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ORIGINAL RESEARCH

Complex and highly saturated soundscapes in restored oak woodlands reflect avian richness and abundance

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Abstract

Temperate woodlands are biodiverse natural communities threatened by land use change and fire suppression. Excluding historic disturbance regimes of periodic groundfires from woodlands causes degradation, resulting from changes in the plant community and subsequent biodiversity loss. Restoration, through prescribed fire and tree thinning, can reverse biodiversity losses, however, because the diversity of woodland species spans many taxa, efficiently quantifying biodiversity can be challenging. We assessed whether soundscapes in an eastern North American woodland reflect biodiversity changes during restoration measured in a concurrent multitrophic field study. In five restored and five degraded woodland sites in Wisconsin, USA, we sampled vegetation, measured arthropod biomass, conducted bird surveys, and recorded soundscapes for five days of every 15-day period from May to August 2022. We calculated two complementary acoustic indices: Soundscape Saturation, which focuses on all acoustically active species, and Acoustic Complexity Index (ACI), which was developed to study vocalizing birds. We used generalized additive models to predict both indices based on Julian date, time of day, and level of habitat degradation. We found that restored woodlands had higher arthropod biomass, and higher richness and abundance of breeding birds. Additionally, soundscapes in restored sites had higher mean Soundscape Saturation and higher mean ACI. Restored woodland acoustic indices exhibited greater magnitudes of daily and seasonal peaks. We conclude that woodland restoration results in higher soundscape saturation and complexity, due to greater richness and abundance of vocalizing animals. This bioacoustic signature of restoration offers a promising monitoring tool for efficiently documenting differences in woodland biodiversity.

Keywords Acoustic complexity index · Arthropods · Bioacoustics · Birds · Habitat degradation · Habitat restoration · Monitoring · Soundscape saturation

Introduction

Worldwide, sixty-one terrestrial ecoregions (Olson et al. 2001) are dominated by woodland habitats, from the Mediterranean woodlands of southwestern Europe to the eucalypt woodlands of eastern Australia and the pine woodlands of western North America (Appendix S1: Table S1). Woodlands are defined by their canopy cover, which is intermediate between that of savannas and forests, and open understory conditions (Curtis 1959; Epstein 2017). North American woodlands and savannas are diverse and include longleaf pine ecosystems in the southeast, ponderosa pine woodland in the west, Garry oak woodland in the northwest, and oak woodland and in the Midwestern USA (i.e., north-central USA from Ohio to North and South Dakota, extending south to Missouri; U.S. Census Bureau). In the United States prior to European settlement, woodland habitats covered more than 50 million hectares, and were maintained by periodic groundfires resulting from natural ignition sources and/or cultural burning practices (Abrams et al. 2022; Mariani et al. 2022).

In the USA, two Midwestern ecoregions are dominated by fire-dependent open woodlands and savannas (Central

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Forest-grasslands Transition and Ozark Mountain Forests; Appendix S1: Table S1), while an additional two have interspersed open woodland habitats (Appalachian Mixed Mesophytic Forests and Central U.S. Hardwood Forests; Appendix S1: Table S2). In these ecoregions, oaks (*Quercus* sp.) are a foundational genus because of their dominance and key role in structuring the ecosystem (Hanberry and Nowacki 2016), and support high diversity of folivorous arthropods (Tallamy and Shropshire 2009), mast-dependent species (i.e., species that feed on acorns; McShea et al. 2007), and species adapted to the permanently open canopy structure and high-light conditions of oak woodlands (Hanberry and Nowacki 2016). Ecological management of temperate woodlands benefits species across multiple taxa, including plant communities in southern USA oak woodlands (Vander Yacht et al. 2020), flower-visiting insects in southeastern USA temperate forest (Campbell et al. 2018), and woodland-adapted bird species of conservation concern in the eastern USA, including Red-headed Woodpeckers (Frei et al. 2020) and Eastern Whip-poor-wills (Cink et al. 2020). Woodland and savanna communities have been reduced drastically, and in the case of Midwestern USA oak savannas, less than 1% remain (Nuzzo 1986). Many remaining woodlands are degraded, with high shrub cover that limits oak regeneration and understory plant diversity. Fire suppression, which has been common since European settlement due to an emphasis on controlling natural fires and limitations placed on cultural burning (Curtis 1959; Abrams et al. 2022; Mariani et al. 2022) leads to a process called mesophication, in which fire-intolerant tree species become established, thus causing shady and humid understory conditions (Nowacki and Abrams 2008). In a positive feedback loop, fires become less common due to high understory moisture, thus allowing more mesic-associated species to grow. While this process is similar to natural succession from open habitats into closed-canopy forest, former oak woodlands often do not transform into high-quality mesic forests with high species diversity, but instead become novel habitats with low species diversity (Rogers et al. 2008; Knoot et al. 2015). Fire suppression and mesophication have raised concern about the persistence of oak woodland habitat (Rhemtulla et al. 2007; Knoot et al. 2015), and can cause woodland degradation even within protected areas. Restoration practices such as prescribed fire and mechanical thinning (Hanberry et al. 2017) are widely used to emulate the effects of natural disturbances which stabilize open woodland ecosystems and have been shown to increase oak regeneration and maintain biodiversity (Brose et al. 2013; Vander Yacht et al. 2020). More broadly, prescribed fire has improved or maintained the quality of woodland ecosystems in ecoregions in western North America (Brown et al. 2019; Hoffman et al. 2019; Saab et al. 2022), Australia (Boer et al. 2009; Burrows and McCaw 2013; Evans and Russell-Smith 2020) and southern Europe (Vilà-Vilardell et al. 2023; Fernández-Guisuraga and Fernandes 2024).

Detecting the effects of woodland restoration requires knowledge of many taxa. Many acoustically active species, including birds, amphibians, and mammals, are influenced by local-scale vegetation characteristics (Parris and McCarthy 1999; Urban and Swihart 2011; Holloway et al. 2012; Barrioz et al. 2013), which in turn are shaped by woodland restoration (Vander Yacht et al. 2020). It is well established that within forested habitats, local-scale vegetation structure can shape sound diversity by influencing the calling animal community (Boelman et al. 2007; Rodriguez et al. 2014; Burivalova et al. 2018). In particular, vegetation structural complexity is associated with greater occurrence and complexity of biotic sounds in forest communities ranging from the UK (Turner et al. 2018), to Sweden (Shaw et al. 2021), to the southern USA (Bobryk et al. 2016). To evaluate the effects of open oak woodland restoration on birds and other woodland species in the Midwestern USA, we used bioacoustics to sample a wide range of acoustically active species.

Bioacoustics is a growing field that intersects with biodiversity monitoring and assessments of ecosystem functioning and habitat quality (Pillay et al. 2019; Bradfer-Lawrence et al. 2020). Bioacoustic monitoring has been used to measure degradation of forest habitat that was associated with reduced species richness and abundance of vocalizing animals (Sueur et al. 2008; Tucker et al. 2014; Burivalova et al. 2021) and has also proved useful for evaluating the success of forest conservation and restoration practices (Gibb et al. 2019; Campos-Cerqueira et al. 2020; Vega-Hidalgo et al. 2021). Soundscapes, which are comprised of the acoustic energy at a given location (Pijanowski et al. 2011), can be characterized by acoustic indices: metrics based on objective features of sound recordings such as pitch and amplitude (Bradfer-Lawrence et al. 2020). Many acoustic indices have been developed (Towsey et al. 2014; Buxton et al. 2018), however a metric that is correlated with biodiversity in a given area may not be correlated with biodiversity in another area (Fuller et al. 2015; Bradfer-Lawrence et al. 2020; Alcocer et al. 2022), thus making it important to evaluate multiple indices and select an ecologically appropriate index for a given taxon and site. Despite this challenge, acoustic indices can capture nuanced differences in seasonal and daily acoustic structure between sites that presence-absence metrics fail to detect (Vega-Hidalgo et al. 2021).

Bird vocalizations dominate the diurnal soundscape in temperate forests (Eldridge et al. 2018), and because birds are good indicators of environmental quality (Hurlbert and Haskell 2003) and have been studied extensively as surrogates for overall biodiversity (Blair 1999; Gregory et al. 2003) their response to woodland restoration may serve as a proxy for the response of other more cryptic taxa (i.e., insect, reptiles, bats). In Midwestern USA woodlands, other common species include mammals (i.e., bats, coyotes, deer, mice, raccoons, squirrels), amphibians (frogs and salamanders) and reptiles (turtles and snakes). For birds in Midwestern USA woodlands, which are better-studied than other taxa, richness and abundance of common species are often lower in sites that have experienced decades of fire suppression than they are in woodlands with intact fire regimes (Reidy et al. 2014; Greenberg et al. 2018; Roach et al. 2019). In addition to differing structural habitat characteristics, lower richness and abundance of birds at fire-suppressed sites may be due to differences in the arthropod community since many woodland birds are dependent on arthropod resources (Holmes and Schultz 1988; Goodbred and Holmes 1996; Burke and Nol 1998). The arthropod response to woodland restoration is diverse (see examples in Moretti et al. 2006; Greenberg et al. 2010; Chitwood et al. 2017; Mason et al. 2021). However certain groups of arthropods may be positively influenced by the complex vegetation structure that results from tree thinning and prescribed fire and often includes canopy gaps, snags, decaying logs, and a diversity of shade-intolerant plant species (Ulyshen 2011; Hanula et al. 2016). For example, pollinating insects that rely on floral resources tend to be more abundant in restored woodlands than in degraded ones (Campbell et al. 2007), and because many caterpillar species are associated with mid-successional tree and shrub species like oaks (*Quercus* sp.) and cherries *(Prunus* sp.; Tallamy and Shropshire 2009; Narango et al. 2020), it is possible that caterpillars are more abundant as well.

To study changes to temperate woodland soundscapes, we selected the Acoustic Complexity Index (ACI; Pieretti et al. 2011) and Soundscape Saturation (Burivalova et al. 2018). ACI was developed to detect rapid changes in frequency over time which are typically a feature of songbird vocalizations and thus this index provides information on avian communities (Pieretti et al. 2011). Soundscape Saturation is based on the acoustic niche hypothesis (Krause 1987) which posits that as a result of natural selection, species sharing the same acoustic space partition that space in terms of time and acoustic frequency. According to this hypothesis, the more species there are in an ecosystem, the more saturated we would expect the soundscape to be (Burivalova et al. 2018).

Temperate forests have strong diel patterns of sound with different taxonomic groups vocalizing at different times of the day (Fuller et al. 2015; Scarpelli et al. 2023a). In many temperate habitats, peak avian activity occurs around dawn (Depraetere et al. 2012; Barbaro et al. 2022; Scarpelli et al. 2023a). The timing and magnitude of seasonal and daily peaks in acoustic activity may be important for detecting differences in restored and degraded oak woodland habitats. For example, as woodlands become degraded due to fire suppression, peaks in acoustic index values are likely to flatten or shift temporally due to loss of species richness, abundance, or changes in community composition, resulting in uniform and low levels of ACI throughout the day or year. Diel patterns in the soundscape are important to consider when assessing habitat quality at different sites (Burivalova et al. 2018, 2019; Bradfer-Lawrence et al. 2019; Vega-Hidalgo et al. 2021). For example, the greatest variation in ACI values occurred during the afternoons in Panama forests (Bradfer-Lawrence et al. 2019). In Indonesian tropical forests, Soundscape Saturation was higher during the day and lower at night in never-logged forests than in degraded areas with selective logging concessions (Burivalova et al. 2019). The factors that explained Soundscape Saturation also changed throughout the day: Soundscape Saturation was correlated with different variables in the morning and in the evening (Burivalova et al. 2018). These examples are all from tropical forests, and the extent to which diel patterns differ between restored and degraded temperate woodlands is unclear.

Temperate soundscapes are also highly seasonal, reflecting the phenology of calling species. The timing and intensity of the onset of vocal activity can be used as an indicator of population recruitment and of phases of the reproductive cycle (Teixeira et al. 2019). For example, avian territorial singing peaks that are short and occur early during the nesting season could indicate nest failure, while longer singing peaks that extend throughout the duration of the nesting season suggest higher likelihood of nest success and potentially double-brooding. In the arctic, where the migratory bird nesting season is short, bioacoustic methods have been developed for estimating arrival date and the start of the nesting season (Oliver et al. 2018).

While soundscapes are often used as a tool for studying biodiversity in tropical forests, they have also been used to assess habitat quality of temperate woodlands (Depraetere et al. 2012; Turner et al. 2018; Le et al. 2018) and temperate forests (Atemasov and Atemasova 2023). Across a gradient of woodland habitat in France, acoustic index values indicated that bird diversity peaked in young woodlands which provide a higher number of microhabitats (Depraetere et al. 2012). In Queensland Australia, differences in woodland condition, related to vegetation, could be detected in soundscapes (Le et al. 2018). In Great Britain coniferous woodlands, acoustic indices reflected vegetation structure, distance to road, management history, and landscape context, resulting in unique soundscapes among sites within the same habitat (Turner et al. 2018).

The goal of this study was to determine the relationship between woodland restoration in southern Wisconsin and acoustic indices, phenology, and diel patterns. We hypothesized that compared to woodlands without intact disturbance regimes, restored woodlands would have more saturated and complex soundscapes with more pronounced daily and seasonal peaks, due to higher richness and abundance of vocalizing species resulting from higher resource and niche availability. We predicted that Soundscape Saturation and Acoustic Complexity Index are (1) higher in restored woodlands with more biodiversity and are (2) characterized by more pronounced daily and seasonal peaks in acoustic activity, reflecting greater biodiversity in restored woodlands.

Methods

Study area

The Baraboo Range (Sauk County, Wisconsin, USA), is a ring of quartzite and sandstone bluffs in southern Wisconsin extending 25-km east to west, 8-km north to south, and reaching a maximum height of 150-m above the surrounding terrain. This is one of the largest blocks of contiguous deciduous forest in the Midwestern USA, and tree communities are dominated by oaks and maples with pockets of coniferous species in ravines and other cool microclimates (Lange 1998). Oak forest, the primary natural cover, consists of red and white oaks, and pre-settlement vegetation cover included fire-adapted habitats, particularly oak savanna, oak woodlands, and bedrock glades (Lange 1998). Blufftops and south sloping hillsides in the south range were historically covered by oak woodlands in the unglaciated western portion and oak savannas in east (Mossman and Lange 1982). Prairie fires were frequent in southern Wisconsin before settlement (Curtis 1959) and likely extended infrequently into the woodlands on the south range (Mossman and Lange 1982). The Baraboo Hills were largely occupied by homesteaders by 1870, and the extensive forests were altered by logging, fire suppression, and plowing with most oak savanna sites converted to agriculture or succeeding to oak woodlands, and oak woodlands in some cases succeeding to maple forests (Mossman and Lange 1982). Following the initial logging in the late 1800s, wildfires sometimes occurred in forests and woodlands (Mossman and Lange 1982), and controlled groundfires may have been used infrequently to maintain woodland pastures for cattle grazing prior to the 1960s. There are no records of fires on our sites from the 1960s until modern restoration efforts.

Study design

In 2022, we established 10 7-ha study sites in upland woodland habitat on properties owned by the Nature Conservancy and the Wisconsin Dept. of Natural Resources (Fig. 1; Table 1). All sites are within and adjacent to several thousand acres of forest habitat and located on blufftops that were historically dominated by open oak woodlands. The degraded sites have oak-hickory overstories and dense understories with remnants of open glade-like ridges still visible despite decades of fire suppression and mesophication. The restored sites have predominantly oak overstories, with sparse mid- and understories, and patches of dense regrowth and brambles resulting from repeated rounds of

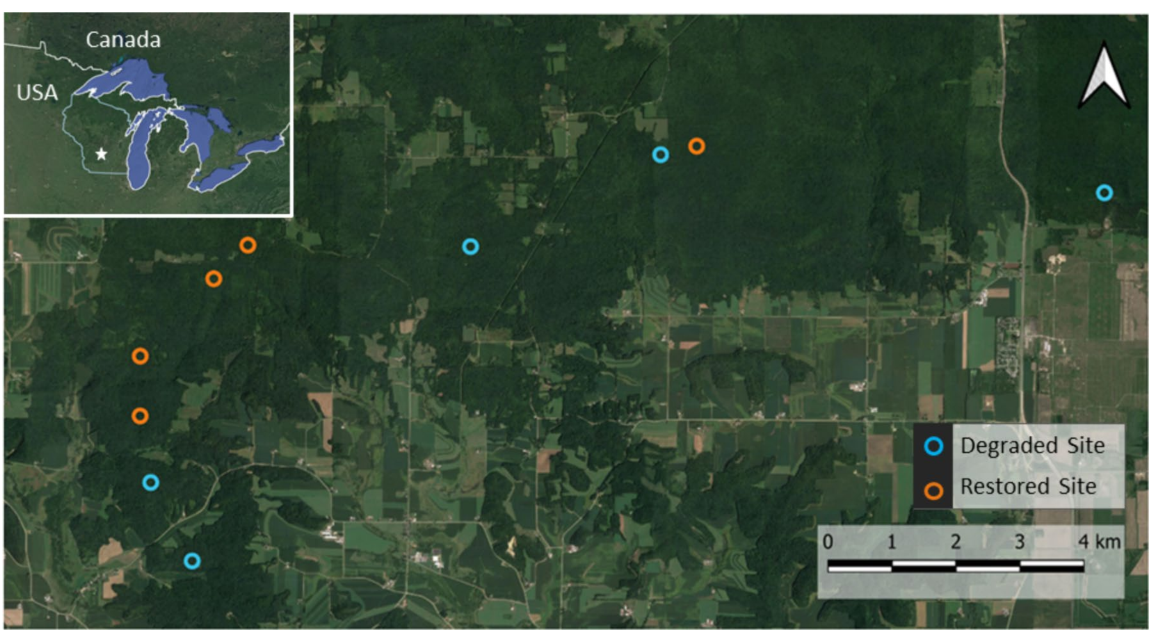

Fig. 1 Study area in Sauk Co., WI, USA. Satellite image shows the southwestern Baraboo Hills with 150 m radius circular study sites (approximately 7-ha) in orange (restored) and blue (degraded sites). One Bioacoustic Audio Recorder location is at the center of each site. Inset shows approximate study area location in southern Wisconsin

Table 1 Study site information for 10 7-ha sites located in the southwestern Baraboo Hills, Sauk Co., WI, USA

Site name		Pair	Burn history	Bedrock	Topography
Restored sites					
1	Happy Hill Woodland	A	Fall 2020	Quartzite	Flat blufftop
2	Schara Rd Woodland	B	Spring 2022	Quartzite	Flat blufftop, south slope
3	Green Forest Preserve	C	Spring 2014, 2015, 2017, 2018, 2019, 2021, 2022	Quartzite	Flat blufftop
4	Hemlock Draw Upland	D	Spring 2017, 2019, 2021	Sandstone	Blufftop, south slope
5	Hemlock Draw North	E	Spring 2021	Sandstone	South slope
Degraded sites					
6	Pan Hollow Upland	A	None	Quartzite	Flat blufftop, south and west slopes
7	Pine Glen Upland	B	None	Quartzite	Blufftop, south slope
8	Misty Valley Upland	C	None	Quartzite	Flat blufftop, south slope
9	Natural Bridge Upland	D	None	Sandstone	Blufftop, south and west slopes
10	Natural Bridge South	E	None	Sandstone	Blufftop, south slope

Sites are paired according to landscape position and geologic characteristics. Burn history includes the season and year of each burn that has occurred as part of the restoration process. No other fires occurred on any of the sites since the 1960s

tree thinning over 2–10 years and 1–5 controlled burns per site. Woodland restoration is ongoing at these sites, with understory thinning, timber stand improvement, and prescribed fire occurring at 1–3-year intervals intended to emulate the historic disturbance regime. Each site is circular, with a 150-m radius and a bioacoustic recording location established at the center. The sites are paired based on landscape position (i.e., hilltop or south-facing slope) and geology (sandstone or quartzite bedrock; Table 1). Sites are separated by > 0.5 km because this exceeds the territory size of all insectivorous birds recorded in this study (Wood Thrush, *Hylocichla mustelina*, and has one of the largest territory sizes, ranging from 0.08 to 4.0 ha; Evans et al. 2020).

Field data collection

We collected field data between 20 May and 10 August 2022, because this time encompasses breeding season for most insectivorous forest birds in southern Wisconsin (Mossman and Lange 1982). Birds establish breeding territories and sing regularly, thus contributing to soundscapes, until the territories dissolve during the post-fledging period in July and August.

Bioacoustics

We used Bioacoustic Audio Recorders (BAR Recorders, Frontier Labs) for all bioacoustic data collection. Each recorder was scheduled to record continuously in 30-min segments with a 44.1 kHz sample rate. Data was saved on secure digital (SD) cards in the Waveform audio file format. Each recorder had an integrated GPS for location and time synchronization, and this was double-checked manually each time a recorder was deployed. Because we had six recorders and ten sites, we developed a staggered system for deploying recorders at a fixed location at each site and rotating through sites during the season so that we had roughly equal numbers of restored and degraded sites being recorded on a given day. The recording location at each site was established 2-m above ground level on the south side of a permanently marked overstory tree trunk. All 10 recording sites were > 200 m from roads or areas with human disturbance because acoustic indices can be highly sensitive to anthropogenic noises (Gibb et al. 2019) such as roads and traffic noise (Ghadiri Khanaposhtani et al. 2019). Additionally, road corridors and forest edges can influence the bird (Fraser and Stutchbury 2004; Battin 2004) and arthropod communities (Burke and Nol 1998; Stireman et al. 2014). Because we were unable to record continuously at all sites, we divided the season into nine 15-day recording periods to capture a range of phenologically distinct times between late-May and early-August. Within each period, we aimed to record continuously for four-five days (96–120 h) per site, because continuous recordings, rather than temporal subsampling, is preferable for characterizing soundscapes (Bradfer-Lawrence et al. 2019).

Vegetation

Within each site we established three sampling points spaced 70–100 m apart where three types of vegetation surveys occurred: canopy oak percent, canopy cover, and herbaceous groundcover. At each sampling point, we identified overstory trees during July using a prism of basal area factor (BAF) 2. Each tree in the variable radius plot was identified to the species level, and the proportion of canopy trees that were Northern Red Oak (*Quercus rubra*) or White Oak (*Q. alba*) was calculated for each point. During July, we took four pictures of the canopy by walking 1-m from the point center in each cardinal direction and holding a camera facing up at 1-m above the ground. We analyzed the pictures using ImageJ software to calculate canopy cover and averaged the four readings from each point. We characterized herbaceous groundcover at every point once during May–June and once during July to account for plant species with different phenologies, as well as within-season growth. At every sampling point, we centered a 50-m transect perpendicular to the slope. At each 1-m intercept along its length, we identified all herbaceous plants that were intersected (Vander Yacht et al. 2020). At three randomly selected locations along the transect, we established a 1-m quadrat (Barrioz et al. 2013) and all plant species within it were tallied and identified to species. To supplement our estimate of herbaceous plant species richness, during each 10-day period, we recorded blooming plant species at six evenly spaced locations along the transect. The sum of all unique plant species recorded at each point was tallied across the season.

Arthropod biomass

We captured arthropods using a malaise trap placed within 100-m of each recorder in locations that were representative of the surrounding habitat and intersected with potential insect flight paths (i.e., deer trails, dry creek beds, or other linear openings in the understory). The traps were in place from 20-May to 10-August and checked once during every 10-day period. Arthropods collected in the traps were weighed in an alcohol-wet state using a lab balance accurate to within 0.01-g following methods in (Hallmann et al. 2017). Before weighing, we removed large grasshoppers (*Orthoptera* sp.) and non-native spongy moth (*Lymantria dispar*) larvae because these are likely not an important food source for insectivorous birds.

Avian point counts

At one or two locations per site spaced > 300 m apart (either one site at the center or two sites on opposite edges) we conducted three 10-min variable-radius point counts between 7 and 29 June. All point counts occurred between 0500 and 1100 to coincide with peak bird activity (Wolf et al. 1995), and every individual bird seen or heard, was recorded, with field-estimated distance from the point center.

Analysis

Bioacoustic data

All statistical analyses were carried out in R version 4.2.2. Due to challenges with equipment, the exact number of recording hours varied within each phenological period. For example, at two sites two days were removed due to storms that caused water droplets to fall directly on the top of the recorder or nearby leaves, thus elevating acoustic indices. Additionally, we limited our recording data to complete 24-h cycles to avoid biasing diel patterns in the soundscape, resulting in a range of 11–22 recording days per management type per phenological period (Table 2). The standard deviations of acoustic indices have been found to stabilize after 120 recording hours in a tropical forest (Bradfer-Lawrence et al. 2019) and our data follow a similar pattern. Plots of mean ACI and soundscape saturation standard deviation stabilize after 120 h in our sites, thus indicating that differences in index values between management types within each phenological period are due to ecological differences rather than short-term variability.

Calculating acoustic indices

To process the bioacoustic recording data, we followed methods described by (Truskinger et al. 2014), and used Analysis Program (Towsey et al. 2018). In order to calculate Soundscape Saturation, we first calculated the acoustic index Power Minus Noise (PMN), which measures the maximum decibel value minus background noise in each of 256 frequency bins that span all frequencies in our recordings (Towsey 2017). This resulted in a matrix of 1440 columns, representing minutes of the day, and 256 rows, representing frequency bins. From PMN, we calculated Soundscape Saturation, with a threshold of 5 dB, following the methods described by (Burivalova et al. 2018). Soundscape Saturation

Table 2 Distribution of dates (and number of hours, in parentheses) of recording data included in analysis of five restored and five degraded oak woodland study sites (7-ha) in the Baraboo Hills (Wisconsin, USA) during 2022

Phenological period	Dates	Restored sites	Degraded sites
Late May	16–31 May	20	22
Early June	1–15 June	21	22
Late June	16–30 June	18	21
Early July	1–15 July	16	11
Late July	16–31 July	22	11
Early August	1–15 August	19	16
Total	15 April – 15 August	116 (2784)	103 (2472)

index reduces the PMN matrix to a single row (one value per minute), indicating the percentage of frequency bins that exceeded the threshold, and thus likely contains a biological sound (Burivalova et al. 2022).

We calculated Acoustic Complexity Index (ACI), again using Analysis Program (Towsey et al. 2018). ACI is a summary index derived from the spectral ACI_{sp} index, which is a 256-element vector that quantifies the relative change in acoustic intensity in each frequency bin of the amplitude spectrogram (Pieretti et al. 2011). ACI summarizes the mid frequency bands only, which includes most bird vocalizations (Pieretti et al. 2011). As with Soundscape Saturation, we calculated one ACI value per minute of each recording. In further analysis steps we truncated the dataset to late spring and summer (20 May–5 August) to overlap with the avian breeding season by removing data recording days outside of this range. Additionally, we limited our soundscape phenology analysis to diurnal acoustic index values (30 min prior to sunrise–30 min after sunset each day) to focus our analysis on diurnal insects and birds. For our diel pattern analysis, we used 24-h soundscapes.

Calibrating acoustic indices and field data

To ensure that diurnal Soundscape Saturation and ACI were sensitive to avian acoustic activity at our study sites, we parameterized linear regression models. We calculated mean diurnal Soundscape Saturation and ACI values for each site during June, the month in which we conducted point counts during peak nesting season and used these as response variables. We totaled site-level bird species richness across the season and calculated the mean raw abundance (number of birds detected during a point count) across the three rounds of point counts conducted at each site. Site-level bird species richness ranged from 26 to 42 and mean raw abundance from 17 to 43. We parametrized two separate univariate models for each acoustic index, one with bird species richness as a predictor, and one with raw bird abundance as a predictor. We assessed the total explanatory power of each model by calculating the adjusted R^2 value.

Modeling acoustic indices

We tested for overall differences in diurnal acoustic indices between restored and degraded sites by calculating means and using Student's t-tests performed on the raw data (site-level acoustic index values for each minute from 30 min before sunrise to 30 min after sunset). To understand how acoustic indices are influenced by woodland restoration, we fit generalized additive models (GAMs; Wood 2011) using the R package 'mgcv' (Wood 2006). For phenology models, we fit one model with diurnal Soundscape Saturation as the response variable and one with diurnal ACI, following the same methods and including the same covariates, described below. Rather than including highly correlated post-treatment effects in the models, we instead used "treatment" as the predictor variable, with two options—restored or degraded. We also included Julian date to account for seasonality and minute of the day (minutes since midnight) to account for diel patterns. We included the GPS coordinates (UTM) of each recorder location as a random variable to account for any spatial autocorrelation. We used gaussian distribution and 'identity' link functions. To achieve normal distribution, ACI was transformed ($1/y^2$) using a box cox transformation in R package 'MASS' (Venables and Ripley 2002), and similarly Soundscape Saturation was transformed $\sqrt{y}$. We checked for collinearity among predictors using R package 'corrplot' (Wei et al. 2022) with a cutoff value of 0.5 and did not include colinear predictors in the same models. We fit all model combinations, including interaction effects among covariates (i.e., allowing one predictor variable to have a different effect on the response variable depending on whether the site was restored or degraded). For all models, we tested different smoothing methods and the restricted maximum likelihood (REML) smoothing parameter estimation method outperformed the minimized generalized cross-validation (GCV) method. For all candidate models, we tested model fit using 'appraise' in R package 'gratia' (Simpson 2023), 'gam.check' and 'concurvity' with a cutoff value of 0.8 in R package 'mgcv' (Wood 2006). We only considered models that met all assumptions and had no collinearity or concurvity between predictors. We used AIC to rank candidate models and plotted seasonal and diel smoothing curves with R package 'ggplot2' (Wickham 2016). The highest-ranking candidate models for ACI (Eq. 1) and Soundscape Saturation (Eq. 2) are:

$$
\begin{aligned}
&1/(AcousticComplexity^2) \sim Treatment + s(Julian, by = Treatment, k = 16)\\
&\quad + s(MinSinceMidnight, by = Treatment),\\
&\quad random = (1||Lat * Long),\ method = "REML"
\end{aligned}
\tag{1}
$$

$$
\begin{aligned}
&\sqrt{SoundscapeSaturation} \sim Treatment + s(Julian,\ by = Treatment,\ k = 16)\\
&\quad + s(MinSinceMidnight,\ by\ =\ Treatment),\\
&\quad random = (1|Lat * Long),\ method = "REML"
\end{aligned}
\tag{2}
$$

For diel pattern models, we followed the same methods as above, using acoustic index data across the full 24-h cycle, and selected the same two models, which again were highest-ranking (Eq. 1 for ACI and Eq. 2 for Soundscape Saturation). We used R package 'ggplot' (Wickham 2016) to visualize results, this time by plotting mean values for each minute of the day at restored and degraded sites.

Vegetation and arthropod summary

To summarize vegetation characteristics at each study site, we calculated the mean canopy oak percent, canopy cover, understory density, and herbaceous species richness from the three sampling points. We calculated mean arthropod biomass per trap-day at each site and tested for differences between restored and degraded sites using a t-test. We plotted seasonal biomass patterns using smoothing curves in R package 'ggplot2' (Wickham 2016).

Avian richness and abundance

To characterize the bird community at each site, we tallied the site-level insectivorous bird species richness and used hierarchical distance sampling (Sillett et al. 2012; Kéry and Royle 2016a) in R package 'unmarked' (Fiske and Chandler 2011) to calculate detection-corrected abundance of the thirteen most abundant species in our study area (Table S4). Detection covariates tested in the global model for each species included hours since sunrise and weather (National Weather Service Code, scale of 0–5 for increasingly poor sky conditions) while density covariates differed by species and included structural habitat measurements (e.g., basal area, understory density, canopy cover), plant and tree species composition, mean arthropod biomass, and soil moisture (measured in the field during June using a handheld soil moisture probe). Covariates with a correlation score of 0.5 or greater (R package 'psych'; Revelle 2023) were not included in the same model. All models fit the assumptions of a Poisson framework and detections best followed a half-normal key function (Kéry and Royle 2016b). We used AIC values to determine the top candidate models for each species (Sillett et al. 2012), i.e. those within 4 of the lowest AIC score using R package 'MuMIn' (Barton 2009). 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). We also tested for overdispersion using the Chi-squared statistic (Reidy et al. 2014; Kéry and Royle 2016c). We summed the predicted territory density per hectare of each species at each site to obtain a site-level male bird density estimate across all common insectivorous bird species.

Results

Restoration of oak woodland sites in the Baraboo Hills resulted in several vegetation changes (Fig. 2). In restored woodlands, mean percent of oak trees in the canopy was 45.4%, compared to 24.5% in degraded sites ($p=0.03$), while mean canopy cover was substantially lower at restored sites (52.8% rather than 79.7%, $p<0.01$; Fig. 2a, Fig. 2b). Mean herbaceous plant species richness was higher at restored sites (25.6 species per point) than it was at degraded sites (13.7 species per point, $p=0.02$; Fig. 2c). Overall arthropod biomass in restored sites was 2.03 mg/trap day, while in

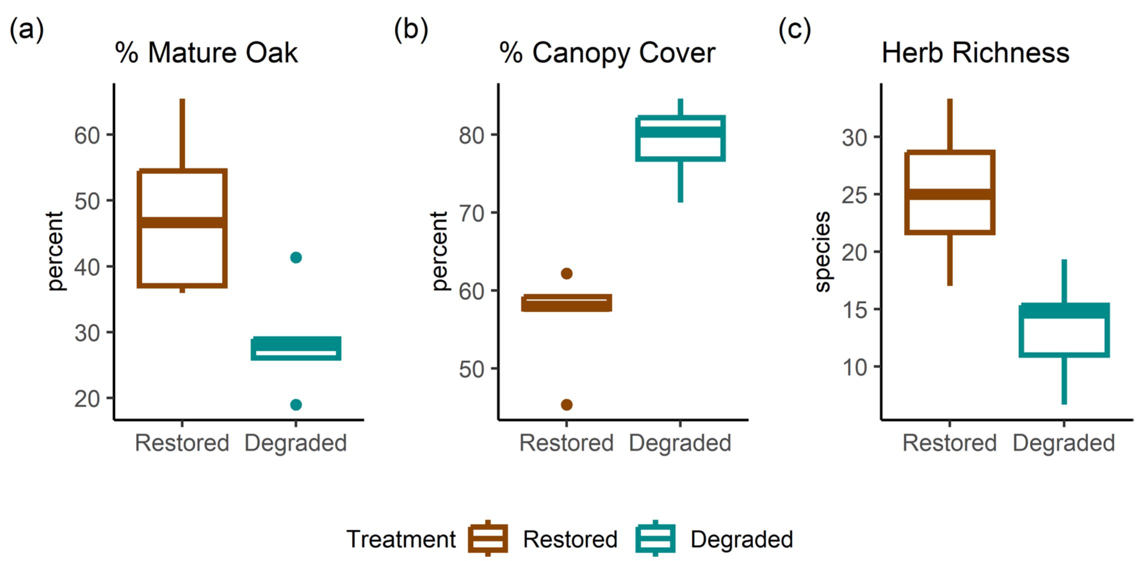

Fig. 2 Vegetation characteristics and measured during May–August 2022 at restored (brown) and degraded (blue) oak woodlands study sites in Sauk Co., WI, USA. Percent mature oak trees (*Quercus* sp.) in the canopy **a**, percent canopy cover **b**, and herbaceous plant species richness **c** are shown. 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

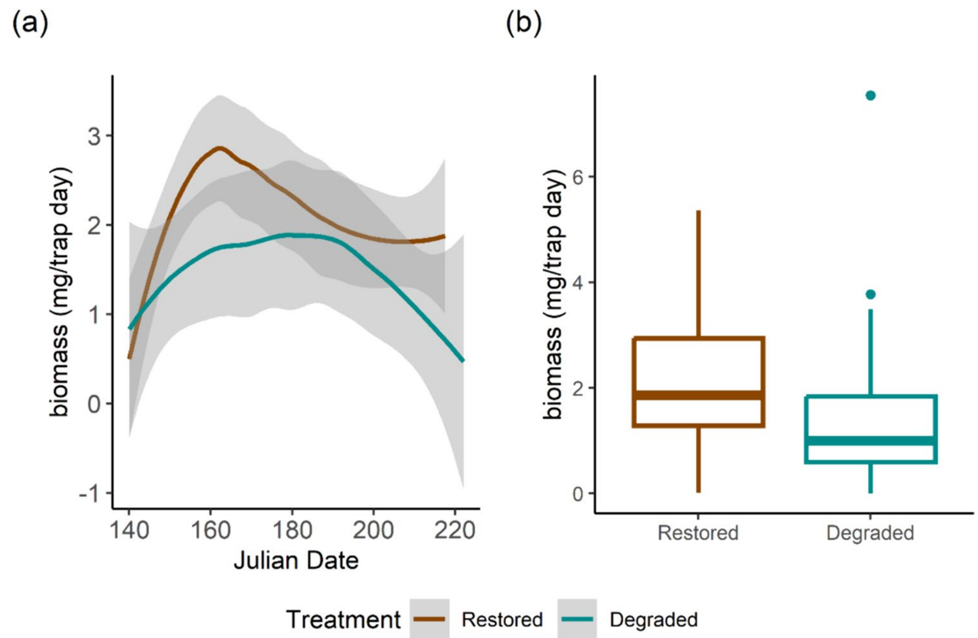

Fig. 3 Mean daily arthropod biomass from May–August 2022 in restored (brown) and degraded (blue) oak woodland study sites in the Sauk Co., WI, USA. Biomass phenology within each habitat type is shown with standard error in gray **a**, and is summarized across the season **b**. The central line within each boxplot **b** 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

degraded sites it was 1.42 mg/trap day (p = 0.02; Fig. 3b). Arthropod biomass exhibited a seasonal peak in early June (Fig. 3a) in both restored and degraded sites, which aligns with avian nesting season in our study area. Differences in arthropod biomass between restored and degraded sites were largest in early June and early August (Fig. 3a). Avian species richness was higher in restored sites (mean 36.8 species, range 28–42) than it was in degraded sites (mean 29.2 species, range 26–34; p < 0.01; Fig. 4a). Finally, avian abundance was higher in restored sites (25.1 territories/ha, range 21.7–29.9) than it was in degraded sites (mean 17.5 territories/ha, range 14.8–20.3; p < 0.01; Fig. 4b; species-specific abundance model results are in Table S4).

We analyzed 1439 diurnal hours across 116 days of bioacoustic data collected in restored sites and 1353 diurnal hours across103 days of bioacoustic data collected in degraded sites between late May and early August 2022 (Table 2). We found that restored woodlands had higher mean diurnal Soundscape Saturation than degraded woodlands during this time (t-test: 31.60% vs. 25.91%, SE = 0.09, p < 0.01). Similarly, restored woodland soundscapes exhibited higher mean diurnal acoustic complexity (0.482 vs.

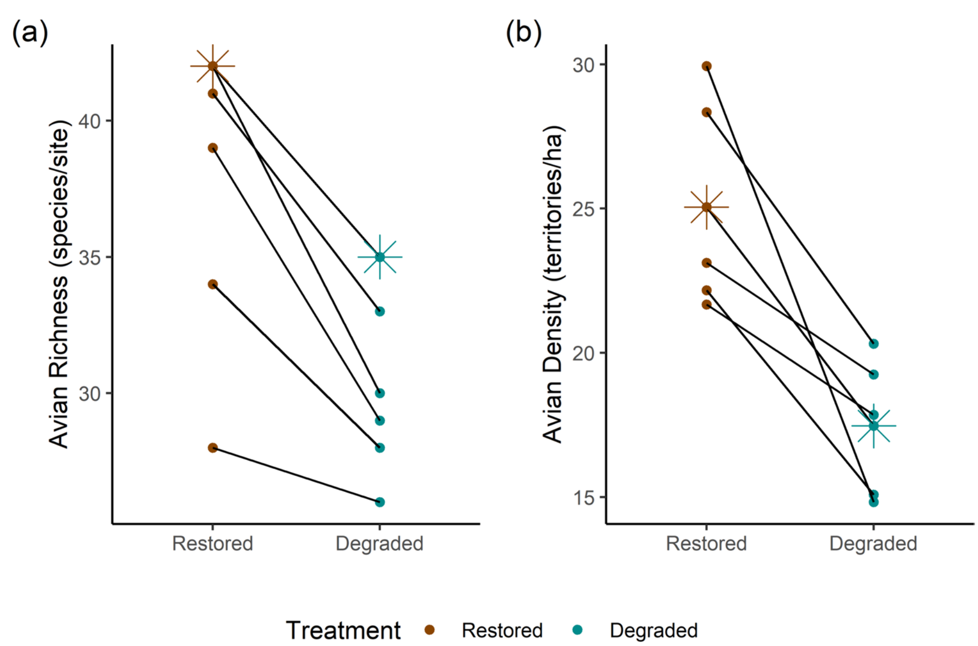

Fig. 4 Total insectivorous bird species richness per site **a** and modeled territory density per hectare of the sixteen most abundant species **b** in southern Wisconsin woodlands. Brown circles indicate restored sites and blue circles indicate degraded sites, connecting lines indicate sites that are paired based on landscape position and geology. Stars indicated cumulative species richness or mean territory density in all restored (brown) and all degraded (blue) sites

Table 3 Top generalized additive models of diurnal Acoustic Complexity Index (ACI) and Soundscape Saturation (SS) predicted by treatment (restored or degraded), Julian date (by treatment), and minute of the day (by treatment)

Covariate	Est	CI	p-value	Adj. R^2
ACI diurnal phenology				0.376
(Int)	0.4807	0.4806–0.4809	< 0.01	
Treatment (Degraded)	− 1.606	− 1.598–− 1.614	< 0.01	
Smooth (Julian) Treat. = Restored			< 0.01	
Smooth (Julian) Treat. = Degraded			< 0.01	
Smooth (Minute) Treat. = Restored			< 0.01	
Smooth (Minute) Treat. = Degraded			< 0.01	
SS diurnal phenology				0.250
(Int)	0.1711	0.1709–0.1713	< 0.01	
Treatment (Degraded)	− 0.3237	− 0.3259–− 0.3215	< 0.01	
Smooth (Julian) Treat. = Restored			< 0.01	
Smooth (Julian) Treat. = Degraded			< 0.01	
smooth(Minute) Treat. = Restored			< 0.01	
Smooth (Minute) Treat. = Degraded			< 0.01	
ACI diel pattern				0.321
(Int)	0.4691	0.4690–0.4692	< 0.01	
Treatment (Degraded)	− 1.606	− 1.598–− 1.614	< 0.01	
Smooth (Julian) Treat. = Restored			< 0.01	
Smooth (Julian) Treat. = Degraded			< 0.01	
Smooth (Minute) Treat. = Restored			< 0.01	
Smooth (Minute) Treat. = Degraded			< 0.01	
SS diel pattern				0.286
(Int)	0.1983	0.1980–0.1985	< 0.01	
Treatment (Degraded)	− 0.4052	− 0.4086–− 0.4020	< 0.01	
Smooth (Julian) Treat. = Restored			< 0.01	
Smooth (Julian) Treat. = Degraded			< 0.01	
Smooth (Minute) Treat. = Restored			< 0.01	
Smooth (Minute) Treat. = Degraded			< 0.01	

0.469, SE < 0.01, $p < 0.01$). The top generalized additive models for both Soundscape Saturation and ACI included treatment (restored or degraded woodland) as well as Julian date and minute of the day as covariates (Table 3). Soundscape Saturation and ACI diurnal phenology models explained 25% and 37.6% of variation respectively, while diel pattern models explained 28.6% and 32.1% of variation (Table 3). All four models included a negative relationship between degraded habitat and acoustic index values (Table 3).

We found that diurnal Soundscape Saturation and ACI in restored sites both exhibit more pronounced seasonal peaks compared to those in degraded sites (Fig. 5). Seasonal peaks occurred in mid-June and in early-July, coinciding with avian nesting season and post-fledging season respectively. We also observed stronger daily soundscape peaks in restored sites compared to degraded sites (Fig. 6), again evident in both acoustic indices. Diurnal acoustic activity peaked around 07:00 and then decreased throughout the day until a secondary evening peak occurred around 19:00, coinciding with the avian dawn and dusk choruses (Fig. 6).

Discussion

In this study, we characterized the vegetation structure and composition, arthropod biomass, bird communities, and soundscapes of restored and degraded oak woodlands in southern Wisconsin. Compared to similar degraded sites without intact disturbance regimes, restored woodland sites had more herbaceous plant richness, higher arthropod biomass, and higher avian species richness and density. This is reflected in two acoustic indices, Soundscape Saturation and Acoustic Complexity Index, which exhibited higher diurnal values throughout the avian breeding season (late-May—early -August) in restored sites. We showed that in restored woodlands, peaks in daily and seasonal Soundscape Saturation and ACI are more pronounced, resulting from complex soundscape diel patterns and phenology.

The vegetation structure and composition of restored woodlands were distinct from those of degraded sites, and were associated with higher arthropod biomass, and insectivorous bird richness and abundance. Restoration involved thinning non-oak species from the canopy prior

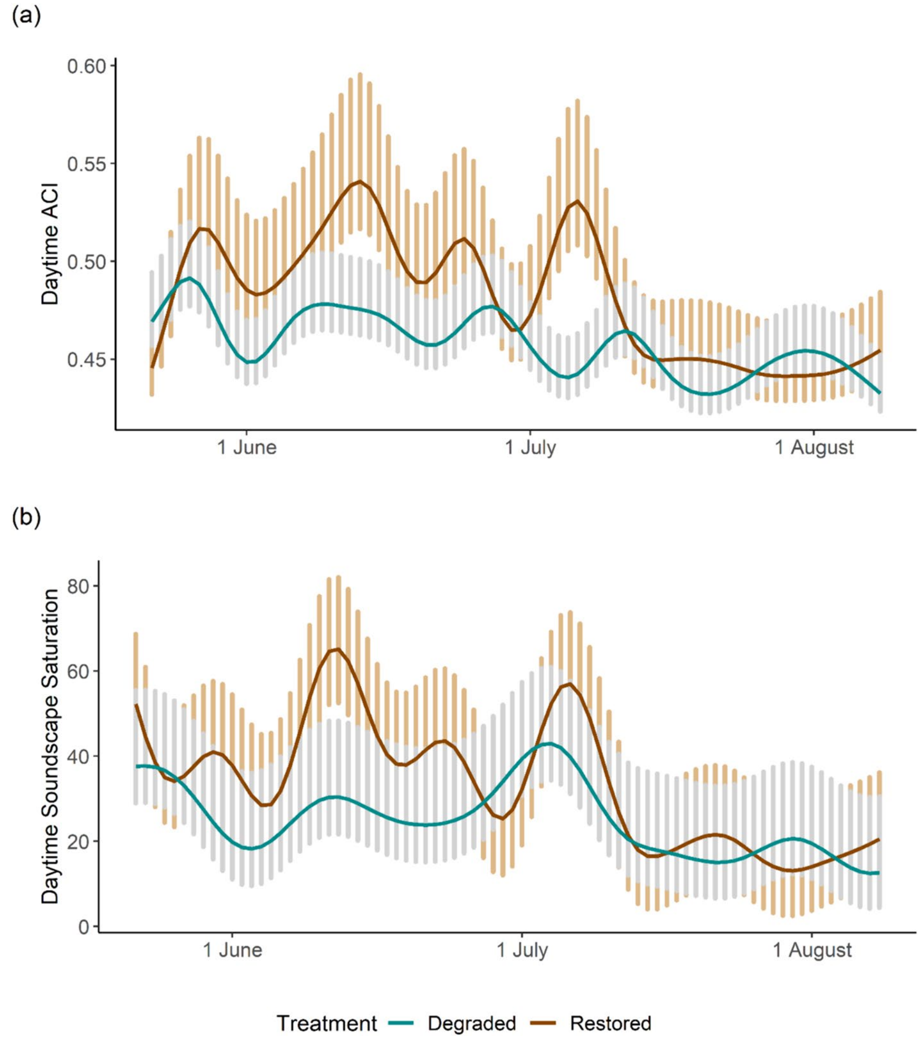

Fig. 5 Modeled diurnal Acoustic Complexity Index (ACI; **a**) and Soundscape Saturation **b** in restored (brown) and degraded (blue) oak woodland sites recorded from late May—early August 2022. Daytime means of the parameters estimated by the model are shown by the dark lines and the modeled range for each day is shown by the lighter vertical line

to conducting prescribed burns, which resulted in both higher percent oaks in the canopy and lower canopy cover in restored sites (Fig. 2a, b). Thus, the overstory tree species composition in restored sites was largely made up of oaks (*Quercus* sp.), which are associated with high arthropod biodiversity and abundance throughout North America (Tallamy and Shropshire 2009; Narango et al. 2020). Additionally, the lower canopy cover and lower understory density in restored sites allowed more sunlight to reach the ground layer, thus supporting higher diversity of herbaceous plants. Arthropod biomass measured in this study included aerial species caught in malaise traps, including bees and wasps, flies, and true bugs. This group of species, while diverse, may have increased in abundance due to the higher ground layer plant diversity, higher percent of oak trees, or the open forest structure itself (i.e., patchier microclimates in the understory resulting from canopy gaps, presence of understory flyways, etc.). In turn, the insectivorous bird community, especially those that forage in the understory where the malaise traps were located, may have responded to higher food resources. Additionally, open canopy structure supports woodland-adapted species that are less common in closed canopy forest (i.e., Red-headed Woodpecker; Frei et al. 2020), while open understory and midstory layers benefit flycatching species by providing more airspace to maneuver while foraging (i.e. Eastern Wood-Pewee; Watt et al. 2020), and patchy ground layer vegetation, including areas of regrowing shrubs and woody vegetation, provide habitat for a understory species (i.e. Mourning Warbler; Pitocchelli 2020).

When considering only the diurnal soundscape, both acoustic indices we calculated tended to be higher in restored sites throughout the season (Fig. 5), however the diel patterns of these indices were more complex (Fig. 6). Both acoustic indices were highest during the day, particularly during the dawn and dusk choruses, and lowest during the night. Soundscape saturation was higher in restored sites than in degraded sites during the day, but during the night there was no difference between sites. ACI was also higher in restored sites than degraded sites during the day, but it

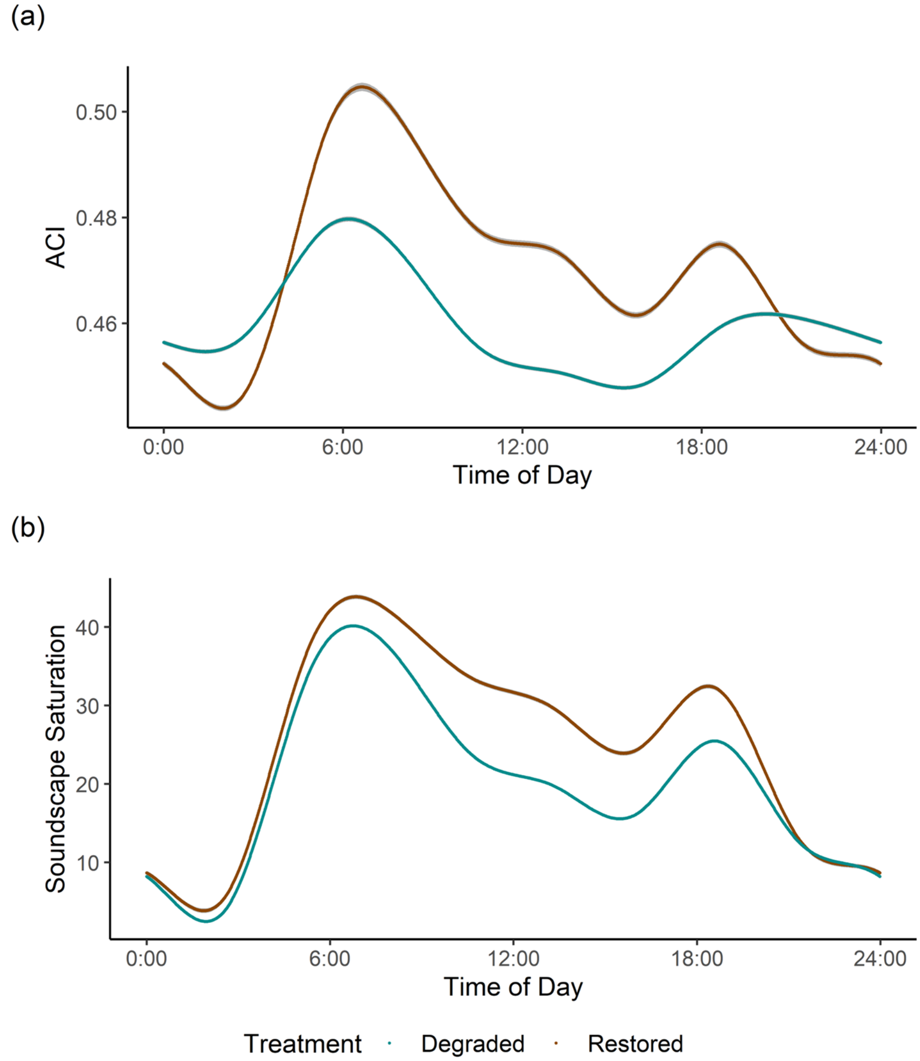

Fig. 6 Mean diel patterns of Acoustic Complexity Index (ACI; **a**) and Soundscape Saturation **b** in restored (brown) and degraded (blue) oak woodland sites recorded from late May-early August 2022. Standard error is shown in light gray (often obscured)

was lower in restored sites during the night. In this study area, the nocturnal soundscape includes tree frogs (*Hyla* sp.) and insects, as well as bats, which call at a frequency that we did not record in this study. It is possible that the denser understory vegetation and more humid conditions in degraded woodlands provides better habitat for some species like frogs. Another potential explanation is that calling insects experience lower predation in degraded sites than in restored sites due to reductions in bird and bat abundance. In Costa Rican rainforests, mature forests had quieter nighttime soundscapes than restoration sites, likely due to the more robust predator community targeting noisy insects (Vega-Hidalgo et al. 2021). Studying woodland and forest biodiversity with bioacoustics can be challenging because vegetation structure influences sound attenuation and thus the likelihood of detecting biotic sounds varies across forest structures, sites, and levels of degradation (Darras et al. 2016; Gibb et al. 2019; Rappaport et al. 2020). Because of this, we chose to limit our field data collection points to a 150 m radius around each recording location, however, the exact sound detection space is unknown. Additionally, restoration activity at the sites used in this analysis has been occurring for a range of 2–10 years per site, and thus these data provide information on short-term restoration effects rather than a final evaluation of open woodland restoration effectiveness. However, long-term open oak woodland restorations in Tennessee (Vander Yacht et al. 2020) and Missouri (Comer et al. 2010) suggest that the vegetation structure and composition trends we witnessed, and the richer avian community that was present in our restored sites is consistent with longer term responses to restoration in woodlands. Finally, the small spatial scale of this study and low number of site replicates limits the generalizability of our results to other woodland ecosystems.

As fire-dependent habitats, oak woodlands are an important component of mosaic landscapes in the Midwestern USA. Within woodlands in eastern and central North America groundfires tend to be low-intensity, patchy and localized, resulting in plant communities of a variety of successional stages existing in close proximity. This can influence the distribution of acoustically active species and be reflected in the soundscape. For example, in a Queensland, Australia mosaic landscape of woodlands and shrublands, insects and birds were associated with both higher shrub and subcanopy cover and thus influenced the soundscape at fine spatial scales (Scarpelli et al. 2023b). Acoustic indices can also be driven by habitat configurational heterogeneity in mosaic landscapes at larger scales (Barbaro et al. 2022), indicating that soundscapes are shaped by more than local habitat characteristics. In this study, we selected sites that were > 200 m from forest edges within the same forest-dominated landscape but were unable to account for variations in the 2500 m radius landscape around each recorder.

Understanding how acoustic indices are related to habitat quality has implications for restoration practices. Acoustic index patterns can be used as benchmarks for achieving success in restoration of degraded lands, and archived sound recordings from high quality habitat can be used to actively facilitate species recolonization in areas where they were locally extirpated (i.e., by luring species into newly restored habitat; Znidersic and Watson 2022). Additionally, soundscape baselines will be important for gauging shifts in calling species communities in ecosystems where climate change could influence soundscape phenology (Scarpelli et al. 2023a) or other attributes. Use of acoustic indices may be a useful assessment and monitoring tool in the 98 ecoregions of the world where temperate woodlands are a dominant or codominant habitat type, an area of approximately 14 million km^2 (Appendix Tables S1 and S2; Olson et al. 2001), particularly in situations in which identifying and monitoring individual species is not practical due to time or expertise constraints, or where a streamlined monitoring approach is beneficial.

Woodland and savanna degradation is widespread throughout fire-adapted and fire-dependent landscapes of the world (Kelly et al. 2020; Roces-Díaz et al. 2022), and affects the capacity of protected areas set aside for biodiversity conservation to fulfill their role of providing high quality habitat if they are not actively restored and maintained with historic disturbance regimes in mind. While a growing body of research, particularly in Australia and western North America, indicates that that low-intensity prescribed fire can increase ecosystem resilience and biodiversity, many woodland ecosystems are either understudied or degraded due to fire suppression (Hunter and Robles 2020; Kelly et al. 2020; Roces-Díaz et al. 2022). Our results indicate that woodland restoration facilitates complex and saturated soundscapes, resulting from higher avian species richness and abundance. In temperate woodlands, the diurnal soundscape is dominated by birds (Eldridge et al. 2018), which are good indicators of habitat quality (Hurlbert and Haskell 2003), and may reflect the responses of other, more cryptic, taxa. For example, the restored sites in this study also had higher arthropod biomass. Thus, the increased diurnal Soundscape Saturation and ACI values we measured in restored sites, as well as more the pronounced phenological and diel patterns, are indicators of woodland restoration.

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Author contribution statement MEP, HSSCS, ZB, and AMP formulated the idea and developed methodology, MEP and HSSCS conducted fieldwork, MEP, HSSCS, and ZB processed soundscape data and performed statistical analysis, MEP and AMP wrote the manuscript, HSSCS and ZB provided editorial advice.

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Availability of data and material The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability All code used in this analysis is available publicly in R packages.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

Consent to participate Not applicable.

Consent for publications Not applicable.

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