRDS TO FOREST DISTURBANCE IN THE ARKANSAS
OZARKS: IMPACTS OF UNEVEN-AGED MANAGEMENT, ICE DAMAGE, AND
WOODLAND RESTORATION

RESPONSE OF BREEDING BIRDS TO FOREST DISTURBANCE IN THE ARKANSAS
OZARKS: IMPACTS OF UNEVEN-AGED MANAGEMENT, ICE DAMAGE, AND
WOODLAND RESTORATION

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in Biology

By

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ABSTRACT

Forests of the Ozarks are important breeding grounds for many bird species, each with specific habitat requirements. Natural and anthropogenic disturbance events can alter vegetational structure of forests, thereby influencing communities of breeding birds. The objectives of my study were to examine the response of breeding birds and their habitat to three types of forest disturbance: (1) uneven-aged management, (2) ice damage, and (3) woodland restoration.

Avian and vegetation surveys were conducted during the 2008, 2009, and 2010 breeding seasons (May-June) in the Ozark National Forest, Arkansas. Each site was surveyed for birds four times a season using fixed-radius point counts. For objective (1), I compared control and thinned plots (n=32 total) immediately after treatment (1994, data from a previous study) and fifteen years post-treatment (2008). Although vegetation differed between treatments in 1994, avian species richness, community composition, and occupancy for three of four populations (representing different nesting guilds) were similar among treatments. Fifteen years later, original differences in habitat had diminished and bird communities were still similar between treatments. For objective (2), I compared sites with high and low ice damage (n=32 total) one year before and two years after a 2009 ice storm. High damage sites had more open canopy and woody debris ground cover, but avian species richness, community composition, and occupancy of three populations (representing different nesting guilds) did not differ between years for either treatment. For objective (3), I compared recently restored woodland and mature forest sites (n=16 total) for three years following restoration (burning and thinning). Restored sites resembled woodland, with open canopy and herbaceous ground cover. They also had higher

avian species diversity and more early successional species, cavity-nesters, and some canopy-nesters. These differences diminished with time since fire.

Overall, forest bird communities demonstrated resilience to small-scale canopy openings created by uneven-aged management and ice damage. However, when fire was introduced along with thinning, avian communities shifted towards those more typical of open woodland. To maximize habitat availability for the most number of species, managers should plan for areas of both closed-canopy forest and woodland ecosystems.

Keywords: forest disturbance, habitat structure, uneven-aged management, ice storm damage, oak woodland restoration, forest bird community, Ozark Mountains, Arkansas

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CHAPTER 1

Introduction

The upland oak-hickory forests of the Ozark Mountains are important breeding grounds for many bird species, including resident and migratory populations (James and Neal, 1986; Howell *et al.*, 2000), some of which are in decline (La Sorte *et al.*, 2007). The heterogeneity in vertical structure typical of these forests provides varied nesting habitat for a diverse suite of species (James, 1971). Some species make use of leaf litter and saplings near the forest floor to fashion their nests [e.g., Ovenbird (*Seiurus aurocapillus*)]. Others prefer to nest in shrubby undergrowth that occurs in canopy openings [e.g., Hooded Warbler (*Setophaga citrina*)]. Most species, however, nest in the canopy [e.g., Red-eyed Vireo (*Vireo olivaceus*)] or in tree cavities [e.g., woodpeckers (*Picoides* spp.)]. Decades of research have demonstrated strong associations between birds and vegetative characteristics of their nesting habitat [see any species account in The Birds of North America Online (Poole, 2005)]. Habitat characteristics can change though, and sometimes quite unexpectedly, following ecological disturbance.

White and Pickett (1985) define disturbance as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment”. Disturbance displaces or inhibits established individuals and provides other individuals with an opportunity to take advantage of a changing resource (Sousa, 1984). In the past, the term disturbance carried with it a negative connotation of destruction; however, more recent ecological theory attributes natural heterogeneity (in landscapes and biotic communities) to disturbance events (Brawn *et al.*, 2001).

Throughout time, forest ecosystems (including those of the Ozarks) have periodically experienced natural disturbances such as tree-fall, fire, drought, wind, and disease (Runkle, 1985; Abrams, 1992). With the dispersal of Native Americans across North America, and the subsequent settlement of Europeans, a new category of disturbance emerged: anthropogenic.

Historic accounts of the Ozarks and dendrochronological studies document intensive timber harvests (Strausberg and Hough, 1997) and periodic human-set fires (Batek *et al.*, 1999; Stambaugh and Guyette, 2006) during the 18th and 19th centuries. Today old growth forests are uncommon in the Ozarks (Stahle and Chaney, 1994) because few escaped logging during westward expansion. In addition, current oak forests exhibit different structure and species composition compared to historic accounts (Foti, 2004), in part because fire suppression during the 20th century contributed to the development of densely stocked, closed canopy forests with shade-tolerant species in the understory.

At the close of the 20th century, management strategies shifted towards returning forests to a more natural disturbance regime. This approach involved utilizing less destructive methods of timber harvest (such as uneven-aged management) and reintroducing fire into areas that were once fire-adapted ecosystems. Along with these controlled approaches to forest management, natural disturbance continues to occur periodically (e.g., insect outbreaks and ice storms). Both anthropogenic and natural disturbances are now part of the modern day disturbance regime of the Ozark forests.

Disturbance, whether anthropogenic or natural, has the potential to influence breeding birds by changing habitat structure. This study examines the response of breeding birds and their habitat to three types of forest disturbance in the Ozark National Forest, Arkansas. In Chapter 2, my objective was to examine the short- and long-term response of breeding bird communities and populations to uneven-aged management (a method of logging in which individuals or small groups of trees are selected for harvest). Species richness and community composition, as well as site occupancy of four populations of birds (representing different nesting guilds), were compared among mature forest and managed sites immediately after harvest (1994) and fifteen

years later (2008). In Chapter 3, I explore how bird communities and populations responded to structural damage caused by a severe 2009 ice storm. Sites with high and low levels of structural damage were compared in terms of avian species richness, community composition, and site occupancy for three populations (representing different nesting guilds) during one breeding season before and two seasons after the ice storm. In Chapter 4, my goal was to determine whether oak woodland restoration practices in a section of the Ozark National Forest have been successful in returning closed-canopy forests to a more open-canopy, woodland state, and whether bird communities and populations have responded to associated changes in vegetation structure. I evaluated differences in habitat characteristics, avian species richness, and community composition between recently restored and control sites for three breeding seasons following restoration treatments. Conclusions and implications from these studies are summarized in Chapter 5.

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CHAPTER 2

Short- and long-term response of breeding birds to uneven-aged management in the Ozark Mountains, Arkansas

Abstract

Uneven-aged silvicultural practices mimic gap-creating natural disturbances and promote habitat heterogeneity in forests, which supports a variety of breeding birds. Few studies have examined the long-term implications of such management. I investigated the response of breeding birds and their habitat to two categories of thinning (understory only, and understory + canopy) immediately after treatment (1994) and fifteen years post-treatment (2008). Avian and vegetation surveys were conducted during the breeding season (May-June) in the Ozark National Forest, Arkansas. Avian species richness and community composition did not vary with intensity of management or time. The early successional species Indigo Bunting (*Passerina cyanea*) had higher occupancy on the most intensely managed plots in 1994. Despite changes in habitat characteristics, the shrub-nesting Hooded Warbler (*Wilsonia citrina*), ground-nesting Ovenbird (*Seiurus aurocapillus*), and canopy-nesting Eastern Wood-Pewee (*Contopus virens*) showed no immediate response to treatment. Fifteen years later, there were no differences among treatments for any species, however overall occupancy was lower for Eastern Wood-Pewees and Indigo Buntings, and higher for Hooded Warblers. These results suggest that uneven-aged management has a short-lived positive effect for some early successional species, but no effect on other forest species, which seem resilient to changes in habitat associated with this practice. Thus, uneven-aged management is recommended when a goal of timber harvest is to maintain the integrity of forest structure and minimize impact on the bird community over time.

Keywords: uneven-aged management, habitat structure, forest bird community, Eastern Wood-Pewee, Ovenbird, Hooded Warbler, Indigo Bunting, Ozark Mountains, Arkansas

1. Introduction

Heterogeneity in forested landscapes historically has been maintained by natural disturbances such as lightning-induced fires, floods, disease outbreaks, and tree-falls (Sousa, 1984; Brawn *et al.*, 2001). These disturbances can promote local and regional biodiversity (Angelstam, 1998). As human populations have grown, the influence of anthropogenic disturbances on natural habitats has become similarly important in affecting the ecology of forests. These impacts can be destructive, as in the case of habitat loss and degradation from urban and agricultural development, but they might also be beneficial to forest ecosystems, as in the case of some types of forest management (Sallabanks and Arnett, 2005).

Humans have impacted forests in the United States since before European settlement, but large-scale manipulation of forest habitat accelerated during the 19th and 20th centuries as humans became more efficient in clearing forested land for agriculture and harvesting forest resources for timber (Strausberg and Hough, 1997). Two major approaches to harvesting trees in forests are: even-aged management and uneven-aged management. Even-aged management (e.g., clear-cutting, shelterwood cuts) creates forest stands that are dominated by one age-class, while uneven-aged management (e.g., single-tree and group selection) produces stands representing at least three or more age classes (Smith, 1997). Even-aged management has been criticized not only for its appearance after harvest, but also for its impacts on hydrologic and ecosystem processes (McDermott and Wood, 2009). Uneven-aged harvesting has become more common because it maintains a relatively more intact forest ecosystem than even-aged harvesting (Sallabanks and Arnett, 2005). Uneven-aged stands typically have a well-developed understory and subcanopy because frequent canopy gaps temporarily release plants in these layers from competition (Thompson *et al.*, 1995).

Although uneven-aged management generates less change in vegetation structure and tree species composition than even-aged management (Thompson *et al.*, 1995), these changes in habitat still have the potential to influence populations and communities of forest wildlife such as mammals (Thompson *et al.*, 2003), reptiles (Renken *et al.*, 2004), and especially birds [see Thompson *et al.* (1995) and Vanderwel *et al.* (2007)]. In recent years, more studies have examined the effects of uneven-aged practices on forest breeding birds, which demonstrate species-specific structural habitat requirements (James, 1971; Holmes and Sherry, 2001). Changes in avian communities (e.g., species diversity) tend to be minimal (Campbell *et al.*, 2007; Tozer *et al.*, 2010), so many studies focus on population-level responses (Sallabanks and Arnett, 2005). In general, species associated with mature forest habitat [e.g., Wood Thrush (*Hylocichla mustelina*), Ovenbird (*Seiurus aurocapillus*)] have shown negative population responses (i.e., declines in abundance or density), while gap-dependent and edge species [e.g., Indigo Bunting (*Passerina cyanea*), Hooded Warbler (*Wilsonia citrina*)] have had positive population responses (i.e., increases in abundance or density) to uneven-aged treatments (Thompson *et al.*, 1995; Annand and Thompson, 1997; Gram *et al.*, 2003; Campbell *et al.*, 2007; Tozer *et al.*, 2010). Understanding the effects of management practices on bird populations and communities is a growing concern, especially in light of estimates of population declines in the last few decades (Robbins *et al.*, 1989; La Sorte *et al.*, 2007).

The upland oak-hickory forests of the Ozark Mountains are important breeding grounds for many bird species, including resident and migratory populations (Donovan *et al.*, 1995; Howell *et al.*, 2000). This study investigated the response of breeding birds to vegetational changes on forested plots, which were managed in 1993-94 as part of a long-term study on the effects of selection cutting in oak-hickory stands in the Ozark National Forest (USDA Forest

Service, 1990). Two stages of silvicultural treatments were implemented. Understory treatments involved intensive thinning of understory vegetation on plots to lower competition for desirable sapling tree species, while full treatments incorporated thinning of both understory and canopy trees (Rodewald, 1995). In 1994, Rodewald and Smith (1998) surveyed these managed sites, along with control sites, for breeding birds and habitat characteristics. In the short-term, they found fewer understory nesters [e.g., Ovenbirds and Worm-eating Warblers (*Helmitheros vermivorus*)] and Acadian Flycatchers (*Empidonax virescens*), a canopy nester, on both types of managed plots. They also found a higher abundance of the canopy-nesting Eastern Wood-Pewee (*Contopus virens*) on both types of managed plots, and a higher abundance of the open-nesting Indigo Bunting on full treatment plots.

Since the Rodewald and Smith (1998) study, ecological succession is likely to have influenced forest structure on these plots. Johnson *et al.* (2002) described the development of a forest stand as proceeding through four stages: stand initiation, stem exclusion, understory reinitiation, and complex. Stands not subjected to extensive overstory removal develop towards the complex stage, in which natural mortality of overstory trees creates canopy gaps irregularly over time and space. These gap-scale disturbances help to maintain uneven-aged forests, but so does selective logging, which can mimic natural disturbances such as tree-falls. If the uneven-aged management applied in 1993-94 served as a gap-scale disturbance, then given fifteen years to develop, we might expect forest plots to have similar structural characteristics regardless of treatment.

Compared to the literature on short-term responses to uneven-aged practices, fewer studies have examined the long-term effects on birds and their forest habitat. Some studies in primarily deciduous forest have shown that the benefits of selective cutting to early successional

species is short lived, with populations returning to pre-cut numbers in fewer than 8-10 years (Robinson and Robinson, 1999; Jobes *et al.*, 2004; Heltzel and Leberg, 2006; Campbell *et al.*, 2007). Correspondingly, these studies also found that mature forest species were less negatively affected on treated plots over time.

The objective of this study was to examine the responses of breeding birds and their habitat to uneven-aged management immediately following treatment and fifteen years post-treatment. I examined bird responses in terms of species richness and composition (community-level) and site occupancy (population-level), which can be defined as the proportion of sites occupied by a species (MacKenzie *et al.*, 2006). Habitat responses were measured by comparing structural variables known to be important in bird-habitat relationships (e.g., canopy cover, shrub cover) (James, 1971). I predicted that one year after harvest, early successional species would be favored over late successional species (and differences in habitat would reflect this pattern); however, after fifteen years of stand development, the effects of silvicultural treatments on birds and habitat would diminish.

2. Materials and methods

2.1 Study areas and management history

The study area was located in the Big Piney District of the Ozark National Forest, in Newton and Pope counties, Arkansas, U.S.A. (35°43'13"N, 93°05'45"W) (Figure 1). Elevation of the study sites ranged from 400-620 m. The canopy of this upland forest was composed primarily of white oak (*Quercus alba* L.), northern red oak (*Q. rubra* L.), black oak (*Q. velutina* Lam.), and mockernut hickory (*Carya tomentosa* (L.) Nutt.). The understory was composed

primarily of red maple (*Acer rubrum* L.), blackgum (*Nyssa sylvatica* Marsh.), flowering dogwood (*Cornus florida* L.), and black cherry (*Prunus serrotina* Ehrh).

In April 2007, the 32 survey points of Rodewald and Smith (1998) were reestablished within or nearby sixteen 4.5 ha research plots created by the USDA Forest Service in the early 1990s as part of a study on uneven-aged forest management practices (USDA Forest Service, 1990). In spring 1993, eight of the sixteen plots were subjected to thinning treatments in which all understory trees of unmerchantable species greater than 1.4 m in height and less than 14 cm in diameter at breast height (dbh) were cut. From late summer through fall 1993, the forest overstories of these eight understory-treated plots were thinned to 15-19 m²/ha basal area. Overstory thinning involved harvesting merchantable trees and cutting all unmerchantable and poorly formed desirable tree species above 14 cm dbh. Also at this time, eight more plots received only the understory thinning treatment. The result included eight full treatment plots (understory + overstory) and eight understory treatment plots (understory only). Each treated plot had one survey point located near its center for a total of eight understory-treated points and eight full-treated points. In addition, sixteen control points were located in adjacent, untreated forest with visual similarity to pre-cut conditions of managed plots. These points were at least 100 m from the edges of managed plots. All points were spaced a minimum of 150 m from one another. For more details on thinning treatments and site selection, see Rodewald (1995).

2.2 Field sampling

For each of the 32 survey sites, four avian point count surveys were conducted by two observers (two surveys each) during the 2008 breeding season (mid-May through June). During these ten-minute surveys (conducted between 0600 to 1000 hours), the species and number of all birds seen or heard within a 50 m radius were recorded (Hutto *et al.*, 1986). Surveys were not

performed under adverse weather conditions (e.g., rain, wind) in order to maximize likelihood of detection (Martin *et al.*, 1997). These surveys were performed similarly to Rodewald (1995) in order to compare data from 1994 and 2008.

Using a modified protocol of James and Shugart (1970), four circular vegetation plots were established for each point count to measure habitat characteristics. One plot was located at the center of the point count, and three others were positioned 35 m from the point count center in three directions: 120, 240, and 360°. Within a 5 m radius of the center of each vegetation plot, the following measurements were taken: canopy height, percent canopy cover (measured via spherical densiometer), number of saplings greater than 0.5 m in height in two diameter size categories [small (0-2.5 cm) and large (2.5-8 cm), measured 10 cm above ground], and percent ground cover (below 0.5 m) of grass, shrub, forb, fern, leaf litter, log, and rock/soil (estimated visually). Within an 11.3 m radius, I counted the number of trees in three dbh size categories: small (8-23 cm), medium (23-38 cm), and large (>38 cm). Also within the 11.3 m radius, I measured the vegetation profile at five locations (selected via random number generator) along each of two transects running north/south and east/west through the plot. I placed a vertical pole at each random location and counted the points where vegetation made contact between 0-1 m and 1-2 m. See Table 1 for a description of variables and abbreviations.

2.3 Statistical analyses

Bird species that do not normally breed in the oak-hickory stands in the Ozarks or that were detected only once were not included in the analyses. For a complete list of species detected during the 1994 and 2008 surveys, see Appendix 1. Mean number of detections per survey for each species was calculated for each treatment for comparison with results from Rodewald (1995) (see Appendix 2).

Bird community analysis was performed using COMDYN4 (Hines *et al.*, 1999), which computes parameters reflecting spatial and temporal changes in communities based on the underlying jackknife estimator proposed by Burnham and Overton (1979), applied to species richness by Boulinier *et al.* (1998), and applied to community-dynamic parameters by Nichols *et al.* (1998). Community parameters (defined below with respect to this study) were estimated by comparing species detection patterns from presence/absence data between treatments within each year. COMDYN4 utilizes summary data, which required collapsing detection histories for each species across sites within the three treatments for each year. For more detail on the specifics of data entry for COMDYN4, see Hines *et al.* (1999). A subset of eight control survey points was randomly selected for analysis to avoid an inflated species richness estimate due to unequal sample sizes between control and full/understory plots. Species richness (N) refers to the number of species occurring in a treatment area at a given time. Extinction probability ($1-\phi$) is the proportion of species that go locally extinct between two treatments. Species turnover ($1-\gamma$) is the proportion of species present in one treatment that are not present another treatment. The rate of increase in species richness (λ) is a ratio of the estimated number of species present in one treatment to the estimated number present in another treatment. Finally, the number of locally colonizing species (B) is an estimate of the number of species present in one treatment that are not present in another treatment (Hines *et al.*, 1999).

Four bird species were selected for population analysis based on their nesting guild, potential to be influenced by management (Rodewald and Smith, 1998), and suitable detection histories. Eastern Wood-Pewees (EAWP) are canopy-nesters whose abundance has been shown to increase with decreasing canopy cover and increasing small trees 7-22 cm dbh (McCarty, 1996). Ovenbirds (OVEN) are ground-nesters that favor closed canopy forests with less shrub

cover at ground-level (Porneluzi *et al.*, 2011). Hooded Warblers (HOWA) are shrub-nesters associated with mature forests with enough tree-gaps to create a well-developed shrub layer (Chiver *et al.*, 2011). Indigo Buntings (INBU) nest in sizable open areas or near edges of forests where extensive shrub layers have developed (Payne, 2006).

An information-theoretic approach was used to evaluate single-season models relating site occupancy (Ψ) to habitat characteristics, while accounting for detectability (p), in program PRESENCE (MacKenzie *et al.*, 2002). Candidate models were developed for each year based on habitat variables known to influence population parameters and detectability for each bird species [i.e., percent canopy cover, percentage of ground covered by shrub, number of small saplings (which indicated the developmental stage of a shrub layer), and number of small trees]. Based on initial analyses, observer effects were not helpful in modeling detectability so they were not included in model sets. Models were ranked according to Akaike's Information Criterion (AIC) and, when necessary, adjusted for small sample size (AIC_c) and overdispersion of the data (QAIC_c) (Burnham and Anderson, 2002). Due to model selection uncertainty (i.e., some Δ AIC_c values for models differed by ≤ 2.0), model averaging was used to estimate the relationship between habitat covariates and probabilities of occupancy and detection, which were then estimated using habitat covariate means for each treatment type (Burnham and Anderson, 2002). Standard error and confidence interval estimates were calculated using the Delta method, as described by Cooch and White (2011).

Using JMP[®] (SAS Institute Inc., 2010), I performed principle components analysis (PCA) on 15 vegetation characteristics to examine habitat relationships among treatments within years. Components with eigenvalues greater than 1.5 were retained in the PCA. Original variables with correlations $>|0.4|$ with PC1 and PC2 were used to name axes. Prior to PCA, some

variables were either log, square-root, or arcsine transformed to improve homogeneity of variance and normality (Sokal and Rohlf, 1995). I performed multivariate analysis of variance (MANOVA) on these variables, testing the effect of treatment within each year. Discriminant analysis (DA) was used to determine which variables best discriminated between forest treatments within each year. Finally, differences between treatments within years were examined for each variable using one-way analysis of variance (ANOVA).

3. Results

3.1 Avian community

For each year, a total of 128 point count surveys were completed and analyzed. In 1994, there were a total of 795 individuals of 31 species detected. In 2008, there were 702 total individuals representing 27 species detected.

The results of the community analysis showed that species richness did not differ between treatments in either year (Table 2). Parameter estimates for community dynamics indicated that community composition also remained the same. In most treatment comparisons, the extinction probability, species turnover, rate of species increase, and locally colonizing species had confidence intervals that included null values, thus these parameters did not indicate significant change in the communities. The only exceptions occurred when comparing control to full treatments in 1994, when probability of extinction was 0.34 ± 0.14 , and in 2008, when the estimated rate of species increase was 1.24 ± 0.13 . Detection probabilities were not different between years for each treatment ($0.47 < P < 0.97$), so the alternative estimate of the rate of increase in species richness ($\text{alt}\lambda$) was used (Hines *et al.*, 1999).

3.2 Avian populations

Eastern Wood-Pewees had overall naïve occupancies of $\Psi = 0.84$ in 1994 and $\Psi = 0.28$ in 2008. In 1994, canopy cover was moderately useful in modeling occupancy (sum of model weights, $\Sigma w_i = 0.37$) (Table 3). In 2008, models including small trees had the most support from the data ($\Sigma w_i = 0.73$). However in both years, evidence for the effects of these covariates was weak since confidence intervals for their beta estimates included zero (Table 4). Estimates for EAWP occupancy were lower in 2008 than in 1994 for all treatments. Occupancy was similar across treatments in 1994; however, it was more variable in 2008, with understory treatment plots tending to have lower occupancy (although confidence intervals overlapped). In both years, detectability models including small saplings had support (1994, $\Sigma w_i = 0.54$; 2008, $\Sigma w_i = 0.41$), but there was evidence for an effect only in 1994 ($\beta = -0.244 \pm 0.189$). Detection estimates were similar across treatments in both years, but were higher in 1994 than in 2008 (Table 5).

Ovenbirds had overall naïve occupancies of $\Psi = 0.72$ in 1994 and $\Psi = 0.94$ in 2008. In 1994, both canopy and shrub cover were useful for modeling OVEN occupancy, but canopy cover was relatively more important (canopy cover $\Sigma w_i = 0.68$, shrub cover $\Sigma w_i = 0.37$) (Table 3). Probability of OVEN occupancy increased with increasing canopy cover ($\beta = 0.851 \pm 0.603$). Canopy cover was also useful in modeling occupancy in 2008 ($\Sigma w_i = 0.63$); however, its effect ($\beta = -2.520 \pm 1.983$) was uncertain since the confidence interval around the beta estimate included zero (Table 4). In both years, OVEN occupancy was fairly high (>0.89) in all treatments (Table 5). Detection probability increased as shrub cover increased in both years, but the effect was small (Table 4) so estimates remained similar among treatments, although higher overall in 2008 compared to 1994 (Table 5).

Hooded Warblers had overall naïve occupancies of $\Psi = 0.16$ in 1994 and $\Psi = 0.81$ in 2008. In 1994, the intercept model had a $w_i = 0.45$ and was only slightly improved by adding the habitat covariate of canopy cover to model occupancy ($\Delta AIC_c = 2.22$) (Table 3). In 2008, the number of small saplings was useful for modeling HOWA occupancy ($\Sigma w_i = 0.78$), but evidence for an effect was weak (Table 4). Occupancy was similar between treatments within 1994 and 2008, and higher overall in 2008 (Table 5). Detection rates were not influenced by number of saplings in 1994, however in 2008, detectability increased slightly with increasing number of saplings (Table 4). Probability of detection did not differ between treatments within either year, but it was generally higher in 2008 (Table 5).

Indigo Buntings had overall naïve occupancies of $\Psi = 0.44$ in 1994 and $\Psi = 0.16$ in 2008. In both years, canopy cover was useful in modeling INBU occupancy (1994, $\Sigma w_i = 0.72$; 2008, $\Sigma w_i = 0.63$) (Table 3), but there was only weak evidence for a negative effect in 1994 and no evidence for an effect in 2008 (Table 4). In 2008, the number of small saplings had a positive effect on INBU occupancy ($\Sigma w_i = 0.34$; $\beta = 0.258 \pm 0.251$). Occupancy was higher overall in 1994, when control plots had lower occupancy than full treatment plots (Table 5). In 2008, occupancy was similar across treatments. Adding covariates to models for detectability did not improve the intercept model, so occupancy was modeled separately. Detection rates of INBU were the same across years (Table 5).

3.3 Habitat characteristics

PCA showed the first three principal components explained ~63% of the variance in 1994 and ~58% in 2008. In 1994, several variables had either high or negative loadings on the first component (Table 6), but PC1 was not successful in contrasting plots according to treatment (Figure 2). The second component, however, was successful in contrasting control with treated

plots in 1994, when canopy height, shrub cover, high vegetation profile, large saplings, and large trees had high positive loadings on PC2. In 2008, none of the principal components were successful in contrasting treatments, perhaps because of within treatment variation (Figure 2). See Table 6 for a complete list of numerical loadings on the first three principal components for each year.

Results of the MANOVAs showed a significant effect of treatment for 1994 ($F_{2,29} = 12.44, P < 0.001$), but not 2008 ($F_{2,29} = 3.07, P = 0.06$). Discriminant analysis showed that different variables were more important in discriminating between treatments for each year. In 1994, large saplings contributed most to discrimination among treatments ($F_{2,29} = 26.33, P < 0.0001$). Shrub cover ($F_{2,28} = 36.44, P < 0.001$), grass cover ($F_{2,27} = 26.33, P < 0.001$), forb cover ($F_{2,26} = 8.55, P < 0.05$), small saplings ($F_{2,25} = 7.00, P < 0.01$), and low vegetation profile ($F_{2,24} = 4.75, P < 0.05$), were the next most important variables in discriminating between treatments in 1994. There were fewer variables in 2008 that were important in discriminating between treatments; these included large saplings ($F_{2,29} = 4.65, P < 0.05$) and small saplings ($F_{2,28} = 3.19, P = 0.06$).

Within year univariate comparisons of habitat variables across treatments showed that there were more differences in habitat variables between treatments in 1994 than 2008 (Table 7). In 1994, shrub cover was lower and forb cover was higher in understory plots than in control or full plots; full treatment plots had more log cover and small saplings, and fewer large trees than other treatments; and control plots had denser high vegetation profiles than treated plots. Full plots had a denser low vegetation profile than control plots, and understory plots had fewer small trees than control plots. Finally, in 1994, control plots had more large saplings than understory plots, which had more than full plots. In 2008, understory plots had denser low vegetation

profiles, more small saplings, and fewer small trees than control plots. Full treatment plots had more large saplings than control plots in 2008.

4. Discussion

Silvicultural treatments did not influence avian community parameters, as evidenced by the similarity in species richness and composition between treatments within and across the years 1994 and 2008. Likewise, the probability of occupancy for Eastern Wood-Pewees (EAWP), Ovenbirds (OVEN), and Hooded Warblers (HOWA) was similar between treatments one year after harvest. However, Indigo Buntings (INBU) increased in occupancy in response to full harvest in 1994. In 2008, estimates suggested that occupancy was similar between treatments for all species. Looking across years, probability of occupancy decreased for EAWP and INBU, and increased for HOWA within each treatment. OVEN occupancy remained the same across the years.

The similarity in species richness and composition between treatments and between years is not completely unexpected. Although previous studies have found higher species diversity in recently treated plots (<5 years) (Annand and Thompson, 1997; Baker and Lacki, 1997; Campbell *et al.*, 2007) and lower diversity in older treated plots (>10 years) (Jobes *et al.*, 2004; Campbell *et al.*, 2007; McDermott and Wood, 2009), these differences are usually negligible (Sallabanks and Arnett, 2005). In a study on the short-term effects of group-selection harvesting on bird communities in a hardwood forest, Tozer *et al.* (2010) found no difference in percent similarity between pre- and post-harvest breeding bird communities in group-selection and reference stands. Uneven-aged management, such as group and single-tree selection harvest, retains much of the vegetation structure of a mature forest, while creating small canopy gaps.

With less intensive management, it is more common to find reports of the relative abundance of populations responding to silvicultural treatments, rather than communities experiencing species turnover (Sallabanks and Arnett, 2005). Perhaps these gaps, and the subsequent shrub and sapling layers that develop, help support early-successional species that are already present in lower numbers in the mature forest community.

The results from the population analysis for Indigo Buntings support this conclusion. In the year after treatment, these early-successional/open-habitat nesters were present in control plots, but they showed higher occupancy in full treatment plots. However, given 15 years, not only was INBU occupancy lower overall, but the difference in occupancy between control and full treatments disappeared. These results are similar to other research that has shown a temporary positive response of early-successional species to harvesting (Probst *et al.*, 1992; Robinson and Robinson, 1999; Heltzel and Leberg, 2006; McDermott and Wood, 2009). The change in occupancy over time could be explained by the increase in canopy cover and decrease in the number of small saplings in 2008 relative to 1994. Previous studies show INBU prefer to nest in harvested areas that tend to have less canopy closure and more low vegetative cover (Annand and Thompson, 1997; Alterman *et al.*, 2005; Heltzel and Leberg, 2006).

Ground-nesting Ovenbirds did not decline in harvested plots in 1994 as predicted, or as reported by Rodewald and Smith (1998). This result is surprising, given the many studies that have documented negative responses of OVEN to selection harvests (for recent examples, see Annand and Thompson, 1997; Jobes *et al.*, 2004; Holmes and Pitt, 2007). One explanation could be that differences in canopy cover among treatments were not great enough to influence OVEN. My results indicate that OVEN occupancy increased with greater canopy cover, however canopy cover did not differ between treatments in either year. Another possibility is that no decline was

detected because Ovenbirds sometimes exhibit delayed responses (two years) to selection cuts (Tozer *et al.*, 2010). Ovenbirds, like some other mature forest species, might be more resistant to disturbances like selective logging than previously thought (Costello *et al.*, 2000; Campbell *et al.*, 2007). Evidence for this last point might lie in the result that Ovenbird occupancy was still high and similar among all treatments fifteen years after treatment.

Canopy-nesting Eastern Wood-Pewees did not respond to harvest in 1994, which contradicts Rodewald and Smith's (1998) finding that EAWP abundance increased with intensity of management. One explanation for this discrepancy could be that detection probability was lower in control plots relative to harvested plots in 1994. Perhaps including detectability in population estimates (which was not done in the earlier study) equalized occupancy between treatments. In 2008, EAWP occupancy estimates were still similar among treatments, and lower overall than 1994. Research shows mixed responses of EAWP to uneven-aged management. Some studies document no difference between reference and harvest stands (Annand and Thompson, 1997; Jobes *et al.*, 2004). Others have found that EAWP initially increase in abundance after harvest, but eventually (after about seven years) their numbers drop (Robinson and Robinson, 1999; Campbell *et al.*, 2007). The results for EAWP in this study suggest they were resilient to habitat changes after harvest, but they declined in later years (Crawford *et al.*, 1981). Since the effects of habitat covariates were uncertain, it is not possible to determine whether this decline was in response to canopy cover or small trees.

Shrub-nesting Hooded Warblers also did not respond to silvicultural treatments in 1994. Some studies have shown that HOWA populations are not affected by harvesting (Heltzel and Leberg, 2006), however others have shown they tend to increase with treatments that create dense understory vegetation (Annand and Thompson, 1997; Baker and Lacki, 1997; Robinson

and Robinson, 1999). This study found less of an influence of post-management understory development (i.e., small saplings and shrubs) on HOWA occupancy than anticipated. In 2008, HOWA occupancy rates were higher overall, but this could not be explained by the habitat variables used to model HOWA occupancy since there were fewer small saplings and higher percent canopy closure. Perhaps other habitat covariates (e.g., percent shrub cover) would be more useful for modeling HOWA occupancy in the future.

Vegetation analyses indicated that timber harvests initially affected habitat variables such as shrub cover, saplings, and trees; however, these patterns did not persist through time. In 2008, there was higher percent canopy cover, yet there were fewer trees in larger size classes. Perhaps the explanation can be linked to oak decline in Ozark forests (Heitzman, 2003; Heitzman *et al.*, 2007). In the early 2000s, advanced stand age, prolonged droughts, and the outbreak of an endemic beetle, the red oak borer (*Enaphalodes rufulus* Haldeman), contributed to the degradation and death of many oak trees, particularly northern red oaks (*Quercus rubra*) (Starkey *et al.*, 2004). Haavik and Stephen (2010) showed that borer-infested trees that died during this outbreak were suppressed individuals that competed poorly for resources. Vegetation in plots might have responded differently to the oak decline event based on their management history. Perhaps trees in previously thinned plots experienced less competition, and thus fared better during the oak decline event compared to control plots, which were likely more densely stocked. Higher oak mortality in control plots would have a tendency to create more gaps, thus opening the canopy, just as selective cutting did years earlier in the treated plots. In this scenario, not only would oak decline equalize habitat characteristics such as canopy cover among treatments, but it would also allow surviving trees to develop fuller canopies.

Two important limitations of this study warrant consideration. First, the study design includes survey points that potentially lack independence. The 32 survey points were grouped across six sites, with four to eight points at each site. Thus, surveys from the points at one site might be more similar to each other than to points from other sites. In addition, some birds are capable of moving over areas larger than the treatment plots, which could have led to double counting of individuals at neighboring point counts. I attempted to minimize this possibility by conducting surveys at neighboring points in as quick of succession as possible, while recording suspected duplicate detections and excluding these from analyses. A second limitation involves the lack of data for sequential years. Tozer *et al.* (2010) showed some birds responded in the second, but not first, year after harvest. Data illustrating a time-series (including year prior to harvest) would allow stronger inference for what environmental factors influence birds.

This study examined community and population parameters obtained from point counts; however, for a more comprehensive understanding of the effects of uneven-aged management on bird populations, research should also track nest success and fledgling survival. Recent studies in Ohio reveal that natal home ranges are much larger than breeding territories, and that fledglings of mature forest species often utilize habitat different from that of their natal nests (e.g., OVEN fledglings utilize regenerating clearcuts) (Vitz and Rodewald, 2006, 2010). Thus, management decisions based solely on the needs of breeding adults might neglect habitat requirements of fledglings.

Conclusion

The results of this study support others that demonstrate the resiliency of bird communities and populations, particularly mature forest species, to uneven-aged management. Selection harvests mimic disturbances like tree-falls, which cause small scale habitat changes

common in natural disturbance regimes (Thompson *et al.*, 1995; Seymour *et al.*, 2002). These results also support previous studies showing that the immediate effects of silvicultural treatments diminish over time (Robinson and Robinson, 1999; Campbell *et al.*, 2007), with early successional species benefiting initially, but not after 15 years of regeneration within gaps. Thus, managers seeking harvest techniques that minimize effects on breeding birds could use uneven-aged selection methods at intervals allowing sufficient time for recovery of vegetation and bird populations.

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Tables

Table 1. Structural habitat variables measured in vegetation plots.

Habitat Variable	Abbreviation
<u>Measured within 5 m radius</u>	
Mean canopy height	CanHt
Mean percent canopy cover	CanCov
Percent grass cover (below 0.5 m)	P-Grass
Percent shrub cover (below 0.5 m)	P-Shrub
Percent forb (below 0.5 m)	P-Forb
Percent fern cover (below 0.5 m)	P-Fern
Percent log cover (below 0.5 m)	P-Log
Percent leaf litter cover (below 0.5 m)	P-Leaf
Number of small saplings 0-2.5 cm	Sap1
Number of large saplings 2.5-8 cm	Sap2
<u>Measured within 11.3 m radius</u>	
Low vegetation profile (number of contacts 0-1 m)	L-Hits
High vegetation profile (number of contacts 1-2 m)	H-Hits
Number of small trees 8-23 cm dbh	Tree3
Number of medium trees 23-38 cm dbh	Tree4
Number of large trees >38 cm dbh	Tree5

Table 2. Avian community parameters^a, standard errors (SE), and 95% confidence intervals (CI) estimated by comparing bird species detected in 1994 and 2008 on plots in the Ozark National Forest, Arkansas. Treatment types include control (C, no cut), understory (U, understory cut only), full (F, understory and overstory cut); n=8 for all treatments.

Year	Comparison	Parameter	Estimate	SE	95% CI		
					Lower	Upper	
1994	<i>Richness</i>	N_C	26.97	4.89	23.00	40.04	
		N_U	31.16	5.29	25.00	44.14	
		N_F	26.33	2.18	25.00	33.36	
	<i>Dynamics</i>	C-U	$1 - \phi$	0.07	0.08	0.00	0.27
			$1 - \gamma$	0.13	0.11	0.00	0.35
			alt λ	1.09	0.12	0.85	1.37
			B	6.00	5.94	0.00	19.72
		C-F	$1 - \phi$	0.34	0.14	0.06	0.47
			$1 - \gamma$	0.15	0.14	0.00	0.30
			alt λ	1.09	0.10	0.92	1.30
			B	8.45	4.89	0.00	21.69
		U-F	$1 - \phi$	0.21	0.13	0.00	0.45
			$1 - \gamma$	0.15	0.10	0.00	0.38
			alt λ	1.00	0.10	0.83	1.24
			B	1.81	3.56	0.00	12.28
		2008	<i>Richness</i>	N_C	23.45	3.66	21.00
N_U	26.55			3.76	23.00	36.16	
N_F	30.76			4.93	26.00	43.19	
<i>Dynamics</i>	C-U		$1 - \phi$	0.01	0.06	0.00	0.19
			$1 - \gamma$	0.15	0.09	0.00	0.31
			alt λ	1.10	0.11	0.87	1.32
			B	3.29	3.94	0.00	14.31
	C-F		$1 - \phi$	0.00	0.06	0.00	0.23
			$1 - \gamma$	0.17	0.11	0.00	0.35
			alt λ	1.24	0.13	1.05	1.56
			B	7.30	5.79	0.00	20.38
	U-F		$1 - \phi$	0.00	0.03	0.00	0.13
			$1 - \gamma$	0.06	0.08	0.00	0.26
			alt λ	1.13	0.12	0.92	1.38
			B	4.21	5.40	0.00	18.06

^a N - estimated number of species present
 $1 - \phi$ - estimated extinction probability
 $1 - \gamma$ - estimated species turnover
alt λ - estimated rate of change of species richness
 B - estimated local colonizing species

Table 3. Model selection results for occupancy (Ψ) and detection (p) probability of bird species representing four nesting guilds surveyed in 1994 and 2008 in the Ozark National Forest, Arkansas. Models include the intercept only (.) and combinations of covariates (described in Table 1).

Species	Year	Model	ΔAIC_c^a	K	$-2L$	w_i	
Eastern Wood-Pewee (canopy-nester)	1994	$\Psi(\cdot), p(\text{Tree3})$	0.00 ^b	3	169.3	0.32	
		$\Psi(\cdot), p(\cdot)$	0.06	2	173.43	0.31	
		$\Psi(\text{CanCov}), p(\text{Tree3})$	1.54	4	167.93	0.15	
		$\Psi(\text{CanCov}), p(\cdot)$	2.06	3	173.04	0.11	
		$\Psi(\text{CanCov}+\text{Tree3}), p(\cdot)$	3.60	4	171.67	0.05	
		$\Psi(\text{CanCov}+\text{Tree3}), p(\text{Tree3})$	3.78	5	167.69	0.05	
		2008	$\Psi(\text{Tree3}), p(\cdot)$	0.00	3	76.59	0.33
	$\Psi(\text{Tree3}), p(\text{Tree3})$		0.65	4	74.62	0.24	
	$\Psi(\cdot), p(\cdot)$		1.41	2	80.45	0.16	
	$\Psi(\cdot), p(\text{Tree3})$		2.23	3	78.82	0.11	
	$\Psi(\text{CanCov}+\text{Tree3}), p(\cdot)$		2.52	4	76.49	0.09	
	$\Psi(\text{CanCov}+\text{Tree3}), p(\text{Tree3})$		3.36	5	74.50	0.06	
	Ovenbird (ground-nester)		1994	$\Psi(\text{CanCov}), p(\cdot)$	0.00 ^b	3	148.64
		$\Psi(\text{CanCov}), p(\text{P-Shrub})$		0.33	4	145.96	0.20
$\Psi(\cdot), p(\cdot)$		0.39		2	152.02	0.19	
$\Psi(\text{CanCov}+\text{P-Shrub}), p(\cdot)$		0.76		4	146.48	0.16	
$\Psi(\text{P-Shrub}), p(\cdot)$		1.22		3	150.13	0.13	
$\Psi(\text{CanCov}+\text{P-Shrub}), p(\text{P-Shrub})$		2.02		5	144.71	0.09	
2008		$\Psi(\text{CanCov}), p(\cdot)$		0.00	3	172.34	0.31
		$\Psi(\cdot), p(\cdot)$	0.88	2	175.40	0.20	
		$\Psi(\text{CanCov}), p(\text{P-Shrub})$	1.44	4	171.53	0.15	
		$\Psi(\text{CanCov}+\text{P-Shrub}), p(\cdot)$	2.11	4	172.20	0.11	
		$\Psi(\cdot), p(\text{P-Shrub})$	2.58	3	174.92	0.09	
		$\Psi(\text{P-Shrub}), p(\cdot)$	2.63	3	174.97	0.08	
		$\Psi(\text{CanCov}+\text{P-Shrub}), p(\text{P-Shrub})$	3.60	5	171.38	0.05	

Table 3. continued

Species	Year	Model	ΔAIC_c^a	K	$-2L$	w_i
Hooded Warbler (understory-nester)	1994	$\Psi(\cdot), p(\cdot)$	0.00	2	50.77	0.45
		$\Psi(\text{CanCov}), p(\cdot)$	2.22	3	50.54	0.15
		$\Psi(\cdot), p(\text{Sap1})$	2.40	3	50.72	0.14
		$\Psi(\text{Sap1}), p(\cdot)$	2.44	3	50.76	0.13
		$\Psi(\text{CanCov}), p(\text{Sap1})$	4.82	4	50.52	0.04
		$\Psi(\text{CanCov+Sap1}), p(\cdot)$	4.83	4	50.53	0.04
		$\Psi(\text{Sap1}), p(\text{Sap1})$	4.99	4	50.69	0.04
		$\Psi(\text{CanCov+Sap1}), p(\text{Sap1})$	7.63	5	50.50	0.01
	2008	$\Psi(\text{Sap1}), p(\cdot)$	0.00 ^b	3	161.11	0.42
		$\Psi(\text{Sap1}), p(\text{Sap1})$	1.73	4	160.2	0.17
		$\Psi(\text{CanCov+Sap1}), p(\cdot)$	2.20	4	160.97	0.14
		$\Psi(\cdot), p(\cdot)$	2.97	2	169.65	0.09
		$\Psi(\cdot), p(\text{Sap1})$	3.61	3	167.06	0.07
		$\Psi(\text{CanCov+Sap1}), p(\text{Sap1})$	4.03	5	160.09	0.06
		$\Psi(\text{CanCov}), p(\cdot)$	5.10	3	169.51	0.03
$\Psi(\text{CanCov}), p(\text{Sap1})$		5.89	4	167.05	0.02	
Indigo Bunting (open-nester)	1994	$\Psi(\text{CanCov}), p(\cdot)$	0.00	3	112.13	0.54
		$\Psi(\text{CanCov+Sap1}), p(\cdot)$	2.16	4	111.67	0.18
		$\Psi(\text{Sap1}), p(\cdot)$	2.66	3	114.79	0.14
		$\Psi(\cdot), p(\cdot)$	2.82	2	117.40	0.13
	2008	$\Psi(\text{CanCov}), p(\cdot)$	0.00	3	44.40	0.39
		$\Psi(\cdot), p(\cdot)$	0.75	2	47.60	0.27
		$\Psi(\text{CanCov+Sap1}), p(\cdot)$	0.99	4	42.77	0.24
		$\Psi(\text{Sap1}), p(\cdot)$	2.68	3	47.08	0.10

^a Minimum values of AIC_c for each species and year, 1994 and 2008 respectively, were: Eastern Wood-Pewee, 99.63 and 83.45; Hooded Warbler, 128.92 and 178.70; Ovenbird, 55.18 and 104.31; and Indigo Bunting, 118.99 and 51.26.

^b The ΔAIC_c values in these model sets represent $\Delta QAIC_c$ values corrected for overdispersion.

Table 4. Model-averaged estimates (β), standard errors (SE), and 95% confidence intervals (CI) of untransformed regression coefficients for covariates affecting occupancy (Ψ) and detection (p) probabilities of bird species representing four nesting guilds surveyed in 1994 and 2008 in the Ozark National Forest, Arkansas. Descriptions of covariates are given in Table 1.

Species	Year	Covariate	β	SE	95% C.I.		
					Lower	Upper	
Eastern Wood-Pewee	1994	Ψ intercept	2.294	1.207	-0.619	5.207	
		CanCov	0.212	0.342	-0.021	0.444	
		p intercept	0.125	0.289	-0.043	0.292	
		Tree3	-0.244	0.189	-0.315	-0.173	
	2008	Ψ intercept	0.319	1.091	-2.057	2.695	
		Tree3	1.987	1.208	-0.920	4.894	
		p intercept	-1.212	0.499	-1.709	-0.715	
		Tree3	-0.058	0.308	-0.245	0.129	
Ovenbird	1994	Ψ intercept	2.586	2.043	-6.193	11.365	
		CanCov	0.851	0.603	0.096	1.606	
		P-Shrub	0.494	0.626	-0.317	1.304	
		p intercept	-0.767	0.528	-1.352	-0.182	
		P-Shrub	0.094	0.095	0.075	0.112	
	2008	Ψ intercept	4.480	2.200	-5.152	14.112	
		CanCov	-2.520	1.983	-10.332	5.291	
		p intercept	0.334	0.196	0.257	0.410	
Hooded Warbler	1994	Ψ intercept	-1.114	0.742	-1.454	1.454	
		p intercept	-1.258	0.736	-2.700	0.184	
	2008	Ψ intercept	2.439	1.263	-0.800	5.678	
		Sap1	1.736	1.115	-0.782	4.255	
		p intercept	0.313	0.289	0.144	0.482	
		Sap1	0.091	0.122	0.061	0.121	
	Indigo Bunting	1994	Ψ intercept	0.635	0.803	-0.938	2.209
			CanCov	-2.253	1.414	-5.023	0.518
p intercept			-0.547	0.307	-1.149	0.056	
2008		Ψ intercept	-0.849	1.204	-6.666	4.967	
		CanCov	-0.735	0.545	-2.872	1.403	
		Sap1	0.258	0.251	0.174	0.343	
		p intercept	-1.748	0.886	-6.801	3.304	

Table 5. Estimated probabilities of occupancy (Ψ) and detectability (p), standard errors (SE), and 95% confidence intervals (CI) of four bird species representing different nesting guilds in 1994 and 2008 on managed plots in the Ozark National Forest, Arkansas.

Species	Year	Trt ^a	Ψ	SE	95% CI		p	SE	95% CI	
					Lower	Upper			Lower	Upper
Eastern Wood-Pewee	1994	C	0.912	0.103	0.908	0.915	0.504	0.001	0.454	0.553
		U	0.909	0.100	0.908	0.910	0.571	0.018	0.541	0.600
		F	0.900	0.091	0.891	0.909	0.546	0.008	0.509	0.583
	2008	C	0.743	0.212	0.494	0.896	0.226	0.061	0.142	0.339
		U	0.265	0.135	0.049	0.719	0.236	0.096	0.176	0.310
		F	0.543	0.039	0.488	0.596	0.230	0.072	0.156	0.326
Ovenbird	1994	C	0.953	0.008	0.919	0.973	0.328	0.004	0.208	0.460
		U	0.886	0.035	0.757	0.951	0.294	0.003	0.206	0.456
		F	0.906	0.067	0.882	0.925	0.319	0.008	0.200	0.443
	2008	C	0.991	0.022	0.982	0.995	0.584	0.003	0.565	0.603
		U	0.953	0.049	0.171	0.999	0.587	0.004	0.568	0.606
		F	0.996	0.013	0.909	1.000	0.576	0.003	0.558	0.593
Hooded Warbler	1994	C	0.247 ^b	0.138	0.189	0.811	0.578 ^b	0.054	0.536	0.618
		U								
		F								
	2008	C	0.850	0.077	0.671	0.940	0.641	0.017	0.608	0.675
		U	0.971	0.040	0.876	0.994	0.670	0.019	0.633	0.708
		F	0.941	0.057	0.908	0.962	0.658	0.016	0.626	0.690
Indigo Bunting	1994	C	0.551	0.031	0.418	0.676	0.367 ^b	0.0710	0.241	0.514
		U	0.630	0.085	0.599	0.659				
		F	0.833	0.171	0.679	0.943				
	2008	C	0.291	0.151	0.248	0.338	0.161 ^b	0.113	0.036	0.495
		U	0.246	0.091	0.081	0.547				
		F	0.378	0.063	0.204	0.591				

^aTreatments (Trt) included control (C, no cut), understory (U, understory cut only), and full (F, understory and overstory cut).

^bHabitat covariates were not useful in modeling these parameters, so estimates were constant across treatments.

Table 6. Habitat variables and their respective loadings on the first three principal components for comparisons between treatments within years. Descriptions of variables are given in Table 1.

Habitat variable	1994			2008		
	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3
CanHt	0.55	0.58	-0.13	0.74	-0.18	-0.08
CanCov	-0.09	0.39	-0.12	0.39	-0.02	-0.71
P-Grass	-0.20	-0.18	-0.39	-0.15	-0.29	0.30
P-Shrub	0.19	0.53	0.72	0.72	-0.44	-0.23
P-Forb	0.76	-0.06	-0.46	0.27	-0.11	0.68
P-Fern	0.54	0.12	0.19	0.51	0.32	0.30
P-Log	-0.89	-0.18	-0.05	-0.72	0.35	-0.41
P-Leaf	0.29	-0.66	0.32	-0.35	0.40	0.38
L-Hits	0.75	-0.25	0.17	0.67	-0.09	0.33
H-Hits	-0.09	0.76	0.38	0.45	0.69	-0.06
Sap1	0.59	-0.10	0.64	0.57	0.10	-0.19
Sap2	-0.26	0.88	-0.12	0.17	0.88	-0.07
Tree3	-0.65	0.27	0.28	-0.77	-0.23	0.02
Tree4	-0.66	-0.10	0.22	-0.66	-0.39	-0.12
Tree5	0.42	0.62	-0.51	0.73	-0.30	-0.12
Proportion of variance explained	0.28	0.21	0.14	0.32	0.15	0.11
Total proportion of variance explained		0.63			0.58	

Table 7. Mean, standard error (SE), ANOVA results, and Tukey HSD relationships between treatments, for habitat variables measured in 1994 and 2008 in the Ozark National Forest, Arkansas. Treatments included control (C, no cut, n=16), understory (U, understory cut only, n=8), and full (F, both understory and overstory cut, n=8). Treatment abbreviations not connected by the same letter are significantly different. Descriptions of variables are given in Table 1.

Habitat Variable	Year	Control Mean (SE)	Understory Mean (SE)	Full Mean (SE)	$F_{2,29}$	P	Tukey HSD
CanHt	1994	26.89 (0.98)	26.66 (0.40)	23.44 (0.94)	3.08	0.06	
	2008	20.27 (0.71)	20.47 (0.61)	19.13 (0.75)	0.73	0.49	
CanCov	1994	82.98 (1.40)	82.06 (2.76)	79.05 (2.14)	1.05	0.36	
	2008	95.60 (0.68)	97.17 (0.32)	94.84 (0.72)	2.29	0.12	
P-Grass	1994	2.68 (0.56)	2.80 (1.74)	3.56 (1.33)	0.43	0.65	
	2008	5.14 (0.86)	3.13 (0.44)	4.75 (1.08)	0.76	0.48	
P-Shrub	1994	20.25 (1.53)	6.45 (1.01)	16.61 (2.58)	14.86	<0.001	C _a U _b F _a
	2008	42.57 (3.79)	46.34 (4.50)	32.84 (3.13)	2.27	0.12	
P-Forb	1994	30.30 (1.52)	43.35 (3.18)	32.02 (4.54)	6.06	<0.01	C _a U _b F _a
	2008	8.76 (2.16)	4.72 (1.40)	9.31 (1.23)	1.20	0.32	
P-Fern	1994	1.01 (0.50)	2.35 (2.34)	1.90 (0.98)	0.13	0.88	
	2008	1.80 (0.66)	1.13 (0.95)	4.53 (2.09)	1.50	0.24	
P-Log	1994	2.12 (0.26)	3.20 (0.49)	5.26 (0.64)	13.41	<0.001	C _a U _a F _b
	2008	8.59 (0.82)	7.78 (1.51)	11.06 (1.77)	1.58	0.22	
P-Leaf	1994	43.13 (2.36)	42.35 (4.28)	41.07 (6.14)	0.07	0.93	
	2008	32.04 (4.37)	34.44 (4.84)	35.97 (3.98)	0.19	0.83	
L-Hits	1994	72.69 (6.13)	86.13 (8.95)	120.75 (19.49)	4.65	<0.05	C _a U _{ab} F _b
	2008	22.77 (2.43)	21.53 (1.81)	22.75 (1.83)	0.05	0.96	
H-Hits	1994	19.44 (2.28)	4.00 (1.34)	5.38 (2.40)	15.18	<0.001	C _a U _b F _b C _a U _b
	2008	10.16 (1.44)	16.3 (2.06)	15.22 (1.03)	4.68	<0.05	F _{ab}
Sap1	1994	182.31 (12.47)	152.13 (12.83)	270.34 (32.11)	8.16	<0.01	C _a U _a F _b C _a U _b
	2008	101.32 (10.94)	150.96 (18.14)	129.97 (14.03)	3.73	<0.05	F _{ab}
Sap2	1994	25.50 (2.87)	2.34 (0.78)	0.00 (0.00)	85.78	<0.001	C _a U _b F _c C _a U _{ab}
	2008	7.81 (1.27)	11.00 (1.57)	14.97 (2.00)	5.27	<0.05	F _b C _a U _b
Tree3	1994	61.06 (4.42)	38.75 (4.36)	47.13 (8.18)	4.33	<0.05	F _{ab} C _a U _b
	2008	8.66 (1.05)	4.94 (0.24)	7.06 (0.92)	3.72	<0.05	F _{ab}
Tree4	1994	22.69 (2.07)	21.25 (3.05)	20.63 (2.64)	0.19	0.82	

	2008	3.50 (0.35)	2.66 (0.46)	3.34 (0.56)	0.94	0.40	
Tree5	1994	9.56 (1.33)	9.88 (1.84)	2.13 (0.88)	6.63	<0.01	C _a U _a F _b
	2008	2.67 (0.32)	2.88 (0.27)	1.75 (0.23)	3.21	0.06	

Figures

Figure 1. Location of study sites in the Ozark National Forest near Pelsor, Arkansas. State highways labeled by pentagons. Other symbols represent avian point count sites from three treatments: control (no cut, n=16), understory (understory cut only, n=8), and full (understory and overstory cut, n=8).

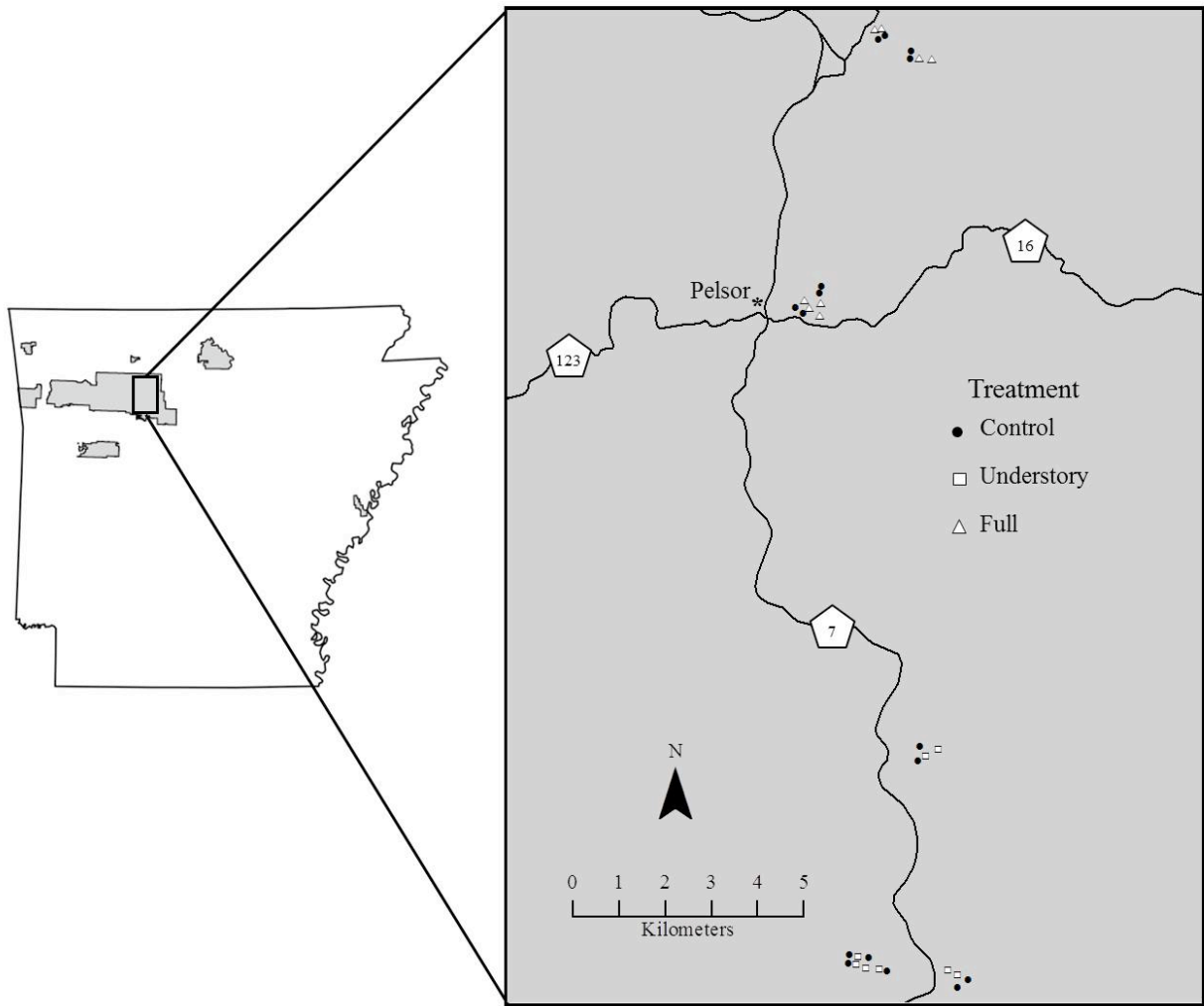
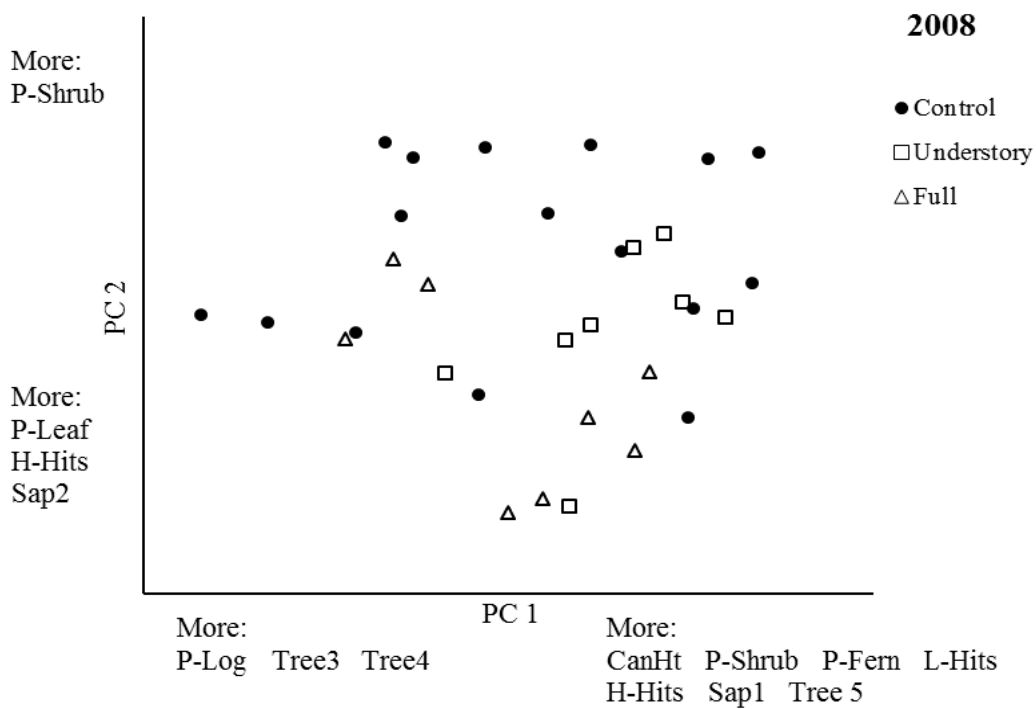
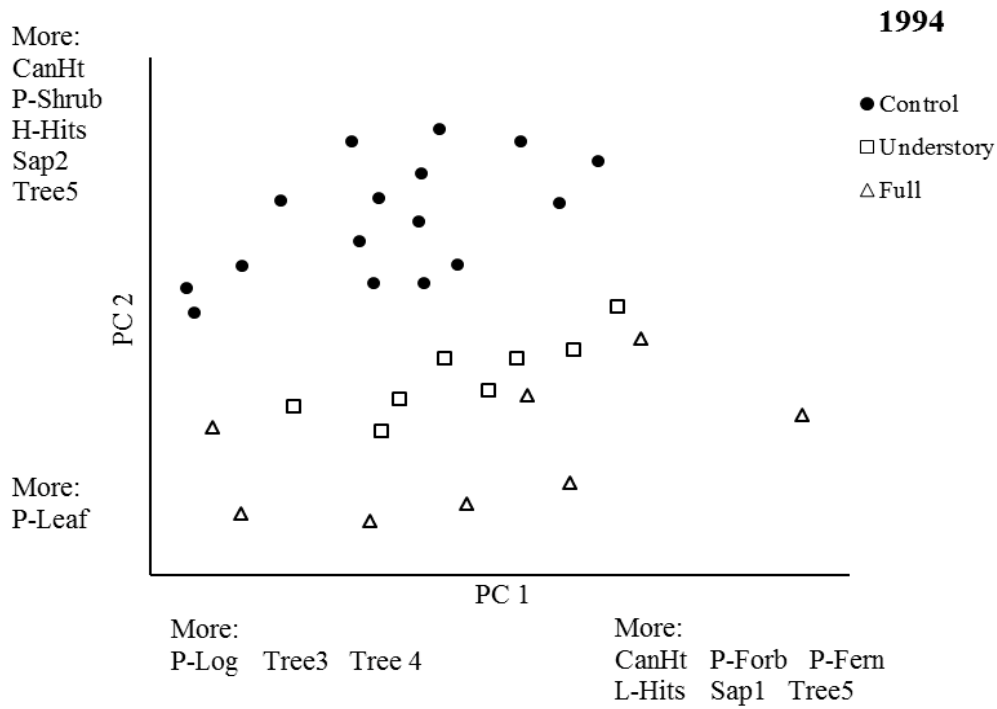


Figure 2. Plots of the first two principle components based on 15 habitat variables measured in 1994 and 2008 on control (no cut, n=16), understory (understory cut only, n=8), and full (understory and overstory cut, n=8) treatment plots in the Ozark National Forest, Arkansas. Descriptions of variables are given in Table 1.



Appendix 1. Bird species detected within 50 m radius point counts conducted in 1994 and 2008 on plots in the Ozark National Forest, Arkansas.

Both Years	1994 Only
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)	Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)
Red-bellied Woodpecker (<i>Melanerpes carolinus</i>)	Downy Woodpecker (<i>Picoides pubescens</i>)
Hairy Woodpecker (<i>Picoides villosus</i>)	Eastern Phoebe (<i>Sayornis phoebe</i>)
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	Great-crested Flycatcher (<i>Myiarchus crinitus</i>)
Eastern Wood-Pewee (<i>Contopus virens</i>)	American Crow (<i>Corvus brachyrhynchos</i>)
Acadian Flycatcher (<i>Empidonax virescens</i>)	Eastern Towhee (<i>Pipilo erythrophthalmus</i>)
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	Chipping Sparrow (<i>Spizella passerina</i>)
Red-eyed Vireo (<i>Vireo olivaceus</i>)	Field Sparrow (<i>Spizella pusilla</i>)
Blue Jay (<i>Cyanocitta cristata</i>)	Blue Grosbeak (<i>Guiraca caerulea</i>)
Carolina Chickadee (<i>Poecile carolinensis</i>)	
Tufted Titmouse (<i>Baeolophus bicolor</i>)	2008 Only
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	Broad-winged Hawk (<i>Buteo platypterus</i>)
Carolina Wren (<i>Thryothorus ludovicianus</i>)	Red-tailed Hawk (<i>Buteo jamaicensis</i>)
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i>)	Barred Owl (<i>Strix varia</i>)
Wood Thrush (<i>Hylocichla mustelina</i>)	White-eyed Vireo (<i>Vireo griseus</i>)
Black-throated Green Warbler (<i>Setophaga virens</i>)	Cedar Waxwing (<i>Bombycilla cedrorum</i>)
Cerulean Warbler (<i>Setophaga cerulea</i>)	Nashville Warbler (<i>Vermivora ruficapilla</i>)
Black-and-White Warbler (<i>Mniotilta varia</i>)	American Redstart (<i>Setophaga ruticilla</i>)
Worm-eating Warbler (<i>Helmitheros vermivorus</i>)	Northern Cardinal (<i>Cardinalis cardinalis</i>)
Ovenbird (<i>Seiurus aurocapillus</i>)	American Goldfinch (<i>Carduelis tristis</i>)
Kentucky Warbler (<i>Oporornis formosus</i>)	
Hooded Warbler (<i>Wilsonia citrina</i>)	
Summer Tanager (<i>Piranga rubra</i>)	
Scarlet Tanager (<i>Piranga olivacea</i>)	
Indigo Bunting (<i>Passerina cyanea</i>)	
Brown-headed Cowbird (<i>Molothrus ater</i>)	

Appendix 2. Mean number of detections per survey and standard error (SE) of breeding birds in 2008 on control and thinned plots in the Ozark National Forest, Arkansas. Treatments included control (no cut, n=64 surveys), understory (understory cut only, n=32 surveys), and full (both understory and overstory cut, n=32 surveys).

Species	Control Mean (SE)	Understory Mean (SE)	Full Mean (SE)
Red-bellied Woodpecker (<i>Melanerpes carolinus</i>)	0.05 (0.03)	0.00 (0.00)	0.03 (0.03)
Hairy Woodpecker (<i>Picoides villosus</i>)	0.05 (0.03)	0.03 (0.03)	0.06 (0.04)
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	0.03 (0.02)	0.09 (0.05)	0.13 (0.13)
Eastern Wood-Pewee (<i>Contopus virens</i>)	0.14 (0.05)	0.03 (0.01)	0.13 (0.06)
Acadian Flycatcher (<i>Empidonax vireescens</i>)	0.31 (0.07)	0.25 (0.10)	0.13 (0.06)
White-eyed Vireo (<i>Vireo griseus</i>)	0.00 (0.00)	0.00 (0.00)	0.06 (0.06)
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	0.08 (0.03)	0.09 (0.05)	0.09 (0.04)
Red-eyed Vireo (<i>Vireo olivaceus</i>)	1.86 (0.13)	1.34 (0.14)	1.66 (0.16)
Blue Jay (<i>Cyanocitta cristata</i>)	0.02 (0.02)	0.00 (0.00)	0.03 (0.03)
Carolina Chickadee (<i>Poecile carolinensis</i>)	0.05 (0.03)	0.13 (0.09)	0.28 (0.16)
Tufted Titmouse (<i>Baeolophus bicolor</i>)	0.02 (0.02)	0.03 (0.03)	0.03 (0.03)
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	0.03 (0.02)	0.09 (0.05)	0.09 (0.04)
Carolina Wren (<i>Thryothorus ludovicianus</i>)	0.14 (0.05)	0.03 (0.03)	0.13 (0.06)
Blue-gray Gnatcatcher (<i>Polioptila caerulea</i>)	0.20 (0.05)	0.22 (0.07)	0.34 (0.09)
Wood Thrush (<i>Hylocichla mustelina</i>)	0.14 (0.04)	0.22 (0.10)	0.25 (0.10)
Black-throated Green Warbler (<i>Setophaga virens</i>)	0.13 (0.05)	0.25 (0.10)	0.03 (0.03)
Cerulean Warbler (<i>Setophaga cerulea</i>)	0.02 (0.02)	0.00 (0.00)	0.03 (0.03)
Black-and-White Warbler (<i>Mniotilta varia</i>)	0.22 (0.06)	0.44 (0.12)	0.59 (0.13)
Worm-eating Warbler (<i>Helmitheros vermivorus</i>)	0.06 (0.04)	0.22 (0.00)	0.19 (0.07)
Ovenbird (<i>Seiurus aurocapillus</i>)	0.80 (0.08)	0.41 (0.10)	0.75 (0.08)
Kentucky Warbler (<i>Oporornis formosus</i>)	0.09 (0.04)	0.06 (0.04)	0.06 (0.04)
Hooded Warbler (<i>Wilsonia citrina</i>)	0.63 (0.10)	1.09 (0.19)	0.56 (0.15)
Scarlet Tanager (<i>Piranga olivacea</i>)	0.14 (0.04)	0.16 (0.07)	0.13 (0.06)
Northern Cardinal (<i>Cardinalis cardinalis</i>)	0.00 (0.00)	0.03 (0.03)	0.06 (0.04)
Indigo Bunting (<i>Passerina cyanea</i>)	0.08 (0.04)	0.03 (0.03)	0.03 (0.03)
Brown-headed Cowbird (<i>Molothrus ater</i>)	0.05 (0.03)	0.03 (0.03)	0.00 (0.00)
American Goldfinch (<i>Carduelis tristis</i>)	0.03 (0.03)	0.06 (0.04)	0.03 (0.03)

CHAPTER 3

Response of breeding birds to ice storm damage in the Ozark Mountains, Arkansas

Abstract

In January 2009, a severe ice storm in southern and midwestern states caused significant structural damage to forests, creating canopy gaps and heavy woody debris on the forest floor. Many studies have shown birds to respond to structural changes in vegetation, but few have documented the response in the context of ice damage. The objective of this study was to examine how breeding bird communities and populations responded to changes in habitat caused by the 2009 ice storm in the Ozark National Forest, Arkansas. Using fixed radius point counts and vegetation plots, I surveyed areas exhibiting high and low levels of ice damage during the breeding seasons of 2008, 2009, and 2010. Species richness and community composition were compared across years. Habitat variables affected by the storm were used to model occupancy for three migratory species representing different nesting requirements along a gradient from closed canopy interior forest [Ovenbird (*Seiurus aurocapillus*)] to gap-dependent interior forest [Hooded Warbler (*Wilsonia citrina*)] to early successional/edge habitat [Indigo Bunting (*Passerina cyanea*)]. The storm significantly decreased canopy cover and increased woody debris in heavily damaged sites, however avian species richness and community composition were not affected by the changes in habitat. Likewise, there was no population-level response from Ovenbirds, Hooded Warblers, or Indigo Buntings. This study suggests that avian communities and certain migratory populations in the Ozark National Forest were resistant to change following a catastrophic ice storm.

Keywords: ice storm damage, habitat structure, forest bird community, Ovenbird, Hooded Warbler, Indigo Bunting, Ozark Mountains, Arkansas

1. Introduction

Disturbance can be defined as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” (White and Pickett, 1985). The effects of disturbance events can range from mild to severe, and this continuum is influenced by the areal extent, magnitude, and frequency of disturbance events. Ice storms are a type of weather-related disturbance that can cause natural and socioeconomic devastation (NOAA, 2000). The National Weather Service defines an ice storm as an occasion in which freezing rain leads to structural damage or significant accumulation of ice (>0.6 cm). The frequency of ice storms in the United States has been estimated as high as 16 events per year over a 13 year period (1982-1994), with an area stretching from Texas to New England experiencing a major ice storm at least once a decade (Irland, 2000).

Ice storms (also known as glaze events) can greatly influence the structure and composition of forests. Bragg et al. (2003) describes the nature of damage to trees, which can be immediate (e.g., permanent bending, loss of limbs and crowns, uprooted individuals) or delayed (e.g., increased susceptibility to insects or disease). The extent of damage depends on the amount of ice accumulation, as well as a stand's history and composition. Ice damage can generate a large quantity of woody debris, which increases the risk and severity of fires. In addition, the loss of certain size classes (especially canopy dominants) or species of trees can lead to shifts in composition and predictable successional changes that are similar to what has been observed in forests gaps created by tree fall or uneven-aged management (e.g., group selection or single-tree harvests) (Rhoads *et al.*, 2002; Darwin *et al.*, 2004).

The changes in forest structure and composition following an ice storm have implications for wildlife, particularly breeding birds, which are considered especially sensitive to alterations in habitat characteristics important to foraging and nesting (James, 1971; Holmes and Sherry, 2001). The few studies examining the response of birds to ice damage have come from a 1998 ice storm that severely affected areas of southeastern Canada and northeastern United States. One study on wintering birds used Christmas Bird Count data from Québec to show that the abundance of species such as Hairy Woodpecker (*Picoides villosus*) and Black-Capped Chickadee (*Parus atricapillus*) was more likely to increase on control versus affected sites, while the abundance of Brown Creeper (*Certhia americana*) and Downy Woodpecker (*Picoides pubescens*) decreased on affected sites (Blais *et al.*, 2001). A study on Cerulean Warblers (*Setophaga cerulea*) in Ontario found that the year following the storm, reproductive output declined, however the population responded the following year by increasing territory size, and reproductive output subsequently increased (Jones *et al.*, 2001). Faccio's (2003) study of forest breeding birds in Vermont indicated a decline in the abundance of forest-interior ground/shrub gleaners [e.g. Ovenbird (*Seiurus aurocapillus*)] and forest-interior canopy gleaners [e.g. Red-eyed Vireo (*Vireo olivaceus*) and Blackburnian Warbler (*Dendroica fusca*)]. To understand the variation in responses to ice damage, we need research representing more than just one storm in one area of North America. To my knowledge, no studies have been conducted on ice damage and breeding birds in the forests of the southeastern U.S.

In late January 2009, an ice storm of great magnitude traveled across southern and midwestern states. Up to 6 cm of ice and 33 cm of snow accumulated in parts of affected areas. Arkansas was one of the hardest hit states, with hundreds of thousands of residences without power for weeks. Damage was extensive to property, utilities, and the surrounding landscape

(NOAA, 2009). The storm also affected research sites in the Ozark National Forest where I had conducted avian surveys during the previous breeding season as part of another study (Chapter 2). Based on aerial surveys, 20 percent of the Ozark National Forest was estimated to have severe damage amounting to greater than 50 percent crown loss and/or bole damage (USDA Forest Service, 2009). Thus, this storm event presented an opportunity to investigate the effects of ice damage on breeding bird populations with a novel storm event in a southern forest.

The upland oak-hickory forests of the Ozark Mountains are important breeding grounds for many bird species, including resident and migratory populations (Donovan *et al.*, 1995; Howell *et al.*, 2000). The disturbance regime of the area includes uneven-aged timber harvest, which as Faccio (2003) notes, mimics natural events such as gaps created by ice damage. Thus, we can look to the many studies on responses of birds to selective logging to generate predictions for the effects of ice damage. Selective logging increases habitat heterogeneity, which is often associated with an increase in bird species richness (Baker and Lacki, 1997; Campbell *et al.*, 2007). An open canopy allows sunlight to reach the forest floor, which enhances the development of understory growth, a change that favors shrub-nesters adapted to forest gaps and edges such as Hooded Warbler (*Wilsonia citrina*) and Indigo Bunting (*Passerina cyanea*), but not closed-canopy, interior ground-nesters such as Wood Thrush (*Hylocichla mustelina*) and Ovenbird (Crawford *et al.*, 1981; Annand and Thompson, 1997; Baker and Lacki, 1997; Alterman *et al.*, 2005). Ice damage and selective logging differ, however, because trees are removed after selective logging, but they remain after ice damage. Ice storm debris increases horizontal and vertical complexity of ground cover, which may negatively influence ground-nesting species that prefer an open forest floor.

The objective of this study was to examine how breeding bird communities and specific populations responded to changes in habitat after the 2009 ice storm. Data were collected the breeding season before and two seasons after the storm. Responses were measured in terms of species richness and composition (community-level) and site occupancy (population-level), which can be defined as the proportion of sites occupied by a species (MacKenzie *et al.*, 2006). Habitat response was measured by comparing structural variables likely to be influenced by ice damage and known to be important in bird-habitat relationships (James, 1971). I predicted that species richness would increase and community composition would reflect more early successional species in areas affected by the storm. In addition, these areas would exhibit lower occupancy for ground-nesting species that prefer open understory and closed canopy forest because of newly created canopy gaps and heavy debris loads on the ground. In contrast, species that prefer to nest in dense undergrowth associated with gaps and edges would have higher occupancy in damaged areas.

2. Materials and methods

2.1 Study area

As part of a another study (see Chapter 2), 32 survey points from a study by Rodewald and Smith (1998) were reestablished in 2008. All points were spaced a minimum of 150 m from one another. These sites were located in the Big Piney Ranger District of the Ozark National Forest, in Newton and Pope counties, Arkansas, U.S.A. (35°43'13"N, 93°05'45"W) (Figure 1). Elevation of the study sites ranged from 400-620 m. The canopy of this upland forest was composed primarily of white oak (*Quercus alba* L.), northern red oak (*Q. rubra* L.), black oak (*Q. velutina* Lam.), and mockernut hickory (*Carya tomentosa* (L.) Nutt.). The understory was

composed primarily of red maple (*Acer rubrum* L.), blackgum (*Nyssa sylvatica* Marsh.), flowering dogwood (*Cornus florida* L.), and black cherry (*Prunus serrotina* Ehrh).

2.2 Field sampling

For each of the 32 survey sites, four avian point count surveys were conducted by two observers (two surveys each) throughout the 2008, 2009, and 2010 breeding seasons (mid-May through June). Surveys from 2008 represent pre-ice storm surveys and surveys in 2009 and 2010 represent post-ice storm surveys. During these ten-minute surveys (conducted between 0600 to 1000 hours), the species and number of all birds seen or heard within a 50 m radius were recorded (Hutto *et al.*, 1986). Surveys were not performed under adverse weather conditions (e.g., rain, wind) in order to maximize likelihood of detection (Martin *et al.*, 1997).

Using a modified protocol of James and Shugart (1970), four circular vegetation plots were established for each point count to measure habitat characteristics. One plot was located at the center of the point count, and three others were positioned 35 m from the point count center in three directions: 120, 240, and 360°. Within a 5 m radius of the center of each vegetation plot, the following habitat variables likely to be influenced by ice damage were measured: percent canopy cover (measured via spherical densiometer), number of small saplings [greater than 0.5 m in height and between 0-2.5 cm in diameter (measured 10 cm above ground)], and percent ground covered by woody debris (estimated visually). Within an 11.3 m radius, evidence of ice damage was recorded including: number of downed crowns and branches from trees in three diameter at breast height (dbh) size categories [small (8-23 cm), medium (23-38 cm), and large (>38 m)], number of bent saplings (0-8 cm dbh), percentage of plot covered by downed crown, branches, and boles.

2.3 Statistical analyses

Aerial surveys conducted by the USDA Forest Service (2009) indicated that the 16 northern sites (Figure 1) in this study were in an area with hardwoods that experienced greater than 50 percent crown loss, bole damage, and blow down; however, the 16 southern sites were in an area with little damage. To verify whether this difference in damage levels was evident on the ground, an index of ice damage for each vegetation plot was calculated by summing the values for numbers of downed crowns and branches from trees in the three size classes, number of bent saplings, and percentages of the plot covered by downed crown, branches, and boles. Index values were averaged across the four vegetation plots per survey point, yielding a mean index value for each survey point. These values supported that the more northern survey points (n=16) were subject to higher levels of ice damage (mean index = 57.42 ± 4.60) with all indices above values of 25, and the more southern sites (n=16) were subject to lower levels of ice damage (mean index = 5.75 ± 1.37) with all indices below values of 25. Thus, the survey sites were divided into two categories, points with high levels of ice damage and points with low levels of ice damage.

To test for differences in habitat characteristics between plots from the two categories of ice damage across years, I applied multivariate analysis of variance (MANOVA) with a repeated measures design using JMP[®] (SAS Institute Inc., 2010). Three habitat variables were analyzed based on their likelihood to be influenced by ice damage: high canopy cover, woody debris ground cover, and number of small saplings. To improve homogeneity of variance and normality, arcsine transformations were performed on canopy and ground cover, and a log transformation was performed on small saplings (Sokal and Rohlf, 1995).

Bird species that do not normally breed in the oak-hickory stands in the Ozarks, that were simply flying over, or that were detected only once over the three years of the study were not included in the analyses. For a complete list of species detected during the 2008, 2009, and 2010 surveys, see Appendix 1. Mean number of detections per survey was calculated for each species in areas with high and low levels of ice damage (see Appendix 2).

Bird community analysis was performed using program COMDYN4 (Hines *et al.*, 1999), which computes parameters reflecting spatial and temporal changes in communities based on the underlying jackknife estimator proposed by Burnham and Overton (1979), applied to species richness by Boulinier *et al.* (1998), and applied to community-dynamic parameters by Nichols *et al.* (1998). Community parameters (defined below with respect to this study) were estimated by comparing species detection patterns from presence/absence data within the two categories of ice damage between 2008-2009, and then between 2009-2010. COMDYN4 utilizes summary data, which required collapsing detection histories for each species across sites within the two categories of ice damage for each year. For more detail on the specifics of data entry for COMDYN4, see Hines *et al.* (1999). Species richness (N) refers to the number of species occurring in an area at a given time. Extinction probability ($1-\phi$) is the proportion of species that go locally extinct between two time periods. Species turnover ($1-\gamma$) is the proportion of species present at time two that were not present at time one. The rate of increase in species richness (λ) is a ratio of the estimated number of species present at time two to the estimated number present at time one. Finally, the number of locally colonizing species (B) is an estimate of the number of species present at time two that were not present at time one (Hines *et al.*, 1999).

Three bird species were selected for population analysis based on their nesting habitat preferences (Crawford *et al.*, 1981), potential to be influenced by ice damage (Faccio, 2003), and

suitable detection histories. Ovenbirds (OVEN) are ground-nesters that favor the interior of closed canopy forests with less shrub cover at ground-level (Porneluzi *et al.*, 2011). Hooded Warblers (HOWA) are shrub-nesters that are associated with mature forests with enough tree-gaps to create a well-developed shrub layer (Chiver *et al.*, 2011). Indigo Buntings (INBU) nest in sizable open areas or near edges of forests where extensive shrub layers have developed (Payne, 2006).

An information-theoretic approach was used to evaluate single-season models relating site occupancy (Ψ) to habitat characteristics, while accounting for detectability (p), in program PRESENCE (MacKenzie *et al.*, 2002). Candidate models were developed for each year based on habitat variables influenced by the ice storm that could influence probability of occupancy and/or detectability for each bird species [i.e., percent canopy cover, percentage of ground covered by woody debris, number of small saplings (which indicated the developmental stage of a shrub layer)]. Based on initial analyses, observer effects were not helpful in modeling detectability so they were not included in model sets. Models were ranked according to Akaike's Information Criterion (AIC) and, when necessary, adjusted for small sample size (AIC_c) and overdispersion of the data ($QAIC_c$) (Burnham and Anderson, 2002). When there was model selection uncertainty (i.e., multiple models had ΔAIC_c values ≤ 2.0), model averaging was used to estimate the relationship between habitat covariates and probabilities of occupancy and detection, which were then estimated using habitat covariate means for high and low categories of ice damage (Burnham and Anderson, 2002). Standard error and confidence interval estimates were calculated using the Delta method, as described by Cooch and White (2011).

3. Results

3.1 Habitat characteristics

Responses of percent high canopy cover, percent woody debris ground cover, and number of small saplings across three years are given in Table 1. Results of the repeated measures MANOVA indicated there was an interaction between ice damage category and year for each of the variables (Table 2). High ice damage (HID) sites decreased in mean percent canopy cover from 2008 to 2009 more so than low ice damage (LID) sites; and although HID sites recovered some canopy cover in 2010, the difference between HID and LID sites persisted (Figure 2). HID sites increased in mean percent woody debris ground cover from 2008 to 2009 while LID sites decreased; however, this difference became less pronounced in 2010 when HID sites showed a decrease in woody debris. HID sites decreased in mean number of small saplings from 2008 to 2009 while LID sites showed no change; however, HID sites recovered to original levels by 2010.

3.2 Avian community

For each year, a total of 128 point count surveys were completed and analyzed. In 2008, there were a total of 720 individuals of 32 species detected. In 2009, there were 646 total individuals representing 30 species detected. In 2010, there were 691 total individuals representing 34 species detected.

The results of the community analysis showed that although species richness tended to be higher in HID areas compared to LID in all years (Figure 3), confidence intervals overlapped so this difference was not significant (Table 3). Species richness in LID areas was less variable over the years than in HID areas, which tended to decline in richness (although not significantly) the breeding season after the storm, and subsequently increase the following year.

Parameter estimates for temporal variation in communities reflected the stability of the richness estimates (Table 3). In HID areas, extinction probability, species turnover, rate of species increase, and locally colonizing species had confidence intervals that included null values, thus these parameters did not indicate significant change in the communities. The same held true for LID areas, although there were approximately three locally colonizing species from 2009 and 2010. Detection probabilities were not different between years for each area ($0.26 < P < 0.70$), so the alternative estimate of the rate of increase in species richness ($\text{alt}\lambda$) was used (Hines *et al.*, 1999).

3.3 Avian populations

Ovenbirds had overall naïve occupancies of $\Psi = 0.94$, 0.69 , and 0.75 in the years 2008, 2009, and 2010, respectively. In 2008, estimated occupancy was close to 1.0 for both areas of high and low ice damage (Figure 4, Table 4). In 2009, occupancy decreased for both categories of ice damage, and the estimate was lower for LID sites than HID sites (although not significantly). By 2010, occupancy was similar again between both categories of ice damage, but still slightly lower than in 2008.

Each year, different models demonstrated support ($\Delta\text{AIC} < 2.0$) according to their relative fit in the candidate set (Table 5). In 2008, the only occupancy model with a covariate to reach convergence and show support suggested that OVEN occupancy decreased with increasing woody debris ($w_i = 0.32$), but the direction of this effect was unclear since the beta estimate confidence interval overlapped zero (Table 6). In 2009, occupancy models including small saplings and canopy cover had the most support (sum of weights, small saplings $\Sigma w_i = 0.65$, canopy cover $\Sigma w_i = 0.39$). There was weak evidence that OVEN occupancy decreased with increasing saplings and canopy cover. In 2010, the model of occupancy with intercept only was

not improved by including habitat covariates. The model with the most support suggested small saplings negatively influenced detectability ($w_i = 0.58$), but the effect had only weak support so detectability estimates for HID and LID were similar. In fact, detectability was comparable for all areas of ice damage across all years (Table 4).

Hooded Warblers had overall naïve occupancies of $\Psi = 0.81, 0.78,$ and 0.78 in the years 2008, 2009, and 2010, respectively. In 2008, estimated occupancy was >0.90 for both HID and LID areas (Figure 4, Table 4). In 2009, occupancy was estimated at nearly 1.0 for both areas (which makes estimating standard error difficult, as seen by the zero value for 2009 LID). In 2010, occupancy declined somewhat in both areas, but both estimates remained high (>0.85).

The occupancy model with most support in 2008 included small saplings ($w_i = 0.62$), with HWA occupancy increasing as saplings increased (Tables 5, 6). In 2009, the occupancy model including canopy cover and small saplings had the most support ($w_i = 0.99$). There was strong evidence that occupancy increased with increasing saplings and weak evidence that occupancy decreased with increasing canopy cover. In 2010, the occupancy models with most support included canopy cover ($\Sigma w_i = 0.30$), which had a small, positive effect. Supported models also included small saplings ($\Sigma w_i = 0.94$), although evidence for their positive effect was not strong. Adding covariates to models for detection probability did not improve model fit so estimates were the same for both areas of ice damage within each year, with detection being highest in 2009, and lowest in 2008 (Table 4).

Indigo Buntings had overall naïve occupancies of $\Psi = 0.16, 0.31,$ and 0.41 in the years 2008, 2009, and 2010, respectively. Estimated occupancy was the same for both ice damage categories in 2008, and there was little change in 2009 (Figure 4, Table 4). Both areas showed an

increase in occupancy in 2010, with LID areas exhibiting a slightly larger increase, but not enough to distinguish LID from HID.

The occupancy model with intercept only received the most support in 2008 ($w_i = 0.59$) (Table 5), hence the identical estimates for INBU occupancy for both categories of ice damage (Table 4). In 2009, two models (intercept only and intercept + canopy) received the most support. Evidence indicated that canopy cover had a negative effect on occupancy (Table 6). In 2010, the model with most support included saplings ($w_i = 0.77$), but their positive effect on occupancy had only weak evidence. Adding covariates to models for detection probability did not improve model fit so estimates were the same for both areas of ice damage within each year. Detectability also did not differ across years (Table 4).

4. Discussion

The 2009 ice storm decreased canopy cover and increased woody debris in high ice damage areas, however bird communities and certain populations did not respond as predicted to these shifts in habitat. Species richness and composition in the years following the storm remained relatively similar to pre-storm richness in both high and low damage sites. Although there was some annual fluctuation in occupancy, high damage sites did not exhibit lower occupancy of Ovenbirds, a mature forest species, or higher occupancy of Hooded Warblers and Indigo Buntings, which are associated with gaps and edges.

The responses of canopy cover and woody debris the season following the storm were expected since the ice storm uprooted entire trees and knocked down limbs and crowns. The second season after the storm, the canopy had begun to recover, but not to pre-storm levels. Canopies of trees affected by a 1998 ice storm in the northeastern U.S. demonstrated a similar

delayed recovery, possibly due to the physiological shock of growing under different conditions (Rhoads *et al.*, 2002). The response of saplings, however, did not fit predictions. I expected saplings to increase in number following the storm as found by (Darwin *et al.*, 2004), but instead there was a decline in saplings in 2009, followed by a recovery to pre-storm levels in 2010. A delay in sapling growth could be explained by large amounts of downed woody debris, which compress and shade out young saplings. Faccio (2003) noted a two to three year delay in positive responses of saplings to light gaps created by the 1998 ice storm.

Bird communities did not increase in species richness in high damage sites, which contradicts the only other study to look at the effects of a severe ice storm on bird diversity (Faccio, 2003). However, this result is not completely surprising considering that canopy gaps were small-scale and canopy closure, although less in high damage sites, was still around seventy percent. This lack of response in species richness and turnover has also been found in studies on selective logging, which is thought to mimic natural events such as tree-falls and ice storms (Campbell *et al.*, 2007; McDermott and Wood, 2009; Tozer *et al.*, 2010).

Populations of bird species representing different nesting habitats did not demonstrate predicted responses. Site occupancy of the Ovenbird, a ground-nester of the interior forest, did not decline after the 2009 storm, which contradicts many studies that have shown a negative response of Ovenbirds to forest disturbance [ice storm, Faccio (2003); tornado damage, (Prather and Smith, 2003), selective logging (Annand and Thompson, 1997; Rodewald and Smith, 1998; Jobes *et al.*, 2004)]. The gap-dependent, shrub-nesting Hooded Warbler maintained high probability of occupancy in both ice damage categories throughout the study. This result supports findings of other studies conducted in the Ozarks, which demonstrated little response of Hooded Warblers to disturbances such as tornados (Prather and Smith, 2003) and selective

logging (Rodewald and Smith, 1998). Although Indigo Buntings demonstrated a trend for increased occupancy after the ice storm, this response did not differ between high and low damaged sites. This result is unexpected since evidence shows this edge-adapted, shrub-nesting species responds positively to gap-creating forest disturbances such as tornados (Prather and Smith, 2003) and selective logging (Rodewald and Smith, 1998; Robinson and Robinson, 1999; Gram *et al.*, 2003).

Although populations did not demonstrate predicted responses, there was evidence that habitat covariates (which were influenced by the ice storm) were important to modeling occupancy. Canopy cover and small saplings were important to Ovenbirds in 2009, although the direction of the effect was inconclusive. The number of saplings positively influenced Hooded Warblers in 2008 and 2009. Canopy cover negatively influenced Indigo Buntings in 2009, and the number of saplings was important in 2010, although the direction of the effect was inconclusive. The importance of these covariates in modeling occupancy suggests that although this specific storm did not induce a drastic response from bird populations, there is still potential for more damaging ice storms to influence populations.

Still, it remains that the 2009 ice storm, although detectably destructive to Ozark forest structure, was not severe enough to meaningfully affect the bird community or certain migratory populations. One explanation for this result could be that the small-scale forest gaps created by the storm were within the range of normal disturbance periodically experienced by these birds. Ice storms, tornados, tree-falls, and selective logging produce similar changes in forest structure. These disturbances might be infrequent when considered individually, but their combined occurrences might have provided opportunities for forest birds to adapt to associated changes in habitat. Another explanation invokes site fidelity in birds, which have long been documented to

return to sites where they have bred previously (for review, see Greenwood and Harvey, 1982). Switzer (1993) suggested that site fidelity varies inversely with territory quality heterogeneity; thus, in a relatively homogenous environment, such as mature interior forest, birds would be less likely to abandon previous nesting sites, even if habitat characteristics were different from the previous breeding season. Relatively high site fidelity has been documented in Ovenbirds, Hooded Warblers, and Indigo Buntings (see Schlossberg, 2009).

A limitation of this study concerns the design, which consisted of a modest number of survey points ($n = 32$) that potentially lacked independence. The points were grouped across six sites, with four to eight points at each site. Surveys from the points at one site might be more similar to each other than to points from other sites. In addition, some birds are capable of moving over areas larger than the survey radius, which could have led to double counting of individuals at neighboring point counts. I attempted to minimize this possibility by conducting surveys at neighboring points in quick succession, while recording suspected duplicate detections and excluding these from analyses. Future research should include more survey sites to maximize the number of detections so that the responses of as many bird species as possible can be analyzed. These sites should also be spaced far enough apart to insure independence.

Future research should also investigate how ice damage affects aspects of breeding birds other than just occupancy. Presence of a species does not guarantee nesting success in a habitat, nor that young survive after fledging. A more complete understanding of the effects of severe ice storms on breeding birds can only be gained by following parents and their young through the entire breeding season. For example, Jones *et al.* (2001) found that reproductive success of Cerulean Warblers declined the year after the 1998 ice storm in the Northeast; but in the following year they increased their territory sizes and improved reproductive success. Future

analysis could also compare the responses of resident versus migratory species since residents might respond stronger to ice damage because they are present for the winter disturbance.

Conclusion

Despite changes in habitat characteristics after a severe ice storm in 2009, breeding bird communities and populations in a forest of the southeastern U.S. were resistant to change. This finding supports the conclusion that what humans see as catastrophic damage may not be perceived the same way by birds selecting nest sites. Currently there are too few studies of the effects of ice storm damage on breeding birds to make broad generalizations, but this study contributes to the slowly growing literature on the subject.

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Tables

Table 1. Habitat variable means, standard error (SE), and 95% confidence intervals (CI) for survey sites in the Ozark National Forest, Arkansas, that experienced high (n=16) and low (n=16) levels of ice damage from a 2009 winter storm. The year 2008 represents pre-ice storm vegetation, while 2009 and 2010 represent vegetation from the two breeding seasons following the ice storm.

Variable	Year	Ice Damage	Mean	SE	95% CI	
					Lower	Upper
Canopy Cover	2008	High	89.99	1.33	87.37	92.61
		Low	93.79	0.82	92.19	95.40
	2009	High	69.02	2.80	63.52	74.52
		Low	90.41	1.59	87.29	93.54
	2010	High	75.77	2.43	71.00	80.54
		Low	91.42	1.35	88.76	94.07
Woody Debris	2008	High	10.39	1.04	8.36	12.42
		Low	7.62	0.90	5.86	9.39
	2009	High	13.91	1.39	11.18	16.63
		Low	5.33	0.85	3.66	6.99
	2010	High	10.94	0.97	9.03	12.85
		Low	5.13	0.64	3.88	6.37
Small Saplings	2008	High	117.19	11.54	94.56	139.82
		Low	128.91	15.17	99.18	158.64
	2009	High	78.14	6.28	65.83	90.45
		Low	131.72	25.67	81.41	182.03
	2010	High	106.52	7.54	91.75	121.29
		Low	126.64	18.61	90.17	163.11

Table 2. Results of MANOVA for habitat characteristics on vegetation plots of survey sites damaged by a 2009 ice storm in the Ozark National Forest, Arkansas. Categories of ice damage include high (n=16) and low (n=16). The year 2008 represents pre-ice storm vegetation, while 2009 and 2010 represent vegetation from the two breeding seasons following the ice storm.

Percent high canopy cover

Source	DF _{num}	DF _{den}	<i>F</i>	<i>P</i>
Ice Damage	1	30	44.35	<0.01
Year	2	29	33.74	<0.01
Ice Damage*Year	2	29	15.11	<0.01
Ice Damage ₀₈₋₀₉	1	30	31.03	<0.01
Ice Damage ₀₈₋₁₀	1	30	14.69	<0.01

Percent woody debris

Source	DF _{num}	DF _{den}	<i>F</i>	<i>P</i>
Ice Damage	1	30	45.46	<0.01
Year	2	29	1.47	0.25
Ice Damage*Year	2	29	4.75	<0.05
Ice Damage ₀₈₋₀₉	1	30	9.77	<0.05
Ice Damage ₀₈₋₁₀	1	30	4.05	0.05

Number of small saplings

Source	DF _{num}	DF _{den}	<i>F</i>	<i>P</i>
Ice Damage	1	30	1.82	0.19
Year	2	29	9.33	<0.01
Ice Damage*Year	2	29	6.43	<0.01
Ice Damage ₀₈₋₀₉	1	30	7.09	<0.05
Ice Damage ₀₈₋₁₀	1	30	0.19	0.66

Table 3. Avian community parameters^a, bootstrap averages, standard errors (SE), and 95% confidence intervals (CI) estimated by comparing bird species detected in 2008, 2009, and 2010 point count surveys in areas with high (n=16) and low (n=16) levels of ice damage from a 2009 winter storm in the Ozark National Forest, AR.

Ice Damage	Parameter	Estimate	Bootstrap Average	SE	95% CI		
					Lower	Upper	
High	N_{2008}	35.54	36.64	5.09	30.00	47.29	
	N_{2009}	30.07	31.28	3.61	27.00	40.06	
	N_{2010}	40.92	40.41	6.32	28.00	51.33	
	2008-09	1 - ϕ	0.06	0.07	0.07	0.00	0.24
		1 - γ	0.00	0.04	0.06	0.00	0.20
		alt λ	0.90	0.91	0.08	0.76	1.07
		B	0.00	1.31	2.85	0.00	9.56
	2009-10	1 - ϕ	0.10	0.07	0.09	0.00	0.28
		1 - γ	0.13	0.15	0.11	0.00	0.38
		alt λ	1.04	1.04	0.13	0.79	1.28
		B	13.90	12.05	6.88	0.00	24.45
	Low	N_{2008}	26.50	28.16	3.07	25.00	37.78
N_{2009}		25.50	24.17	1.75	22.00	27.50	
N_{2010}		28.25	28.09	1.54	26.00	31.50	
2008-09		1 - ϕ	0.02	0.10	0.09	0.00	0.32
		1 - γ	0.00	0.04	0.06	0.00	0.24
		alt λ	0.88	0.88	0.08	0.73	1.04
		B	0.00	1.04	1.90	0.00	6.86
2009-10		1 - ϕ	0.01	0.07	0.08	0.00	0.25
		1 - γ	0.10	0.16	0.11	0.00	0.39
		alt λ	1.18	1.19	0.13	1.00	1.50
		B	3.04	5.57	2.64	0.50	10.86

^a N - estimated number of species present
1 - ϕ - estimated extinction probability
1 - γ - estimated species turnover
alt λ - estimated rate of change of species richness
 B - estimated local colonizing species

Table 4. Estimated probabilities of occupancy (Ψ) and detection (p), standard error (SE), and 95% confidence intervals (CI) of three breeding bird species pre-ice storm (2008) and two years post-ice storm (2009, 2010) in the Ozark National Forest, AR.

Species	Year	Ice Damage	Ψ	SE	95% CI		p^a	SE	95% CI	
					Lower	Upper			Lower	Upper
Ovenbird	2008	High	0.973	0.057	0.006	1.000	0.572	0.109	0.552	0.664
		Low	0.968	0.060	0.012	1.000				
	2009	High	0.825	0.113	0.799	0.848	0.531	0.135	0.486	0.575
		Low	0.611	0.144	0.207	0.904				
	2010	High	0.802	0.085	0.588	0.920	0.536	0.086	0.447	0.624
		Low	0.802	0.085	0.588	0.920				
Hooded Warbler	2008	High	0.914	0.065	0.687	0.981	0.589	0.050	0.489	0.682
		Low	0.947	0.051	0.697	0.993				
	2009	High	0.997	0.008	0.994	0.999	0.760	0.043	0.666	0.834
		Low	1.000	0.000	0.012	1.000				
	2010	High	0.851	0.079	0.612	0.954	0.643	0.056	0.614	0.671
		Low	0.957	0.049	0.439	0.998				
Indigo Bunting	2008	High	0.389	0.326	0.042	0.903	0.121	0.108	0.018	0.501
		Low	0.389	0.326	0.042	0.903				
	2009	High	0.427	0.042	0.268	0.606	0.349	0.137	0.273	0.434
		Low	0.329	0.145	0.082	0.725				
	2010	High	0.715	0.202	0.204	0.999	0.218	0.054	0.130	0.341
		Low	0.982	0.106	0.123	0.999				

^a Years with one value for p had similar probability of detection in both high and low areas of ice damage.

Table 5. Model^a selection results for occupancy (Ψ) and detection (p) probability of three bird species with different nesting habitat preferences pre-ice storm (2008) and two years post-storm (2009, 2010) in the Ozark National Forest, AR.

Species	Year	Model	$\Delta AICc^b$	K	$-2L$	w_i
Ovenbird (forest interior, ground-nester)	2008	$\Psi(\cdot), p(\cdot)$	0.00 ^c	2	175.40	0.68
		$\Psi(\text{Debris}), p(\cdot)$	1.50	3	174.71	0.32
	2009	$\Psi(\text{Sap1}), p(\cdot)$	0.00 ^c	3	153.60	0.33
		$\Psi(\text{CanCov+Sap1}), p(\cdot)$	1.35	4	152.41	0.17
		$\Psi(\text{CanCov}), p(\cdot)$	1.82	3	155.70	0.13
		$\Psi(\cdot), p(\cdot)$	2.10	2	158.66	0.11
		$\Psi(\text{Debris+Sap1}), p(\cdot)$	2.22	4	153.42	0.11
		$\Psi(\text{Debris}), p(\cdot)$	3.36	3	157.49	0.06
		$\Psi(\text{CanCov+Debris+Sap1}), p(\cdot)$	3.66	5	152.21	0.05
		$\Psi(\text{CanCov+Debris}), p(\cdot)$	4.16	4	155.66	0.04
	2010	$\Psi(\cdot), p(\text{Sap1})$	0.00	3	159.75	0.58
		$\Psi(\cdot), p(\text{Debris+Sap1})$	2.33	4	159.74	0.18
		$\Psi(\cdot), p(\cdot)$	3.80	2	165.80	0.09
		$\Psi(\cdot), p(\text{Debris})$	5.43	3	165.18	0.04
		$\Psi(\text{Debris}), p(\cdot)$	5.88	3	165.63	0.03
$\Psi(\text{CanCov}), p(\cdot)$		5.96	3	165.71	0.03	
$\Psi(\text{Sap1}), p(\cdot)$		6.05	3	165.80	0.03	
$\Psi(\text{Debris+Sap1}), p(\cdot)$		8.20	4	165.61	0.01	
$\Psi(\text{CanCov+Debris}), p(\cdot)$		8.22	4	165.63	0.01	
$\Psi(\text{CanCov+Sap1}), p(\cdot)$		8.30	4	165.71	0.01	
$\Psi(\text{CanCov+Debris+Sap1}), p(\cdot)$	10.65	5	165.61	0.00		
Hooded Warbler (forest gap, shrub-nester)	2008	$\Psi(\text{Sap1}), p(\cdot)$	0.00 ^c	3	161.07	0.62
		$\Psi(\text{CanCov+Sap1}), p(\cdot)$	2.26	4	161.02	0.20
		$\Psi(\cdot), p(\cdot)$	3.15	2	169.65	0.13
		$\Psi(\text{CanCov}), p(\cdot)$	5.28	3	169.51	0.04
	2009	$\Psi(\text{CanCov+Sap1}), p(\cdot)$	0.00	4	120.39	0.90
		$\Psi(\text{Sap1}), p(\cdot)$	4.33	3	128.00	0.10
		$\Psi(\cdot), p(\cdot)$	15.67	2	143.67	0.00
		$\Psi(\text{CanCov}), p(\cdot)$	16.02	3	141.56	0.00
	2010	$\Psi(\text{Sap1}), p(\cdot)$	0.00 ^c	3	152.64	0.66
		$\Psi(\text{CanCov+Sap1}), p(\cdot)$	1.71	4	151.94	0.28
		$\Psi(\cdot), p(\cdot)$	5.47	2	162.31	0.04
		$\Psi(\text{CanCov}), p(\cdot)$	7.66	3	162.29	0.01

Table 5. continued

Species	Year	Model	ΔAIC_c	K	$-2L$	w_i
Indigo Bunting (forest edge, shrub-nester)	2008	$\Psi(\cdot), p(\cdot)$	0.00 ^c	2	47.60	0.59
		$\Psi(\text{CanCov}), p(\cdot)$	2.32	3	47.46	0.18
		$\Psi(\text{Sap1}), p(\cdot)$	2.44	3	47.59	0.17
		$\Psi(\text{CanCov+Sap1}), p(\cdot)$	4.90	4	47.41	0.05
	2009	$\Psi(\cdot), p(\cdot)$	0.00 ^c	2	91.33	0.42
		$\Psi(\text{CanCov}), p(\cdot)$	0.37	3	89.25	0.35
		$\Psi(\text{Sap1}), p(\cdot)$	2.28	3	91.16	0.13
		$\Psi(\text{CanCov+Sap1}), p(\cdot)$	2.98	4	89.24	0.09
	2010	$\Psi(\text{Sap1}), p(\cdot)$	0.00 ^c	3	87.87	0.77
		$\Psi(\text{CanCov+Sap1}), p(\cdot)$	2.62	4	87.87	0.21
		$\Psi(\cdot), p(\cdot)$	8.04	2	99.78	0.01
		$\Psi(\text{CanCov}), p(\cdot)$	9.03	3	98.12	0.01

^a Models include the intercept only (\cdot) and combinations of covariates that represent percent canopy cover (CanCov), percent ground covered by woody debris (Debris), and number of small saplings (Sap1).

^b Minimum values of AIC_c for each species and year, 2008, 2009, and 2010 respectively, were: Ovenbird, 177.84, 139.23, and 166.24; Hooded Warbler, 107.08, 112.35, and 127.54; and Indigo Bunting, 45.84, 95.74, and 84.25.

^c The ΔAIC_c values in these model sets represent $\Delta QAIC_c$ values corrected for over-dispersion.

Table 6. Model-averaged estimates (β) of untransformed regression coefficients for covariates^a affecting occupancy (Ψ) and detection (p) probabilities of three breeding bird species pre-ice storm (2008) and two years post-ice storm (2009, 2010) in the Ozark National Forest, AR.

Species	Year	Covariate	β	SE	95% CI		
					Lower	Upper	
Ovenbird (forest interior, ground-nester)	2008	Ψ intercept	3.721	1.950	-4.760	12.202	
		Debris	-0.351	0.686	-1.034	0.332	
		p intercept	0.288	0.446	0.208	0.368	
	2009	Ψ intercept	0.999	0.794	0.187	1.811	
		CanCov	-0.287	0.349	-0.589	0.014	
		Sap1	-0.943	0.911	-3.097	1.210	
		p intercept	0.124	0.544	-0.055	0.304	
	2010	Ψ intercept	1.396	0.532	0.354	2.438	
		p intercept	0.036	0.242	-0.439	0.511	
		Sap1	-0.612	0.323	-1.246	0.021	
	Hooded Warbler (forest gap, shrub-nester)	2008	Ψ intercept	2.625	0.926	0.810	4.441
			Sap1	2.381	1.102	0.222	4.541
p intercept			0.359	0.206	-0.044	0.762	
2009		Ψ intercept	7.637	3.725	0.336	14.937	
		CanCov	-3.218	1.708	-6.567	0.130	
		Sap1	12.329	5.887	0.790	23.868	
		p intercept	1.151	0.235	0.691	1.611	
2010		Ψ intercept	2.426	1.022	0.106	4.746	
		CanCov	0.158	0.254	0.004	0.311	
		Sap1	3.175	1.514	-1.962	8.312	
		p intercept	0.590	0.242	0.466	0.713	

Table 6. continued

Species	Year	Covariate	β	SE	95% CI	
					Lower	Upper
Indigo Bunting (forest edge, shrub-nester)	2008	Ψ intercept	-0.451	1.370	-3.137	2.234
		p intercept	-1.988	1.016	-3.979	0.003
	2009	Ψ intercept	-0.505	0.612	-0.992	-0.018
		CanCov	-0.272	0.269	-0.403	-0.141
		p intercept	-0.622	0.604	-0.978	-0.267
	2010	Ψ intercept	2.446	2.097	-1.664	6.556
		Sap1	8.482	5.498	-2.293	19.258
		p intercept	-1.277	0.316	-1.897	-0.657

^a Covariates represent percent canopy cover (CanCov), percent ground covered by woody debris (Debris), and number of small saplings (Sap1).

Figures

Figure 1. Location of study sites in the Ozark National Forest near Pelsor, Arkansas. State highways labeled by pentagons. Closed circles represent northern sites (n=16), which experienced higher levels of ice damage (index > 25). Open circles represent southern sites (n=16), which experienced lower levels of ice damage (index < 25).

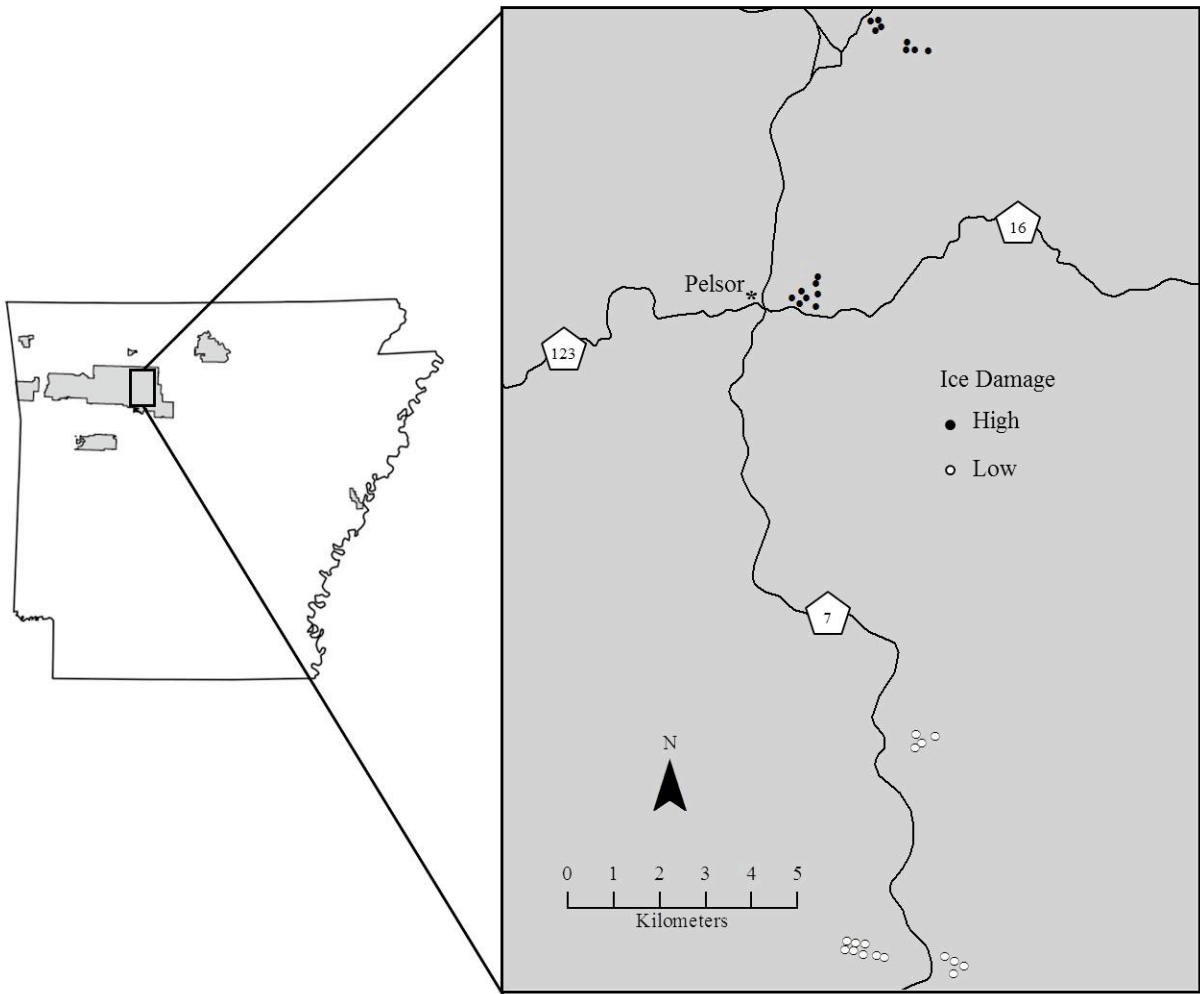


Figure 2. Habitat variable means (\pm SE) for survey sites in the Ozark National Forest, Arkansas, that experienced high (n=16) and low (n=16) levels of ice damage from a 2009 winter storm. The year 2008 represents pre-ice storm vegetation, while 2009 and 2010 represent vegetation from the two breeding seasons following the ice storm.

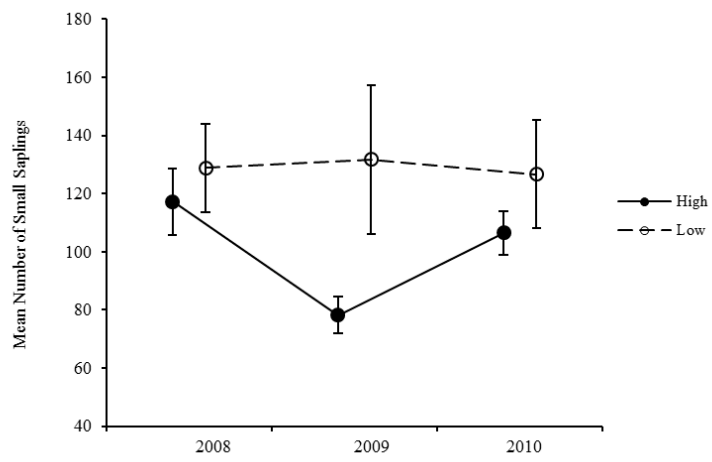
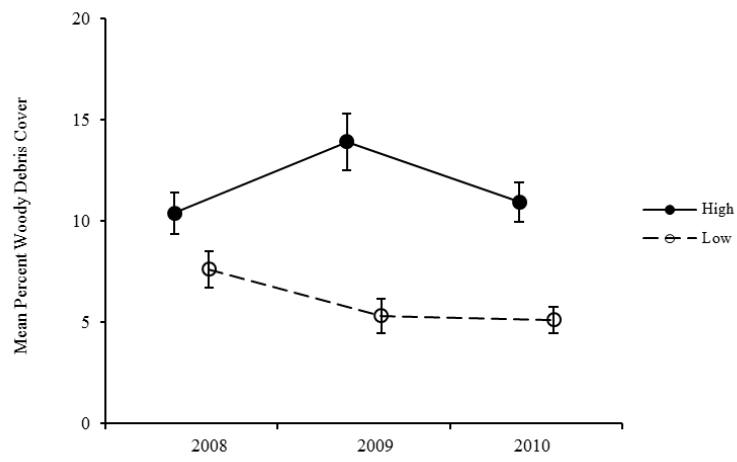
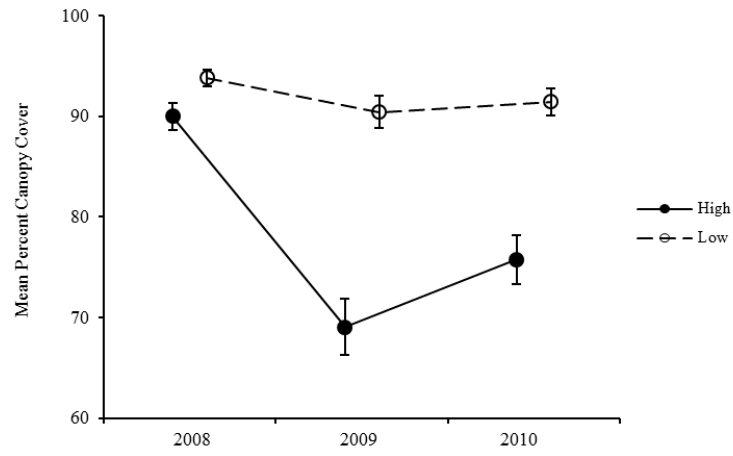


Figure 3. Estimates of total avian species richness (\pm SE) across survey points that experienced high (n=16) and low (n=16) levels of ice damage from a 2009 winter storm in the Ozark National Forest, Arkansas. The year 2008 represents pre-ice storm richness, while 2009 and 2010 represent richness from the two breeding seasons following the ice storm.

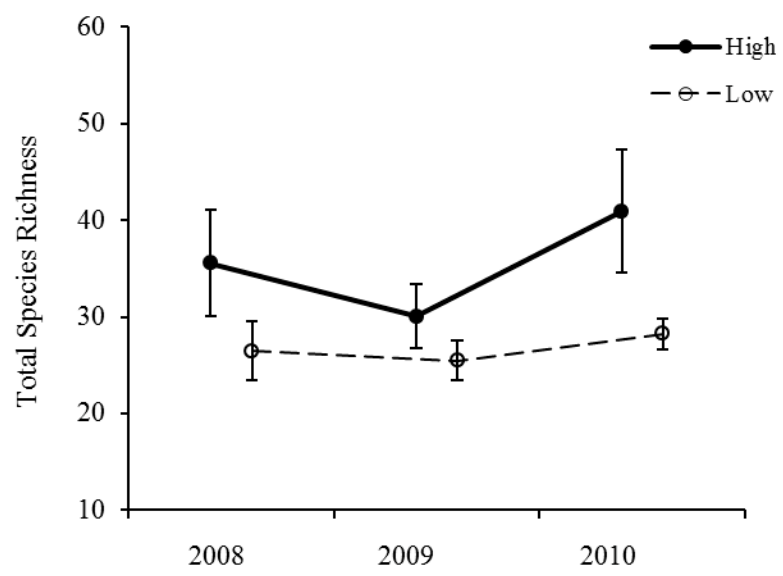
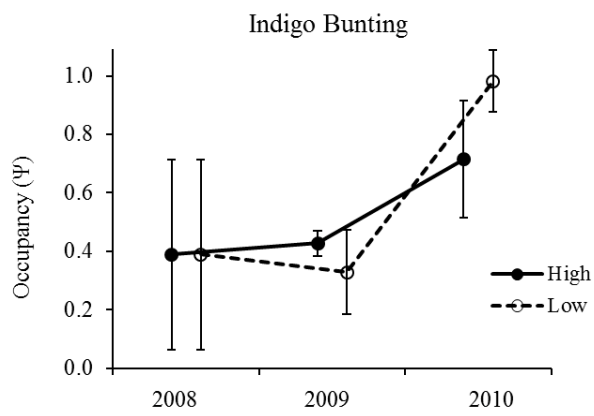
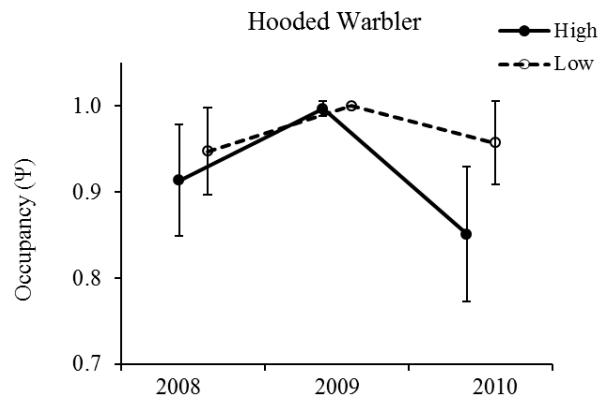
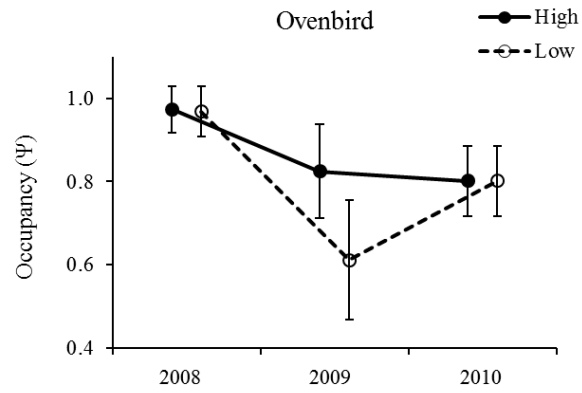


Figure 4. Estimated probabilities of occupancy ($\Psi \pm SE$) of breeding birds in areas the Ozark National Forest, Arkansas, that experienced high (n=16) and low (n=16) levels of ice damage from a 2009 winter storm. Species include: Ovenbird (forest-interior, ground-nester), Hooded Warbler (forest gap, shrub-nester), and Indigo Bunting (forest edge, shrub-nester). The year 2008 represents pre-ice storm occupancy, while 2009 and 2010 represent occupancy from the two breeding seasons following the ice storm.



Appendix 1. Bird species detected within 50 m radius point counts conducted in 2008, 2009, and 2010 in the Ozark National Forest, AR.

All Years	2008 and 2009
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	Barred Owl (<i>Strix varia</i>)
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)	Eastern Phoebe (<i>Sayornis phoebe</i>) White-eyed Vireo (<i>Vireo griseus</i>)
Hairy Woodpecker (<i>Picoides villosus</i>)	
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	2009 and 2010
Eastern Wood-Pewee (<i>Contopus virens</i>)	Red-bellied Woodpecker (<i>Melanerpes carolinus</i>)
Acadian Flycatcher (<i>Empidonax virescens</i>)	
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	
Red-eyed Vireo (<i>Vireo olivaceus</i>)	2008 Only
Blue Jay (<i>Cyanocitta cristata</i>)	Broad-winged Hawk (<i>Buteo platypterus</i>)
American Crow (<i>Corvus brachyrhynchos</i>)	American Redstart (<i>Setophaga ruticilla</i>)
Carolina Chickadee (<i>Poecile carolinensis</i>)	Summer Tanager (<i>Piranga rubra</i>)
Tufted Titmouse (<i>Baeolophus bicolor</i>)	
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	2010 Only
Carolina Wren (<i>Thryothorus ludovicianus</i>)	Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i>)	Downy Woodpecker (<i>Picoides pubescens</i>)
Wood Thrush (<i>Hylocichla mustelina</i>)	Eastern Towhee (<i>Pipilo erythrophthalmus</i>)
Ovenbird (<i>Seiurus aurocapillus</i>)	Yellow-throated Warbler (<i>Setophaga dominica</i>)
Worm-eating Warbler (<i>Helmitheros vermivorus</i>)	Yellow-breasted Chat (<i>Icteria virens</i>)
Black-and-White Warbler (<i>Mniotilta varia</i>)	
Kentucky Warbler (<i>Oporornis formosus</i>)	
Hooded Warbler (<i>Wilsonia citrina</i>)	
Cerulean Warbler (<i>Setophaga cerulea</i>)	
Black-throated Green Warbler (<i>Setophaga virens</i>)	
Scarlet Tanager (<i>Piranga olivacea</i>)	
Northern Cardinal (<i>Cardinalis cardinalis</i>)	
Indigo Bunting (<i>Passerina cyanea</i>)	
Brown-headed Cowbird (<i>Molothrus ater</i>)	
American Goldfinch (<i>Carduelis tristis</i>)	

Appendix 2. Mean number of detections per survey and standard error (SE) of bird species in areas of the Ozark National Forest, Arkansas, that experienced high (n=64) and low (n=64) levels of ice damage from a 2009 winter storm. The year 2008 represents pre-ice storm detections, while 2009 and 2010 represent detections from the two breeding seasons following the ice storm.

Species	Ice Damage	2008 Mean (SE)	2009 Mean (SE)	2010 Mean (SE)
Red-tailed Hawk	H	0.03 (0.02)	0.00 (0.00)	0.02 (0.02)
(<i>Buteo jamaicensis</i>)	L	0.00 (0.00)	0.00 (0.00)	0.03 (0.02)
Barred Owl	H	0.02 (0.02)	0.03 (0.02)	0.00 (0.00)
(<i>Strix varia</i>)	L	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Ruby-throated Hummingbird	H	0.00 (0.00)	0.03 (0.02)	0.02 (0.02)
(<i>Archilochus colubris</i>)	L	0.02 (0.02)	0.05 (0.03)	0.00 (0.00)
Red-bellied Woodpecker	H	0.06 (0.03)	0.00 (0.00)	0.02 (0.02)
(<i>Melanerpes carolinus</i>)	L	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Downy Woodpecker	H	0.00 (0.00)	0.00 (0.00)	0.05 (0.03)
(<i>Picoides pubescens</i>)	L	0.00 (0.00)	0.00 (0.00)	0.02 (0.02)
Hairy Woodpecker	H	0.09 (0.04)	0.17 (0.05)	0.16 (0.04)
(<i>Picoides villosus</i>)	L	0.02 (0.02)	0.11 (0.05)	0.08 (0.04)
Pileated Woodpecker	H	0.09 (0.03)	0.06 (0.04)	0.00 (0.00)
(<i>Dryocopus pileatus</i>)	L	0.06 (0.03)	0.03 (0.02)	0.00 (0.00)
Eastern Wood-Pewee	H	0.14 (0.05)	0.17 (0.05)	0.19 (0.05)
(<i>Contopus virens</i>)	L	0.09 (0.04)	0.05 (0.03)	0.08 (0.04)
Acadian Flycatcher	H	0.25 (0.06)	0.17 (0.05)	0.22 (0.05)
(<i>Empidonax virescens</i>)	L	0.25 (0.07)	0.19 (0.05)	0.11 (0.04)
White-eyed Vireo	H	0.03 (0.02)	0.02 (0.02)	0.00 (0.00)
(<i>Vireo griseus</i>)	L	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Yellow-throated Vireo	H	0.13 (0.04)	0.00 (0.00)	0.13 (0.04)
(<i>Vireo flavifrons</i>)	L	0.05 (0.03)	0.05 (0.03)	0.13 (0.03)
Red-eyed Vireo	H	1.86 (0.12)	1.19 (0.10)	1.50 (0.11)
(<i>Vireo olivaceus</i>)	L	1.56 (0.12)	1.66 (0.11)	1.56 (0.11)
Blue Jay	H	0.03 (0.02)	0.00 (0.00)	0.02 (0.02)
(<i>Cyanocitta cristata</i>)	L	0.00 (0.00)	0.02 (0.02)	0.00 (0.00)
American Crow	H	0.00 (0.00)	0.00 (0.00)	0.02 (0.02)
(<i>Corvus brachyrhynchos</i>)	L	0.00 (0.00)	0.05 (0.35)	0.00 (0.00)
Carolina Chickadee	H	0.17 (0.06)	0.11 (0.04)	0.05 (0.03)
(<i>Poecile carolinensis</i>)	L	0.08 (0.03)	0.14 (0.04)	0.30 (0.11)
Tufted Titmouse	H	0.03 (0.02)	0.03 (0.02)	0.09 (0.04)
(<i>Baeolophus bicolor</i>)	L	0.02 (0.02)	0.00 (0.00)	0.09 (0.04)

Appendix 2 (cont.)

Species	Ice Damage	2008 Mean (SE)	2009 Mean (SE)	2010 Mean (SE)
White-breasted Nuthatch	H	0.06 (0.04)	0.23 (0.07)	0.25 (0.08)
(<i>Sitta carolinensis</i>)	L	0.06 (0.03)	0.14 (0.05)	0.19 (0.07)
Carolina Wren	H	0.13 (0.04)	0.11 (0.04)	0.03 (0.02)
(<i>Thryothorus ludovicianus</i>)	L	0.09 (0.04)	0.11 (0.04)	0.22 (0.08)
Blue-gray Gnatcatcher	H	0.34 (0.07)	0.39 (0.08)	0.22 (0.06)
(<i>Polioptila caerulea</i>)	L	0.14 (0.04)	0.39 (0.06)	0.28 (0.06)
Wood Thrush	H	0.23 (0.07)	0.05 (0.02)	0.02 (0.02)
(<i>Hylocichla mustelina</i>)	L	0.16 (0.06)	0.03 (0.02)	0.02 (0.02)
Ovenbird	H	0.80 (0.08)	0.55 (0.08)	0.69 (0.11)
(<i>Seiurus aurocapillus</i>)	L	0.59 (0.09)	0.33 (0.07)	0.38 (0.07)
Worm-eating Warbler	H	0.09 (0.04)	0.03 (0.02)	0.05 (0.03)
(<i>Helmitheros vermivorus</i>)	L	0.17 (0.05)	0.20 (0.05)	0.19 (0.05)
Black-and-White Warbler	H	0.42 (0.08)	0.50 (0.01)	0.38 (0.06)
(<i>Mniotilta varia</i>)	L	0.33 (0.07)	0.33 (0.01)	0.44 (0.07)
Kentucky Warbler	H	0.09 (0.04)	0.06 (0.03)	0.11 (0.05)
(<i>Oporornis formosus</i>)	L	0.06 (0.03)	0.00 (0.00)	0.00 (0.00)
Hooded Warbler	H	0.52 (0.10)	0.67 (0.09)	0.50 (0.08)
(<i>Wilsonia citrina</i>)	L	0.95 (0.12)	0.77 (0.09)	0.77 (0.10)
Cerulean Warbler	H	0.03 (0.02)	0.05 (0.03)	0.08 (0.03)
(<i>Setophaga cerulea</i>)	L	0.00 (0.00)	0.00 (0.00)	0.03 (0.02)
Black-throated Green Warbler	H	0.02 (0.02)	0.16 (0.05)	0.14 (0.05)
(<i>Setophaga virens</i>)	L	0.25 (0.07)	0.00 (0.00)	0.00 (0.00)
Scarlet Tanager	H	0.13 (0.04)	0.25 (0.06)	0.14 (0.04)
(<i>Piranga olivacea</i>)	L	0.16 (0.05)	0.13 (0.05)	0.22 (0.05)
Northern Cardinal	H	0.03 (0.02)	0.06 (0.04)	0.02 (0.02)
(<i>Cardinalis cardinalis</i>)	L	0.02 (0.02)	0.03 (0.02)	0.03 (0.02)
Indigo Bunting	H	0.03 (0.02)	0.16 (0.05)	0.17 (0.05)
(<i>Passerina cyanea</i>)	L	0.08 (0.04)	0.17 (0.07)	0.14 (0.06)
Brown-headed Cowbird	H	0.14 (0.04)	0.02 (0.02)	0.08 (0.06)
(<i>Molothrus ater</i>)	L	0.03 (0.02)	0.00 (0.00)	0.00 (0.00)
American Goldfinch	H	0.02 (0.02)	0.05 (0.03)	0.08 (0.03)
(<i>Carduelis tristis</i>)	L	0.06 (0.02)	0.03 (0.00)	0.08 (0.03)

CHAPTER 4

Response of breeding birds to woodland restoration in the Ozark Mountains, Arkansas

Abstract

Oak woodlands, which are transitional communities between prairie and forest, have declined significantly in the last century. Recent efforts to restore oak woodlands involve reducing tree density via mechanical thinning and prescription fire, which also promotes herbaceous ground cover. The shift in vegetation from closed-canopy forest to open woodland can affect bird species that use these areas for breeding. This study examines the response of vegetation and bird communities to woodland restoration in the Ozark National Forest, Arkansas. Using fixed radius avian point counts and vegetation plots, I surveyed eight recently restored woodland points and eight control points in untreated, closed-canopy forest during the breeding seasons of 2008, 2009, and 2010. Results indicate restoration efforts were successful in creating a woodland-like habitat with fewer trees, less canopy cover, and more herbaceous ground cover. Bird communities showed higher species richness and different composition in restored versus control sites. Across years, restored sites consistently hosted more total birds, and more open-nesters [e.g. Indigo Bunting (*Passerina cyanea*), Yellow-Breasted Chat (*Icteria virens*)], cavity-nesters [e.g. Hairy Woodpecker (*Picoides villosus*)], and some canopy-nesters [e.g. Blue-gray Gnatcatcher (*Polioptila caerulea*)]. Understory-nesters, such as the Ovenbird (*Seiurus aurocapillus*), were less common in restored sites. Restoration efforts in the Ozark National Forest have begun to return both vegetation and bird communities to an oak woodland state; however, without periodic fire, this diverse and imperiled ecosystem will likely not persist.

Keywords: oak woodland restoration, habitat structure, forest bird community, nesting guild, Ozark Mountains, Arkansas

1. Introduction

Oak woodlands and savannas are fire-adapted ecosystems characterized by oaks (*Quercus* spp.), low tree density, and an herbaceous understory of grasses and forbs (Nuzzo, 1986; Nelson, 2005). Although the distinction between “woodland” and “savanna” is sometimes unclear, woodlands are generally considered to have more trees (and subsequent canopy cover, 30-70%) than savannas (10-30% canopy cover) (Brawn *et al.*, 2001; Nelson, 2005). These transitional communities between prairie and forests were once common in parts of the U.S. prior to European settlement, with an estimated coverage in the Midwest of more than 11 million hectares; however, the current extent of these ecosystems is estimated to be less than 1% of their former range because of loss or degradation due to agricultural conversion, urban development, and logging practices (Nuzzo, 1986; McPherson, 1997). Woodlands and savannas have especially suffered from a lack of fire because low intensity fires occurring at regular intervals (1-10 years) are thought to have been a major part of the historical disturbance regime that helped maintain these ecosystems prior to the fire suppression campaigns of the 20th century (Abrams, 1992). With no fires to interrupt ecological succession, the remaining areas of woodlands and savannas have developed into closed-canopy forests with shade-tolerant, woody understories (Bray, 1960; Nuzzo, 1986).

Improved understanding of the historical prevalence and current imperilment of oak woodlands (Noss and Peters, 1995) has motivated management plans for returning densely forested areas to open woodlands (McPherson, 1997; Johnson *et al.*, 2002). In 2001, the USDA Forest Service and other partners initiated a landscape-scale woodland restoration project to restore over 25,000 hectares of primarily oak ecosystems in the Ozark National Forest, Arkansas (Andre *et al.*, 2009). The project focuses on six restoration areas scattered across the Big Piney

Ranger District. The major goals are to reduce tree density (i.e., basal area) through silvicultural treatments, and to reintroduce fire into ecosystems where it had been suppressed since the mid-1900s. Decreasing basal area by mechanical thinning reduces competition for resources among trees and reduces canopy cover, which allows light to reach the forest floor, promoting the growth of understory vegetation (Johnson *et al.*, 2002). Frequent, low intensity fires help regenerate oaks, reduce midstory and understory strata by removing fire-intolerant saplings and shrubs, and promote the growth of grasses and forbs (Barnes and Van Lear, 1998; Artman *et al.*, 2001; Brose *et al.*, 2006). The result is an open woodland habitat with less canopy cover and an understory dominated by herbaceous cover.

The shift in species composition and structure of the forest that occurs with woodland restoration influences wildlife communities. Of particular concern are Neotropical migratory bird species that breed in the Ozarks, some populations of which have declined in the last half-century (Robbins *et al.*, 1989; Askins, 2000; La Sorte *et al.*, 2007). Removal of overstory trees reduces nesting sites for birds that utilize the canopy, but promotes woody understory growth, which benefits shrub-nesting species (Rodewald and Smith, 1998; Greenberg *et al.*, 2007). When thinning is combined with repeated fire, however, shrub and sapling densities eventually decline, creating an open understory with higher amounts of herbaceous cover (Peterson and Reich, 2001), which then decreases availability of shrub nesting habitat. In addition to nesting habitat, woodland restoration affects food availability for birds, which promotes generalists and lower canopy foragers in savannas (Davis *et al.*, 2000), and insectivores in closed-canopy forests (Au *et al.*, 2008). Thus, the changes in nesting habitat and food availability due to woodland restoration support bird species typically associated with early successional or forest edge

habitats, while discouraging species associated with interior, closed-canopy forests (Hunter *et al.*, 2001).

Since the restoration project in the Ozark National Forest began, progress has primarily been gauged via plant communities, although some research has investigated the responses of small mammals and birds (Brown, 2005; Andre *et al.*, 2007). Brown (2005) found that oak woodland restoration in the Ozarks led to more diverse avian communities in which open-habitat nesters, such as the Indigo Bunting (*Passerina cyanea*), were the most commonly encountered species. Canopy nesters [e.g. Red-eyed Vireo (*Vireo olivaceus*)] and ground-nesters [e.g. Ovenbird (*Seiurus aurocapillus*)] were more common in untreated forests. Brown's study was conducted in a restoration area called Middle Fork, one of six treatment units associated with the restoration project. No published studies have considered how birds in other areas of the restoration project have responded to thinning and burning treatments.

Further research is needed to explore how birds are responding to management in other restoration units in the Ozark National Forest, particularly since this project represents the first of this scale for the Arkansas Ozarks, which occur on the eastern edge of the historical distribution of midwestern oak savanna (McPherson, 1997). Thus, my objective was to determine the response of avian communities and populations to woodland restoration in the Piney restoration area, and to link these responses to changes in forest structure. To accomplish this, I surveyed bird communities in recently restored woodland sites and mature forest control sites over three years following thinning and burning treatments. I predicted that vegetation structure in restored sites would reflect conditions found in open woodlands (i.e., fewer trees, less canopy cover, more herbaceous ground cover). In addition, bird species associated with early successional and edge habitats [e.g. Indigo Bunting, Yellow-Breasted Chat (*Icteria virens*)] would be more

common in recently restored sites, while mature forest species [e.g. Red-eyed Vireo, Ovenbird, Worm-eating Warbler (*Helmitheros vermivorous*)] would be more common in control sites.

2. Materials and methods

2.1 Study area and management history

The study area was located in the Piney restoration area (about 5,000 hectares) of the Big Piney Ranger District of the Ozark National Forest, in Johnson County, Arkansas, U.S.A. (35°34'45"N, 93°14'34"W). Elevation of the study sites ranged from 400-575 m. The canopy of this upland forest was composed primarily of white oak (*Quercus alba* L.), northern red oak (*Q. rubra* L.), black oak (*Q. velutina* Lam.), and mockernut hickory (*Carya tomentosa* (L.) Nutt.). The understory was composed primarily of red maple (*Acer rubrum* L.), blackgum (*Nyssa sylvatica* Marsh.), black locust (*Robinia pseudoacacia* L.), and black cherry (*Prunus serrotina* Ehrh).

In ArcGIS® Desktop (ESRI, 2006), I used data layers for land cover and restoration practices (burning and thinning) provided by the USDA Forest Service (Ozark-St. Francis National Forests) to select sixteen recently restored survey points in mixed hardwood cover at least 300 m from the boundaries of treatment areas and at least 250 m apart from one another. When ground-truthed, the number of restored survey sites was narrowed to eight due to issues with accessibility and actual management history. Elevation, aspect, and slope were similar for all points. Treated points were located in areas mechanically thinned to 10-15 m²/ha and burned in 2004, and then burned again in 2007. Both burns were early growing season, low intensity fires with the goal of reducing fuel loads. Eight control points were located in adjacent, untreated forest (Figure 1).

2.2 Field sampling

For each of the 16 survey sites, four avian point count surveys were conducted by two observers (two surveys each) throughout the 2008, 2009, and 2010 breeding seasons (mid-May through June). During these ten-minute surveys (conducted between 0600 to 1000 hours), the species and number of all birds seen or heard within a 50 m radius were recorded (Hutto *et al.*, 1986). Surveys were not performed under adverse weather conditions (e.g., rain, wind) in order to maximize likelihood of detection (Martin *et al.*, 1997).

Using a modified protocol of James and Shugart (1970), two circular vegetation plots were established for each point count to measure habitat characteristics. One plot was located at the center of the point count, and another was positioned 35 m from the point count center in one of three randomly chosen directions: 120, 240, or 360°. Within a 5 m radius of the center of each vegetation plot, the following measurements were taken: canopy height, percent canopy cover (measured via spherical densiometer), number of saplings greater than 0.5 m in height in two diameter size categories [small (0-2.5 cm) and large (2.5-8 cm), measured 10 cm above ground], and percent ground cover (below 0.5 m) of grass, shrub, forb, fern, leaf litter, log, and rock/soil (estimated visually). Within an 11.3 m radius, I counted the number of trees in three diameter at breast height (dbh) size categories: small (8-23 cm), medium (23-38 cm), and large (>38 m). I also measured the vertical structure of vegetation using a vegetation profile board modified from Nudds (1977) at 10 m from the center in two directions (90° and 270°). See Table 1 for a description of variables and abbreviations.

2.3 Statistical analyses

Using JMP[®] (SAS Institute Inc., 2010), I performed principle components analysis (PCA) on 13 habitat variables to examine relationships among vegetation characteristics and

recently restored and control sites. Variables with PC loadings $>|0.4|$ were used in naming axes. Prior to PCA, some variables were either log or arcsine transformed to improve homogeneity of variance and normality (Sokal and Rohlf, 1995). I performed multivariate analysis of variance (MANOVA) on these variables, testing the effect of treatment within each year. Discriminant analysis (DA) was used to determine which variables best discriminated between forest treatments within each year. Finally, between treatment differences within years were examined for each variable using univariate F -tests.

Bird species that do not normally breed in the oak-hickory stands in the Ozarks, that were simply flying over, or that were detected only once over the three years of the study were not included in analyses. For a complete list of common and scientific names of species detected in 2008, 2009, and 2010 surveys, see Appendix 1.

Bird community analysis was performed using COMDYN4 (Hines *et al.*, 1999), which computes parameters reflecting spatial and temporal changes in communities based on the underlying jackknife estimator proposed by Burnham and Overton (1979), applied to species richness by Boulinier *et al.* (1998), and applied to community-dynamic parameters by Nichols *et al.* (1998). Community parameters (defined below with respect to this study) were estimated by comparing species detection patterns from presence/absence data between restored and control sites within each year. COMDYN4 utilizes summary data, which required collapsing detection histories for each species across sites within the three treatments for each year. For more detail on the specifics of data entry for COMDYN4, see Hines *et al.* (1999). Species richness (N) refers to the number of species occurring in an area at a given time. Extinction probability ($1-\phi$) is the proportion of species that go locally extinct when comparing control to restored sites. Species turnover ($1-\gamma$) is the proportion of species present in restored sites that are not present in control

sites. The rate of increase in species richness (λ) is a ratio of the estimated number of species present in restored sites to the estimated number present in control sites. Finally, the number of locally colonizing species (B) is an estimate of the number of species present in restored sites that are not present in control sites (Hines *et al.*, 1999).

Within each year, mean number of detections per survey occasion was calculated for each species at each point in restored and control sites. These species were classified into the following nesting guilds: canopy (included both sub-canopy and canopy nesters), cavity, understory (forest ground and shrub nesters) and open (open or edge habitat nesters). PCA was used to examine the ordination of plots based on mean number of detections for each bird species. Species with PC loadings $>|0.4|$ were used in naming axes. Within each year, the mean number of detections was compared between restored and control sites using the Wilcoxon sign-ranked test since count data could not be transformed to a normal distribution. Small sample size prohibited the use of software that would allow for estimates of population parameters that take into account heterogeneity in detection probability among treatments, species, or observers (Buckland *et al.*, 2001).

3. Results

3.1 Habitat characteristics

PCA of the habitat variables showed the first two principal components explained over 63% of the variance each year (Table 2). Restored and control plots were contrasted best in all years by PC1, on which canopy cover, leaf litter, small trees, and large trees had high positive loadings and grass, forb, low vegetation profile, high vegetation profile, and small saplings had high negative loadings (Table 2). Contrasts became less distinct in 2009 and 2010 (Figure 2).

MANOVA showed a significant effect of treatment in 2008 ($F_{1,14} = 4.97, P < 0.05$), 2009 ($F_{1,14} = 6.40, P < 0.05$), and 2010 ($F_{1,14} = 12.05, P < 0.05$). DA showed that in 2008, small trees ($F_{1,14} = 25.94, P < 0.01$) and grass ($F_{1,13} = 17.42, P < 0.01$) were important in discriminating between treatments; this trend continued into 2009 (small trees, $F_{1,14} = 10.17, P < 0.01$; grass, $F_{1,13} = 9.70, P < 0.01$). In 2010, these variables were still important (small trees, $F_{1,14} = 36.78, P < 0.01$; grass, $F_{1,12} = 4.96, P < 0.05$), but so too were medium trees ($F_{1,13} = 9.77, P < 0.01$).

Within year comparisons of habitat variables between treatments in each year showed that recently restored sites had more grass and forb ground cover, and vertical vegetation was denser. In 2008, small sapling density was higher in restored sites. In all years, control sites had more canopy cover, log ground cover, small trees, and large trees. Shrub ground cover and number of large saplings were greater in control sites in 2008. For habitat variable means, standard errors, and test results, see Table 3.

3.2 Avian community

For each year, a total of 64 point count surveys were completed and analyzed. In 2008, there were a total of 386 individuals of 33 species detected. In 2009, there were 373 total individuals representing 28 species detected. In 2010, there were 402 total individuals representing 33 species detected. Some species were detected only in recently restored woodland sites, while others were detected only in mature forest control sites (Appendix 1).

Community analysis showed differences in species richness and composition between restored and control sites in all years. In 2009 and 2010, recently restored sites had higher species richness (N) than control sites (Table 4). In 2008, confidence intervals overlapped for species richness; however, in this year (as well as 2008 and 2009) the rate of change in species richness (λ) was positive, indicating an increase in the number of species in restored sites when

compared to control sites. Detection probabilities were not different between treatments each year ($0.26 < P < 0.75$), so the alternative estimate of the rate of increase in species richness ($\text{alt}\lambda$) was used. In all years, species turnover ($1-\gamma$) occurred between control and restored sites, and restored sites had a significant number of locally colonizing species (B). Only 2010 exhibited a significant probability of extinction ($1-\phi$) for species found in control sites when compared to restored sites.

3.3 Avian populations

PCA using bird species abundance showed that the first two principal components explained at least 33% of the variance each year (Table 5). Restored and control plots were contrasted best in all years by PC1, on which Hairy Woodpecker, Carolina Wren, Blue-gray Gnatcatcher, Yellow-breasted Chat, and Indigo Bunting had high positive loadings, and Ovenbird and Worm-eating Warbler had high negative loadings (Table 5, see Appendix 1 for scientific names). PC2 did not successfully contrast treatment sites, but seemed to reflect some within treatment variation in abundances of various species. Contrasts between treatment sites on PC1 became less distinct over time (Figure 3).

In 2008, there were more total birds detected per point count in restored versus control sites, which was a pattern also seen for canopy, cavity, and open-nesting guilds (Table 6). Species exhibiting more detections in restored sites were: Eastern Wood-Pewee, Blue-gray Gnatcatcher, and Cerulean Warbler (canopy-nesters); Hairy Woodpecker, Carolina Chickadee, White-breasted Nuthatch, and Carolina Wren (cavity-nesters); and Yellow-breasted Chat and Indigo Bunting (open-nesters). The understory-nesting guild and its members the Ovenbird and Worm-eating Warbler were detected more often in control sites.

In 2009, number of detections for total birds and the guilds of canopy, cavity, and open-nesters remained higher in restored sites (Table 7). The canopy-nesting Blue-gray Gnatcatcher, cavity-nesting Hairy Woodpecker, and open-nesting Yellow-throated Vireo, Yellow-breasted Chat, and Indigo Bunting were detected more often in restored sites. Although the understory-nesting guild did not differ in detections between restored and control sites, Ovenbirds were detected more often (and only) in control sites.

In 2010, total birds, cavity-nesters, and open-nesters were detected more often in restored sites (Table 8). The individual species from these guilds that were more common in restored sites were Hairy Woodpecker and Carolina Wren (cavity), and Yellow-breasted Chat and Indigo Bunting (open). The number of detections for canopy-nesters did not differ between treatments, but Blue-Gray Gnatcatchers were detected more often in restored sites. Likewise, the number of understory-nesters detected overall was not different between treatments; however, Hooded Warblers were more common in restored sites, while Ovenbirds were more common in control sites.

4. Discussion

Restoration efforts in the Piney unit of the woodland ecosystem restoration project were successful in creating habitat resembling oak woodlands that supported bird communities distinct from surrounding closed-canopy forest. In restored sites, bird communities had higher species richness and different species composition compared to control sites. Restored sites consistently hosted species typically associated with early successional habitats, such as Indigo Bunting and Yellow-breasted Chat, but they did not support mature, interior forest birds like the Ovenbird. Differences between restored and control sites diminished with time since burn.

Recently restored woodland sites and mature forest sites were distinct in their vegetative structure in all years. Restored sites exhibited characteristics of oak woodlands such as less canopy cover, fewer trees, and more prominent herbaceous ground cover. Control sites maintained more canopy cover, log ground cover, and trees. Similar results were reported by other studies examining the effects of thinning and/or prescription burns on forest vegetation (Blake, 2005; Hartung and Brawn, 2005; Jenkins and Jenkins, 2006; Au *et al.*, 2008). Although several habitat variables suggested restored sites were approaching a woodland state, the presence of thick understory vegetation (evidenced by greater vegetation profiles) in restored sites indicated that treated sites were not completely restored. Future burns at regular intervals should help reduce this flush of woody growth and promote herbaceous ground cover (Nuzzo, 1986; Brawn *et al.*, 2001).

Avian community richness was greater and species composition was different in recently restored sites compared to mature forest sites. Community dynamics indicated species turnover, an increase in species richness, and significant numbers of colonizing species when comparing control to restored sites. When examining community composition, restored sites hosted more early successional species (e.g., Indigo Bunting, Yellow-breasted Chat), and some species that were never recorded in control sites (e.g., White-eyed Vireo, Blue-winged Warbler, Prairie Warbler, Eastern Towhee). Likewise, control sites hosted species commonly associated with mature, closed-canopy forest, some of which were never detected in restored sites (e.g., Acadian Flycatcher, Ovenbird, Black-throated Green Warbler). Brown (2005) also found higher diversity of birds on restored sites in the Middle Fork unit of the this woodland restoration project. The increase in species richness is likely due to the nature of woodland as a transitional stage between prairie and forest. The heterogeneity in habitat characteristics can meet the needs (both

nesting and foraging) of a wider variety of birds than either prairie or forest alone (Temple, 1998).

The number of detections for individual species was also influenced by woodland restoration. Total number of birds detected was greater in restored sites in all years, which was due in large part to open-nesters. These results are consistent with studies showing early successional species to be more common in restored savannas or woodlands (Blake, 2005; Brawn, 2006; Grundel and Pavlovic, 2007; Comer *et al.*, 2011). Most species in this guild nest in habitat characterized by openings or edges with shrubby growth or low scrub (Baicich and Harrison, 1997), which were key features of the recently restored sites (i.e., 60-70% canopy cover, thick vegetation <2 m tall). Yellow-breasted Chat and Indigo Bunting were more common in restored sites across years, which is consistent with Brown (2005). All other open-nesters tended to be detected more often on restored sites (and sometimes only on restored sites) but their numbers were not great enough to show a significant difference.

The cavity-nesting guild was also more common in restored sites in all years. In 2008, four species of cavity nesters (Hairy Woodpecker, Carolina Chickadee, White-breasted Nuthatch, and Carolina Wren) were detected more often in restored sites. Woodpeckers, chickadees, and nuthatches nest and forage on snags (Bagne *et al.*, 2008), which can be created by fire (Horton and Mannan, 1988; Harrod *et al.*, 2009). Recently burned sites might have had more snags to provide nesting and foraging habitat for these species, thus resulting in more individuals; however, since snags were not counted, this explanation is speculative. Hairy Woodpeckers were the only cavity-nester to remain more common in restored sites in 2009 and 2010. As time since fire passes, snag abundance decreases (Drapeau *et al.*, 2009), so perhaps there were fewer snags to support all cavity nesting species.

Canopy-nesters initially were more common in restored areas, which can be attributed to species that utilize openings in mature forests like Eastern Wood-Pewee (McCarty, 1996), Blue-gray Gnatcatcher (Kershner and Ellison, 2012), and Cerulean Warbler (Hamel, 2000). As time since treatment increased, only the Blue-gray Gnatcatcher remained more common in restored sites. The similarity between treatments in detections of canopy-nesters in 2010 might indicate that the canopy was beginning to close, which is supported by the 10% increase in canopy cover when comparing 2008 to 2010. Based on Brown (2005), I expected some canopy species would be less common in restored sites (e.g., Red-eyed-Vireo, Acadian Flycatcher), however their numbers of detections were similar between treatments. This result is not surprising since some studies have shown no response of mature forest canopy-nesters to woodland restoration (Blake, 2005; Brawn, 2006). Perhaps a more substantial reduction in canopy cover (e.g., to oak savanna levels of 10-30%) is necessary to induce significant responses in some canopy-nesters.

Understory-nesters were the only guild that demonstrated more detections per survey in mature forest sites than woodland sites (but only for 2008). This difference was mostly due to Ovenbird and Worm-eating Warbler, which both nest on the ground in leaf litter of interior forests (Baicich and Harrison, 1997). Ovenbird was the only understory-nester to remain more common in control sites in all years. In 2009, Hooded Warbler was detected more often in restored woodlands, which offset the general trend for understory birds to be more common in mature forest. Unlike the Ovenbird, Hooded Warblers are gap-dependent forest birds that nest in low, shrubby habitat, which was plentiful in restored sites, as evidenced by the dense vegetation profile. It is likely this thick undergrowth was also one factor that deterred Ovenbirds and Worm-eating Warblers from nesting in restored sites since they are associated with less dense understories (Baicich and Harrison, 1997; Burke and Nol, 1998).

Management of the Piney unit in the Ozark National Forest using mechanical thinning and periodic fire seems to be working to meet the goals of the woodland restoration project. The number of trees and canopy cover has decreased, and ground cover contains more grasses and forbs. In response, bird communities have shifted to resemble those found in oak woodlands in other parts of the U.S. (Brawn *et al.*, 2001). Some studies suggest using either thinning or burning (instead of both approaches) does not effectively restore closed-canopy forests to open woodlands (Au *et al.*, 2008; Comer *et al.*, 2011). This study demonstrates that a combined approach helps get managers close to their goal, and it does so rather quickly (<4 years). Few studies have tracked vegetation and birds beyond one or two years post-treatment (Artman *et al.*, 2001). This study suggests that restored woodland communities change with time since fire, which highlights that fire intervals should be kept regular or else the distinction between woodlands and the surrounding forest begins to fade.

As compelling as these results appear, interpretation and generalization must proceed with caution for several reasons. First, a small number of treatment units were available for study due to mixed management histories. The size and accessibility of the units were also limiting, thus only eight points per treatment could be surveyed. Second, since birds are mobile there is potential for some surveys points to lack independence given their proximity; however, I attempted to minimize this by limiting the point count radius to 50 m and omitting suspected repeat detections from analysis. Third, since pre-restoration data were not available, this study assumes that there were no differences between restored and control sites before treatment. Given the similarities between control sites, this assumption is likely met. Finally, the small data set could not be analyzed with software that computes estimates for population parameters that take into account heterogeneity in detectability among species, sites, or observers. It is possible

that birds were more easily detected in restored sites because visibility is improved in open habitat. If this is true, then diversity and number of detections could be underestimated in control sites. Although population analysis did not take into account detectability, community analysis indicated there was no difference in detection probability between treatments.

Conclusion

This study provides evidence that woodland restoration via thinning and burning has been partially successful in returning at least one area of the Ozark National Forest to woodland-like conditions, both in terms of vegetation and bird communities. However, three years after the most recent burn, bird communities and vegetation structure demonstrated less distinction than one year after fire. Thus, these areas still require periodic fire to continue and maintain a complete transition from closed-canopy forest to open woodland. Although some forest understory-nesting species might decline locally with continued restoration, this study indicates that there are more canopy, cavity, and open-nesting species that benefit from the establishment of oak woodlands in the Ozarks.

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Tables

Table 1. Structural habitat variables measured in vegetation plots at recently restored woodland and mature forest control sites in the Ozark National Forest, Arkansas.

Habitat Variable	Abbreviation
<hr/> Measured within 5-m radius <hr/>	
Mean percent canopy cover	CanCov
Percent grass cover (below 0.5 m)	Grass
Percent shrub cover (below 0.5 m)	Shrub
Percent forb (below 0.5 m)	Forb
Percent fern cover (below 0.5 m)	Fern
Percent log cover (below 0.5 m)	Log
Percent leaf litter cover (below 0.5 m)	Leaf
Number of small saplings 0-2.5 cm	Sap1
Number of large saplings 2.5-8 cm	Sap2
<hr/> Measured within 11.3-m radius <hr/>	
Low vegetation profile (number squares $>1/2$ obscured by vegetation form 0-1 m)	LowVP
High vegetation profile (number squares $>1/2$ obscured by vegetation form 1-2 m)	HighVP
Number of small trees (8-23 cm dbh)	Tree3
Number of medium trees (23-38 cm dbh)	Tree4
Number of large trees (>38 cm dbh)	Tree5

Table 2. Habitat variables and their respective loadings on the first two principal components measured over three years at recently restored woodland and mature forest control sites in the Ozark National Forest, Arkansas. Definitions of variables are given in Table 1.

Habitat variable	2008		2009		2010	
	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2
CanCov	0.92	-0.03	0.90	0.14	0.79	0.32
Grass	-0.84	-0.17	-0.84	-0.12	-0.86	-0.14
Shrub	0.50	-0.43	0.04	0.88	-0.04	0.88
Forb	-0.81	0.13	-0.79	-0.38	-0.81	-0.32
Leaf	0.81	0.45	0.89	-0.19	0.91	-0.29
Log	0.62	-0.13	-0.24	0.14	0.09	0.48
LowVP	-0.88	-0.08	-0.85	0.21	-0.79	-0.01
HighVP	-0.89	0.00	-0.64	0.42	-0.75	0.02
Sap1	-0.59	0.52	-0.45	0.64	-0.45	0.69
Sap2	0.64	0.36	0.62	-0.04	0.31	-0.36
Tree3	0.94	-0.05	0.90	0.07	0.94	0.11
Tree4	0.57	-0.73	0.27	0.56	0.77	-0.03
Tree5	0.71	0.56	0.78	0.22	0.73	-0.03
Proportion of variance explained	0.58	0.13	0.48	0.15	0.49	0.15
Total proportion of variance explained	0.71		0.63		0.64	

Table 3. Means, standard errors (SE), and results of *F* tests of 13 vegetation variables measured over three years in recently restored woodland and mature forest control plots (n=8 each) in the Ozark National Forest, Arkansas. Significant differences indicated by bold text.

Habitat Variable	Year	Restored Mean (SE)	Control Mean (SE)	<i>F</i> _{1,14}	<i>P</i>
Canopy Cover	2008	61.29 (5.33)	93.89 (0.61)	52.86	<0.001
	2009	53.82 (9.32)	90.95 (2.90)	16.64	<0.01
	2010	69.16 (8.75)	95.61 (0.80)	11.40	<0.01
Percent Grass	2008	21.50 (4.41)	1.31 (0.37)	40.14	<0.001
	2009	17.75 (4.44)	0.69 (0.42)	30.76	<0.001
	2010	17.56 (4.43)	1.75 (0.56)	24.03	<0.001
Percent Shrub	2008	25.13 (4.41)	43.00 (5.69)	6.11	<0.05
	2009	26.35 (5.38)	25.63 (5.49)	0.00	0.986
	2010	28.19 (5.03)	29.75 (6.23)	0.07	0.798
Percent Forb	2008	33.13 (7.78)	4.50 (1.71)	17.41	<0.001
	2009	21.56 (5.25)	1.75 (0.83)	24.39	<0.001
	2010	27.19 (6.40)	1.63 (0.40)	29.06	<0.001
Percent Log	2008	9.13 (2.12)	36.50 (6.14)	18.36	<0.001
	2009	17.19 (3.09)	52.94 (7.51)	19.58	<0.001
	2010	15.56 (3.90)	49.69 (7.76)	13.45	<0.01
Percent Leaf	2008	10.38 (1.15)	13.75 (1.28)	4.01	0.065
	2009	9.13 (1.54)	12.06 (5.60)	0.01	0.908
	2010	6.44 (0.36)	11.88 (4.21)	1.66	0.218
Low Veg Profile	2008	13.16 (0.89)	5.50 (1.11)	20.57	<0.001
	2009	14.03 (0.44)	9.91 (0.58)	29.18	<0.001
	2010	42.97 (3.41)	26.06 (3.33)	9.30	<0.01
High Veg Profile	2008	49.31 (5.84)	12.97 (3.02)	21.51	<0.001
	2009	62.72 (6.17)	37.88 (3.89)	9.27	<0.01
	2010	48.56 (0.91)	33.03 (3.39)	9.54	<0.01
Sapling 1	2008	178.94 (42.09)	95.94 (14.83)	5.73	<0.05
	2009	104.00 (19.63)	94.63 (43.51)	1.29	0.275
	2010	123.81 (10.44)	113.44 (31.33)	1.09	0.315
Sapling 2	2008	1.44 (0.50)	6.00 (1.16)	18.08	<0.001
	2009	1.06 (0.48)	3.38 (0.66)	10.84	<0.01
	2010	2.13 (0.59)	3.81 (0.69)	3.84	0.070
Tree 3	2008	2.56 (0.52)	14.94 (2.03)	55.31	<0.001
	2009	1.69 (0.630)	10.81 (1.84)	31.68	<0.001
	2010	2.13 (0.46)	13.88 (1.40)	59.00	<0.001
Tree 4	2008	3.38 (0.49)	5.25 (0.91)	3.94	0.083
	2009	3.50 (0.70)	4.06 (0.80)	0.32	0.579
	2010	2.81 (0.52)	5.44 (1.4)	4.59	0.050
Tree 5	2008	0.69 (0.21)	2.25 (0.40)	11.80	<0.01
	2009	0.50 (0.19)	1.31 (0.23)	7.85	<0.05
	2010	1.06 (0.29)	2.31 (0.37)	7.39	<0.05

Table 4. Avian community parameters^a, bootstrap averages, standard errors (SE), and 95% confidence intervals (CI) estimated by comparing bird species detected in 2008, 2009, and 2010 point count surveys in recently restored woodland and mature forest control sites (n=8 each) in the Ozark National Forest, Arkansas.

Year	Parameter	Estimate	Bootstrap Average	SE	95% CI	
					Lower	Upper
2008	N_{Control}	22.36	23.88	3.75	19.00	34.12
	N_{Restored}	31.22	32.32	3.78	28.00	43.24
	$1 - \phi$	0.14	0.16	2.85	0.00	0.46
	$1 - \gamma$	0.42	0.44	0.11	0.23	0.63
	$\text{alt}\lambda$	1.47	1.47	0.16	1.19	1.87
	B	12.10	12.36	5.49	0.47	22.70
2009	N_{Control}	18.25	18.48	2.38	16.00	25.50
	N_{Restored}	27.35	28.23	1.48	26.00	31.40
	$1 - \phi$	0.03	0.08	0.09	0.00	0.31
	$1 - \gamma$	0.40	0.41	0.11	0.15	0.62
	$\text{alt}\lambda$	1.63	1.63	0.17	1.39	2.00
	B	9.67	11.37	2.63	5.17	15.89
2010	N_{Control}	20.55	22.10	1.43	20.00	24.79
	N_{Restored}	26.47	28.02	1.38	26.47	30.95
	$1 - \phi$	0.26	0.27	0.11	0.03	0.48
	$1 - \gamma$	0.43	0.44	0.10	0.24	0.63
	$\text{alt}\lambda$	1.30	1.30	0.06	1.24	1.44
	B	11.31	11.95	2.92	5.93	16.82

^a N - estimated number of species present

$1 - \phi$ - estimated extinction probability

$1 - \gamma$ - estimated species turnover

$\text{alt}\lambda$ - estimated rate of change of species richness

B - estimated local colonizing species

Table 5. Loading scores of bird species for the first two principal components from PCA using mean detections per point count (n=32) on restored woodland and control forest sites in the Ozark National Forest, Arkansas. A dash indicates a species was not detected that year.

Species	Code	2008		2009		2010	
		PC 1	PC 2	PC 1	PC 2	PC 1	PC 2
Yellow-billed Cuckoo	YBCU	-	-	-	-	-0.29	-0.31
Ruby-throated Hummingbird	RTHU	-0.16	-0.11	0.41	0.48	-0.04	0.53
Red-bellied Woodpecker	RBWO	0.30	0.58	0.38	0.09	0.08	-0.29
Downy Woodpecker	DOWO	0.22	0.43	-	-	0.30	-0.18
Hairy Woodpecker	HAWO	0.50	0.25	0.74	0.37	0.66	-0.15
Pileated Woodpecker	PIWO	-	-	0.12	-0.49	-	-
Eastern Wood-Pewee	EAWP	0.51	0.43	0.03	-0.13	0.16	-0.14
Acadian Flycatcher	ACFL	-0.41	-0.04	-	-	-	-
White-eyed Vireo	WEVI	0.61	-0.70	-	-	0.43	-0.04
Yellow-throated Vireo	YTVI	0.21	0.17	0.44	-0.51	0.08	-0.12
Red-eyed Vireo	REVI	-0.27	0.13	0.03	0.26	-0.42	0.41
Blue Jay	BLJA	0.20	0.38	0.32	-0.72	0.35	0.42
Carolina Chickadee	CACH	0.47	0.36	-0.06	-0.03	0.61	-0.23
Tufted Titmouse	TUTI	0.05	-0.05	0.22	0.14	0.49	0.42
White-breasted Nuthatch	WBNU	0.75	-0.10	0.57	-0.52	0.21	0.50
Carolina Wren	CARW	0.67	-0.03	0.50	0.11	0.65	0.39
Blue-gray Gnatcatcher	BGGN	0.83	0.02	0.72	0.53	0.49	0.67
Ovenbird	OVEN	-0.48	-0.15	-0.43	0.01	-0.49	-0.23
Worm-eating Warbler	WEWA	-0.47	-0.30	-0.45	0.16	-0.46	0.35
Blue-winged Warbler	BWWA	0.61	-0.70	-	-	0.74	-0.44
Black-and-white Warbler	BAWW	-0.48	-0.15	-0.31	0.41	0.07	0.13
Kentucky Warbler	KEWA	0.37	0.58	0.33	0.32	-	-
Hooded Warbler	HOWA	-0.11	0.52	0.61	-0.05	0.50	0.72
Cerulean Warbler	CERW	0.85	-0.23	0.52	0.44	0.21	0.66
Pine Warbler	PIWA	0.28	-0.54	-	-	-0.27	-0.15
Yellow-throated Warbler	YTWA	0.10	0.06	0.25	0.29	-	-
Prairie Warbler	PRAW	0.61	-0.70	0.34	-0.74	0.39	-0.13
Black-throated Green Warbler	BTNW	0.14	0.45	-0.45	0.01	-0.36	-0.25
Yellow-breasted Chat	YBCH	0.59	-0.12	0.68	-0.25	0.83	-0.37
Eastern Towhee	EATO	0.16	0.29	0.28	-0.69	0.58	-0.31
Scarlet Tanager	SCTA	-0.08	0.42	0.09	0.42	-0.56	0.26
Summer Tanager	SUTA	0.31	0.50	0.20	0.29	-0.33	-0.13
Northern Cardinal	NOCA	-0.31	-0.11	-	-	-0.33	-0.13
Indigo Bunting	INBU	0.88	0.17	0.57	-0.11	0.81	0.03
Brown-headed Cowbird	BHCO	-	-	-	-	0.60	-0.41
American Goldfinch	AMGO	-0.13	-0.12	0.45	0.54	0.01	0.76
Proportion of variance explained		0.21	0.14	0.18	0.15	0.21	0.14

Table 6. Mean detections and standard error (SE) per point count for bird nesting guilds and species detected in 2008 on recently restored woodland and mature forest control sites (n=8 each) in the Ozark National Forest, Arkansas. Significant differences indicated by bold text.

Species	Restored		Control		Wilcoxon Test	
	Mean	SE	Mean	SE	Z	P
Total birds	8.34	0.48	3.65	0.42	-3.31	<0.001
Canopy-nesters	2.50	0.31	1.80	0.23	-1.90	<0.05
Ruby-throated Hummingbird	0.00	0.00	0.03	0.03	0.88	0.382
Eastern Wood-Pewee	0.38	0.08	0.09	0.07	-2.28	<0.05
Acadian Flycatcher	0.00	0.00	0.06	0.04	1.37	0.170
Red-eyed Vireo	1.06	0.14	1.33	0.23	1.12	0.264
Blue Jay	0.06	0.06	0.00	0.00	-0.88	0.382
Blue-gray Gnatcatcher	0.50	0.09	0.00	0.00	-3.56	<0.001
Cerulean Warbler	0.13	0.06	0.00	0.00	-2.52	<0.05
Pine Warbler	0.09	0.05	0.09	0.07	0.39	0.700
Black-throated Green Warbler	0.06	0.04	0.03	0.03	-0.54	0.587
Summer Tanager	0.03	0.03	0.00	0.00	-0.88	0.382
Scarlet Tanager	0.13	0.07	0.16	0.07	0.35	0.723
Understory-nesters	0.47	0.17	1.31	0.27	2.33	<0.05
Ovenbird	0.00	0.00	0.41	0.13	2.49	<0.05
Worm-eating Warbler	0.00	0.00	0.25	0.09	2.50	<0.05
Black-and-white Warbler	0.03	0.03	0.19	0.08	1.60	0.109
Kentucky Warbler	0.09	0.05	0.00	0.00	-1.37	0.171
Hooded Warbler	0.34	0.12	0.31	0.09	-0.11	0.914
Northern Cardinal	0.00	0.00	0.03	0.03	0.88	0.382
Cavity-nesters	1.78	0.20	0.38	0.13	-3.23	<0.01
Red-bellied Woodpecker	0.19	0.07	0.06	0.04	-1.49	0.114
Downy Woodpecker	0.06	0.04	0.03	0.03	-0.54	0.587
Hairy Woodpecker	0.31	0.10	0.06	0.04	-2.03	<0.05
Carolina Chickadee	0.47	0.13	0.13	0.07	-2.21	<0.05
Tufted Titmouse	0.03	0.03	0.00	0.00	-0.88	0.382
White-breasted Nuthatch	0.41	0.12	0.09	0.07	-1.98	<0.05
Carolina Wren	0.31	0.10	0.00	0.00	-2.50	<0.05
Open-nesters	3.59	0.27	0.16	0.10	-3.40	<0.001
White-eyed Vireo	0.06	0.04	0.00	0.00	-0.88	0.382
Yellow-throated Vireo	0.13	0.11	0.00	0.00	-1.37	0.171
Blue-winged Warbler	0.06	0.04	0.00	0.00	-8.75	0.282
Yellow-throated Warbler	0.06	0.04	0.09	0.07	-0.39	0.700
Prairie Warbler	0.03	0.03	0.00	0.00	-8.75	0.382
Yellow-breasted Chat	0.44	0.09	0.00	0.00	-2.84	<0.01
Eastern Towhee	0.09	0.05	0.00	0.00	-1.37	0.171
Indigo Bunting	2.69	0.18	0.03	0.03	-3.46	<0.001
American Goldfinch*	0.03	0.03	0.63	0.63	-	-

*Wilcoxon test could not successfully be calculated.

Table 7. Mean detections and standard error per point count for bird nesting guilds and species detected in 2009 on recently restored woodland and mature forest control sites (n=8 each) in the Ozark National Forest, Arkansas. Significant differences indicated by bold text.

Species	Restored		Control		Wilcoxon Test	
	Mean	SE	Mean	SE	Z	P
Total birds	7.75	0.23	3.63	0.44	-3.32	<0.001
Canopy-nesters	2.47	0.30	1.50	0.17	-2.34	<0.05
Ruby-throated Hummingbird	0.13	0.07	0.03	0.03	-1.11	0.267
Eastern Wood-Pewee	0.09	0.05	0.06	0.06	-0.83	0.405
Red-eyed Vireo	1.19	0.08	1.22	0.14	0.05	0.956
Blue Jay	0.03	0.03	0.00	0.00	-0.88	0.382
Tufted Titmouse	0.06	0.04	0.00	0.00	-1.37	0.170
Blue-gray Gnatcatcher	0.66	0.14	0.00	0.00	-3.21	<0.01
Cerulean Warbler	0.13	0.07	0.00	0.00	-1.77	0.076
Black-throated Green Warbler	0.00	0.00	0.03	0.03	0.88	0.382
Summer Tanager	0.06	0.04	0.03	0.03	-0.54	0.587
Scarlet Tanager	0.13	0.09	0.13	0.05	0.68	0.498
Understory-nesters	1.00	0.16	1.19	0.19	0.64	0.489
Ovenbird	0.00	0.00	0.25	0.13	2.14	<0.05
Worm-eating Warbler	0.03	0.03	0.13	0.07	1.11	0.267
Black-and-white Warbler	0.28	0.10	0.50	0.11	1.36	0.173
Kentucky Warbler	0.03	0.03	0.00	0.00	-0.88	0.382
Hooded Warbler	0.66	0.14	0.31	0.14	-1.61	0.108
Cavity-nesters	1.84	0.25	0.75	0.25	-2.21	<0.05
Red-bellied Woodpecker	0.13	0.09	0.00	0.00	-1.37	0.171
Hairy Woodpecker	0.41	0.09	0.09	0.05	-2.39	<0.05
Pileated Woodpecker*	0.06	0.04	0.06	0.04	-	-
Carolina Chickadee	0.25	0.11	0.19	0.10	-0.41	0.638
White-breasted Nuthatch	0.44	0.12	0.16	0.08	-1.67	0.094
Carolina Wren	0.56	0.18	0.25	0.14	-1.73	0.083
Open-nesters	2.44	0.43	0.19	0.09	-3.05	<0.01
Yellow-throated Vireo	0.19	0.06	0.00	0.00	-2.52	<0.05
Yellow-throated Warbler	0.06	0.06	0.00	0.00	-0.88	0.382
Prairie Warbler	0.06	0.04	0.00	0.00	-1.37	0.170
Yellow-breasted Chat	0.38	0.13	0.00	0.00	-2.49	<0.05
Eastern Towhee	0.06	0.04	0.00	0.00	-1.37	0.170
Indigo Bunting	1.59	0.32	0.19	0.09	-2.82	<0.01
American Goldfinch	0.09	0.05	0.00	0.00	-1.78	0.075

*Wilcoxon test could not successfully be calculated.

Table 8. Mean detections and standard error (SE) per point count for bird nesting guilds and species detected in 2010 on recently restored woodland and mature forest control sites (n=8 each) in the Ozark National Forest, Arkansas. Significant differences indicated by bold text.

Species	Restored		Control		Wilcoxon Test	
	Mean	SE	Mean	SE	Z	P
Total birds	7.84	0.40	4.31	0.34	-3.32	<0.001
Canopy-nesters	2.41	0.29	1.66	0.33	-0.26	0.791
Yellow-billed Cuckoo	0.00	0.00	0.06	0.04	1.37	0.170
Ruby-throated Hummingbird	0.03	0.03	0.00	0.00	-0.88	0.382
Eastern Wood-Pewee	0.31	0.16	0.09	0.07	-1.03	0.303
Red-eyed Vireo	1.38	0.15	1.41	0.12	0.11	0.914
Blue Jay	0.03	0.03	0.00	0.00	-0.88	0.382
Blue-gray Gnatcatcher	0.44	0.13	0.06	0.06	-2.32	<0.05
Cerulean Warbler	0.09	0.07	0.00	0.00	-1.37	0.171
Pine Warbler	0.00	0.00	0.03	0.03	0.88	0.382
Black-throated Green Warbler	0.00	0.00	0.19	0.12	1.77	0.076
Summer Tanager	0.00	0.00	0.03	0.03	0.88	0.382
Scarlet Tanager	0.13	0.07	0.31	0.09	1.51	0.131
Understory-nesters	1.16	0.14	1.31	0.31	0.21	0.832
Ovenbird	0.00	0.00	0.34	0.15	2.14	<0.05
Worm-eating Warbler	0.06	0.06	0.19	0.06	1.65	0.100
Black-and-white Warbler	0.59	0.08	0.56	0.19	-0.62	0.536
Hooded Warbler	0.50	0.07	0.19	0.06	-2.58	<0.01
Northern Cardinal	0.00	0.00	0.03	0.03	0.88	0.382
Cavity-nesters	2.19	0.16	0.56	0.19	-2.59	<0.01
Red-bellied Woodpecker*	0.03	0.03	0.03	0.03	-	-
Downy Woodpecker	0.06	0.04	0.00	0.00	0.17	0.143
Hairy Woodpecker	0.35	0.07	0.13	0.07	-2.00	<0.05
Carolina Chickadee	0.31	0.16	0.13	0.09	-0.97	0.332
Tufted Titmouse	0.18	0.34	0.06	0.04	-1.49	0.135
White-breasted Nuthatch	0.19	0.08	0.06	0.06	-1.35	0.178
Carolina Wren	0.53	0.12	0.15	0.07	-2.46	<0.05
Open-nesters	2.63	0.50	0.25	0.13	-3.28	<0.01
White-eyed Vireo	0.13	0.07	0.00	0.00	-1.77	0.076
Yellow-throated Vireo*	0.06	0.06	0.03	0.03	-	-
Blue-winged Warbler	0.13	0.07	0.00	0.00	-1.77	0.076
Prairie Warbler	0.03	0.03	0.00	0.00	-0.88	0.382
Yellow-breasted Chat	0.59	0.16	0.00	0.00	-3.20	<0.01
Eastern Towhee	0.13	0.07	0.00	0.00	-1.77	0.076
Indigo Bunting	1.38	0.18	0.22	0.10	-3.25	<0.01
Brown-headed Cowbird	0.13	0.09	0.00	0.00	-1.37	0.171
American Goldfinch	0.06	0.04	0.00	0.00	-1.37	0.170

*Wilcoxon test could not successfully be calculated.

Figures

Figure 1. Location of study sites in the Piney restoration area of the Ozark National Forest (in gray on state map), Arkansas. Recently restored woodland sites (n=8) were located in areas previously burned (gray) and thinned (dotted). Control forest sites (n=8) were located in adjacent untreated forest.

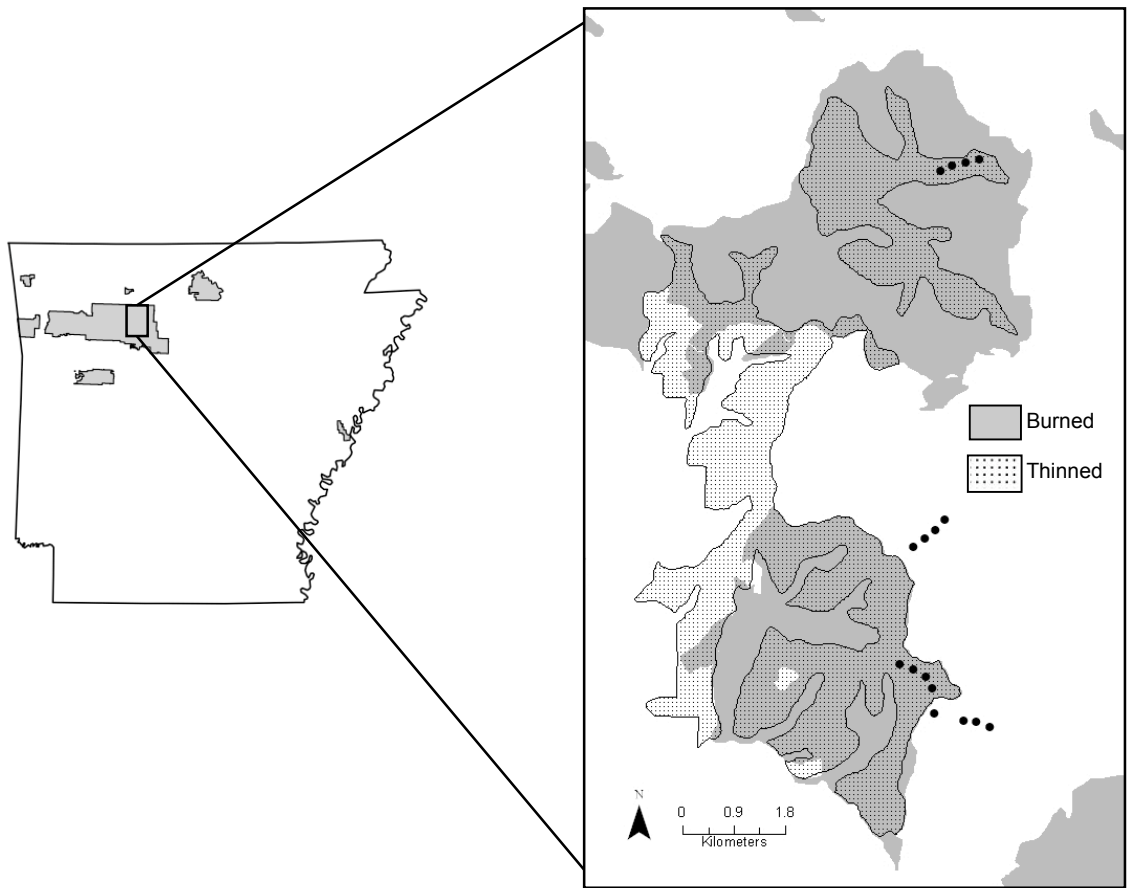


Figure 2. Plots of the first two principal components based on 13 habitat variables measured in recently restored woodland and mature forest control plots (n=8 each) in the Ozark National Forest, Arkansas. Definitions of variables are given in Table 1.

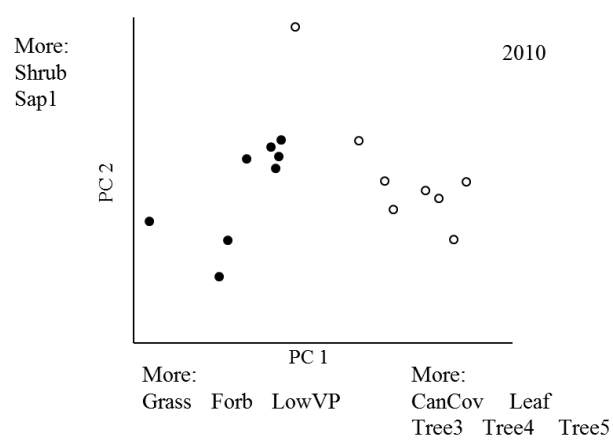
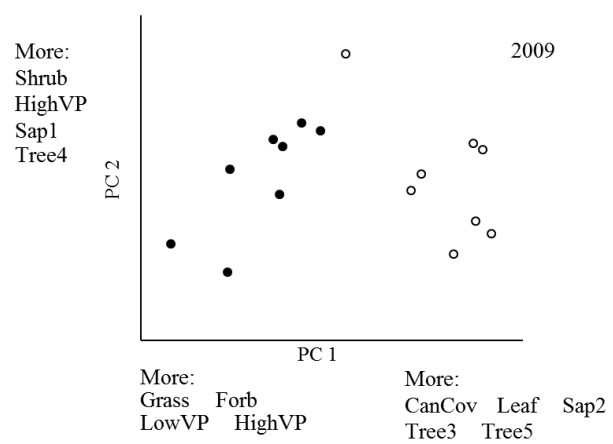
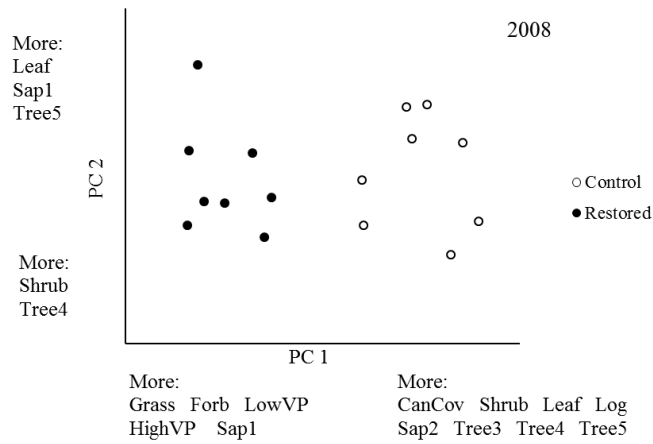
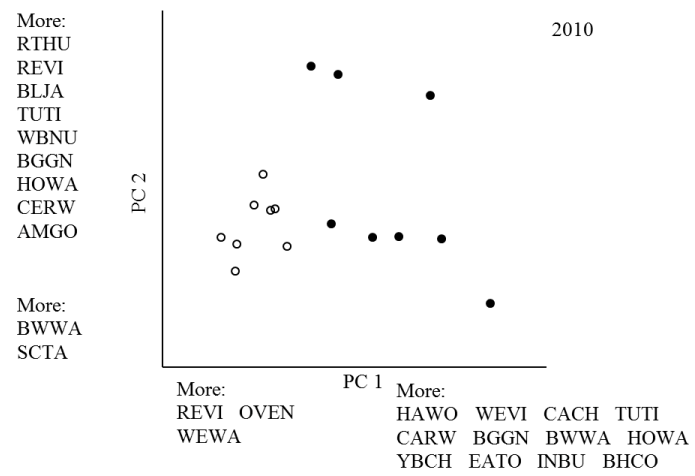
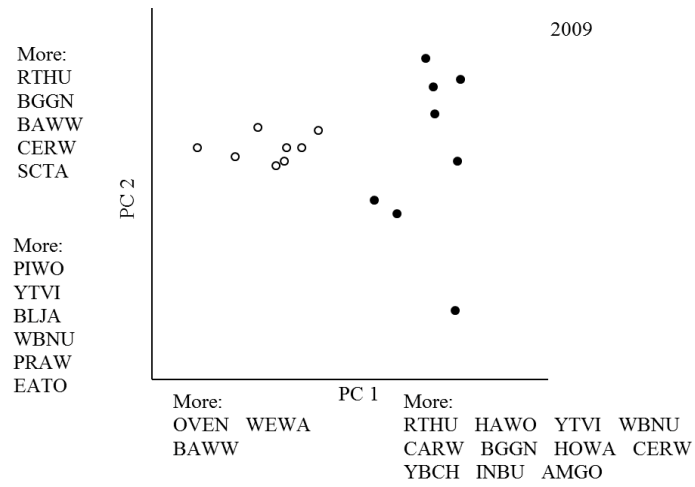
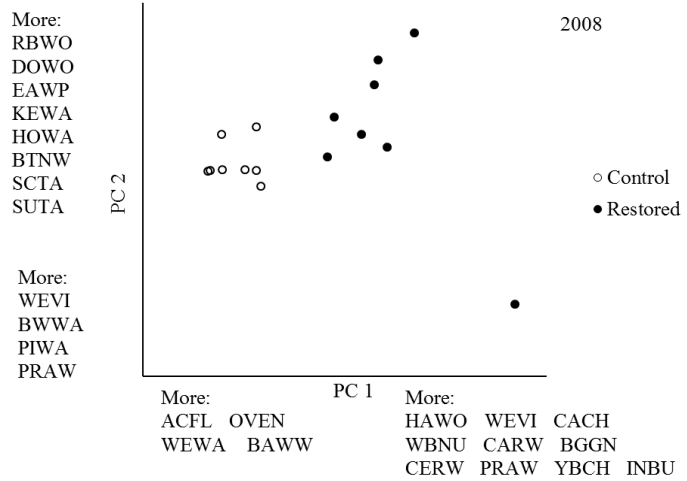


Figure 3. Plots of first two principal components based on mean number of detections for bird species surveyed on recently restored woodland and mature forest control sites (n=8 each) in the Ozark National Forest, Arkansas. Species codes are defined in Table 5.



Appendix 1. Bird species detected within 50 m radius point counts conducted during the breeding season in 2008, 2009, and 2010 in recently restored woodland and mature forest (control) sites in the Ozark National Forest, Arkansas.

Both Sites	Restored Only
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)	Red-headed Woodpecker (<i>Melanerpes erythrocephalus</i>)
Red-bellied Woodpecker (<i>Melanerpes carolinus</i>)	White-eyed Vireo (<i>Vireo griseus</i>)
Downy Woodpecker (<i>Picoides pubescens</i>)	Blue Jay (<i>Cyanocitta cristata</i>)
Hairy Woodpecker (<i>Picoides villosus</i>)	Blue-winged Warbler (<i>Vermivora cyanoptera</i>)
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	Kentucky Warbler (<i>Oporornis formosus</i>)
Eastern Wood-Pewee (<i>Contopus virens</i>)	Cerulean Warbler (<i>Setophaga cerulea</i>)
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	Prairie Warbler (<i>Setophaga discolor</i>)
Red-eyed Vireo (<i>Vireo olivaceus</i>)	Yellow-breasted Chat (<i>Icteria virens</i>)
Carolina Chickadee (<i>Poecile carolinensis</i>)	Eastern Towhee (<i>Pipilo erythrophthalmus</i>)
Tufted Titmouse (<i>Baeolophus bicolor</i>)	Brown-headed Cowbird (<i>Molothrus ater</i>)
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	
Carolina Wren (<i>Thryothorus ludovicianus</i>)	<hr/> Control Only <hr/>
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i>)	Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)
Worm-eating Warbler (<i>Helmitheros vermivorus</i>)	Acadian Flycatcher (<i>Empidonax virens</i>)
Black-and-White Warbler (<i>Mniotilta varia</i>)	Ovenbird (<i>Seiurus aurocapillus</i>)
Hooded Warbler (<i>Wilsonia citrina</i>)	Northern Cardinal (<i>Cardinalis cardinalis</i>)
Pine Warbler (<i>Setophaga pinus</i>)	
Yellow-throated Warbler (<i>Setophaga dominica</i>)	
Black-throated Green Warbler (<i>Setophaga virens</i>)	
Summer Tanager (<i>Piranga rubra</i>)	
Scarlet Tanager (<i>Piranga olivacea</i>)	
Indigo Bunting (<i>Passerina cyanea</i>)	
American Goldfinch (<i>Spinus tristis</i>)	

CHAPTER 5

Conclusion

Overall, forest bird communities in the Arkansas Ozarks demonstrated resilience to small-scale canopy openings created by disturbance events such as uneven-aged management and ice storm damage. However, when both fire and thinning were used in woodland restoration, avian communities and populations responded as predicted based on their nesting habitat requirements.

Uneven-aged management initially altered vegetation characteristics in treated plots, however these changes did not immediately influence avian communities or certain populations (other than benefiting Indigo Buntings). After fifteen years, the contrast between treatment plots in terms of habitat structure disappeared, and avian community and population parameters, although different overall from 1994, were still similar among treatments (including Indigo Buntings). These results indicate that uneven-aged management is an appropriate approach to timber harvest when the goal is to maintain the integrity of forest structure and minimize the short- and long-term impacts on the bird community over time.

Likewise, although a 2009 ice storm resulted in structural damage (in the form of canopy gaps and woody debris), avian communities and populations were unaffected. Avian species diversity and community composition remained similar to pre-storm levels in both high and low damage sites. Site occupancy fluctuated annually for Ovenbirds, Hooded Warblers, and Indigo Buntings, but these variations were consistent between high and low damage sites. The length of the study (i.e., two years post-storm) might not have been long enough to detect a delayed response; however, it is also likely that the frequent, but small, canopy openings and associated debris did not alter habitat structure enough to deter ground-nesters or attract gap-dependent species.

Woodland restoration, however, resulted in dramatic changes in vegetation characteristics, and avian communities and populations reflected these changes. Sites that were thinned and burned resembled woodland habitat with a more open canopy and herbaceous ground cover. Recently restored sites had higher avian species richness and communities composed of more early successional species, such as the Yellow-breasted Chat and Indigo Bunting. Some cavity- and canopy-nesters typical of more open forests were also more common in restored sites. Mature forest sites exhibited lower species richness, but more understory nesters like the Ovenbird and Worm-eating Warbler. These differences were most pronounced a year after the second fire treatment, and they diminished with time since fire. These results indicate restoration efforts have been partly successful in converting closed-canopy forest to a woodland-like state; however, fire treatments should be continued at regular intervals to achieve the desired goals of the project.

The overall results of this study suggest that small-scale forest disturbances, such as canopy gaps created by uneven-aged management or ice damage, have less influence on communities of forest birds than the combined effects of thinning and burning. Perhaps the responses of bird populations to woodland restoration might not have been as pronounced if detectability had been taken into account (as in the uneven-aged management and ice damage studies). Even if this is the case, vegetation and community analyses (which did account for detectability) indicated distinct differences between recently restored woodland and mature forest sites.

Another explanation could be that the nature of disturbance caused by uneven-aged management and ice damage is similar to that of tree-falls, which are disturbance events commonly experienced by birds living in mature forests. Fire, on the other hand, is less frequent

and has greater potential to remove woody understory and promote herbaceous growth. When these two disturbance events occur together, there is a shift from a forest with a few scattered gaps to an open woodland. Both ecosystems host unique assemblages of bird species, and thus, management plans should incorporate areas of both closed-canopy forest and woodland ecosystems in order to maximize habitat availability for breeding birds of the Ozark Mountains.