

Persche, M. E., H. S. S. C. Sagar, and A. M. Pidgeon. 2025. Influence of woodland management within interior forests on foliage arthropods and avian insectivores. *Avian Conservation and Ecology* 20(1):20. <https://doi.org/10.5751/ACE-02858-200120>

Copyright © 2025 by the author(s). Published here under license by the Resilience Alliance. Open Access. CC-BY 4.0

Research Paper

Influence of woodland management within interior forests on foliage arthropods and avian insectivores

Maia E. Persche¹ , H. S. Sathy Chandra Sagar¹  and Anna M. Pidgeon¹ 

¹Department of Forest and Wildlife Ecology, University of Wisconsin-Madison

ABSTRACT. Eastern North American woodlands have become rare and degraded by land use conversion and fire suppression, which prevents regeneration of oaks and other shade-intolerant species. The persistence of woodlands now hinges on management using prescribed fire and tree thinning. Simultaneously, most contiguous forests have been lost to deforestation and fragmentation. Converting patches within these forests into woodlands could support a diversity of bird species, but may deter those needing mature forests, creating a potential trade-off. In a three-year field study in the Midwestern USA, we examined the effects of woodland management within interior forests on foliage arthropod biomass, and insectivorous bird species richness and mass-abundance relationships, which describe the energetic limit of a community. Mass-abundance relationships are considered integral to ecological communities and, in ecosystems without anthropogenic threats, typically show a negative relationship between species' body mass and their abundance because of higher energy requirements for larger species; deviations indicate biodiversity responses to habitat disturbances. Working in two managed and two unmanaged woodland sites from 2021 to 2023, we conducted 3809 arthropod branch surveys, captured, banded, and weighed 535 insectivores of 32 avian species, and documented 43 insectivores on point counts. We found that foliage arthropod biomass was higher in managed sites during 2021 and 2022 but not 2023, and that managed woodlands supported higher richness of understory insectivores, all insectivores, and early-successional species, and equal richness of ground foragers and mature forest specialists. The insectivorous bird community in managed sites had significant negative mass-abundance upper bounds limits in all years, while in unmanaged sites this relationship was nonsignificant and appeared to vary widely between years, potentially reflecting differences in arthropod resource availability. Thus, although the anticipated trade-off between woodland management and mature forest bird conservation was not strongly evident, the inconsistent mass-abundance relationships in unmanaged sites suggest lower resilience to resource variability.

L'influence de la gestion des forêts intérieures sur les arthropodes du feuillage et les insectivores aviaires

RÉSUMÉ. Les forêts de l'est de l'Amérique du Nord sont devenues rares et se sont dégradées en raison de la conversion des terres et de la suppression des incendies, ce qui empêche la régénération des chênes et d'autres espèces intolérantes à l'ombre. Aujourd'hui, la persistance des zones boisées dépend de la gestion des feux dirigés et de l'éclaircissement des arbres. Simultanément, la plupart des forêts d'un seul tenant ont été détruites par la déforestation et la fragmentation. La conversion de parcelles de ces forêts en zones boisées peut favoriser la diversité des espèces d'oiseaux, mais elle est susceptible de décourager celles qui ont besoin de forêts matures, ce qui appelle un arbitrage. Dans le cadre d'une étude de terrain de trois ans dans le Midwest américain, nous avons examiné les effets de la gestion des forêts intérieures sur la biomasse des arthropodes du feuillage, la richesse des espèces d'oiseaux insectivores et les relations masse-abondance, qui décrivent la limite énergétique d'une communauté. Les relations masse-abondance sont considérées comme partie intégrante des communautés écologiques et, dans les écosystèmes qui ne sont pas soumis à des menaces anthropogéniques, elles montrent généralement une relation négative entre la masse corporelle des espèces et leur abondance en raison des besoins énergétiques plus élevés des espèces de grande taille. Les écarts traduisent les réponses de la biodiversité aux perturbations de l'habitat. En travaillant sur deux sites boisés gérés et deux sites non gérés entre 2021 et 2023, nous avons mené 3809 enquêtes sur les branches d'arthropodes; capturé, bagué et pesé 535 insectivores de 32 espèces aviaires; et documenté 43 insectivores lors de comptages ponctuels. Nous avons constaté que la biomasse des arthropodes du feuillage était plus élevée dans les sites gérés en 2021 et 2022, mais pas en 2023. Par ailleurs, les forêts gérées abritaient une plus grande richesse d'insectivores du sous-bois, de tous les insectivores et d'espèces de début de transition, ainsi qu'une richesse égale de fourrageurs au sol et de spécialistes des forêts matures. Dans les sites gérés, la communauté des oiseaux insectivores présentait des limites supérieures négatives significatives de la masse-abondance pour toutes les années. Dans les sites non gérés, cette relation n'était pas significative et semblait varier considérablement d'une année à l'autre, ce qui pourrait traduire des différences dans la disponibilité des ressources en arthropodes. Ainsi, même si l'arbitrage attendu entre la gestion des forêts et la conservation des oiseaux des forêts matures n'était pas des plus évidents, l'incohérence des relations masse-abondance dans les sites non gérés suggère une plus faible résilience à la variabilité des ressources.

Key Words: *breeding habitat; insect decline; Lepidoptera; restoration; trophic relationship*

INTRODUCTION

Insect decline, likely resulting from habitat loss and intensifying agricultural practices, has been widely documented in the temperate zone (Dirzo et al. 2014, Hallmann et al. 2014). Insectivorous birds, which are facing steep declines in North America (Rosenberg et al. 2019, Tallamy and Shriver 2021), tend to establish territories preferentially in areas with higher arthropod density (Burke and Nol 1998, Moorman et al. 2012). Caterpillars are an especially crucial resource for nesting forest birds, and reductions in their biomass during the breeding season have been linked to lower nest success and population growth of insectivorous birds (Holmes and Schultz 1988, Narango et al. 2018). In eastern North America, restoring oak (*Quercus* spp.) woodlands through prescribed fire and tree thinning can promote plant and thus insect abundance and diversity (Campbell et al. 2007, Vander Yacht et al. 2020), and given the role of oaks as a keystone genera (Narango et al. 2020), may increase caterpillar abundance and diversity as well. However, within contiguous forest patches that support bird communities requiring mature forest, the influence of woodland restoration is less clear. On one hand, increased arthropod biomass could support more insectivorous bird territories, while on the other, more open canopy and understory conditions maintained by fires could reduce habitat quality for mature forest specialists.

Throughout the 1900s, many mature forest bird species experienced population declines related to habitat loss and fragmentation (Thompson et al. 2002). In particular, habitat degradation from exurban housing development in forests reshapes the bird community by reducing populations of forest specialists and Neotropical migrants (Suarez-Rubio et al. 2011, Lumpkin and Pearson 2013). Mature forest specialists are also highly vulnerable to brood parasitism from Brown-headed Cowbirds (*Molothrus ater*; Brittingham and Temple 1983), a species native to the short-grass plains of central North America that extended its range into the eastern forests following agriculture and forest fragmentation (Thompson et al. 2002, Lowther 2020). Within interior forests, Brown-headed Cowbirds tend to occur in greater numbers in logged areas than in unlogged areas (Annand and Thompson 2018). Additionally, insect resources may be lower near forest edges than in forest interiors, potentially because of warmer and drier microclimates (Burke and Nol 1998, Van Wilgenburg et al. 2001), or the effects of introduced plant species (Gavier-Pizarro et al. 2010, Stireman et al. 2014). Compounding these threats, nearly all insectivorous forest specialists in eastern North America are long-distance migrants and for many of these, habitat loss has occurred in all parts of their annual cycles (Faaborg et al. 2010). The populations of many forest birds continue to decline (Rosenberg et al. 2019). Thus, although oak woodland management within interior forests is likely not as disruptive as timber harvest or exurban development is for mature forest bird species, understanding potential threats of management for this vulnerable group of birds will be useful in making informed conservation planning and habitat management decisions.

Open forests, woodlands, savannas, and barrens are often the focus of restoration efforts (Brawn et al. 2001) because they were an integral component of North American landscapes prior to European settlement (Nowacki and Abrams 2008, Hanberry et al. 2020). Woodlands are distinguished by their canopy cover,

which is intermediate between that of savannas and forests, and their open understory conditions (Curtis 1959, Epstein 2017). The sparse tree canopies and canopy gaps of woodlands allow light to reach the ground layer, thus supporting high plant and insect diversity (Nowacki and Abrams 2008, Hanberry and Nowacki 2016). Woodlands in eastern North America are typically fire-maintained with patches of dense shrub regrowth occurring between fires (Hanberry et al. 2017, Abella et al. 2020). Fire suppression has led to denser tree canopies and understory shrub and sapling growth, which have resulted in woodland understory microclimates becoming more humid, shady, and cool through a process called mesophication (Nowacki and Abrams 2008). Mesophication causes declines in many ground layer plant and insect species (Campbell et al. 2007, Rogers et al. 2008, Hanula et al. 2015), and eventually precludes the regeneration of shade-intolerant tree species including oaks. Oaks are foundational species that provide food, foraging habitat, nest sites, and suitable microclimates for a wide variety of species (Hanberry and Nowacki 2016, Narango et al. 2020), thus, their failure to regenerate threatens the persistence of woodland ecosystems (Knoot et al. 2015). These changes have been widespread across eastern North America, affecting eastern forests (Hanberry et al. 2020), Midwestern oak savannas and woodlands (Nuzzo 1986, Rogers et al. 2008), and southeastern oak and pine ecosystems (Hanberry et al. 2018). Although timber harvesting has been suggested as a way to maintain open habitat structure in the absence of fire, this strategy often leads to patchworks of dense forest and regenerating clearcuts that differ from historic conditions in which large early successional patches and extensive dense forests were uncommon, and thus may not provide adequate habitat for woodland species (Hanberry and Thompson 2019).

To restore and maintain woodlands and open ecosystems, land managers and conservationists have increasingly turned to practices like tree thinning and prescribed fire that mimic natural disturbance regimes (Brawn et al. 2001, Hanberry et al. 2017). Although management for open ecosystem restoration has been shown to increase herbaceous plant species richness (Vander Yacht et al. 2020), the response of the arthropod community can be more variable. In particular, arthropod responses to prescribed fire appear to be species-specific, indicating that generalizing across the entire arthropod community within an ecosystem may be misleading (Hanula and Wade 2003). On one hand, understory thinning, removal of invasive shrub species, and prescribed fire may increase the richness and abundance of arthropods (Campbell et al. 2007, Lettow et al. 2018, Mason et al. 2021). Conversely, prescribed fire may negatively affect arthropod biomass, abundance, and burn-year species richness (Underwood and Quinn 2010, Jacobs et al. 2015, Chitwood et al. 2017). Additionally, many caterpillars and other folivorous arthropods specialize in foraging on certain tree species or genera (Tallamy and Shropshire 2009, Narango et al. 2020), and thus management that favors some tree species and removes other species could influence arthropod biomass.

The response of the eastern North American bird community to woodland restoration is generally characterized by positive responses among early-successional and open-habitat species and neutral or negative responses among mature forest species (Barrioz et al. 2013, Reidy et al. 2014, Greenberg et al. 2018, Roach et al. 2019). In particular, ground foraging species may be

negatively affected by the loss of leaf litter following prescribed burning (Greenberg et al. 2007, Vander Yacht et al. 2016). Bird community responses to logging practices within contiguous forests could parallel those of woodland restoration responses. In response to even- and uneven-age timber harvesting within interior forests, increased richness and abundance of early-successional and gap-dependent species has been documented (Thompson et al. 1996, Gram et al. 2003, Annand and Thompson 2018). This is usually accompanied by a temporary reduction in the abundance of a few mid- and late-successional forest dependent species (Thompson et al. 1996, Gram et al. 2003, Annand and Thompson 2018). For example, Ovenbirds (*Seiurus aurocapilla*), a ground-nesting forest specialist, declined in response to timber harvest in New Brunswick, Canada, and then gradually returned to pre-harvest density during the next five years (Haché et al. 2013). However, following a timber harvest in the Missouri Ozarks (USA), the density of mature forest specialists did not return to pre-harvest levels after more than a decade (Morris et al. 2013). Similarly, logging treatments in the Missouri Ozarks caused declines of mature forest birds in nearby unlogged reference plots, indicating that landscape configuration influences population density of some species (Gram et al. 2003).

The extent to which differences in arthropod resource availability between managed and unmanaged woodlands influence fundamental ecosystem properties is unclear. For example, habitats with low arthropod biomass could limit the abundance of species in higher trophic levels, as evidence suggests that insectivorous species may be resource-limited in certain temperate situations (i.e., birds: Holmes and Schultz 1988, Rodenhouse and Holmes 1992; and bats: Zahn et al. 2007). This would then have implications for resource or energy partitioning among higher trophic levels. One fundamental property of ecological communities is a negative relationship between species' body size and their abundance (Damuth 1981, White et al. 2007). This has been observed over large geographic areas (i.e., globally, larger species of mammalian herbivores tend to have lower population densities than smaller species; Damuth 1981). However, at local scales, the relationship between body mass and abundance tends to be polygonal rather than linear, with a negative upper bounds slope (i.e., the linear relationship of the 97th percentile of the data), as in the cases of British woodland and farmland bird assemblages (Blackburn et al. 1993) and understory insectivores in Himalayan forests (Srinivasan 2013). Because mass-abundance relationships are thought to be determined by the energy available in a given system, plotting the upper bounds slope illustrates the energetic limit of a given community (Blackburn et al. 1993, White et al. 2007, Srinivasan 2013). Changes to the slope of the upper-bounds limit can result from anthropogenic disturbance to ecological communities and are associated with subtle biodiversity responses, including changes to community structure and function (Cosset et al. 2020).

Mass-abundance relationships can differ in response to ecosystem change; for example, degradation from logging resulted in more steeply negative mass-abundance slopes in Himalayan forests, indicating greater resource competition (Srinivasan 2013). Additionally, species interactions can influence mass-abundance relationships: mass-abundance slopes in mixed species flocks in southern India and Sri Lanka were less negative than they were for the whole bird community, indicating that flocking behavior

can reduce resource competition and limitation, especially for larger species (Sreekar et al. 2015). In temperate woodlands adapted over millennia to periodic disturbance, years of fire suppression and consequent mesophication could substantially alter resource availability, and thus mass-abundance relationships. Thus, insectivorous bird mass-abundance relationships could vary between habitat being managed with prescribed burns and tree thinning, and unmanaged habitat.

Few studies have taken a multitrophic approach to understanding ecological responses to oak woodland management (i.e., tree thinning and prescribed burning used to promote open canopy and midstory vegetation, patchy understory vegetation, diverse herbaceous ground layers, and oak regeneration), or have examined temperate bird community structure through the lens of mass-abundance relationships. The goal of this study was to determine whether oak woodland management within contiguous forests results in changes to understory arthropod biomass, and whether any differences detected in resource availability are reflected in species richness and mass-abundance relationships of insectivorous birds. We examined the species richness of all insectivores, as well as of four overlapping guilds: understory insectivores, ground foragers, mature forest specialists, and early-successional species (Table 1). We included understory insectivores because this is an ecologically important group of birds that can function as ecological indicators of land-use intensity and deforestation (Bregman et al. 2014, Sreekar et al. 2015). We included ground foragers and mature forest specialists because we anticipated that members of these guilds may have negative responses to woodland management (Greenberg et al. 2007, Reidy et al. 2014, Roach et al. 2019) and are often a conservation priority in extensively forested landscapes. Finally, we included early-successional species because this guild contains many species that are facing long-term declines (Brawn et al. 2001, Rosenberg et al. 2019, Fink et al. 2022). We examined mass-abundance relationships of all insectivores in managed and unmanaged sites, hypothesizing that the upper bounds slope would be more steeply negative in unmanaged sites, indicating greater resource competition from low arthropod availability.

METHODS

Study area

At the eastern edge of the Driftless Region in the northern Midwest (USA), the Baraboo Hills of southern Wisconsin were dominated by oak woodlands prior to European settlement (Rhemtulla et al. 2007, 2009, Knoot et al. 2015). Because of fire suppression, forest composition has shifted toward mesic species including maples (*Acer* sp.), elms (*Ulmus* sp.), ashes (*Fraxinus* sp.), and basswood (*Tilia* sp.) in a novel forest succession trajectory (Knoot et al. 2015). Conservation efforts beginning in the early 1900s have resulted in a predominately forested landscape (> 80 km²) that supports a diverse bird community (Mossman and Lange 1982).

Study design

We established four 15-ha study sites in upland woodland habitat on properties owned by the Nature Conservancy and the Wisconsin Department of Natural Resources. Sites were separated by > 0.5 km because this distance exceeds the territory diameter of all insectivorous birds recorded in this study (Wood

Thrush [*Hylocichla mustelina*] has one of the largest territory sizes, ranging from 0.08 to 4.0 ha; Evans et al. 2020). Additionally, all sites were > 200 m from a road or other hard forest edge, embedded within several thousand hectares of contiguous habitat, and situated on flat or south-sloping aspects. Sites were all > 300 m from streams, which can be a source of emergent aquatic insects where abundance of insectivorous birds is high (Iwata et al. 2003, Schilke et al. 2020). The unmanaged sites, Pan Hollow Uplands (PHUP) and Natural Bridge North (NBNO) have oak-hickory overstories and dense mid- and understories

Table 1. Forty-three forest and woodland insectivore species included in this analysis, with information about their guild (s), and their population trend in Wisconsin (+ increasing population, - decreasing, ~ stable or mixed). Total number of mist net captures are reported in managed (M) and unmanaged (U) sites, with the higher number of captures bolded. U = understory insectivore; G = ground forager; F = mature forest specialist, E = early-successional species. See Appendix 1 for species scientific names.

Species	U	G	F	E	WI Pop. Trend	Captures	
						M	U
Acadian Flycatcher	X		X		~	1	1
American Redstart	X				+	99	10
American Robin		X			-	22	13
Baltimore Oriole					~	3	0
Black-capped Chickadee	X				-	3	6
Blue-gray Gnatcatcher					-	8	0
Blue-winged Warbler	X			X	~	7	0
Brown Creeper			X		~	1	0
Chestnut-sided Warbler	X			X	~	2	0
Cerulean Warbler			X		~	0	0
Chipping Sparrow	X				-	1	0
Common Yellowthroat	X			X	~	0	0
Downy Woodpecker					+	6	7
Eastern Towhee		X		X	~	19	3
Eastern Wood-Pewee	X		X		+	29	17
Field Sparrow	X			X	-	0	0
Gray Catbird	X			X	~	20	7
Great Crested Flycatcher					~	0	0
Hairy Woodpecker			X		+	1	2
Hooded Warbler	X		X		-	1	9
House Wren	X			X	+	20	1
Indigo Bunting	X			X	~	37	9
Least Flycatcher					~	0	0
Mourning Warbler	X			X	-	13	0
Northern Cardinal	X				+	4	4
Northern Flicker		X			~	2	1
Ovenbird		X	X		-	7	26
Pileated Woodpecker			X		+	0	0
Red-bellied Woodpecker			X		+	0	0
Red-eyed Vireo			X		~	2	3
Red-headed Woodpecker					+	1	0
Rose-breasted Grosbeak					+	34	14
Ruby-throated Hummingbird					+	0	0
Scarlet Tanager			X		~	3	7
Song Sparrow	X			X	-	1	0
Tufted Titmouse					+	0	1
Veery		X	X		~	7	9
White-breasted Nuthatch					+	1	3
Wood Thrush		X	X		+	7	17
Yellow Warbler	X			X	~	0	0
Yellow-bellied Sapsucker			X		~	1	2
Yellow-billed Cuckoo					+	0	0
Yellow-throated Vireo					~	0	0

with the remnants of open glade-like ridges or areas of open oak-dominated overstories still visible. The managed sites, Happy Hill Woodland (HHWO) and Hemlock Draw South (HDSO) have predominantly white oak overstories and open mid- and understories due to periodic thinning and prescribed burning conducted by The Nature Conservancy throughout 2016–2023 (see Table S1 for a complete management history of each site). HDSO was burned four times and thinned five times from 2014 to 2023, while HHWO was burned two times and thinned two times from 2018 to 2022. Aside from these treatments conducted by the Nature Conservancy, there is no record of logging or fires on any of the four sites since at least the 1960s. We paired each managed site with an unmanaged site with similar topography and bedrock type. HDSO and NBNO are both at the top of steep south-facing hillsides with sandstone bedrock, and the shape of these sites is determined by topography, with the north side of both sites situated on the top of crescent-shaped bluffs and the south side situated on the upper third of the south slope. HHWO and PHUP are located on flat or mild south-slopes at the top of large quartzite bluffs, and these sites are rectangular. In each site, we established a network of 10 mist net locations spaced 60–100 meters apart and connected by narrow trails.

Field data collection

Data collection occurred during May–August from 2021 to 2023 at HDSO, HHWO, and PHUP, and 2022–2023 at NBNO. At each point, we established a 50-m transect marked in 1-m increments running perpendicular to the slope. At each increment, we categorized the groundcover as herbaceous (forbs, grasses, sedges), bare soil, or other (Barrioz 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 (DBH between 2.54 and 12.70-cm) within each circle (Barrioz et al. 2013, Vander Yacht et al. 2020). Using a Haglof Vertex set to 3 m basal area factor we tallied a set of overstory trees at each site and identified them to species, making note of snags. We took four pictures of the canopy by walking 1-m from the point center in each cardinal direction and holding a camera flat at 1-m above the ground. We analyzed the pictures using ImageJ software to calculate percent canopy cover and averaged the four readings from each location.

Once every 10-days from mid-May until early August we surveyed foliage arthropods following the Caterpillars Count! protocol (Hurlbert et al. 2019). At each sampling point, we marked five 50-leaf branches within 10-m of each mist net location using flagging and a unique code. Branches were selected so that common understory tree and shrub species were evenly represented, and less common species were also included in the study. We counted each arthropod in the 50-leaf area, estimated its length to the nearest mm, identified it to order, and uploaded a picture to iNaturalist to verify our identification. In total, we conducted 3809 branch samples.

To estimate bird species richness, we designed two points per study site as avian point count locations, separated by > 300 m. During late May and June of each study year we conducted three 10-minute point counts at each point count location between 0500 and 1100. Every individual bird seen or heard within a 150 m radius was recorded.

To estimate mass abundance ratios, we used data from bird banding at each site, following the Monitoring Avian Productivity and Survivorship Program protocols (MAPS Program, Institute for Bird Populations). Starting during MAPS Period Four (1 June) we operated each banding station once during every 10-day period until Period Ten (early August), opening nets within 30 minutes of sunrise and closing six hours later. Total net-hours of operation in 2021 was 849.7 in managed sites and 426 in unmanaged, while in 2022 it was 713.9 (managed) and 806 (unmanaged), and in 2023 it was 704 (managed) and 599 (unmanaged). All mist nets were 12 m long, 2.6 m high, 30- or 36 mm mesh size, and divided into four horizontal shelves. After nets were open, we checked them every 30-min throughout the six hours and brought any captured birds to a central banding location to process. Each bird was fitted with a uniquely numbered USGS aluminum band, weighed with a spring scale, and the bird's sex and age were determined based on plumage and molt characteristics (Pyle 2022). For this study, we used data only from a bird's initial capture each year, and excluded hatch-year individuals.

Data analysis

We calculated herbaceous cover percent, bare soil percent cover, and understory density (stems/m²) at each sampling point. We calculated the percentage of overstory trees (> 12.70 cm DBH) in the variable radius plots that were in the genus *Quercus* (either Red Oak, *Quercus rubra*, or White Oak, *Q. alba*). We then calculated mean herbaceous plant cover, understory density, oak percent, and canopy cover at each site. Because vegetation characteristics did not change between years, we calculated mean values for each characteristic in managed and unmanaged sites across all three years of the study, and performed t-tests to check for differences.

Arthropod biomass was estimated using order-specific allometric equations based on length (Rogers et al. 1977, Sabo et al. 2002, Gruner 2003). We calculated total arthropod biomass (mg/50 leaves) of each branch sample, and then tested for differences in overall biomass per 50 leaves between managed and unmanaged sites during each year using a t-test. To visualize distribution of arthropod biomass across each season, we fit a smoothing curve (R package ggplot2; Wickham 2016) with arthropod biomass as the response variable and Julian date as the predictor variable in managed and unmanaged sites.

We limited our analysis of birds to insectivores, defined as species that feed on > 50% insect material during the breeding season (Billerman et al. 2022). We further divided birds into ground foragers (species that forage predominantly on and under vegetation and duff on the ground) and understory insectivores (i.e., species that forage predominantly on vegetation below 3 m; Billerman et al. 2022). Mature forest specialists and early-successional species were designated using a combination of the Birds of the World database and classifications in the Supplementary Information of Farwell et al. (2020). To determine how effectively our point counts characterized the avian community, we calculated species accumulation curves for each guild within managed and unmanaged sites using R package vegan (Oksanen et al. 2025) from data collected during point counts in all three study years. To understand whether species composition of bird communities differed between managed and

unmanaged sites, we used non-metric dimensional scaling in R package vegan (Oksanen et al. 2025). We examined each guild as well as all insectivorous species.

We examined the mass-abundance relationships of adult insectivorous forest birds, including all insectivorous species we captured in mist nets (Table 1). We tested for differences in mass-abundance upper-bounds limits in managed and unmanaged habitats using quantile regression (Koenker 2005) in the R package quantreg (Koenker 2022). We analyzed each year separately, and set the upper bounds limit (tau) to 0.97, because we wanted to capture the upper edge of the polygonal shape that resulted from plotting mass-abundance data, which likely includes the most resource-limited species (Blackburn et al. 1993). We tested other tau levels from 0.90 to 0.99 to verify that general patterns were consistent. We first calculated the mean body mass of each species in each treatment type in each year, analyzing males and females separately to account for sexual dimorphism. We standardized capture rates by mist netting effort (total net hours in each habitat type over all study years) and used this as a proxy of abundance for each species:

$$\text{Abundance} = (\text{Individuals Captured} / \text{Total Net Hours per Treatment Group}) * 100$$

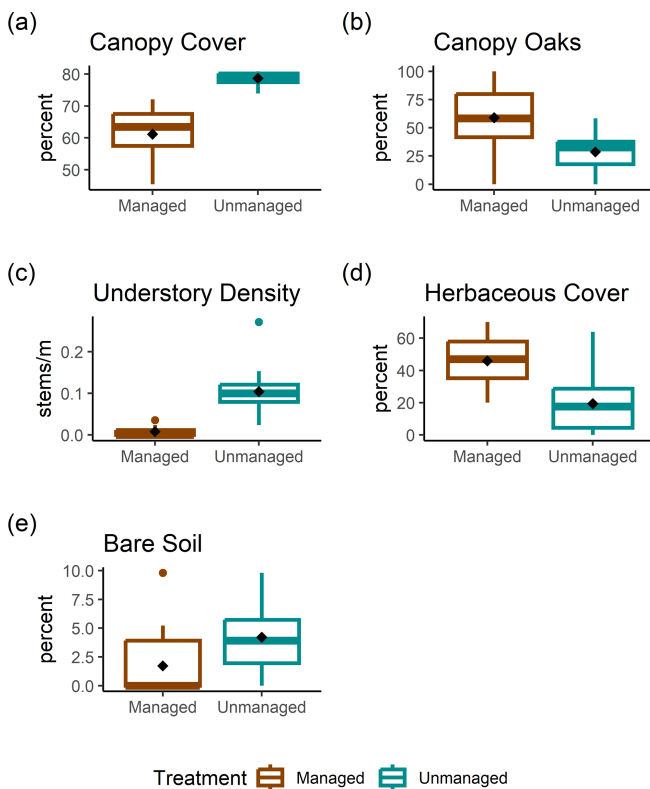
We considered the slope of the upper bounds limit to be statistically significant, and thus indicate an ecological pattern, if $p \leq 0.10$ (Arnold 2010).

RESULTS

Oak woodland management resulted in significant changes to vegetation structure and reflected the goals of oak habitat restoration. Compared to unmanaged sites, managed sites had lower percent canopy cover (61.2 ± 1.7 SE vs. 78.6 ± 0.4 SE; $p < 0.01$), higher percent of oak trees in the canopy (58.0 ± 5.8 SE vs. 28.7 ± 3.7 SE; $p < 0.01$), lower understory density (0.008 ± 0.003 SE vs. 0.104 ± 0.012 SE stems/m²; $p < 0.01$), higher percent herbaceous groundcover (45.9 ± 3.8 SE vs. 19.4 ± 3.9 SE; $p < 0.01$), and lower percent bare soil groundcover (1.73 ± 0.67 SE vs. 4.21 ± 0.79 SE; $p = 0.02$; Fig. 1). We found that mean arthropod biomass in managed sites was significantly higher than in unmanaged sites in 2021 (26.3 ± 2.09 SE vs. 17.5 ± 1.60 SE mg/50 leaves; $p < 0.01$) and 2022 (9.28 ± 0.766 SE vs. 5.05 ± 0.400 SE mg/50 leaves; $p < 0.01$), but not in 2023 (2.38 ± 0.364 SE vs. 1.99 ± 0.204 SE mg/50 leaves; $p = 0.35$). The difference in arthropod biomass between managed and unmanaged sites was most pronounced during early nesting season, i.e., late-May–June, and in July and August there was no difference in biomass between managed and unmanaged sites (Fig. 2a–c). We observed high densities of cyclic Geometridae caterpillar species across our study area in 2021 and a severe drought in 2023, which reduced caterpillar abundance, resulting in larger differences in caterpillar biomass between years than between managed and unmanaged sites within a given year.

We detected 43 insectivore species during point counts, including 11 species that were not captured in mist nets (Table 1; see Table S2 for scientific names). All species captured in mist nets were also detected on point counts. Of the 43 species detected, 17 were understory insectivores, six were ground foragers, 14 were mature forest specialists, and 11 were early-successional species (Table 1).

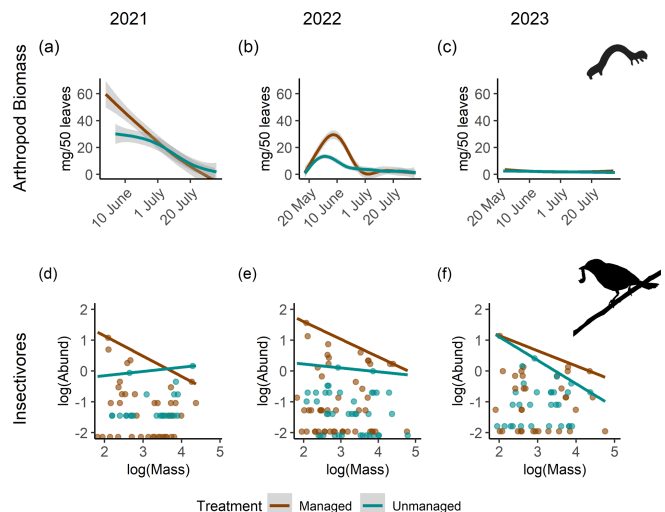
Fig. 1. Vegetation characteristics measured during July and August 2021–2023 at two managed (brown) and two unmanaged (blue) oak woodland study sites in the Baraboo Hills (Sauk Co., WI, USA). Percent canopy cover (a), percent mature oak trees (*Quercus* sp.) in the canopy (b), understory density in stems/m² (c), percent herbaceous plant cover (d), and percent bare soil cover (e) are shown. The central line within each boxplot indicates median, the upper and lower limits of the box indicate 25th and 75th quantiles of the data, and the vertical lines indicates the 95th quantile. Outliers are represented by points.



Species richness was similar between managed and unmanaged sites for ground foragers and mature forest specialists, and slightly higher in managed sites for understory insectivores and all insectivores (Fig. 3). There was higher richness of early-successional species in managed sites (Fig. 3). Species composition differed between managed and unmanaged sites for understory insectivores, mature forest species, and all insectivores, but not for ground-foragers or early-successional species (Fig. 4).

We captured, banded, and released 535 adult individuals of 32 insectivore species from 2021 to 2023. We banded 363 insectivores in managed sites and 172 in unmanaged sites (Table 1). The upper bounds limit of the insectivorous bird community in managed sites had a significantly negative slope in all study years, while in unmanaged years it varied widely and was not significant in any year (Fig. 2 d-f). The slope for managed sites ranged from -0.49 in 2023 to -0.66 in 2021 (Table S3). The intercept for managed

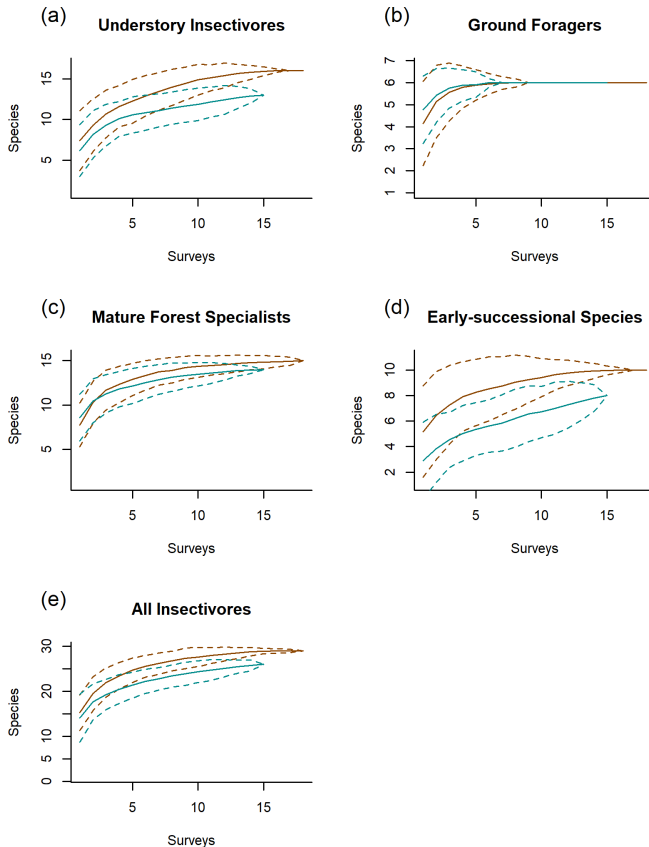
Fig. 2. Foliage arthropod biomass (a-c) and avian mass-abundance relationships (d-f) in two managed (brown) and two unmanaged (blue) oak woodland study sites in the Baraboo Hills (Sauk Co., WI, USA) during 2021–2023. Foliage arthropods were surveyed near each mist net location once during every 10-day period from late May to early August. Mean arthropod biomass phenology, with 95% confidence intervals in light gray, are shown for 2021 (a), 2022 (b), and 2023 (c). Avian mass-abundance upper bounds limits (d-f) depicting the upper 97th percentile of the data, calculated using quantile regression with tau set to 0.97, are shown by the solid lines, while data used in the analysis are represented by dots of a corresponding color. Each dot represents the mean mass (x axis) and abundance (standardized capture rates; y axis) of the birds of a given species and sex captured in a given treatment type (i.e., female Eastern Towhees, *Pipilo erythrophthalmus*, in managed woodland sites).



sites was highest in 2022 (2.74), and lowest in 2023 (2.13; Table S3). The intercept of the unmanaged sites upper bounds line in 2021 (-0.43, $p = 0.10$) and 2022 (0.47, $p = 0.12$) were lower than that of the managed sites, and in 2023, there were no differences between the intercepts (Table S3).

We captured 11 species of mature forest specialists during our study and recorded another three species during point counts (Cerulean Warbler [*Setophaga cerulea*], Pileated Woodpecker [*Dryocopus pileatus*], and Red-bellied Woodpecker [*Melanerpes carolinus*]; Table 1). Of the 11 species captured, five were captured infrequently during the study (< 5 captures; Acadian Flycatcher [*Empidonax virescens*], Brown Creeper [*Certhia americana*], Hairy Woodpecker [*Dryobates villosus*], Red-eyed Vireo [*Vireo olivaceus*], Yellow-bellied Sapsucker [*Sphyrapicus varius*]), five were captured more frequently in unmanaged sites (Hooded Warbler [*Setophaga citrina*], Ovenbird [*Seiurus aurocapilla*], Scarlet Tanager [*Piranga olivacea*], Veery [*Catharus fuscescens*], and Wood Thrush), and one was captured more frequently in managed sites (Eastern Wood-Pewee [*Contopus virens*]; Table 1). We captured eight early-successional species and recorded an

Fig. 3. Species accumulation curves for four insectivorous forest bird guilds, as well as all species included in the study, in managed (brown) and unmanaged (blue) oak woodland study sites in the Baraboo Hills (Sauk Co., WI, USA). The confidence intervals shown by the dotted lines represent two standard deviations. Point counts were conducted three times per site between late-May and late-June 2021–2023.

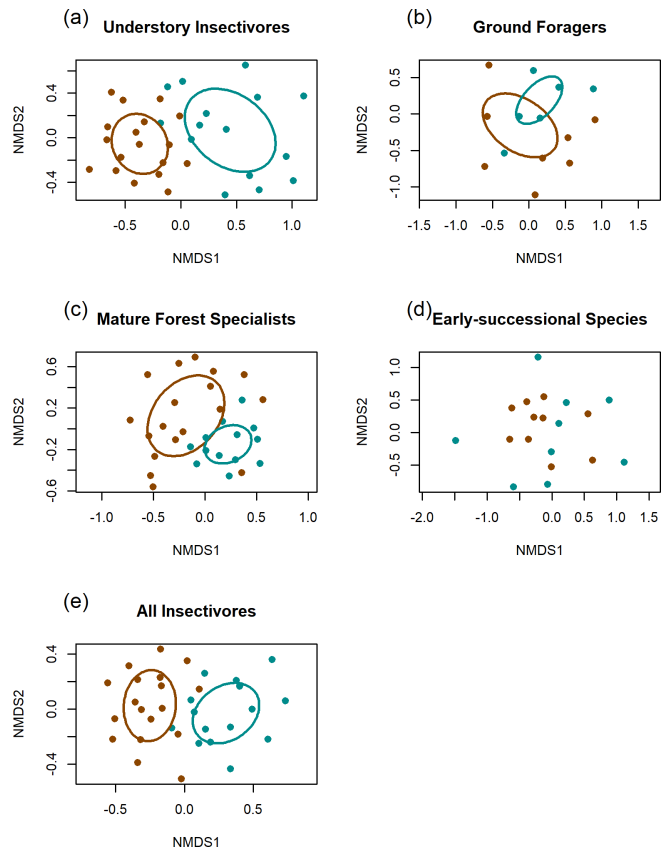


additional three species on point counts in managed sites (Common Yellowthroat [*Geothlypis trichas*], Field Sparrow [*Spizella pusilla*], and Yellow Warbler [*Setophaga petechia*]; Table 1). Four early-successional species were only captured in managed sites (Blue-winged Warbler [*Vermivora cyanoptera*], Chestnut-sided Warbler [*Setophaga pensylvanica*], Mourning Warbler [*Geothlypis philadelphia*], and Song Sparrow [*Melospiza melodia*]), and the remaining four species were captured more frequently in managed sites than in unmanaged sites (Eastern Towhee [*Pipilo erythrophthalmus*], Gray Catbird [*Dumetella carolinensis*], House Wren [*Troglodytes aedon*], Indigo Bunting [*Passerina cyanea*]; Table 1).

DISCUSSION

As habitat management and restoration play an increasingly central role in temperate forest conservation, understanding the influences of these processes on vegetation, arthropods, and insectivorous birds is important for promoting biodiversity and supporting trophic webs. We found that oak woodland management resulted in habitats with open canopies, high oak

Fig. 4. Non-metric dimensional scaling of four insectivorous forest bird guilds, as well as all species included in the study, in managed (brown) and unmanaged (blue) oak woodland study sites in the Baraboo Hills (Sauk Co., WI, USA). Each point represents one point count, and ellipses show the standard deviation of the center of each treatment group. Point counts were conducted three times per site between late-May and late-June 2021–2023.



dominance, low understory density, high herbaceous plant cover, and low bare soil cover (Fig. 1). Managed sites had equal or higher arthropod biomass per leaf in the understory (Fig. 2), and equal or higher richness of insectivorous birds (Fig. 3) than unmanaged sites. For the insectivorous bird community in managed sites, the mass-abundance upper bounds slope was significantly negative in all years, while in unmanaged sites it varied substantially and was nonsignificant.

We found that in 2021 and 2022 arthropod biomass per leaf was higher in the understories of managed woodlands than in the understories of comparable unmanaged sites. In 2023, arthropod biomass was low throughout our study area, likely due to a severe drought, and while arthropod biomass was slightly higher in managed sites this difference was not statistically significant. The lower caterpillar biomass in dense unmanaged sites in our study area parallels findings from Britain that linked moth decline to intensifying silvicultural practices that reduced availability of open woodlands and lightly-grazed areas (Fox 2013). On the other hand, logging treatments in an Indiana (USA) deciduous forest

reduced Lepidopteran species richness by 40%, highlighting the importance of unlogged areas in maintaining landscape-level richness (Summerville 2011). Because we only recorded arthropod abundance and biomass, rather than species identity, it is possible that management treatments in our study area reduced species richness of arthropods without causing declines in overall abundance. However, the fact that our managed sites were embedded within a contiguous forest extending for thousands of hectares, and that management treatments did not involve extensive logging of canopy trees, may have buffered the arthropod community against potential negative effects.

We documented similar or greater species richness in managed sites of all insectivores, as well as the four guilds that we examined, despite hypothesizing that management would negatively influence richness of ground-foragers and mature forest specialists. Bird communities in managed and unmanaged sites differed in composition as well, particularly among understory insectivores and all insectivores. Although mature forest bird community composition was also different between managed and unmanaged sites, this difference was small, and ground forager communities were not distinct. We lacked sufficient detections of early-successional species in unmanaged sites to calculate an ellipsis for this guild, but the distribution of data (Fig. 4e) suggests that these communities were not distinct. Of the 43 insectivorous species found in our study area, nine are experiencing recent (2007–2021) negative population trends in Wisconsin, while 15 are experiencing positive trends (Fink et al. 2022; Table 1). Among the guilds we investigated, mature forest specialists included the most species with increasing trends (six of 15 species are increasing while two are declining), and understory insectivore include the most species with decreasing population trends (six of 17 species are declining while four are increasing). Of the declining species detected during this study, five were captured more often in managed sites, three were captured more often in unmanaged sites, and one was never captured but was only documented during point counts in managed sites. This indicates that, from a species richness perspective, woodland management within mature forest landscapes can benefit a diverse array of species, particularly early-successional species and understory insectivores, while maintaining richness and community composition of ground foragers and mature forest specialists. Early successional species, some of which are facing regional and/or long-term declines (Brawn et al. 2001, Rosenberg et al. 2019, Fink et al. 2022), have previously been associated with savanna restorations and timber harvests (Davis et al. 2000, Gram et al. 2003). Fire-dependent habitats like oak woodlands are by nature patchy and ephemeral (Brawn et al. 2001), thus providing habitat for a diversity of species that reach peak abundances at different stages of post-disturbance regrowth (see examples in Chandler et al. 2009, Schlossberg et al. 2010, Morris et al. 2013).

We found higher abundance of small-bodied insectivores in managed woodland sites than in unmanaged sites during all three study years. This trend was especially driven by the high density of American Redstarts (*Setophaga ruticilla*) in managed sites ($n = 99$), by far the most abundant species in our study area (Table 1). However, other small-bodied understory insectivores were captured more frequently in managed sites as well, including Blue-winged Warbler, Blue-gray Gnatcatcher (*Poliophtila caerulea*), Eastern Wood-Pewee, House Wren, Indigo Bunting, and

Mourning Warbler. These differences in abundance could be related to differences in arthropod biomass per leaf between managed and unmanaged sites, which were most pronounced during late-May and June and coinciding with peak bird nesting activity in our study area (Mossman and Lange 1982). However, we did not include avian abundance and arthropod biomass in the same model, and thus other factors may also have contributed to the lower avian abundance. For example, habitat structure, particularly understory and midstory density, could influence availability of nesting locations for certain bird species. Although it is likely that understory arthropod communities are relatively similar to those in the midstory and canopy (Hirao et al. 2009, Šigut et al. 2018), we did not test this directly. We also assumed that bird species foraged on all tree species that we quantified arthropod availability for, despite evidence that some species forage preferentially (Holmes and Robinson 1981, Hartung and Brawn 2005, Wood et al. 2012).

We hypothesized that mass-abundance upper bounds limits would be more steeply negative in unmanaged sites because of higher resource competition for limited arthropod resources. However, we instead found that mass-abundance relationships in unmanaged sites were nonsignificant and appeared to vary widely between years, while in managed sites, mass-abundance relationships were consistent between all study years. Arthropod biomass was extremely high in our study area in 2021, above average in 2022, and very low in 2023 because of a drought. In unmanaged sites, we captured more small-bodied birds and fewer large-bodied birds during the arthropod resource shortage in 2023 than in the previous years, perhaps resulting from increased resource competition. By contrast, mass-abundance relationships in managed sites remained stable in 2023, suggesting that fundamental properties of the insectivorous bird community in managed sites are more resilient to short-term resource shortages. This could be a result of food resources we were unable to quantify, including seeds and berries, and arthropods on the foliage of herbaceous plants, in the bark of trees, in the soil, or in the leaf-litter. Davis et al. (2000) found that savanna restoration using prescribed fire in Minnesota, USA led to increases in omnivorous ground-foraging species such as Eastern Towhee, Chipping Sparrow (*Spizella passerina*), Field Sparrow, and Song Sparrow. In our study, the higher cover of herbaceous plants and lower bare soil groundcover in managed sites suggests that managed woodland habitat has more diverse arthropod habitat beyond what we were able to measure on understory foliage. Although mesic forests near streams and in cool microclimates have been shown to provide more stable insect resources throughout the summer (Persche and Pidgeon 2020, Schilke et al. 2020), we did not find the same effect in upland mesic forest on former oak woodland sites.

Although mature forest specialists continued to use managed sites during all three study years, capture rates tended to be lower than they were in unmanaged sites, particularly for Hooded Warbler, Scarlet Tanager, Ovenbird, and Wood Thrush. For these species, the trade-off between managing for woodland conditions and conserving contiguous mature forest habitat was the most pronounced. Hooded Warbler, Ovenbird, and Wood Thrush have previously been documented responding negatively to logging (Haché et al. 2013, Morris et al. 2013) or woodland restoration (Artman et al. 2001, Greenberg et al. 2007, Vander Yacht et al.

2016). However, in the case of Wood Thrush and Hooded Warbler, which use areas of dense understory resulting from canopy gaps in mature forests (Whittam et al. 2002, Evans et al. 2020, Mumme et al. 2023), population increases during the years following logging have also been observed (Gram et al. 2003, Morris et al. 2013, Sheehan et al. 2014). We observed territories of all three species entirely or partially within management units, particularly 2–3 years after thinning or burning treatments, in areas of dense understory regrowth. Thus, although mature forest specialists may have lower densities after woodland management treatment, these effects are likely to last only for a few years and affect few species (Thompson et al. 1996, Vander Yacht et al. 2016, Annand and Thompson 2018). Long-term monitoring of population trends during repeated cycles of woodland management will help determine whether Hooded Warbler, Ovenbird, and Wood Thrush populations ever reach pre-disturbance densities (see Morris et al. 2013). Our sites are separated by > 1 km and so we were not able to test for negative effects of management carrying over into birds in unmanaged sites, as observed by Gram et al. (2003) and Morris et al. (2013). However, we anecdotally noticed high density of Wood Thrush and Ovenbird territories in unmanaged habitat adjacent to management units, potentially resulting from displaced territories within the units or increased habitat quality at the management unit edge. Some of the negative effects of habitat fragmentation (i.e., brood parasitism from Brown-headed Cowbirds, increased nest predation) that have been hypothesized to influence birds in woodland management units as well, may be buffered by the surrounding extensive forest (Gram et al. 2003).

Ovenbirds and Wood Thrush are ground foragers, and their foraging habitat may have been negatively influenced by management. For example, Haché et al. (2013) found that litter invertebrate abundance decreased and Ovenbird territories were larger following selection timber harvesting. Prescribed fire can have negative effects on ground-dwelling invertebrate species as well (Verble-Pearson 2014, Chitwood et al. 2017). Although we were unable to quantify litter invertebrates in our study area, this could have been one of the reasons for the lower Ovenbird and Wood Thrush abundance in managed sites. However, we found a lower percent of bare soil in managed sites than unmanaged sites, despite periodic prescribed burning, and other ground foragers, including American Robin (*Turdus migratorius*), Eastern Towhee, Northern Flicker (*Colaptes auratus*), and Veery had similar or higher capture rates in managed sites.

In regions where woodlands and forests have largely been converted to agriculture or other human-modified environments, effectively balancing the needs of a diverse group of species is necessary. This is particularly true when considering woodland restoration within large forest preserves that are rare strongholds for mature forest bird species. We found that oak woodland management within extensive mature forests was associated with equal or higher understory arthropod biomass, equal or higher insectivore richness, and stable mass-abundance relationships between years with vastly different arthropod resources. In unmanaged sites, mass-abundance relationships were not significant in any year and appeared to vary widely, suggesting lower resilience to arthropod variability. Four mature forest specialists were less abundant in managed sites, while eight early-

successional species were more abundant. Examining multi-trophic systems and mass-abundance relationships of insectivorous birds within extensive forests can illuminate more subtle biodiversity responses to habitat degradation or management than are usually studied. To our knowledge, this is the first inquiry into the mass-abundance relationships of temperate forest insectivores, and the first application of this approach to assess the influence of habitat management on breeding birds.

Acknowledgments:

This material is based upon work supported by the National Institute of Food and Agriculture, United States Department of Agriculture, McIntire Stennis project 1023332, as well as a Dickie Family Sauk County Educational Fellowship and a Wisconsin Society for Ornithology research grant. We would like to thank the many people who helped collect field data, including L. Berman, O. Beaupre, K. Brunk, C. Chorzempa, J. Christianson, H. Cox, J. Furchgott, S. Gomez-maier, L. Hartman, A. Olah, J. Schneidermann, A. Shchur, J. Shanks, A. Tveite. Thank you to U. Srinivasan and three anonymous reviewers for providing feedback on earlier versions of this manuscript. We are grateful to The Nature Conservancy and the Wisconsin Department of Natural Resources for land access, the many land stewards working on these sites, and the 535 understory insectivores we banded and measured for this study.

LITERATURE CITED

- Abella, S. R., K. S. Menard, T. A. Schetter, L. R. A. Sprow, and J. F. Jaeger. 2020. Rapid and transient changes during 20 years of restoration management in savanna-woodland-prairie habitats threatened by woody plant encroachment. *Plant Ecology* 221:1201-1217. <https://doi.org/10.1007/s11258-020-01075-4>
- Annand, E. M., and F. R. I. Thompson III. 2018. Forest bird response to regeneration practices in central hardwood forests. *Journal of Wildlife Management* 61:159-171. <https://doi.org/10.2307/3802425>
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* 74:1175-1178. <https://doi.org/10.2193/2009-367>
- Artman, V. L., E. K. Sutherland, and J. F. Downhower. 2001. Prescribed burning to restore mixed-oak communities in southern Ohio: effects on breeding-bird populations. *Conservation Biology* 15:1423-1434. <https://doi.org/10.1111/j.1523-1739.2001.00181.x>
- Barrioz, S., P. Keyser, D. Buckley, D. Buehler, and C. Harper. 2013. Vegetation and avian response to oak savanna restoration in the Mid-South USA. *American Midland Naturalist* 169:194-213. <https://doi.org/10.1674/0003-0031-169.1.194>
- Billerman, S. M., B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg, editors. 2022. *Birds of the world*. Cornell Laboratory of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow>

- Blackburn, T. M., V. K. Brown, B. M. Doube, J. J. D. Greenwood, J. H. Lawton, and N. E. Stork. 1993. The relationship between abundance and body size in natural animal assemblages. *Journal of Animal Ecology* 62:519-528. <http://www.jstor.org/stable/5201> <https://doi.org/10.2307/5201>
- Brawn, J. D., S. K. Robinson, and F. R. I. Thompson. 2001. The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology, Evolution, and Systematics* 32:251-276. <https://doi.org/10.1146/annurev.ecolsys.32.081501.114031>
- Bregman, T. P., C. H. Sekercioglu, and J. A. Tobias. 2014. Global patterns and predictors of bird species responses to forest fragmentation: implications for ecosystem function and conservation. *Biological Conservation* 169:372-383. <https://doi.org/10.1016/j.biocon.2013.11.024>
- Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *Bioscience* 33:31-35. <https://doi.org/10.2307/1309241>
- Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. *Auk* 115:96-104. <https://doi.org/10.2307/4089115>
- Campbell, J. W., J. L. Hanula, and T. A. Waldrop. 2007. Effects of prescribed fire and fire surrogates on floral visiting insects of the blue ridge province in North Carolina. *Biological Conservation* 134:393-404. <https://doi.org/10.1016/j.biocon.2006.08.029>
- Chandler, R. B., D. I. King, and C. C. Chandler. 2009. Effects of management regime on the abundance and nest survival of shrubland birds in wildlife openings in northern New England, USA. *Forest Ecology and Management* 258:1669-1676. <https://doi.org/10.1016/j.foreco.2009.07.025>
- Chitwood, M. C., M. A. Lashley, B. L. Sherrill, C. Sorenson, C. S. DePerno, and C. E. Moorman. 2017. Macroarthropod response to time-since-fire in the longleaf pine ecosystem. *Forest Ecology and Management* 391:390-395. <https://doi.org/10.1016/j.foreco.2017.02.038>
- Cosset, C. C. P., J. J. Gilroy, U. Srinivasan, M. G. Hethcoat, and D. P. Edwards. 2020. Mass-abundance scaling in avian communities is maintained after tropical selective logging. *Ecology and Evolution* 10:2803-2812. <https://doi.org/10.1002/ece3.6066>
- Curtis, J. T. 1959. The vegetation of Wisconsin: an ordination of plant communities. University of Wisconsin Press, Madison, Wisconsin, USA.
- Damuth, J. 1981. Population density and body size in mammals. *Nature* 290:699-700. <https://doi.org/10.1038/290699a0>
- Davis, M. A., D. W. Peterson, P. B. Reich, M. Crozier, T. Query, E. Mitchell, J. Huntington, and P. Bazakas. 2000. Restoring savanna using fire: impact on the breeding bird community. *Restoration Ecology* 8:30-40. <https://doi.org/10.1046/j.1526-100x.2000.80005.x>
- Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. *Science* 345:401-406. <https://doi.org/10.1126/science.1251817>
- Epstein, E. E. 2017. Natural communities, aquatic features, and selected habitats of Wisconsin. Chapter 7 in *The ecological landscapes of Wisconsin: an assessment of ecological resources and a guide to planning sustainable management*. PUB-SS-1131H 2017. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.
- Evans, M., E. Gow, R. R. Roth, M. S. Johnson, and T. J. Underwood. 2020. Wood Thrush (*Hylocichla mustelina*), version 1.0. In A. F. Poole, editor. *Birds of the world*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.woothr.01>
- Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, D. J. Levey, P. P. Marra, C. L. Merkord, E. Nol, S. I. Rothstein, T. W. Sherry, T. S. Sillett, F. R. Thompson, and N. Warnock. 2010. Conserving migratory land birds in the New World: Do we know enough? *Ecological Applications* 20:398-418. <https://doi.org/10.1890/09-0397.1>
- Farwell, L. S., P. R. Elsen, E. Razenkova, A. M. Pidgeon, and V. C. Radeloff. 2020. Habitat heterogeneity captured by 30-m resolution satellite image texture predicts bird richness across the United States. *Ecological Applications* 30:e02157. <https://doi.org/10.1002/eap.2157>
- Fink, D., T. Auer, A. Johnston, M. Strimas-Mackey, S. Ligocki, O. Robinson, W. Hochachka, L. Jaromczyk, A. Rodewald, C. Wood, I. Davies, and A. Spencer. 2022. eBird status and trends. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Fox, R. 2013. The decline of moths in Great Britain: a review of possible causes. *Insect Conservation and Diversity* 6:5-19. <https://doi.org/10.1111/j.1752-4598.2012.00186.x>
- Gavier-Pizarro, G. I., V. C. Radeloff, S. I. Stewart, C. D. Huebner, and N. S. Keuler. 2010. Rural housing is related to plant invasions in forests of southern Wisconsin, USA. *Landscape Ecology* 25:1505-1518. <https://doi.org/10.1007/s10980-010-9516-8>
- Gram, W. K., P. A. Porneluzi, R. L. Clawson, J. Faaborg, and S. C. Richter. 2003. Effects of experimental forest management on density and nesting success of bird species in Missouri Ozark forests. *Conservation Biology* 17:1324-1337. <https://doi.org/10.1046/j.1523-1739.2003.02171.x>
- Greenberg, C. H., A. L. Tomcho, J. D. Lanham, T. A. Waldrop, J. Tomcho, R. J. Phillips, and D. Simon. 2007. Short-term effects of fire and other fuel reduction treatments on breeding birds in a southern Appalachian upland hardwood forest. *Journal of Wildlife Management* 71:1906-1916. <https://doi.org/10.2193/2006-070>
- Greenberg, C. H., J. Tomcho, A. Livings-Tomcho, J. D. Lanham, T. A. Waldrop, D. Simon, and D. Hagan. 2018. Long-term avian response to fire severity, repeated burning, and mechanical fuel reduction in upland hardwood forest. *Forest Ecology and Management* 424:367-377. <https://doi.org/10.1016/j.foreco.2018.05.014>
- Gruner, D. S. 2003. Regressions of length and width to predict arthropod biomass in the Hawaiian Islands. *Pacific Science* 57:325-336. <https://doi.org/10.1353/psc.2003.0021>

- Haché, S., M. A. Villard, and E. M. Bayne. 2013. Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird. *Ecology* 94:861-869. <https://doi.org/10.1890/12-1025.1>
- Hallmann, C. A., R. P. B. Foppen, C. A. M. van Turnhout, H. de Kroon, and E. Jongejans. 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature* 511:341-343. <https://doi.org/10.1038/nature13531>
- Hanberry, B. B., D. C. Bragg, and H. D. Alexander. 2020. Open forest ecosystems: an excluded state. *Forest Ecology and Management* 472:118256. <https://doi.org/10.1016/j.foreco.2020.118256>
- Hanberry, B. B., D. C. Bragg, and T. F. Hutchinson. 2018. A reconceptualization of open oak and pine ecosystems of eastern North America using a forest structure spectrum. *Ecosphere* 9(10): e02431. <https://doi.org/10.1002/ecs2.2431>
- Hanberry, B. B., J. M. Kabrick, P. W. Dunwiddie, T. Hartel, T. B. Jain, and B. O. Knapp. 2017. Restoration of temperate savannas and woodlands. Pages 142-157 in S. K. Allison and S. D. Murphy, editors. *Routledge handbook of ecological and environmental restoration*. Routledge, London, UK. <https://doi.org/10.4324/9781315685977-11>
- Hanberry, B. B., and G. J. Nowacki. 2016. Oaks were the historical foundation genus of the east-central United States. *Quaternary Science Reviews* 145:94-103. <https://doi.org/10.1016/j.quascirev.2016.05.037>
- Hanberry, B. B., and F. R. Thompson III. 2019. Open forest management for early successional birds. *Wildlife Society Bulletin* 43:141-151. <https://doi.org/10.1002/wsb.957>
- Hanula, J. L., S. Horn, and J. J. O'Brien. 2015. Have changing forests conditions contributed to pollinator decline in the southeastern United States? *Forest Ecology and Management* 348:142-152. <https://doi.org/10.1016/j.foreco.2015.03.044>
- Hanula, J. L., and D. D. Wade. 2003. Influence of long-term dormant-season burning and fire exclusion on ground-dwelling arthropod populations in longleaf pine flatwoods ecosystems. *Forest Ecology and Management* 175:163-184. [https://doi.org/10.1016/S0378-1127\(02\)00130-5](https://doi.org/10.1016/S0378-1127(02)00130-5)
- Hartung, S. C., and J. D. Brawn. 2005. Effects of savanna restoration on the foraging ecology of insectivorous songbirds. *Condor* 107:879-888. <https://doi.org/10.1093/condor/107.4.879>
- Hirao, T., M. Murakami, and A. Kashizaki. 2009. Importance of the understory stratum to entomofaunal diversity in a temperate deciduous forest. *Ecological Research* 24:263-272. <https://doi.org/10.1007/s11284-008-0502-4>
- Holmes, R. T., and S. K. Robinson. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. *Oecologia* 48:31-35. <https://doi.org/10.1007/BF00346985>
- Holmes, R. T., and J. C. Schultz. 1988. Food availability for forest birds: effects of prey distribution and abundance on bird foraging. *Canadian Journal of Zoology* 66:720-728. <https://doi.org/10.1139/z88-107>
- Hurlbert, A., T. Hayes, T. McKinnon, and C. Goforth. 2019. Caterpillars count! A citizen science project for monitoring foliage arthropod abundance and phenology. *Citizen Science: Theory and Practice* 4:1. <https://doi.org/10.5334/cstp.148>
- Iwata, T., S. Nakano, and M. Murakami. 2003. Stream meanders increase insectivorous bird abundance in riparian deciduous forests. *Ecography* 26:325-337. <https://doi.org/10.1034/j.1600-0587.2003.03355.x>
- Jacobs, K. A., B. Nix, and B. C. Scharenbroch. 2015. The effects of prescribed burning on soil and litter invertebrate diversity and abundance in an Illinois Oak Woodland. *Natural Areas Journal* 35:318-327. <https://doi.org/10.3375/043.035.0214>
- Knoot, T. G., M. E. Shea, L. A. Schulte, J. C. Tyndall, M. D. Nelson, C. H. Perry, and B. J. Palik. 2015. Forest change in the driftless area of the Midwest: from a preferred to undesirable future. *Forest Ecology and Management* 341:110-120. <https://doi.org/10.1016/j.foreco.2014.12.013>
- Koenker, R. 2005. *Quantile regression*. Cambridge University Press, Cambridge, UK. <https://doi.org/10.1017/CBO9780511754098>
- Koenker, R. 2022. *quantreg*.
- Lettow, M. C., L. A. Brudvig, C. A. Bahlai, J. Gibbs, R. P. Jean, and D. A. Landis. 2018. Bee community responses to a gradient of oak savanna restoration practices. *Restoration Ecology* 26:882-890. <https://doi.org/10.1111/rec.12655>
- Lowther, P. E. 2020. Brown-headed Cowbird (*Molothrus ater*), version 1.0. In A. F. Poole and F. B. Gill, editors. *Birds of the world*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.bnhcow.01>
- Lumpkin, H. A., and S. M. Pearson. 2013. Effects of exurban development and temperature on bird species in the southern Appalachians. *Conservation Biology* 27:1069-1078. <https://doi.org/10.1111/cobi.12085>
- Mason, S. C., V. Shirey, L. C. Ponisio, and J. K. Gelhaus. 2021. Responses from bees, butterflies, and ground beetles to different fire and site characteristics: a global meta-analysis. *Biological Conservation* 261:109265. <https://doi.org/10.1016/j.biocon.2021.109265>
- Moorman, C. E., L. T. Bowen, J. C. Kilgo, J. L. Hanula, S. Horn, and M. D. Ulyshen. 2012. Arthropod abundance and seasonal bird use of bottomland forest harvest gaps. *Wilson Journal of Ornithology* 124:31-39. <https://doi.org/10.1676/11-020.1>
- Morris, D. L., P. A. Perneluzi, J. Haslerig, R. L. Clawson, and J. Faaborg. 2013. Results of 20 years of experimental forest management on breeding birds in Ozark forests of Missouri, USA. *Forest Ecology and Management* 310:747-760. <https://doi.org/10.1016/j.foreco.2013.09.020>
- Mossman, M. J., and K. I. Lange. 1982. *Breeding birds of the Baraboo Hills, Wisconsin*. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.
- Mumme, R. L., I. Chiver, L. J. Evans Ogden, and B. J. Stutchbury. 2023. Hooded Warbler (*Setophaga citrina*), version 2.0. In P. G. Rodewald, editor. *Birds of the world*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.hoowar.02>
- Narango, D. L., D. W. Tallamy, and P. P. Marra. 2018. Nonnative plants reduce population growth of an insectivorous bird. *Proceedings of the National Academy of Sciences* 115:11549-11554. <https://doi.org/10.1073/pnas.1809259115>

- Narango, D. L., D. W. Tallamy, and K. J. Shropshire. 2020. Few keystone plant genera support the majority of Lepidoptera species. *Nature Communications* 11:5751. <https://doi.org/10.1038/s41467-020-19565-4>
- Nowacki, G. J., and M. D. Abrams. 2008. The demise of fire and “Mesophication” of forests in the Eastern United States. *BioScience* 58:123-138. <https://doi.org/10.1641/B580207>
- Nuzzo, V. A. 1986. Extent and status of midwest oak savanna: presettlement and 1985. *Natural Areas Journal* 6(2):6-36.
- Oksanen, J., G. L. Simpson, F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, P. Solymos, M. H. H. Stevens, E. Szoecs, et al. 2025. *vegan: Community Ecology Package*. R. package. <https://doi.org/10.32614/CRAN.package.vegan>
- Persche, M. E., and A. M. Pidgeon. 2020. Habitat resilience for songbirds: the role of topographic position in a mixed deciduous forest. *Forest Ecology and Management* 472:118238. <https://doi.org/10.1016/j.foreco.2020.118238>
- Pyle, P. 2022. *Identification guide to North American birds, Part I*, 2nd edition. Slate Creek Press, Point Reyes Station, California, USA.
- Reidy, J. L., F. R. Thompson III, and S. W. Kendrick. 2014. Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks. *Forest Ecology and Management* 313:34-46. <https://doi.org/10.1016/j.foreco.2013.10.042>
- Rhemtulla, J. M., D. J. Mladenoff, and M. K. Clayton. 2007. Regional land-cover conversion in the U.S. upper Midwest: magnitude of change and limited recovery (1850–1935–1993). *Landscape Ecology* 22:57-75. <https://doi.org/10.1007/s10980-007-9117-3>
- Rhemtulla, J. M., D. J. Mladenoff, and M. K. Clayton. 2009. Legacies of historical land use on regional forest composition and structure in Wisconsin, USA (mid-1800s–1930s–2000s). *Ecological Applications* 19:1061-1078. <https://doi.org/10.1890/08-1453.1>
- Roach, M. C., F. R. Thompson III, and T. Jones-Farrand. 2019. Effects of pine-oak woodland restoration on breeding bird densities in the Ozark-Ouachita Interior Highlands. *Forest Ecology and Management* 437:443-459. <https://doi.org/10.1016/j.foreco.2018.12.057>
- Rodenhouse, N. L., and R. T. Holmes. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. *Ecology* 73:357-372. <https://doi.org/10.2307/1938747>
- Rogers, D. A., T. P. Rooney, D. Olson, and D. M. Waller. 2008. Shifts in southern Wisconsin forest canopy and understory richness, composition, and heterogeneity. *Ecology* 89:2482-2492. <https://doi.org/10.1890/07-1129.1>
- Rogers, L. E., R. L. Buschbom, and C. R. Watson. 1977. Length-weight relationships of shrub-steppe invertebrates. *Annals of the Entomological Society of America* 70:51-53. <https://doi.org/10.1093/aesa/70.1.51>
- Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra. 2019. Decline of the North American avifauna. *Science* 366:120-124. <https://doi.org/10.1126/science.aaw1313>
- Sabo, J. L., J. L. Bastow, and M. E. Power. 2002. Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of the North American Benthological Society* 21:336-343. <https://doi.org/10.2307/1468420>
- Schilke, P. R., M. Bartrons, J. M. Gorzo, M. J. Vander Zanden, C. Gratton, R. W. Howe, and A. M. Pidgeon. 2020. Modeling a cross-ecosystem subsidy: forest songbird response to emergent aquatic insects. *Landscape Ecology* 35:1587-1604. <https://doi.org/10.1007/s10980-020-01038-0>
- Schlossberg, S., D. I. King, R. B. Chandler, and B. A. Mazzei. 2010. Regional synthesis of habitat relationships in shrubland birds. *Journal of Wildlife Management* 74:1513-1522. <https://doi.org/10.2193/2008-601>
- Sheehan, J., P. B. Wood, D. A. Buehler, P. D. Keyser, J. L. Larkin, A. D. Rodewald, T. B. Wigley, T. J. Boves, G. A. George, M. H. Bakermans, T. A. Beachy, A. Evans, M. E. McDermott, F. L. Newell, K. A. Perkins, and M. White. 2014. Avian response to timber harvesting applied experimentally to manage Cerulean Warbler breeding populations. *Forest Ecology and Management* 321:5-18. <https://doi.org/10.1016/j.foreco.2013.07.037>
- Šigut, M., H. Šigutová, J. Šipoš, P. Pyszek, N. Kotásková, and P. Drozd. 2018. Vertical canopy gradient shaping the stratification of leaf-chewer-parasitoid interactions in a temperate forest. *Ecology and Evolution* 8:7297-7311. <https://doi.org/10.1002/ece3.4194>
- Sreekar, R., U. Srinivasan, C. Mammides, J. Chen, U. Manage Goodale, S. Wimalabandara Kotagama, S. Sidhu, and E. Goodale. 2015. The effect of land-use on the diversity and mass-abundance relationships of understory avian insectivores in Sri Lanka and southern India. *Scientific Reports* 5:11569. <https://doi.org/10.1038/srep11569>
- Srinivasan, U. 2013. A slippery slope: logging alters mass-abundance scaling in ecological communities. *Journal of Applied Ecology* 50:920-928. <https://doi.org/10.1111/1365-2664.12123>
- Stireman III, J. O., H. Devlin, and A. L. Doyle. 2014. Habitat fragmentation, tree diversity, and plant invasion interact to structure forest caterpillar communities. *Oecologia* 176:207-224. <https://doi.org/10.1007/s00442-014-3014-7>
- Suarez-Rubio, M., P. Leimgruber, and S. C. Renner. 2011. Influence of exurban development on bird species richness and diversity. *Journal of Ornithology* 152:461-471. <https://doi.org/10.1007/s10336-010-0605-x>
- Summerville, K. S. 2011. Managing the forest for more than the trees: effects of experimental timber harvest on forest Lepidoptera. *Ecological Applications* 21:806-816. <https://doi.org/10.1890/10-0715.1>
- Tallamy, D. W., and W. G. Shriver. 2021. Are declines in insects and insectivorous birds related? *Ornithological Applications* 123:duaa059. <https://doi.org/10.1093/ornithapp/duaa059>
- Tallamy, D. W., and K. J. Shropshire. 2009. Ranking lepidopteran use of native versus introduced plants. *Conservation Biology* 23:941-947. <https://doi.org/10.1111/j.1523-1739.2009.01202.x>

Thompson III, F. R. I., T. M. Donovan, R. M. Degraaf, J. Faaborg, and S. K. Robinson. 2002. A multi-scale perspective of the effects of forest fragmentation on birds in Eastern forests. *Studies in Avian Biology* 25:8-19.

Thompson III, F. R. I., S. K. Robinson, D. R. Whitehead, and J. D. Brawn. 1996. Management of central hardwood landscapes for the conservation of migratory birds. Pages 117-143 in F. R. Thompson, editor. *Management of Midwestern landscapes for the conservation of Neotropical migratory birds*. General technical report NC-187. U.S. Forest Service, Detroit, Michigan, USA.

Underwood, E. C., and J. F. Quinn. 2010. Response of ants and spiders to prescribed fire in oak woodlands of California. *Journal of Insect Conservation* 14:359-366. <https://doi.org/10.1007/s10841-010-9265-7>

Van Wilgenburg, S. L., D. F. Mazerolle, and K. A. Hobson. 2001. Patterns of arthropod abundance, vegetation, and microclimate at boreal forest edge and interior in two landscapes: implications for forest birds. *Écoscience* 8:454-461. <https://doi.org/10.1080/11956860.2001.11682675>

Vander Yacht, A. L., P. D. Keyser, S. A. Barrioz, C. Kwit, M. C. Stambaugh, W. K. Clatterbuck, and R. Jacobs. 2020. Litter to glitter: promoting herbaceous groundcover and diversity in mid-southern USA oak forests using canopy disturbance and fire. *Fire Ecology* 16:17. <https://doi.org/10.1186/s42408-020-00072-2>

Vander Yacht, A. L., P. D. Keyser, D. A. Buehler, C. A. Harper, D. S. Buckley, and R. D. Applegate. 2016. Avian occupancy response to oak woodland and savanna restoration. *Journal of Wildlife Management* 80:1091-1105. <https://doi.org/10.1002/jwmg.21097>

Verble-Pearson, R. M. 2014. Effects of fire intensity on litter arthropod communities in Ozark oak forests, Arkansas, U.S.A. *American Midland Naturalist* 172:14-24. <https://doi.org/10.1674/0003-0031-172.1.14>

White, E. P., S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution* 22:323-330. <https://doi.org/10.1016/j.tree.2007.03.007>

Whittam, R. M., J. D. McCracken, C. M. Francis, and M. E. Gartshore. 2002. The effects of selective logging on nest-site selection and productivity of Hooded Warblers (*Wilsonia citrina*) in Canada. *Canadian Journal of Zoology* 80:644-654. <https://doi.org/10.1139/z02-039>

Wickham, H. 2016. *ggplot2: Elegant graphics for data analysis*. Springer, Cham, Switzerland. <https://doi.org/10.1007/978-3-319-24277-4>

Wood, E. M., A. M. Pidgeon, F. Liu, and D. J. Mladenoff. 2012. Birds see the trees inside the forest: the potential impacts of

changes in forest composition on songbirds during spring migration. *Forest Ecology and Management* 280:176-186. <https://doi.org/10.1016/j.foreco.2012.05.041>

Zahn, A., L. Rodrigues, A. Rainho, and J. M. Palmeirim. 2007. Critical times of the year for *Myotis myotis*, a temperate zone bat: roles of climate and food resources. *Acta Chiropterologica* 9:115-125. [https://doi.org/10.3161/1733-5329\(2007\)9\[115:CTOTYF\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2007)9[115:CTOTYF]2.0.CO;2)



Appendix 1: Influence of woodland management within interior forests on foliage arthropods and avian insectivores

Maia E. Persche, H. S. Sathya Chandra Sagar, Anna M. Pidgeon

Table S1. Management histories of the two managed woodland sites in the Baraboo Hills (Sauk Co., Wisconsin, USA). HDSO (Hemlock Draw South) and HHWO (Happy Hill Woodland) are both owned and managed by The Nature Conservancy. TSI refers to timber stand improvement and involves harvesting overstory trees to favor oaks and other shade-intolerant species. Thinning refers to felling midstory and understory trees.

		HDSO	HHWO
2014	Fall/Winter	TSI	
2017	Spring	Burned	
2018	Spring		
2018	Fall/Winter	TSI	Thinned
2019	Spring	Burned	
2019	Fall/Winter	TSI	
2020	Fall/Winter	TSI	Burned
2021	Spring	Burned	
2021	Fall/Winter	TSI	Thinned
2022	Spring		
2022	Fall/Winter		Burned
2023	Spring	Burned	

Table S2. Common and scientific names of 43 insectivorous bird species documented between late-May and early-August 2021-2023 in four oak woodland study sites in the Baraboo Hills (Sauk Co., Wisconsin, USA).

Species	Scientific Name
Acadian Flycatcher	<i>Empidonax virescens</i>
American Redstart	<i>Setophaga ruticilla</i>
American Robin	<i>Turdus migratorius</i>
Baltimore Oriole	<i>Icterus galbula</i>
Black-capped Chickadee	<i>Poecile atricapillus</i>
Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>
Blue-winged Warbler	<i>Vermivora cyanoptera</i>
Brown Creeper	<i>Certhia americana</i>
Cerulean Warbler	<i>Setophaga cerulea</i>
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>
Chipping Sparrow	<i>Spizella passerina</i>
Common Yellowthroat	<i>Geothlypis trichas</i>
Downy Woodpecker	<i>Dryobates pubescens</i>
Eastern Towhee	<i>Pipilo erythrophthalmus</i>
Eastern Wood-Pewee	<i>Contopus virens</i>
Field Sparrow	<i>Spizella pusilla</i>
Gray Catbird	<i>Dumetella carolinensis</i>
Great Crested Flycatcher	<i>Myiarchus crinitus</i>
Hairy Woodpecker	<i>Dryobates villosus</i>
Hooded Warbler	<i>Setophaga citrina</i>
House Wren	<i>Troglodytes aedon</i>
Indigo Bunting	<i>Passerina cyanea</i>
Least Flycatcher	<i>Empidonax minimus</i>
Mourning Warbler	<i>Geothlypis philadelphia</i>
Northern Cardinal	<i>Cardinalis cardinalis</i>
Northern Flicker	<i>Colaptes auratus</i>
Ovenbird	<i>Seiurus aurocapilla</i>
Pileated Woodpecker	<i>Dryocopus pileatus</i>
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>
Red-eyed Vireo	<i>Vireo olivaceus</i>
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>
Ruby-throated Hummingbird	<i>Archilochus colubris</i>
Scarlet Tanager	<i>Piranga olivacea</i>
Song Sparrow	<i>Melospiza melodia</i>
Tufted Titmouse	<i>Baeolophus bicolor</i>
Veery	<i>Catharus fuscescens</i>
White-breasted Nuthatch	<i>Sitta carolinensis</i>

Wood Thrush	<i>Hylocichla mustelina</i>
Yellow Warbler	<i>Setophaga petechia</i>
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>
Yellow-throated Vireo	<i>Vireo flavifrons</i>

Table S3. Mass-abundance model output, corresponding to Figure 2d-f.

Year	Model Coefficients	Estimate	Std. Error	t value	p value
2021	(Intercept)	2.45	0.67	3.69	<0.01
	logMass	-0.66	0.22	-2.97	<0.01
	TreatmentUnmanaged	-2.88	1.74	-1.66	0.10
	logMass:TreatmentUnmanaged	0.79	0.49	1.61	0.11
2022	(Intercept)	2.74	0.72	3.83	<0.01
	logMass	-0.57	0.19	-2.97	<0.01
	TreatmentUnmanaged	-2.27	1.44	-1.58	0.12
	logMass:TreatmentUnmanaged	0.45	0.41	1.08	0.28
2023	(Intercept)	2.13	1.05	2.02	0.05
	logMass	-0.49	0.27	-1.79	0.08
	TreatmentUnmanaged	0.50	2.11	0.24	0.81
	logMass:TreatmentUnmanaged	-0.27	0.63	-0.43	0.67