



# Cascading effects of oak woodland management: Higher arthropod biomass, avian richness, and abundance

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## ABSTRACT

Oak woodlands are threatened across North America due to land use change, fire exclusion, and the spread of invasive species following European settlement. Effective conservation of woodlands—and associated biodiversity—is dependent on management (prescribed fire and tree thinning) emulating natural disturbance and historic cultural burning. We examined the effects of woodland management during the avian breeding season in the upper Midwest (WI, USA), collecting data at three trophic levels: vegetation, arthropods, and insectivorous birds. Compared to unmanaged sites, managed sites had lower basal area, understory density and snag abundance, and higher tree diameter, herbaceous plant cover, and soil moisture. Mean caterpillar biomass was higher in managed sites, as was mean aerial insect biomass. Avian species richness was higher in managed sites, and was negatively associated with canopy cover and positively associated with herbaceous plant cover. Detection-corrected abundance estimates of the 21 most common insectivorous bird species indicated that ten species were more abundant in managed sites, four were more abundant in unmanaged sites, and seven were distributed equally. Six of 12 foliage-gleaning species, two of three aerial insectivores, and two of five ground foragers were more abundant in managed sites. For all but two species (American Redstart, *Setophaga ruticilla*; Eastern Wood-Pewee, *Contopus virens*), density of breeding territories was better explained by habitat characteristics than by arthropod resources. Our results indicate that managed woodlands support higher arthropod biomass and have the potential to benefit a wide range of bird species.

## 1. Introduction

North American woodlands, which covered more than 50 million hectares prior to European settlement, are a disappearing habitat type due to long-term fire exclusion, mesophication, and changes in grazing practices (Nowacki and Abrams, 2008; Hanberry et al., 2018, 2020). Prior to settlement, the landscape of the Midwestern USA was dominated by a mix of prairie, savanna, woodland, and forest with woodlands typically defined by canopy cover ranging from 50 % to 75 % (Rhemtulla et al., 2007; Greenberg et al., 2016; Hanberry et al., 2020). Mirroring trends observed throughout the Midwest (Rhemtulla et al., 2007), Wisconsin oak (*Quercus* spp.) woodlands and savannas have been drastically reduced from their former dominance in the southern and central portion of the state (Rhemtulla et al., 2009; Knoot et al., 2015). Around the time of European settlement in the mid-19th century, 46 % of Wisconsin forests were savanna or woodland, and over the last two centuries in the Eastern Broadleaf Forest division in southern Wisconsin,

fire tolerant oak species have decreased from 65 % of trees at the time of settlement to 23 % of trees currently (Hanberry and Dey, 2019). The canopies of southern Wisconsin forests have shifted from mostly oaks to mostly shade-tolerant species (i.e., maples, *Acer* spp., and ashes, *Fraxinus* spp.), and this has been associated with decreased floral diversity (Rogers et al., 2008).

Modern oak woodland management is often intended to emulate the effects of natural disturbance and cultural burning by Indigenous peoples (Greenberg et al., 2016; Abrams et al., 2022) by increasing vegetation heterogeneity (i.e., vertical complexity, treefall gaps, or multiple seral stages in close proximity) through treatments including tree thinning and prescribed fire (Hanberry et al., 2017). These practices are associated with increased oak regeneration and herbaceous plant, arthropod, and bird diversity (Reidy et al., 2014; Campbell et al., 2018; Vander Yacht et al., 2020), however, the cascading effects of habitat management on multitrophic relationships are less clear. The reasons that determine high quality habitats for avian species are complex and

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may be driven by food availability, forest structure, or their interaction (Holmes and Robinson, 1981, Narango et al., 2017, Lister and Garcia, 2018).

Woodland management has the potential to alter the arthropod community through changes to habitat structure, host plant availability, and direct effects of prescribed fire. The distribution of forest arthropods is partially driven by local climatic gradients (Ulyshen, 2011), which can be sensitive to tree thinning (Brooks and Kyker-Snowman, 2008). Arthropod richness and abundance in an ecosystem are positively associated with the proportion of native plants (Burghardt et al., 2010, Stireman et al., 2014). In temperate forests, native caterpillars (Lepidopteran larvae) can reach high densities and thus play an essential role in food webs, both as herbivores and as prey for higher-level consumers (Seifert et al., 2020), including bird species (Holmes and Schultz, 1988, Goodbred and Holmes, 1996). Because many caterpillar species are host-specific, tree species composition can shape Lepidopteran communities (Sigut et al., 2018, Narango et al., 2018). Management to promote oak regeneration may benefit caterpillars, as oaks support high caterpillar diversity across the USA (Narango et al., 2020). And finally, while prescribed fire can be beneficial to some arthropods (Campbell et al., 2007, 2018), it does not always have a positive effect on arthropod abundance and species richness, particularly for ground-dwelling species (Verble-Pearson and Yanoviak, 2014, Chitwood et al., 2017). However, fire exclusion results in dense shady conditions in woodland understories which are associated with declines of woodland Lepidoptera species (van Swaay et al., 2006) and certain pollinators (Campbell et al., 2018).

Woodland management can benefit breeding bird species with specialized habitat requirements, including cavity nesters (Greenberg et al., 2019), and species associated with uneven canopies (i.e., Cerulean Warblers (*Setophaga cerulea*); Boves et al., 2013, Sheehan et al., 2014). More generally, management for woodland conditions shifts the bird community towards early-successional and open-habitat species (Vander Yacht et al., 2016, Greenberg et al., 2018), a group which has been facing declines in North America as disturbance regimes, and thus early-successional habitat, have increasingly been lost (DeGraaf and Yamasaki, 2003, King and Schlossberg, 2014). Additionally, disturbance-dependent forest bird species are facing sharp declines throughout the Eastern USA, including in southern Wisconsin (North American Bird Conservation Initiative, 2025). While generalist species do not respond strongly to management, forest-interior specialists and species associated with the lower forest strata can be adversely affected by prescribed fire and thinning, particularly during the first few years after management (Greenberg et al., 2007, Vander Yacht et al., 2016). Although vegetation habitat characteristics in managed woodlands have been shown to influence bird abundance (Reidy et al., 2014, Vander Yacht et al., 2016, Greenberg et al., 2018), arthropod availability likely plays an important role as well, and few studies have assessed avian response to management in terms of resource availability as well as habitat associations.

During the nesting season, arthropod biomass is a crucial resource for insectivorous birds (Holmes and Schultz, 1988, Goodbred and Holmes, 1996), and songbird territory placement and post-breeding habitat use have been linked to arthropod prey availability (Burke and Nol, 1998, Streby et al., 2011, Jirinec et al., 2016). For example, in Minnesota forests, adult and juvenile American Redstarts (*Setophaga ruticilla*) and Ovenbirds (*Seiurus aurocapilla*) were associated with high shrub-level arthropod density during the post-breeding period (Streby et al., 2011). Ovenbird territories in Ontario were located in areas with significantly higher prey biomass than surrounding areas (Burke and Nol, 1998). High use areas within Wood Thrush (*Hylocichla mustelina*) home ranges in Virginia were characterized by higher biomass of spiders and worm-like invertebrates (Jirinec et al., 2016). Eastern Wood-Pewees (*Contopus virens*) in North Carolina were more abundant in managed woodlands with high abundance of flying insects, compared to nearby unmanaged woodlands (Greenberg et al., 2007, Campbell et al., 2018).

In this study, we took a multitrophic approach to understanding how oak woodland management influences habitat quality and arthropod resource availability for forest songbirds. In particular, our goals were to determine whether woodland management influences (1) caterpillar biomass, (2) aerial insect biomass, (3) avian species richness, and (4) abundance of common avian species. We hypothesized that (1) the open canopy structure, oak prevalence, and plant diversity resulting from management actions provide more and better-quality habitat for caterpillars than is available in unmanaged woodlands. If this is true, we predict that caterpillar biomass is higher in managed than unmanaged woodlands. Similarly, we hypothesized that (2) the changes associated with management actions, particularly higher plant diversity and vegetation structural complexity, contribute to greater habitat quality for aerial insects. Based on this hypothesis we predicted that aerial insect biomass is higher in managed woodlands than in unmanaged woodlands. Our next hypothesis was that (3) managed woodlands provide habitat for both early-successional and forest-adapted bird species whereas unmanaged woodlands have little to no habitat suitable for early-successional species. This hypothesis led to our prediction that avian species richness is higher in managed than unmanaged woodlands. Finally, we hypothesized that (4) the increased abundance of arthropods predicted in managed sites would result in greater insectivorous bird abundance, as long as species-specific habitat associations are present following management. We therefore predicted that for bird species in three of four foraging guilds examined, abundance would be higher in managed than unmanaged woodlands. Table 1 details guild-specific hypotheses, as well as species-specific hypotheses based on habitat associations previously documented in the study area (Mossman and Lange, 1982).

## 2. METHODS

### 2.1. Study System

The South Range of the Baraboo Hills (Sauk County, Wisconsin, USA) is a 40 km by 4–8 km range of quartzite and sandstone bluffs covered by contiguous forest (Fig. 1). Quartzite, which forms the unglaciated bedrock of the central Baraboo Hills, is associated with poorly drained soils, cooler microclimates and mesic conditions, while sandstone and dolomite, which overlie the quartzite in much of the western Baraboo Hills, are associated with well drained soils, warmer microclimates and drier conditions (Mossman and Lange, 1982). Tree communities in this landscape are dominated by oak, maple, and central hardwoods, with conifer relics (Eastern Hemlock, *Tsuga canadensis*, and White Pine, *Pinus strobus*) in some protected stream gorges and rocky slopes. Oak forest, the primary natural cover, consists largely of Red Oak (*Quercus rubra*) and White Oak (*Q. alba*; Lange, 1998). A full list of tree and shrub species documented in our study area is in Table A.2. Pre-European settlement vegetation cover included fire-adapted habitats, particularly oak savanna and woodlands on bluffs and south sloping hillsides, as well as mesic forests on most northern slopes (Mossman and Lange, 1982). Cultural burning by Indigenous people (Abrams and Nowacki, 2008, Abrams et al., 2022), and fires resulting from natural ignition sources (Curtis, 1959) occurred on average every four years in the Baraboo Hills prior to European settlement (Meunier, 2022). By 1870, the Baraboo Hills were homesteaded, and the extensive forests were altered by initial logging and wildfire, followed by fire exclusion and continued logging (Mossman and Lange, 1982).

### 2.2. Study Design

We established ten 5–8 hectare study sites in upland woodland habitat (Fig. 1). Five sites were managed beginning as early as 2005 and five sites were not managed (see Table A.3 for site-specific management details and land ownership). All sites were located > 200 m from a road or other hard forest edge, embedded within several thousand acres of

Table 1

Focal avian species categorized by foraging habitat guild based on species accounts in Birds of the World (Billerman et al# 2022). Predicted response to short-term management (i.e., <10 years) indicates our expectation for each foraging guild, based on arthropod resource availability, and for each species, based on habitat associations previously documented in the Baraboo Hills (Mossman and Lange, 1982). ‘Positive’ indicates a hypothesis that the species or guild will be more abundant in managed sites, while ‘neutral’ indicates no expected difference, and ‘negative’ indicates less abundance in managed sites. For scientific names see Table A.1.

Species	Hypothesized Response to Management
<i>Foliage Gleaning (n = 12)</i>	<b>Positive:</b> More abundant in managed sites due to increased foliage caterpillar biomass due to canopy oak dominance, and sunlight reaching the understory resulting in more annual plant growth and caterpillar habitat
American Redstart	<b>Negative:</b> although associated with forest edges and young forests, nests in pole-sized trees and saplings, which are removed during management
Blue-gray Gnatcatcher	<b>Positive:</b> associated with large White Oaks ( <i>Quercus alba</i> )
Cerulean Warbler	<b>Positive:</b> observed at the tops of mature trees with large crowns near small canopy gaps
Hooded Warbler	<b>Negative:</b> habitat specialist that nests in patches of dense understory in canopy openings within closed-canopy mesic forest
House Wren	<b>Positive:</b> associated with down woody debris (which can persist in managed sites following tree thinning), forest edges, shrubby open areas in the understory and open or semi-open canopies
Indigo Bunting	<b>Positive:</b> associated with forest edges and openings that afford tall exposed sites for singing perches and shrubby growth for nesting
Mourning Warbler	<b>Positive:</b> observed in canopy openings with dense shrubs or tall herbs within extensive forests
Red-eyed Vireo, Rose-breasted Grosbeak, Scarlet Tanager, Yellow-billed Cuckoo	<b>Neutral:</b> did not have strong habitat associations within large forests in this study area
Yellow-throated Vireo	<b>Positive:</b> sporadically observed in deciduous forest canopies near openings and forest edges
<i>Wood-drilling (n = 1)</i>	<b>Positive:</b> More abundant in managed sites due to availability of standing dead trees that support arthropod prey
Red-bellied Woodpecker	<b>Positive:</b> occurs mostly in habitats with semi-open canopy and high importance of oaks
<i>Aerial Insectivore (n = 3)</i>	<b>Positive:</b> More abundant in managed sites due to an increase in space to maneuver during foraging, and increased aerial insect biomass due to structural complexity of vegetation, high oak dominance, diversity of understory microclimates and high herbaceous plant species richness
Acadian Flycatcher	<b>Negative:</b> associated with mature mesic forest with high canopy cover, high humidity, mesophytic trees and shrubs, and relatively open understories with sapling perches that allow for low aerial foraging
Eastern Wood-Pewee	<b>Positive:</b> associated with oak forests with open lower canopies that afforded perches for foraging, and few small trees, conditions that are most common on upper slopes
Great Crested Flycatcher	<b>Positive:</b> associated with open and uneven canopies, which can result from

Table 1 (continued)

Species	Hypothesized Response to Management
<i>Ground Foragers (n = 5)</i>	steep rocky slopes, snags, or woodland management <b>Negative:</b> Less abundant in managed sites due to reductions in leaf litter after prescribed burning, which reduces habitat for arthropod prey
American Robin	<b>Neutral:</b> did not have strong habitat associations within large forests in this study area
Eastern Towhee	<b>Positive:</b> associated with shrubby openings and forest edges
Ovenbird	<b>Negative:</b> associated with stands of small to medium straight-trunked trees which is typical of unmanaged mesic forests. Nests in leaf litter on the ground which is reduced after prescribed fires
Veery	<b>Neutral:</b> although associated with mesic forests and damp sites, also found in thick shrubs or tall herbs which may be common in unmanaged sites as the understory regrows
Wood Thrush	<b>Neutral:</b> associated with high canopy cover, but also frequently nests among dense saplings resulting from treefall gaps and thus may benefit from the patchy understory of managed sites that include regrowing saplings and shrubs

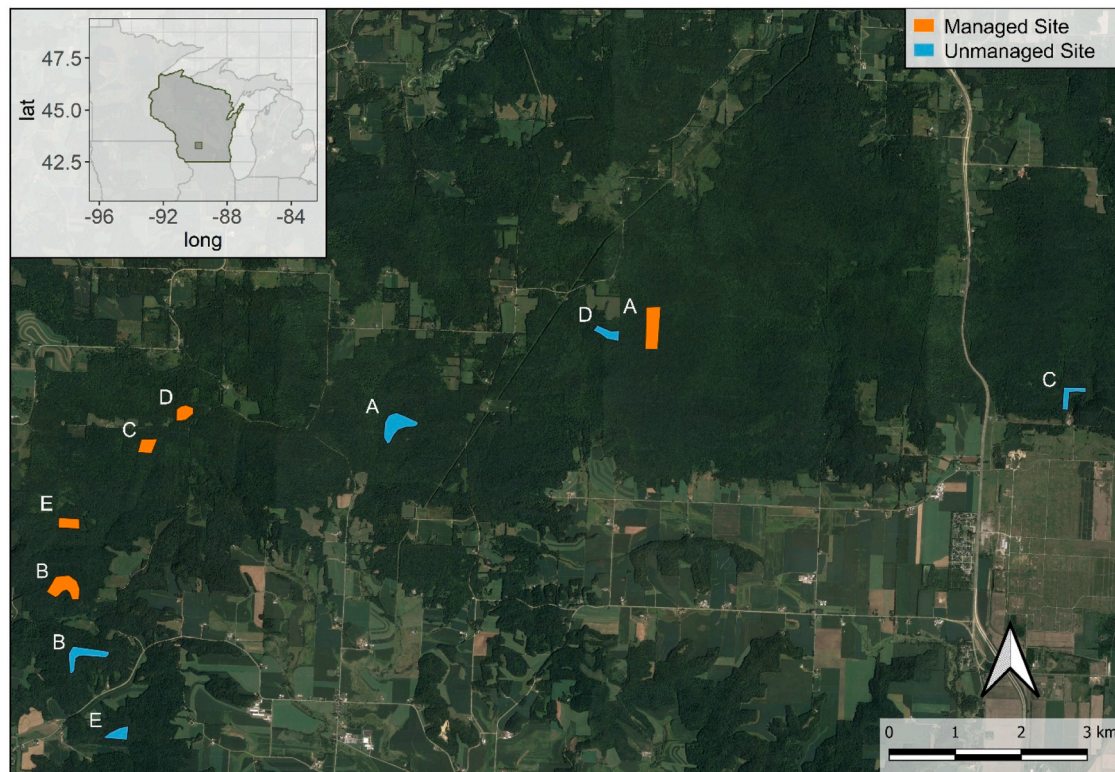
contiguous habitat, and situated on flat or south-sloping aspects. We paired each managed site with an unmanaged site with similar size, landscape context, topography, elevation, and geology. Paired sites were, on average, separated by 5.5 km. In each site, we established a network of 7–10 sampling points for habitat and caterpillar surveys, spaced 60–100 m apart.

The unmanaged sites had oak-hickory (*Quercus* and *Carya* spp.) overstories and dense mid- and understories with the remnants of open glade-like ridges. Red cedars (*Juniperus virginiana*) were established on rocky bluffs of two unmanaged sites, otherwise all tree species within the study sites were deciduous. The managed sites had predominantly White Oak overstories and open mid- and understories due to periodic thinning and low-intensity prescribed burns occurring at 1–3 year intervals (Table A.3). Understory thinning was usually the first management activity in each managed site. It targeted mostly saplings and small trees of ironwood (*Ostrya virginiana*) and shade-tolerant tree species and was nearly complete in some areas. Tree thinning was usually limited and very selective for shade-tolerant species but also included some more intensive canopy removal, always with the goal of increasing fire effect, canopy oak prevalence and oak regeneration (Table A.3). Management on these five sites began as early as 2005 and as recently as 2020, and managed areas ranged in size from 40–80 ha and were all within a matrix of unmanaged forested habitat.

2.3. Field Data Collection

We collected field data between May and August of 2022 and 2023. We assessed differences in vegetation between managed and unmanaged sites by taking measurements at each sampling point during July and August of each year. At each point, we established a 50 m transect marked in 1 m increments running perpendicular to the slope and situated so that the point itself was in the center of the transect, at meter 25 (hereafter referred to as the point center). We categorized the ground-cover directly underneath each 1 m increment as either herbaceous (forbs, grasses, sedges), woody debris (down woody material >7.6 cm, or 3 in., in diameter), or other (Barrios et al., 2013, Vander Yacht et al., 2020). We designated three 3 m radius circles along the transect (at meters 0, 25, and 50) and counted the number of shrubs or saplings





**Fig. 1.** Study area in the central and western Baraboo Hills, Sauk County, Wisconsin. Unmanaged oak woodland sites are shown in blue and managed sites are shown in orange. Letters indicate paired sites, and additional site information can be found in Table A.3. Inset shows approximate location of study area within Wisconsin in the Midwestern USA. Satellite imagery is from Google Earth.

(DBH between 2.54 and 12.70 cm) within each circle (Barrioz et al., 2013, Vander Yacht et al., 2020).

Overstory basal area was obtained at each sampling point center by using variable radius plot sampling with a Haglof Vertex set to 3 m basal area factor. We identified each overstory tree within the plot and recorded the number of snags present. We measured the DBH of the three closest overstory trees (>12.70 cm DBH) to the point center.

We took four pictures of the subcanopy and canopy by walking 1 m from point center in each cardinal direction and holding a smartphone camera flat at 1 m above the ground facing upwards. To focus on the canopy and subcanopy, we avoided branches in the shrub layer by moving slightly from a picture location if necessary, or temporarily moving an understory branch. We analyzed the pictures using ImageJ software to calculate percent canopy cover and averaged the four readings from each location.

To characterize the understory microclimate during avian nesting season, we took five soil moisture readings at a depth of 3–5 cm within a 1 m radius of the point center once during every 10 day period between 25 May and 30 June using a Vegetronix Soil Moisture Meter-200. At the same time, we measured understory humidity using a Kestrel-3000 weather meter hanging from a branch at 1.5 m above the ground within 1 m of the point center.

Once every ten days during avian nesting season (25 May–30 June) we surveyed foliage caterpillars following Caterpillars Count protocols (Hurlbert et al., 2019). We marked five 50-leaf sections of branches (height range 1–2.5 m) within 10 m of each point center using flagging and a unique code. This resulted in 7–10 clusters of 5 branch locations per sites. Branches were selected so that common understory tree and shrub species were evenly represented, and less common species were also included in the study. During each survey, we estimated average leaf length, categorized percent herbivory as: 0 (none), 1 (trace, <5 %), 2 (light, 5–10 %), 3 (moderate, 10–25 %), 4 (>25 %). We counted each caterpillar in the 50-leaf area and estimated its length to the nearest

mm. To measure aerial insect biomass per trap day each season, we set one malaise trap near the center of each study site in a location that was representative of the surrounding habitat and intersected with potential insect flight paths (i.e., a linear opening in the understory). The traps were open continuously between 25 May and 30 June, checked every 1–2 weeks, and specimens were stored in ethanol for later processing.

We designated 1–2 points per study site as avian point count locations. If a site was large enough to accommodate two locations spaced > 300 m apart, we designated two points, otherwise we designated only the center point of the site. This resulted in 17 point count locations, with all five unmanaged sites and two of the managed sites having two point count locations per site (Table A.3). Between 7 and 29 June 2022, and between 26 May and 30 June 2023, we conducted three 10 min unlimited radius point counts at each point count location between 0500 and 1100. Throughout the season we visited each site during the early morning hours (0500–0700) as well as the late morning hours (0700–1100). Every individual bird seen or heard was recorded and the estimated distance and direction from the point center was recorded, according to the following distance bins: 0–10, 10–20, 20–30, 30–40, 40–50, 50–80, 80–100, 100–150, 150–300, > 300 m.

#### 2.4. Analysis

We calculated mean herbaceous plant cover, woody debris cover, understory density, overstory basal area, overstory mean DBH, snag density, and canopy cover for each site. We calculated the percent of overstory trees in the variable radius plot that were either Red Oak or White Oak within each site. We tested for normality using a Shapiro Wilk's test, and assessed differences in mean habitat characteristics between managed and unmanaged sites using nonparametric Wilcoxon rank sum tests. We calculated mean soil moisture and understory humidity from 25 May to 30 June 2022 and 2023 at each site, and again used Wilcoxon rank sum to evaluate differences between sites. We

considered differences in mean habitat characteristics in managed and unmanaged sites to be statistically significant, and thus indicate an ecological pattern, if  $p \leq 0.10$  (Arnold, 2010).

To test our first hypothesis, that caterpillar biomass is higher in managed sites than unmanaged sites, we calculated caterpillar biomass using an allometric equation based on the field-estimated length of each caterpillar we tallied during foliage surveys:  $0.004 \times \text{length (mm)}^{2.64}$  (Rogers et al., 1977; Lany et al., 2016). In our study area, caterpillar biomass varied widely between years, as has been found in other temperate forests (Lany et al., 2016). Because caterpillar abundance and biomass vary significantly across tree species (Butler and Strazanac, 2000; Narango et al., 2017) and can be highly variable within small sample sizes, we decided to calculate means across 2022 and 2023 to use as covariates in our bird abundance models (described below). To assess differences in caterpillar biomass between managed and unmanaged sites, we performed a modified Wilcoxon rank sum test for zero-inflated data using R package ‘ZIR’ (Wang et al., 2023).

To test our second hypothesis, that aerial insect biomass is higher in managed sites than unmanaged sites, we weighed the contents of malaise trap samples. After collection, malaise trap catches were stored in 80 % ethanol and weighed in an alcohol-wet state to optimally preserve samples for later identification. Following methods in (Hallmann et al., 2017), samples were strained through a fine mesh filter (226 micron mesh cone paint strainer) and when the time between alcohol drips reached 10 s, the sample was weighed using a lab balance, accurate to 0.01-g. We removed non-aerial arthropods (spiders, grasshoppers, caterpillars) from the samples prior to weighing them. We tested for normality with a Shapiro Wilk’s test, and performed a nonparametric Wilcoxon rank sum test to assess differences in aerial insect biomass between managed and unmanaged sites.

To test our third prediction, that insectivorous bird species richness is higher in managed sites than unmanaged sites, we tallied all species detected in each site during each year. For three pairs of sites that had different numbers of point count locations (Table A.3) we only considered data from one randomly selected point count location per site. We tested for differences in species richness between managed and unmanaged sites using a paired *t*-test. To test whether differences in bird species richness were explained by habitat conditions in managed and unmanaged sites, we fit linear regressions with vegetation characteristics and arthropod biomass as covariates. The eight vegetation covariates we tested are described in Table A.4, and arthropod covariates included average caterpillar biomass (mg per 50 leaves), and aerial insect biomass (mg per trap day) during June of each study year. All covariates were scaled prior to model fitting. First, we created models with only one covariate, and then combined top covariates into more complex models. We tested for collinearity among covariates using R package ‘corrplot’ (Wei et al., 2022) with a cutoff value of 0.7, and by applying the Variance Inflation Factor (O’Brien, 2007), using the ‘vif’ function in R package ‘car’ (Fox and Weisberg, 2018) with a cut-off value of  $VIF \leq 4$ . We then selected among candidate models using the ‘model.sel’ function in R package ‘MuMIn’ (Barton, 2009), to rank models according to AICc (small-sample corrected Akaike Information Criterion). We assessed the total explanatory power of each top model by calculating the adjusted  $R^2$  value.

Finally, to test our fourth hypothesis, that abundance of bird species in the foliage-gleaning, wood-drilling and aerial insectivore foraging guilds is higher in managed sites due to increased arthropod availability, as long as specific habitat associations are not disrupted by management, we calculated detection-corrected abundance for the 21 most common bird species using hierarchical distance sampling (Buckland et al., 2001; Kéry and Royle, 2016). This framework allowed us to test habitat characteristics and arthropod biomass as covariates, while correcting for imperfect detection (Fiske and Chandler, 2011; Kéry and Royle, 2016). First, we truncated the radius of each point count to 150 m to avoid spatial overlap with adjacent points. We calculated territory density based on the number of singing males, and thus excluded female

birds that were detected visually or by call notes. To avoid model overfitting, we considered species with at least 20 detections during the study period, listed in Table 1.

We used R package ‘unmarked’ (Fiske and Chandler, 2011) to fit distance-based density models for each species with more than 20 detections within 150 m of 17 sampling points (18 species), or within 300 m of 10 sampling points (one per study site) for three species with larger territories that can be heard from longer distances: American Robin, Eastern Towhee, and Wood Thrush. We used hierarchical models that included covariates influencing detectability (detection covariates) as well as territory density (density covariates). Detection covariates tested for each species included: Julian date, start time, temperature, wind, and weather (scale of 0–5 for increasingly poor sky condition). We considered 12 density covariates, including vegetation measurements (canopy cover, basal area, mean overstory DBH, oak percent in the overstory, number of snags, understory density, herbaceous cover, woody debris cover), microclimate characteristics (understory humidity and soil moisture), and arthropod availability (caterpillar biomass and aerial insect biomass; Table A.4). We used point-specific data for model covariates rather than averaging across the study site (see Table A.4 for a complete description of density covariates). All detection and density covariates were scaled prior to model fitting, and covariates with a correlation score of 0.7 or higher were not included in the same model (R package ‘psych’; Revelle, 2023). To ensure that models were based on ecological understanding, we tested only those density covariates for each species that we expected could influence some aspect of foraging or nesting habitat (species-specific tested covariates are listed in Table A.6). To avoid overfitting, we added covariates to models one at a time, starting with detection covariates.

All models fit the assumptions of a Poisson framework and detections of each species best followed half-normal, hazard-rate, exponential, or uniform key functions (Kéry and Royle, 2016), as determined by AICc values ( $\Delta AICc < 2$ ) calculated in the ‘model.sel’ function of R package ‘MuMIn’ (Barton, 2009). We again used AICc values to determine which detection and/or density covariates to include in the top model(s) for each species (Sillett et al., 2012), using the ‘model.sel’ function in R package ‘MuMIn’ (Barton, 2009). To avoid overfitting, we added covariates to models one at a time, starting with detection covariates. We evaluated goodness of fit of top models by using parametric bootstrapping, in which 1000 simulated data sets from our model were refit to the same model and the values of the reference and observed distributions were compared using the Freeman-Tukey fit statistic (Sillett et al., 2012). Model fit is indicated by the observed value not being beyond the 0.05 percentile of the reference distribution (Sillett et al., 2012). We also tested for overdispersion using the Chi-squared statistic (Reidy et al., 2014; Kéry and Royle, 2016) using 2 as a cutoff value. The top model(s) for each species are reported in Table 4, which includes all models within 2 AICc of the top model. For species that did not show strong responses to the density covariates we selected (i.e., null model was the top model), we ran models with management type (managed or unmanaged site) as the only density covariate to test whether a characteristic of managed habitat had not been captured by our models.

### 3. RESULTS

Compared to unmanaged sites, managed sites had significantly ( $p < 0.10$ ) lower basal area, canopy cover, and understory density, and higher mean DBH, oak percent in the overstory, woody debris cover, and herbaceous plant cover (Table 2). There was no difference between number of snags per point. Soil moisture was slightly higher in managed sites, and there was no difference in humidity (Table 2).

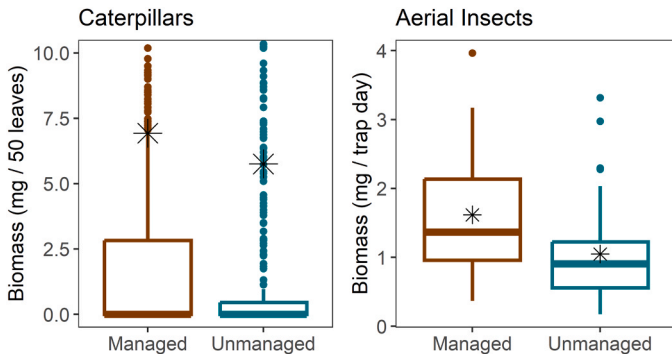
Mean caterpillar biomass per leaf was significantly higher in managed sites ( $6.93 \text{ mg} / 50 \text{ leaves} \pm 0.62 \text{ SD}$ ) than in unmanaged sites ( $5.76 \text{ mg} / 50 \text{ leaves} \pm 0.67 \text{ SD}$ ;  $p < 0.01$ ; Fig. 2).

Similarly, mean aerial insect biomass was higher in managed sites ( $1.62 \text{ mg} / \text{day} \pm 0.14 \text{ SD}$ ) than in unmanaged sites ( $1.05 \text{ mg} / \text{day} \pm$

**Table 2**

Mean vegetation and microclimate characteristics at five managed and five unmanaged oak woodland study sites during 2022 and 2023. P-values of Wilcoxon tests are shown. The larger value of significantly different ( $p \leq 0.10$ ) pairs are bolded.

	Managed Sites		Unmanaged Sites		p-value
	Mean	SD	Mean	SD	
Basal Area (m <sup>2</sup> / ha)	5.98	0.60	<b>8.11</b>	<b>0.81</b>	<b>0.07</b>
Mean DBH (cm)	<b>41.12</b>	<b>3.49</b>	29.64	1.95	<b>0.02</b>
Canopy Cover (percent)	62.91	4.21	<b>75.04</b>	<b>3.87</b>	<b>0.06</b>
Snags (number per point)	1.28	0.51	1.97	0.47	0.42
Oaks in the canopy (percent)	<b>64.68</b>	<b>11.30</b>	43.09	5.73	<b>0.10</b>
Understory Density (stems / m <sup>2</sup> )	0.01	0.002	<b>0.10</b>	<b>0.025</b>	<b>0.01</b>
Herb Cover (percent)	<b>51.68</b>	<b>0.04</b>	18.93	0.04	<b>&lt; 0.01</b>
Woody Debris (percent)	<b>6.16</b>	<b>0.63</b>	3.04	0.40	<b>0.07</b>
Humidity (percent)	56.75	0.98	57.49	0.95	0.48
Soil Moisture (percent)	<b>17.69</b>	<b>0.86</b>	15.33	1.00	<b>0.05</b>

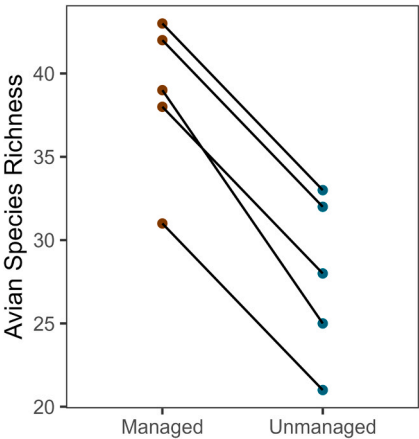


**Fig. 2.** Foliage caterpillar biomass (mg/50 leaves) and aerial insect biomass (alcohol-wet mg/trap day) from 25 May–30 June 2022 and 2023 in managed (brown) and unmanaged (blue) woodland sites in the Baraboo Hills. The central line of each boxplot represents the median, the upper and lower limits of the box represent the 25th and 75th quantiles of the data, and the vertical lines represent the 95th quantile. Outliers are represented by points, and the mean of each group is represented by a black asterisk.

0.11 SD;  $p < 0.01$ ; Fig. 2). Thus, our first and second hypotheses were supported.

We detected 48 insectivorous bird species across the study area (listed with scientific names in Table A.1). As predicted, when summed across two years, there was significantly higher average avian species richness in managed sites than in unmanaged sites ( $38.6 \pm 2.11$  SD vs.  $27.8 \pm 2.22$  SD;  $p < 0.01$ ), and in each pair of sites, the managed site had higher richness (Fig. 3). The same trend was true when richness within each year was considered separately (mean  $33.7$  species  $\pm 1.92$  SD in managed sites and  $23.4$  species  $\pm 1.58$  SD in unmanaged sites,  $p < 0.01$ ). Bird species richness was negatively related to canopy cover and positively related to herbaceous plant cover, with the best model explaining 84 % of the variation in richness across the study area (Table 3). Results of univariate models also indicate that bird richness is negatively related to understory density, snags, and basal area, and positively related to mean DBH, woody debris, oak percent in the canopy, and aerial insect biomass (Table A.5).

We modeled the detection-corrected abundance of the 21 most common insectivorous bird species in this study area (Table 4; Table A.7). These species occurred at different densities across the study area, from 0.02 pairs per hectare (Mourning Warblers in unmanaged habitat) to 9.18 /ha (American Redstart in managed habitat). The most abundant bird species at every site were American Redstart, Blue-gray Gnatcatcher, and Eastern Wood-Pewee. In managed sites, the least abundant species were Wood Thrush, Hooded Warbler, and Acadian Flycatcher, while in unmanaged sites Mourning Warbler, Wood Thrush



**Fig. 3.** Bird richness in managed (brown) and unmanaged (blue) sites across 2022 and 2023 breeding seasons in Baraboo Hills oak woodlands. The black lines connect paired sites (see Table A.3).

**Table 3**

Linear regression explaining avian species richness in managed and unmanaged oak woodlands. Model covariates with estimates (Est.), standard error (SE), t-values (t-val), p-values (p-val), and Adjusted R<sup>2</sup> are reported.

Covariate	Est.	SE	t-val	p-val	Adj. R <sup>2</sup>
Intercept	30.20	0.63	52.89	< 0.01	0.84
Canopy Cover	-3.98	0.79	-5.05	< 0.01	
Herbaceous Cover	3.73	0.79	4.73	< 0.01	

and Veery were least abundant.

In total, ten species were more abundant in managed sites, four were more abundant in unmanaged sites, and seven were distributed equally between managed and unmanaged sites (Fig. 4). We hypothesized that foliage-gleaning birds were more abundant in managed sites because of the higher availability of caterpillar biomass in those sites. We found that six of the twelve foliage-gleaning species were more abundant in managed sites, one was more abundant in unmanaged sites, and five were equally distributed (Fig. 4). The species that was more abundant in unmanaged sites, Hooded Warbler, has habitat associations that are disrupted by management (Table 1). However, of the five species that are equally distributed between managed and unmanaged sites, four do not have strong habitat associations and one has habitat associations consistent with conditions at managed sites (Table 1). Thus, our hypothesis that these species are more abundant in managed sites due to higher arthropod resources, was not supported.

We hypothesized that the wood drilling species was more abundant in managed sites based on our expectation that higher snag density would lead to more foraging and nesting habitat. However, there were more snags in the unmanaged sites (Table 2), and the wood drilling species (Red-bellied Woodpecker) was equally distributed between managed and unmanaged sites (Fig. 4).

We hypothesized that aerial insectivores were more abundant in managed sites due to higher aerial insect biomass, and our hypothesis was supported for two out of three species. The third species, Acadian Flycatcher was more abundant in unmanaged sites (Fig. 4) due to specific habitat requirements being disrupted by management (Table 1).

Finally, we hypothesized that ground foraging species would be less abundant in managed sites because prescribed fire could reduce litter depth, thus limiting nesting and foraging habitat. However, we found that two ground foraging species were more abundant in managed sites (American Robin and Eastern Towhee), and two were more abundant in unmanaged sites (Ovenbird and Veery; Fig. 4). This is partially driven by the habitat associations of Eastern Towhee being consistent with conditions in managed sites, while those of Ovenbird and Veery are



**Table 4**

Top distance-corrected density model(s) for each species. Density covariates, estimates (Est.), standard errors (SE) and p-values (p-val) are included. Results are included for all models with  $\Delta AIC < 2$ , and models are labeled with letters. Additional model outputs are in Table A.7, including the detection covariates included in each model. 'NA' indicates that the model does not include density covariates. Mean territory density per hectare in managed sites (M) and unmanaged sites (U) are reported with the higher value shown in bold. Detection covariates are described in Table A.4, and scientific names of bird species are in Table A.1.

Species	Model	Density Covs.	Est.	SE	p-val	M	U
<i>Foliage-gleaning Species</i>							
American Redstart	A	Caterpillars	0.24	0.11	0.02	<b>9.18</b>	4.29
		Aerial Insects	0.13	0.10	0.17		
		Canopy	−0.43	0.10	< 0.01		
Blue-gray Gnatcatcher	A	Oaks	0.56	0.13	< 0.01	<b>5.79</b>	3.20
Cerulean Warbler	A	Canopy	−0.81	0.25	< 0.01	<b>0.48</b>	0.22
	B	Canopy	−0.64	0.21	< 0.01	<b>1.06</b>	0.34
		DBH	0.56	0.25	0.03		
Hooded Warbler	A	Understory	0.43	0.25	0.09	0.11	<b>0.49</b>
		Oaks	−0.73	0.31	0.02		
	B	Understory	0.54	0.23	0.02	0.17	<b>0.39</b>
House Wren	A	Canopy	−0.61	0.19	< 0.01	<b>1.23</b>	0.22
		Understory	−1.49	0.51	< 0.01		
Indigo Bunting	A	Herbs	0.61	0.12	< 0.01	<b>2.38</b>	1.11
Mourning Warbler	A	Understory	−4.70	2.61	0.07	<b>0.21</b>	0.02
Red-eyed Vireo	A	NA	NA	NA	NA	1.20	1.20
Rose-breasted Grosbeak	A	NA	NA	NA	NA	0.41	0.41
	B	Understory	−0.32	0.22	0.13	<b>0.51</b>	0.39
	C	Canopy	−0.26	0.16	0.11	<b>0.51</b>	0.39
Scarlet Tanager	A	NA	NA	NA	NA	1.00	1.00
Yellow-billed Cuckoo	A	NA	NA	NA	NA	0.25	0.25
Yellow-throated Vireo	A	NA	NA	NA	NA	0.21	0.21
	B	DBH	0.43	0.27	0.11	<b>0.29</b>	0.18
	C	Canopy	−0.37	0.27	0.17	<b>0.27</b>	0.18
<i>Wood-drilling Species</i>							
Red-bellied Woodpecker	A	NA	NA	NA	NA	0.40	0.40
	B	Canopy	−0.33	0.18	0.07	<b>0.58</b>	0.41
	C	Snags	−0.32	0.23	0.17	0.44	0.41
<i>Aerial Insectivores</i>							
Acadian Flycatcher	A	Oaks	−0.60	0.23	< 0.01	0.16	<b>0.34</b>
	B	Humidity	0.66	0.28	0.02	0.25	<b>0.37</b>
	C	NA	NA	NA	NA	0.23	0.23
	D	Canopy	0.47	0.23	0.04	0.18	<b>0.30</b>
Eastern Wood-Pewee	A	Understory	−0.16	0.09	0.07	<b>4.10</b>	3.37
	B	Aerial Insects	0.13	0.07	0.07	<b>4.01</b>	3.45
	C	Basal Area	−0.12	0.08	0.17	<b>3.88</b>	3.51
	D	Oaks	0.10	0.08	0.19	<b>3.93</b>	3.49
Great Crested Flycatcher	A	Oaks	0.84	0.27	< 0.01	<b>0.52</b>	0.22
<i>Ground Foragers</i>							
American Robin	A	DBH	0.35	0.12	< 0.01	<b>1.15</b>	0.66
	B	Canopy	−0.36	0.13	< 0.01	<b>1.09</b>	0.71
Eastern Towhee	A	Understory	−1.22	0.38	< 0.01	<b>1.46</b>	0.43
Ovenbird	A	Herb	−0.50	0.21	0.02	0.22	<b>0.48</b>
	B	Canopy	0.42	0.19	0.03	0.24	<b>0.40</b>
Veery	A	Humidity	0.89	0.36	0.01	0.12	<b>0.22</b>
Wood Thrush	A	NA	NA	NA	NA	0.09	0.09
	B	Oaks	−0.41	0.26	0.11	0.09	<b>0.12</b>

consistent with conditions in unmanaged sites (Table 1).

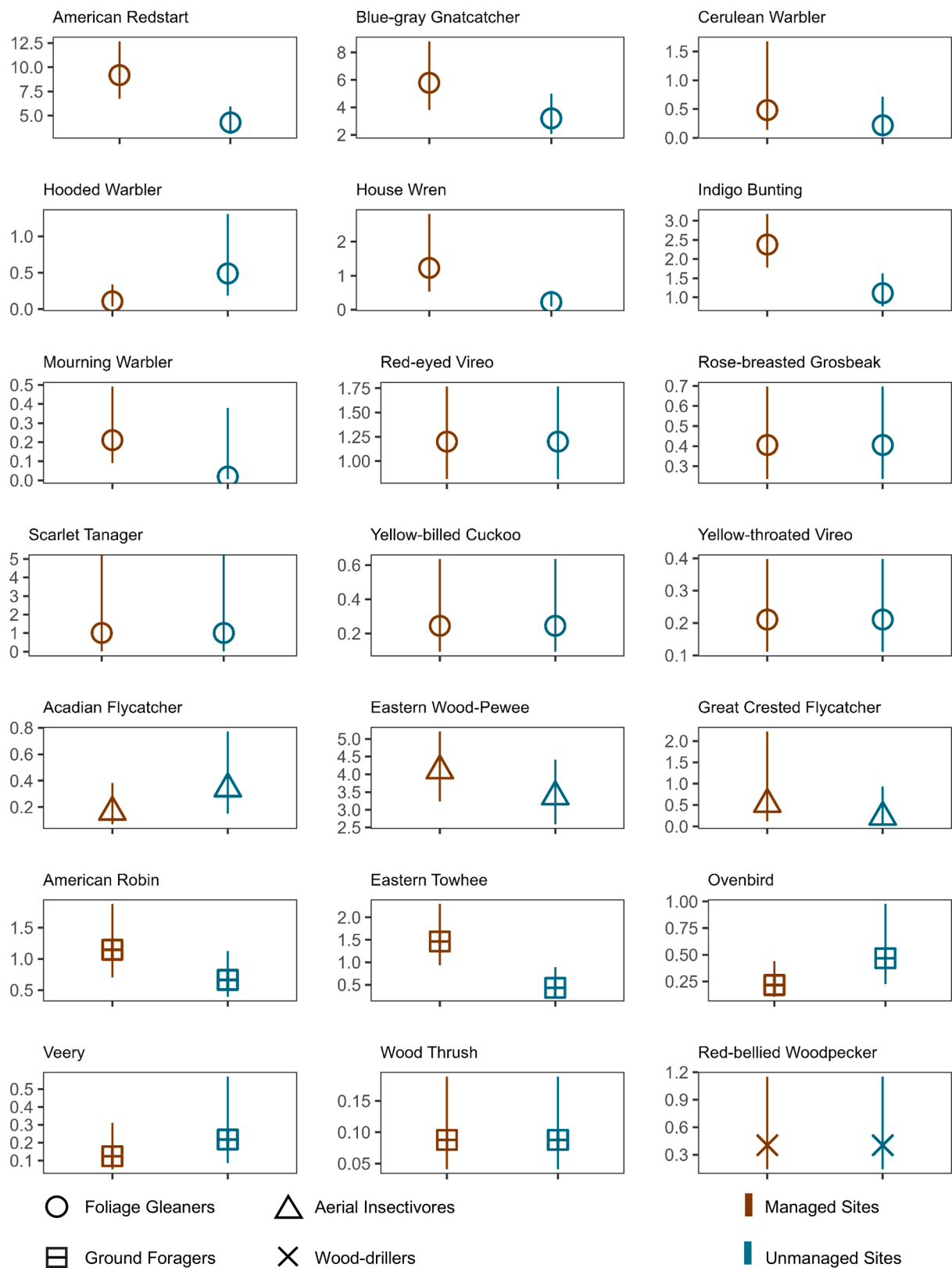
#### 4. DISCUSSION

In this study we showed that management for oak woodland conditions results in distinctive changes to vegetation composition and structure, and we noted strong differences in our managed and unmanaged sites. We found that managed sites had higher caterpillar biomass per leaf and higher aerial insect biomass during the late spring and early summer. Additionally, we found greater avian species richness in managed sites than in comparable unmanaged sites. The abundance of 10 of the 21 most common bird species was higher in managed sites, while abundance of an additional seven species was similar between sites. Only four of 21 bird species had lower abundance in managed sites relative to unmanaged sites, and these differences in abundance were small (<0.4 pairs per hectare). In light of widespread declines in bird populations, managing protected lands for woodland conditions could increase habitat quality for a diverse group of bird species.

As predicted, we found higher caterpillar biomass in managed sites

than in unmanaged sites during June. We assumed that understory caterpillar biomass measured during this study is representative of other vertical layers of the forest, since density of caterpillars across layers was consistent in similar studies (Le Corff and Marquis, 1999, Hirao et al., 2009, Seifert et al., 2020). Additionally, higher caterpillar biomass per leaf in managed woodland understories could be somewhat offset by the lower leaf density in these habitats following thinning of understory shrubs and saplings. Alternatively, fewer leaves with higher caterpillar biomass could increase foraging efficiency for foliage-gleaning birds. In the Midwest, shade-intolerant tree species like oaks likely support higher arthropod biomass than shade-tolerant species like maples (*Acer* sp.), elms (*Ulmus* sp.) and ashes (*Fraxinus* sp.; Narango et al., 2017). Because shade-tolerant saplings are often thinned from managed woodlands, and regenerating oaks are rare in unmanaged woodlands, the shift in understory tree species composition may be responsible for the differences in caterpillar biomass we observed.

As hypothesized, we found higher bird species richness in managed sites compared to unmanaged sites, resulting from early-successional species moving into managed areas (i.e., Gray Catbird, House Wren,



**Fig. 4.** Distance-corrected density estimates of 21 common woodland bird species in managed (brown) and unmanaged (blue) oak woodland habitats in the Baraboo Hills (Sauk Co., WI, USA) during 2022 and 2023. Shapes correspond to foraging habitat guild and vertical lines show standard error. Scientific names are in Table A.1.

Indigo Bunting, Yellow-breasted Chat; scientific names are in Table A.1) and the continued presence of interior forest species (Acadian Flycatcher, Hooded Warbler, Ovenbird), which tended to occur in lower densities in managed sites, but were rarely absent entirely except for nesting seasons immediately following a spring burn. Positive responses of early-successional species to woodland management are well-documented in the eastern USA (Thompson et al., 1996, Gram et al., 2003, King and Schlossberg, 2014, Hanberry and Thompson, 2019). The



continued presence of interior forest species in managed sites was likely due to the extensive forested areas surrounding managed units. This finding is similar to findings from Tennessee, which indicate that the occupancy of most late-successional forest species is not changed by woodland management (Vander Yacht et al., 2016).

Avian species richness was well-explained by two vegetation characteristics that are influenced by woodland management: canopy cover and herbaceous plant cover. The strongest predictor, canopy cover, was negatively correlated with bird richness and was lower in managed sites, while herbaceous plant cover was higher in managed sites and was positively correlated with bird richness (Table 2). In our study area, bird species richness was also positively influenced by mean DBH, woody debris groundcover, and oak percent in the canopy, all of which are higher in managed sites (Table 2). Understory density and basal area, which we found are negatively associated with bird species richness, were both lower in managed sites (Table 2). Finally, and as hypothesized, aerial insect biomass was positively associated with avian species richness, which reflects findings from a southern Appalachian (USA) upland hardwood forest (Greenberg et al., 2007).

We found partial support for our hypothesis that foliage-gleaning, wood-drilling, and aerial insectivore species would be more abundant in managed sites as long as specific habitat associations were not disrupted by management (Table 1). In general, nearly all species responded more strongly to vegetation characteristics rather than arthropod resources. Of the ten species that were more abundant in managed sites, eight had only vegetation characteristics in their top models while two species (American Redstart and Eastern Wood-Pewee) had a combination of vegetation and arthropod biomass covariates in their top models. All three species that were more abundant in unmanaged sites had only vegetation characteristics in their top models.

Within the foliage-gleaning guild, the species that were more abundant in managed sites included five species with well-defined habitat associations (Cerulean Warbler, Blue-gray Gnatcatcher, House Wren, Indigo Bunting, and Mourning Warbler) that had vegetation covariates but not arthropod biomass covariates in their top abundance models. Cerulean Warbler density was higher in places with lower canopy cover and higher DBH, while Blue-gray Gnatcatcher density was higher in places with higher canopy oak percent, and Mourning Warbler density was higher in places with low understory density, and thus a more developed ground layer (Table 4). Similarly, House Wrens, a species typically associated with forest edges, were more abundant in places with low canopy cover and understory density, while Indigo Buntings, another early-successional species, were more abundant in places with high herbaceous plant cover (Table 4). Additionally, the only foliage-gleaning species that was more abundant in unmanaged sites, the Hooded Warbler, was also associated with vegetation characteristics (dense understory conditions and fewer oaks in the overstory) rather than arthropod abundance (Table 4), as hypothesized based on its specialized habitat associations that are more similar to conditions in unmanaged sites (Table 1).

Caterpillar biomass and aerial insect biomass were included as covariates in the top abundance model for only one foliage-gleaning species, American Redstart, which also commonly forages aerially (Table 4). This species was predicted to respond negatively to woodland management due to a loss of nesting sites (Table 1), but instead we found a close relationship between arthropod resources and density. The remaining five foliage-gleaners were equally distributed between managed and unmanaged sites, and their abundance was not strongly influenced by habitat characteristics or arthropod resources, although Rose-breasted Grosbeaks showed a slight negative relationship with canopy cover and understory density and Yellow-throated Vireos had a slight negative relationship with canopy cover and a positive relationship with DBH (Table 4). In these cases, our hypothesis was not supported because, despite higher arthropod resources in managed sites, there were no significant differences in bird abundance.

The wood-drilling species, Red-bellied Woodpecker, was equally

distributed between managed and unmanaged sites, but showed slight negative relationships with canopy cover and snags (Table 4). The number of snags per point was equal between managed and unmanaged sites, contrary to what we had predicted. The unexpectedly high number of snags in unmanaged sites was likely due to high mortality of ash trees (*Fraxinus* sp.) in the canopy resulting from the invasive Emerald Ash Borer (*Agilus planipennis*) which reached our study sites around 2020. From 2021–2023, dead ash trees tended to remain standing in unmanaged sites longer than in managed sites, which were exposed to fire and stronger wind. Additionally, many ash trees had been removed from managed sites prior to 2021. Because we were unable to measure bark-dwelling or saprophytic arthropod biomass during this study, it is possible that Red-bellied Woodpeckers were responding to arthropod resources in the more open canopies of managed sites, rather than simply the availability of snags.

Among the three aerial insectivores, only one (Eastern Wood-Pewee) was associated with aerial insect biomass in our models, in addition to being negatively related to understory density and basal area and positively related to canopy oak percent (Table 4). Great Crested Flycatchers were more abundant in managed sites and were associated with canopy oak percent, while Acadian Flycatchers were more abundant in unmanaged sites and were negatively associated with canopy oak percent and positively associated with understory humidity and canopy cover (Table 4).

The territory densities of all five ground-foraging species were associated with habitat associations rather than arthropod biomass. American Robin and Eastern Towhee were more abundant in managed areas and were associated with high DBH and low canopy cover (American Robin) and low understory density (Eastern Towhee; Table 4). Ovenbirds, which are a mature forest dependent species, were more abundant in unmanaged sites in this study area and were negatively associated with herbaceous plant cover and positively associated with canopy cover (Table 4). This could be related to their use of leaf litter for nest sites as well as foraging (Mossman and Lange, 1982, Porneluzi et al., 2020) or potentially to lower ground-dwelling arthropod biomass, which has been noted following fires (Verble-Pearson and Yanoviak, 2014). Wood Thrush were equally distributed between managed and unmanaged sites but showed a slight negative relationship with canopy oak percent (Table 4). Veeries were more abundant in unmanaged sites and were positively associated with humidity (Table 4), reflecting their association with mesic forests and damp sites (Table 1).

We found that oak woodland management can be beneficial for supporting higher arthropod biomass in the understory, higher bird species richness, and similar or higher abundance of all but three forest bird species. Despite the increased arthropod abundance and biomass in managed sites, the abundances of only two bird species (American Redstart and Eastern Wood-Pewee) of the 21 we examined were related to arthropod abundance rather than vegetation characteristics. However, it is likely that some of the vegetation characteristics we measured (i.e., oak percent in the canopy) are closely related to arthropod biomass, as insect communities on oak species are more speciose and abundant than on other tree species (Tallamy and Shropshire, 2009, Narango et al., 2020). Overall, management in our study area resulted in lower densities of only four forest specialist species. Likely, the surrounding unmanaged forest played a role in the persistence of these interior forest species in managed sites. For a small subset (< 15 %) of the forest-associated bird species (Wood Thrush, Ovenbird, Hooded Warbler, and Veery), we found that managed sites provided habitat only after several years of understory regrowth following prescribed fires. Thus, maintaining patches of shrubs and saplings within managed units, or refraining from yearly prescribed fires, could allow for populations of mature forest species to persist. On the other hand, for early-successional species adapted to frequent disturbances (i.e., Blue-winged Warbler, Field Sparrow, and Indigo Bunting; Greenberg et al., 2016) high fire severity or frequency might be necessary for the

higher tree mortality and patchy understory vegetation necessary for populations to persist (Greenberg et al., 2019). Unsurprisingly, we found that several early-successional species in our study were detected only in managed sites (Chestnut-sided Warbler, Eastern Bluebird, Field Sparrow, Mourning Warbler, Yellow-breasted Chat, Warbling Vireo), and all early successional species for which we modeled abundance (Indigo Bunting, House Wren, Mourning Warbler, Eastern Towhee) were more abundant in managed sites.

The three bird species with the greatest decrease in population density between managed and unmanaged sites (Acadian Flycatcher, Ovenbird, and Hooded Warbler) are all forest specialist Neotropical migrant species that have declined in southern Wisconsin from 2007–2015 (Fink et al., 2022). This underscores the importance of conservation planning at landscape levels to ensure that unmanaged, or carefully managed, mesic forest remains, particularly in places that were not historically woodlands (i.e., stream gorges, north and east slopes, wooded valleys with rich soil). Additionally, all three species are present in managed sites in certain contexts. We found that Ovenbirds tend to be absent the year following a fire, but then return as the leaf litter builds up in subsequent years. Similarly, Hooded Warblers, which depend on dense patches of understory within closed canopy forests, may occur several years following a fire in managed sites, especially in places where less canopy thinning has occurred and sunlight from partial or nearby canopy openings encourages dense shrub regrowth. This is consistent with their tendency to temporarily decline after woodland management treatments in the Southern Appalachians (Greenberg et al., 2007). Managed woodlands are naturally patchy and habitat changes can occur between years depending on small scale differences in fire intensity, tree mortality, and other disturbances (Hanberry et al., 2017), thus creating opportunities for forest-associated birds to establish territories, especially within a large forest matrix.

We caution that this study aimed to understand short-term effects of management on arthropods and birds and may not reflect long-term changes. Consistent management activity in our study sites has been ongoing for three–ten years, while fire exclusion had been in effect since European settlement in the late 19th century. These ecosystems may continue to change under the frequent disturbance management regime. Although our study area likely is representative of large deciduous forests in the Midwestern USA, and our findings regarding bird species responses to woodland management are in line with those of similar studies (Greenberg et al., 2007, Au et al., 2008, Reidy et al., 2014, Vander Yacht et al., 2016), we were limited to ten sites within a small geographic region, thus constraining the scope of this research. Finally, two avian density models should be interpreted with caution: Scarlet Tanager density has a high variation (Table A.7, Fig. 4), likely due to a small sample size, and Yellow-billed Cuckoo density, which can have unreliable estimates when sampling is conducted over 1–2 years or without using playback on point counts due to low detectability (Hughes, 2020).

Woodland habitat management emulates the historic disturbance regime which is necessary for oak woodlands to persist into the future, and is associated with increased arthropod biomass, bird species richness, and density of ten common bird species, relative to unmanaged forest. Focusing management efforts in places where this habitat type occurred historically (i.e., south slopes, places with poor soil, areas where woodlands were documented prior to European settlement) balances the needs of early-successional species and interior forest species that thrive in denser closed-canopy habitat. On the landscape level, management for woodland restoration can foster landscape resilience by maintaining the full range of habitat types and natural disturbance processes known to occur in the upper Midwest (Lawler et al., 2015, Beller et al., 2019, Anderson et al., 2023), while providing high-quality habitat for many insectivorous bird species.

## CRediT authorship contribution statement

**Anna M. Pidgeon:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization.  
**Maia E. Persche:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization.  
**Michael J. Mossman:** Writing – review & editing, Methodology, Conceptualization.

## Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Anna M. Pidgeon reports financial support was provided by National Institute of Food and Agriculture. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122957.

## Data availability

Data will be made available on request.

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