

Hybrid bioacoustic and ecoacoustic analyses provide new links between bird assemblages and habitat quality in a winter boreal forest

Taylor Shaw^{a,*}, Raluca Hedes^b, Arvid Sandstrom^c, Alejandro Ruete^d, Matthew Hiron^e, Marcus Hedblom^f, Sönke Eggers^e, Grzegorz Mikusiński^{b,c}

^a Chair of Geobotany, Faculty of Biology, University of Freiburg, Freiburg, Germany

^b Chair of Wildlife Ecology and Management, Faculty of Environment and Natural Resources, University of Freiburg, Freiburg, Germany

^c School for Forest Management, Swedish University of Agricultural Sciences SLU, Skinnkatteberg, Sweden

^d Greensway AB, Ulls väg 24A, 756 51, Uppsala, Sweden

^e Department of Ecology, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden

^f Department of Urban and Rural development, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden

ARTICLE INFO

Keywords:

Dead wood
Structural heterogeneity
Passive acoustic monitoring
Sweden
Boreal forest
Winter

ABSTRACT

Resident birds in boreal forests can serve as indicators of habitat quality and are often species of conservation interest, particularly in multifunctional forests also used for timber production. To make informed forest management decisions, we must first understand which structural features provide habitats useful for resident birds. This is particularly true in winter, an understudied and critical season for their survival. The objective of this study was to establish reliable methods for monitoring bird presence and activity during winter, and to use these methods to evaluate the relative importance of stand structural features to make inferences about which features support and increase winter survival potential. Using a hybrid bioacoustic and ecoacoustic approach, we tested the ability of acoustic recordings to identify links between bird diversity and components of structural complexity, and compared these results to those from the traditional point count method. We conducted a vegetation survey, point count surveys and collected acoustic recordings from December 2019–February 2020 in 19 sites in a Swedish boreal forest. First, we compared species richness values derived from point counts and bioacoustic monitoring methods. Bioacoustic species richness was significantly higher than point count richness, although only when the time spent identifying species from recordings exceeded the time spent conducting point counts in the field. Next, we demonstrated that bioacoustic species identification yields additional metrics of bird activity that point counts cannot. We tested the response of these metrics, and point count metrics, to variables of structural heterogeneity and complexity of our sites. Almost all bioacoustic metrics increased significantly with increasing structural complexity, while point count richness and abundance did not, indicating that automated recording is more effective in identifying forest patches of high quality in winter. Lastly, using an ecoacoustic approach, we calculated six of the most common acoustic indices and tested if any could effectively reflect the bird-structure relationships described above. Two indices showed significant positive relationships to bioacoustic metrics, demonstrating their potential as biodiversity assessment proxies that respond to differences in habitat quality. This is the first winter acoustic study to monitor bird assemblages in detail; it employed both bioacoustic and multi-index ecoacoustic approaches, which provided evidence that automated acoustic recording can be an effective and superior method for monitoring resident forest birds.

1. Introduction

Boreal and temperate forests have distinct assemblages of year-round resident birds (Barbe et al., 2018; Forsman and Mönkkönen, 2003). Resident birds are often used as indicators of forest naturalness and as

broader environmental indicators applied in monitoring schemes (Oettel and Lapin, 2021; Roberge et al., 2008; Roberge and Angelstam, 2006). In Sweden, for example, out of 16 bird species used in measuring the achievement of the National Environmental Quality Objectives “Sustainable Forests”, 15 are resident birds.

* Corresponding author.

E-mail address: taylor.shaw@biologie.uni-freiburg.de (T. Shaw).

<https://doi.org/10.1016/j.indic.2021.100141>

Received 20 May 2021; Received in revised form 26 July 2021; Accepted 28 July 2021

Available online 29 July 2021

2665-9727/© 2021 The Authors.

Published by Elsevier Inc.

This is an open access article under the CC BY-NC-ND license

(<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

In contrast to migratory species, resident birds must cope with winter conditions signified by food shortage, increased energy demands at low temperatures and reduced vegetation cover, particularly from seasonally leafless deciduous vegetation (Wesołowski et al., 2018). Winter is thus a critical period largely affecting the ability of these species to survive in a forest landscape. Resident birds are sensitive to forestry-induced changes in forest structure (i.e. reduced habitat quality) and habitat loss (Helle and Järvinen 1986; Eggers and Low 2014; Klein et al., 2020), and particularly in the winter season (Turcotte and Desroches 2005). Boreal forests managed for timber production produced stands with more homogenous forest structure, marked by a simplification in understory complexity, unvaried tree age and a scarcity of old, large and dead trees. Together, this reduces nesting, foraging and concealment opportunities for birds and has led to population declines of resident birds and local extinctions of highly specialised species like the white-backed woodpecker (Blicharska et al., 2014; Helle and Järvinen, 1986). Moreover, a large proportion of resident species are cavity-nesters (e.g. woodpeckers, tits, several owls) or also use cavities for roosting; scarcity of trees with cavities in intensively managed forests may therefore affect the potential of winter survival.

Monitoring forest birds in boreal and temperate biomes is largely based on breeding bird surveys in spring, when bird vocalisations are most intense, which encapsulate many species in one visit (e.g. Peterjohn and Sauer, 1994). In spring, point counts usually last 5–10 min (Bibby et al., 2000) and are useful in assessing relative densities and population trends of birds, although longer-lasting point counts provide more accurate estimates (Fuller and Langslow 1984; Hutto et al., 1986; Sorace et al., 2000). Winter surveys are much less common due to generally low detectability of forest birds, lowered accessibility of forest environments due to snow, relatively low densities of birds and the decreasing attractiveness for observers during this time, due to the combination of these factors (Brewer, 1978). The data available to assess the use of different forest structures by resident birds in winter is therefore limited. From the perspective of environmentally sustainable forest management, it is important to have reliable and feasible methods to evaluate to what extent vegetation structures in multipurpose forests provide wintering habitats for resident birds, being both indicator species and often species of conservation interest.

Automated acoustic monitoring has recently become a popular method for detecting vocalising species, particularly birds, because they are highly vocal, play diverse roles in ecosystem functioning and are often used as indicators of environmental change (Gasc et al., 2017). Acoustic monitoring can be employed to identify birds to species level from recordings (bioacoustics) or to quantify patterns of acoustic energy in a soundscape via acoustic indices (ecoacoustics). Acoustic indices can be rapidly extracted from hundreds of hours of recordings without listening to each file, and have been linked to habitat quality, species richness, abundance, phylogenetic and functional diversity (Sueur and Farina 2015; Gasc et al., 2013; Stowell and Sueur, 2020). Acoustic monitoring typically focuses on the breeding season when birds are most vocally active, and these results are often directly compared to point count surveys conducted in the same season (Darras et al., 2018). However, the primary advantage of acoustic monitoring is that devices can be left in situ and programmed to survey regularly, with high temporal resolution, over long time periods. Particularly in winter, acoustic monitoring is advantageous as data can be passively collected and saved while site access is restricted by snow, and retrieved once access is regained. A lack of predictable phenological events such as the dawn chorus and territorial calls associated with breeding make bird vocalisations, which are mostly contact calls, more stochastic in winter; recording at regular intervals (instead of one site visit from point counts) increases the probability of capturing winter bird activity by distributing a similar sampling effort over a longer timeframe.

To our knowledge, three winter acoustic studies exist to date. Krause et al. (2011) and Mullet et al. (2016) sought to broadly characterize the sonic components of a winter soundscape, such as distinguishing bird

calls (biophony) from wind (geophony) or anthropogenic noise from planes, automobiles and snowmobiles (anthrophony). Wolfgang and Haines (2016) evaluated the use of automated call recognition software of wintering birds, but only for 3 species. No studies have examined the usefulness of in-situ automated recorders to monitor the full resident bird assemblage in detail (e.g. richness) to gain insights into their activity and use of vegetation structures throughout the critical winter season. This study sought to do this by 1) collecting bird assemblage metrics via both bioacoustic and traditional point count methods; 2) testing the response of each of these metrics to a gradient of structural heterogeneity; and 3) assessing which acoustic indices, derived from audio recordings, reflect the bird-structure links established above.

2. Materials and methods

2.1. Study area

The study was conducted in Färna Ecopark, Sweden, a 4000-ha area largely devoted to conservation, 2800 ha of which are forested. Färna Ecopark is located in a mosaic coniferous-deciduous boreal landscape intermixed with wetlands and bogs, rocky outcrops and numerous waterbodies and watercourses (Fig. 1). The dominant tree species are Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), silver birch (*Betula pendula*) and European aspen (*Populus tremula*). The climate displays strong temperature variations between seasons, with average temperatures ranging from -5 °C to 0 °C in winter and 15 °C–25 °C in summer. Using data from 2003 to 2013 vegetation inventories of Färna Ecopark in QGIS v.3.10 (QGIS Development Team, 2019), we selected 19 sites within three forest classifications based on proportion of deciduous tree species: 20–50 % deciduous, < 20 % deciduous, and 0 % deciduous (monoculture stands). The 20–50 % deciduous plots were identified in QGIS; the sites in monoculture stands, which are located in “unclassified forest” areas, were selected in situ. This resulted in a gradient of percent deciduous stands, ranging from 0.17 % (conifer monocultures) to 73.30 %. Each site was established as a 50-m radius around a GPS point centre, while ensuring the forest classification in the surrounding 100-m radius remained constant.

2.2. Vegetation survey

Six circular 100 m² subplots were established around the center of each site (n = 114). Each Norway spruce, Scots pine, birch, aspen and black alder (*Alnus glutinosa*) tree with a height greater than 1.5 m was measured for height and diameter at breast height (DBH, measured at 1.3 m from the ground). The height and DBH of each dead tree present were also recorded. From this survey, several vegetation metrics were developed to reflect aspects of species composition and structural diversity, adapted from Storch et al. (2018). These variables include: DBH quadratic mean, DBH standard deviation, mean stand height, stand height standard deviation, total basal area, percentage of total basal area with deciduous trees, mean DBH of standing deadwood, mean diameter of downed deadwood, standing deadwood volume, downed deadwood volume (see Appendix A for details).

2.3. Point count survey

GM conducted two bird surveys at each site from 14.12.19 to 14.03.20. Visits at a given site were separated by a mean of 29.2 days (range: 21–56). All surveys were conducted between 8:00 and 14:20; 26 surveys started before noon and 12 after. Each survey lasted 20 min and all birds seen or heard were recorded, with no distance limit in order for this data to be comparable to the detection radius of an acoustic recorder (Shaw et al., 2021). Final variables from point counts include species richness (hereafter Richness_{pc}) and Abundance per site. Total sampling effort (excluding time spent to access sites) was 40 min per site.

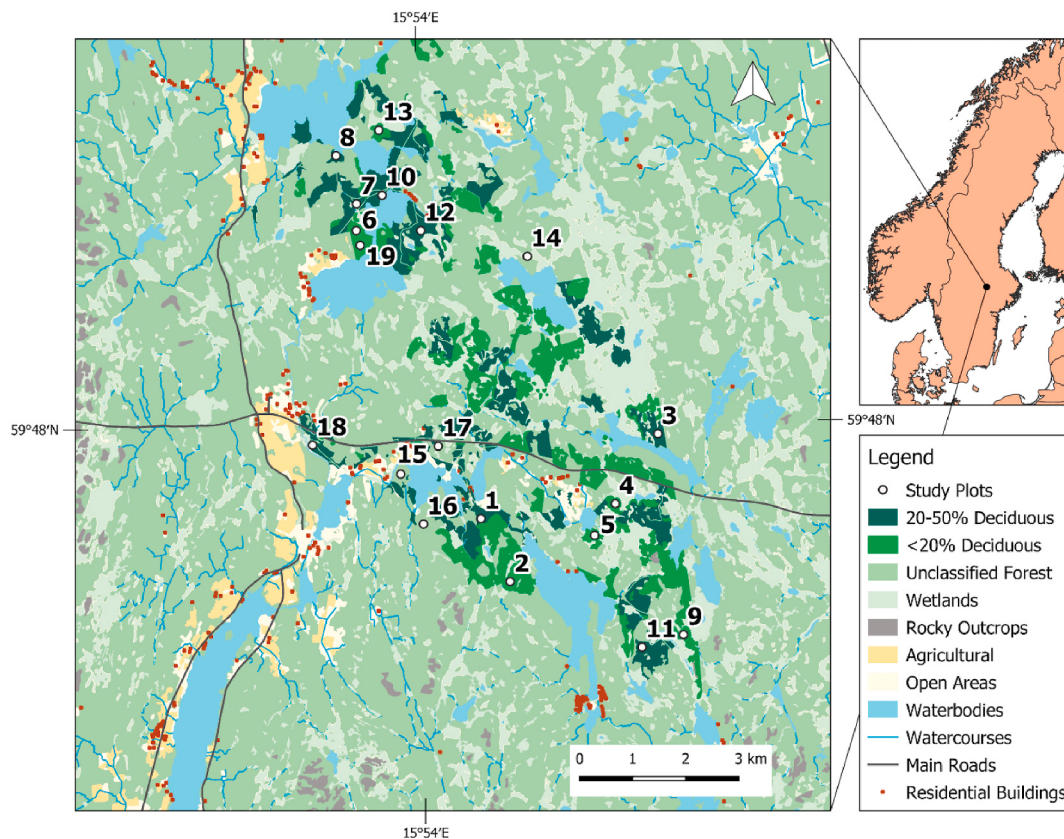


Fig. 1. Map of the study area in Färna Ecopark, Sweden, depicting 19 study sites in a mosaic, multipurpose boreal forest landscape.

2.3.1. Acoustic survey

Acoustic data was collected from December 05, 2019 to February 20, 2020 using automated prototype ‘Soundscape Explorer Terrestrial’ recorders by Luniletronik Cooperativa (Fivizziano, Italy), equipped with an omnidirectional EMY-63M/P microphone (sensitivity: $-38 \text{ dB} \pm 3 \text{ dB}$, signal to noise ratio: $> 60 \text{ dB}$). Recorders were installed 1.6 m high on a tree nearest the site center, with the microphone oriented southwest, away from the prevailing wind direction (Shaw et al., 2021). Devices were programmed to record for 1 min every 10 min, 24 h a day, at a sampling rate of 24 kHz and gain of $+25 \text{ dB}$. In each plot we collected 57 days of recordings within our data collection period, resulting in 8208 1-min recordings per site (2599.2 h total).

2.3.2. Acoustic data processing

As most resident birds are diurnal and point counts were only conducted during daylight hours, only daytime recordings were used for this study. These were determined according to daily sunrise and sunset times based on a common set of coordinates and altitude for all sites ($59^{\circ}47'30.7''\text{N}$, $15^{\circ}53'35.3''\text{E}$ and 123 m.a.s.l., respectively) using the *sunrise.m* function in Octave v5.0.2 (Beauducel, 2020; Eaton et al., 2020). Raw acoustic files can contain sounds originating from non-bird sources (e.g. geophony and anthrophony), thus we first sampled and manually reviewed files to clean the dataset of non-bird vocalisations. This sample consisted of 150 files from each site (2850 total) at 2-h intervals (recordings from 8:30, 10:30, 12:30 and 14:30). We used spectrograms in Kaleidoscope Lite v5.2.1 (Wildlife Acoustics, Inc., 2020) to visually screen the files for non-bird sounds, which we classified as either rain, wind or glitches. Using acoustic indices generated from these files (see section 2.5), we identified index values that enabled us to classify non-bird sounds and clean the entire dataset (details in Appendix B). Following the removal of non-bird vocalisations and non-daytime files, a total of 22565 recordings remained (between 980 and 1426 1-min recordings per site), which were used in later analyses.

2.3.3. Aural identification from recordings

An expert observer with no prior knowledge of the site from which the files originated, identified all detectable bird species. The expert identified 200 random non-consecutive daytime recordings per site ($n = 3800$). Files were randomly selected with the *sample.n* function in the ‘dplyr’ R package (Wickham et al., 2020). From the 200 files per site, a subset of 40 files were randomly selected, resulting in two species richness counts: first, aural identification with a sampling effort equal to that of point counts (40 min per site) hereafter called *Richness_equal*, and second, identifications with a maximized sampling effort greater than the point count survey (200 min per site) hereafter called *Richness_max*.

Abundance cannot be reliably estimated from acoustic recordings; however different metrics can be derived from an aural identification dataset that describe bird activity. We calculated the following variables: No. Occurrences, quantifying the cumulative number of bird observations per site, all species pooled; No. Flocks, quantifying the cumulative number of files capturing mixed-species flock vocalisations per site; and No. Multiple Birds, quantifying the number of files that capture more than one vocalising species within 1 min (excluding mixed species flocks) per site. No. Flocks was identified by clear flocking behaviour, which is an uncountable number of birds calling simultaneously, while No. Multiple Birds is the identification of a single individual and then another individual calling later in the file (e.g. one blue tit vocalising at e.g. 0:11 s, then silence, and at 0:48 a treecreeper vocalisation is also detected).

2.3.4. Acoustic index computation

Using files cleaned of wind, rain, and device glitches, we computed six of the most common acoustic indices used for biodiversity monitoring from the ‘soundecology’ package in R (Villanueva-Rivera and Pijanowski, 2018), as multi-index studies with these indices have been shown to be more effective than single index investigations

(Bradfer-Lawrence et al., 2020). Index descriptions can be found in Table 1. We calculated index means per site, as means are expected to reveal patterns that might otherwise be masked by index variability (Bradfer-Lawrence et al., 2019). All index values were normalized on a scale from 0 to 1 with the *normalize* function in the 'effectsize' package (Ben-Shachar et al., 2020) to facilitate comparisons between indices.

2.4. Data exploration and spatial correlation metrics

A series of additional acoustic indices were used to aid in data cleaning and to account for potential sources of autocorrelation in the data. These indices included the LowFreqCover Index, High Amplitude Index, Background Noise Index, Clipping Index and Signal to Noise Ratio, which were computed using the Ecoacoustic Audio Analysis Software in R (Towsey, 2020). Six spatial variables potentially relevant to our research questions were also calculated per site: 'distance to waterways', 'distance to waterbodies', 'distance to main roads', 'distance to residential buildings' and 'number of residential buildings in a 1000 m radius'. Geospatial analyses were computed in QGIS with the NNJoin Plugin using the Nearest Neighbour Analysis. Vector GIS data was obtained from the Swedish mapping, cadastral and land registration authority 'Lantmäteriet'.

2.5. Statistical analysis

2.5.1. PCA analysis of vegetation variables

All statistical analyses were performed in R v.4.0.2 (R Core Team, 2020). Vegetation metrics were combined using a Principal Component Analysis (PCA) with the singular value decomposition approach, using the *Rprcomp* function with variable centering and scaling. Axis retention was aided by the broken-stick model (Borcard et al., 2011), as this was found to be an accurate stopping rule to estimate the number of significant components (Jolliffe, 2002).

2.6. Comparing species richness between methods

The only metric we could compare directly between point count and aural identification methods was bird richness, thus a two-samples *t*-test was applied to each combination of variables: Richness_pc, Richness_equal and Richness_max.

2.6.1. Bird assemblage metrics in response to forest structure

Next, we sought to investigate forest structure as a direct driver of bird assemblage and activity metrics using the vegetation PCs as independent variables in Generalized Linear Models (GLMs). The three richness metrics, as well as the other bird variables (Abundance, No. Occurrences, No. Flocks and No. Multiple Birds), were each modelled independently as response variables using Gaussian distributions. All GLMs were made using the 'glmmTMB' package (Brooks et al., 2017).

2.6.2. Acoustic indices in response to bird assemblage and forest structure

To investigate if acoustic indices reflect metrics of bird assemblage and activity, we used GLMs to model each acoustic index (ACI, ADI, BIO, EVE, H and NDSI) individually in response to the following independent variables: one assemblage metric at a time (as a direct driver), vegetation PCs (indirect drivers) and their interactions. All models used a Tweedie distribution with a log-link function. Using an information theoretic (IT) approach (Burnham and Anderson, 1998), all models with the same acoustic index response variable can be directly compared; the best-performing model has high predictive value and minimal complexity, with the lowest corrected Akaike information criterion (AICc) (Hurvich and Tsai, 1989). IT-modelling is useful for measuring the relative strength of evidence for competing hypotheses given the data at hand; this approach allowed us to determine the relative strength of a given index to reflect each particular aspect of bird assemblages. This comparison is facilitated by the Akaike weight (*w_i*), which can be

Table 1
Acoustic index descriptions.

Acoustic Index (citation)	Abbreviation	Calculation Details	Interpretation
Acoustic Complexity Index (Pieretti et al., 2011)	ACI	Calculates the difference in amplitude from one specified time to the next, within one frequency band, relative to the total amplitude of that band. The values from each frequency band are then added.	Designed to reflect complex sound; it captures rapid variations in frequency and amplitude that are typical of biophony (especially birdsong). This index typically does not respond to persistent sound such as machinery noise or buzzing insects.
Acoustic Diversity Index (Villanueva-Rivera et al., 2011)	ADI	Divides a recording into frequency bands and applies the Shannon index to each band, only considering signals above an amplitude threshold.	High levels of geophony or anthrophony that extend over the entire spectrogram will result in higher values, while lower values will indicate sound occurring in a narrow frequency band.
Bioacoustic Index (Boelman et al., 2007)	BIO	Computes the area under each curve, including all frequency bands from 2 to 11 kHz with a dB value greater than the minimum dB value for each curve.	A combination of sound intensity and frequency bands occupied. Designed to reflect biophony. Low values indicate little to no acoustic activity.
Evenness Index (Villanueva-Rivera et al., 2011)	EVE	Divides a recording into frequency bands and applies the Gini index to the proportion of signals in each bin above a dB threshold.	If frequency bands are evenly occupied (a very quiet or very noisy file), value will be low. When sounds occur in an isolated range of frequencies, or there is an uneven distribution of sound across the recording, value will be high.
Entropy (Sueur et al., 2008)	H	Assesses the amplitude evenness across frequency bands and time samples. Similar to ADI, but on a finer scale and including narrower frequency bands	Even signals, such as a very quiet or uniformly noisy recording, produce high values. Recordings with very loud bird calls produce low values.
Normalized Difference Soundscape Index (Kasten et al., 2012)	NDSI	Calculated based on a hypothesised categorisation between the frequency spectrum of anthrophony (1 kHz–2kHz) and the frequency range in which biophy typically occurs (2 kHz–11 kHz). The value returned is	Resulting values between -1 and 1, with >0 value indicating biophony dominating the soundscape. Negative values indicate anthrophony is dominating the soundscape.

(continued on next page)

Table 1 (continued)

Acoustic Index (citation)	Abbreviation	Calculation Details	Interpretation
		the ratio between the two components.	

interpreted as the approximate probability that a given model would be the optimal model (lowest AICc) in that set of models, if this test were repeated many times (Burnham and Anderson, 1998).

Model diagnostics were performed with the 'DHARMA' package and model residuals were checked for spatial autocorrelation using the *testSpatialAutocorrelation* function (Hartig, 2020). Any models showing significant autocorrelation via the Moran's I test were further investigated; alternative models using additional spatial and acoustic variables (see section 2.5) were tested to explain spatial autocorrelation patterns and therefore achieve a more accurate estimate of the effect of the main variable in question. The best alternative model was chosen based on the highest Moran's I test p-value and lowest AICc value.

3. Results

3.1. PCA analyses of vegetation and acoustic indices

For vegetation structural variables, Axis 1 accounted for 39.8 % of the variation in our data, and largely reflected variables related to structural heterogeneity and complexity. Quadratic DBH, DBH standard deviation, mean stand height, height standard deviation and basal area contributed to 82.2 % of this axis (Appendix C), and will hereafter be referred to as the Structural Heterogeneity axis. The second axis explained 26.1 % of the variation, with metrics related to standing and downed deadwood volume having the largest contributions (73.8 %; Appendix C); it will be referred to as the Deadwood Volume axis. Two PCs were retained following the broken-stick model, accounting for 65.8 % of the variation in the vegetation structure data. As both axes decrease, the structural heterogeneity and deadwood volume increase, respectively (Appendix C).

3.2. Bird richness: point count versus bioacoustic identification

Of all recordings reviewed for aural identification, 45.1 % of files

contained bird vocalisations (n = 1710); of these files, 116 contained vocalisations too faint to identify, 29 vocalisations identified with uncertainty, and 2427 bird vocalisations identified with certainty (the latter was used for all analyses).

Across all sites, 30 species were identified from point counts, 25 identified from recordings with equal sampling effort and 37 identified from recordings with maximizing sampling effort (Appendix D for species occurrence lists). Species occurring on every or almost every site were similar between methods, including the great spotted woodpecker (*Dendrocopos major*) (point count = 12 sites, bioacoustic ID (40 min) = 14 sites, bioacoustics ID (200 min) = 16 sites), great tit (*Parus major*) (12,15,18) and Eurasian siskin (*Spinus spinus*) (12,13,19). Aural identifications captured six additional species at that frequency, including the goldcrest (*Regulus regulus*) (4,19,19), Eurasian treecreeper (*Certhia familiaris*) (1,17,19), long-tailed tit (*Aegithalos caudatus*) (2,9,19), blue tit (*Cyanistes caeruleus*) (4,13,17), crested tit (*Lophophanes cristatus*) (7,10,16) and Eurasian nuthatch (*Sitta europaea*) (6,8,14), which reveals a detectability bias in the point count method that the recorders did not suffer from. Twenty-five species were identified by both methods at the same site(s); five species were identified only by point count and twelve species only from recordings (see Appendix E for full details and discussion).

Richness_max was significantly higher than Richness_equal and Richness_pc (Fig. 2). On average Richness_equal exceeded Richness_pc, although at seven sites Richness_pc was equal to or exceeded Richness_equal, therefore no statistically significant difference between richness was found between these methods.

3.3. Response of bird assemblage and activity metrics to forest structure

Point count richness, Richness_pc, had no significant relationship to either vegetation PC axis, although both bioacoustic metrics, Richness_equal and Richness_max, increased significantly with higher structural heterogeneity (PC1) (Fig. 3). Neither bioacoustic richness metrics had a significant relationship to deadwood (PC2).

Mean Abundance per site, derived from point count data, was 9.68 (SD $\pm$ 6.89) individuals. Means for the following three bird activity metrics derived from acoustic recordings were: No. Occurrences 127.63 ($\pm$ 53.14), No. Flocks 25.74 ($\pm$ 9.49) and No. Multiple Birds 30.16 ($\pm$ 17.62). No. Occurrences and No. Multiple Birds increased significantly with structural heterogeneity and complexity (PC1), while Abundance and No. Flocks did not (Fig. 4). None of these metrics

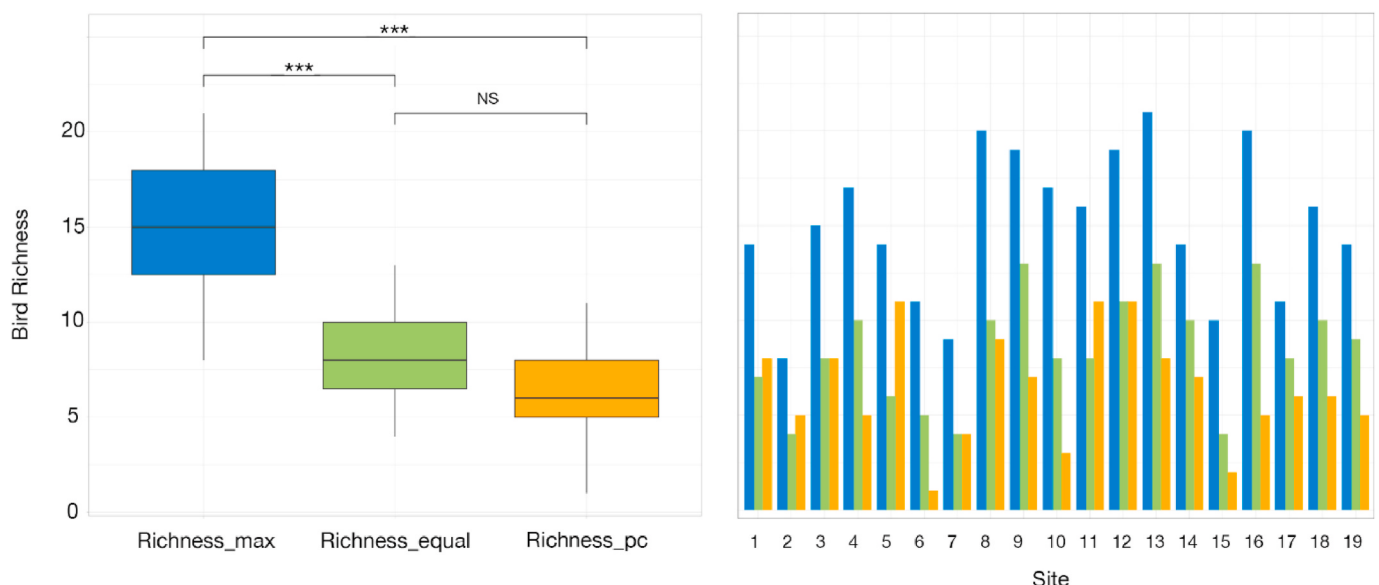


Fig. 2. Bird richness data, by method and by site. Significance notation from two-samples *t*-test: NS = not significant, * <0.05, ** <0.01, *** <0.001.

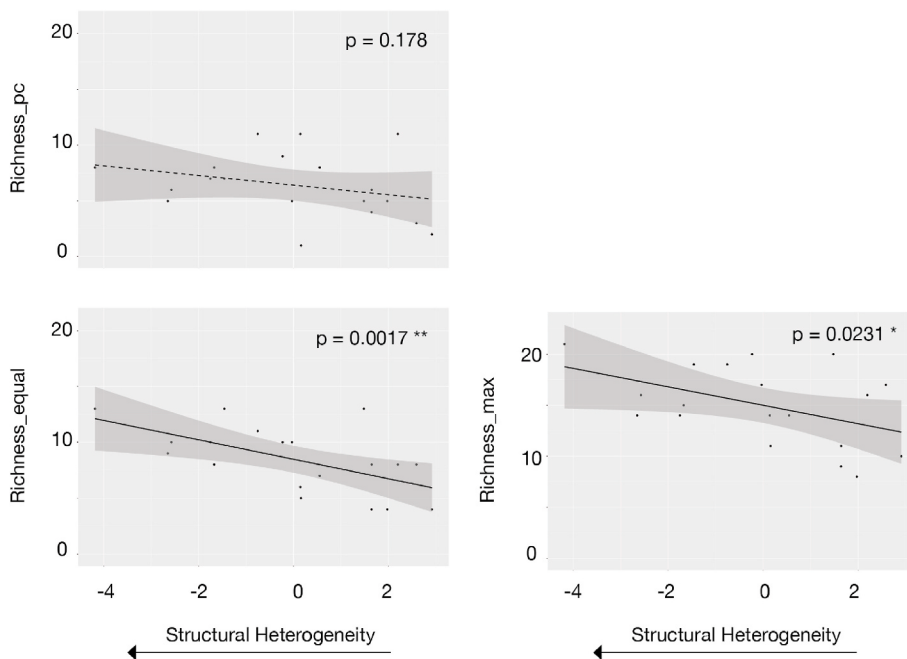


Fig. 3. The response of bird richness to vegetation PCA axis 1 and 2. Richness_pc was derived from point count data; Richness_equal was derived from acoustic recordings with a sampling effort equal to that of the point count (40 min per site); Richness_max is derived from acoustic recordings with a maximized sampling effort (200 min per site). Decreasing values on the Structural Heterogeneity axis indicate higher structural heterogeneity. Solid lines indicate a significant relationship, dashed lines indicate non-significance, shaded areas indicate 95 % confidence interval.

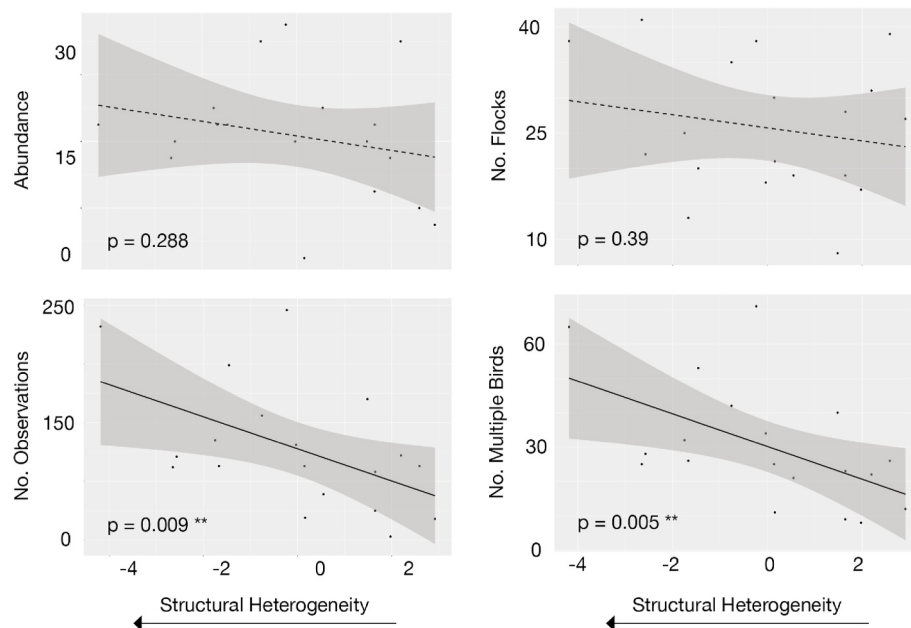


Fig. 4. The response of bird assemblage metrics to vegetation PCA axis 1. Abundance was derived from point count data; No. Visits, No. Flocks and No. Multiple Birds was derived from acoustic recordings. Decreasing values on the Structural Heterogeneity axis indicate higher structural heterogeneity. Solid lines indicate a significant relationship, dashed lines indicate non-significance, shaded areas indicate 95 % confidence interval.

showed significant relationships to deadwood (PC2).

3.4. Relationship of acoustic indices to bird metrics

The ACI and BIO indices increased significantly with higher bird assemblage and activity values: Richness_equal, Richness_max, No. Occurrences and No. Multiple Birds (Fig. 5). ACI and BIO indices reflect multiple facets of bird assemblage and activity, although w_i values indicate they reflect certain aspects more strongly than others (Table 2). No. Multiple Birds, followed by No. Occurrences, are the variables with the strongest positive relationship to ACI values, while Richness_max is most strongly related to BIO values. The other acoustic indices (ADI,

EVE, H, NDSI) showed no relationship to bird assemblage metrics.

3.5. Spatial autocorrelation

None of the models with bird metrics as the response variable (Figs. 3 and 4) showed spatial autocorrelation, and neither did ADI, BIO, EVE nor H acoustic indices. However, two NDSI and four ACI models showed significant spatial autocorrelation. The landscape metrics ‘number of residential buildings in a 1000 m radius’, ‘distance to waterbodies’ and ‘distance to waterways’ accounted for spatial autocorrelation in ACI models, however no spatial metrics explained the autocorrelation in NDSI models. Instead, LowFreqCover (an acoustic index capturing low-

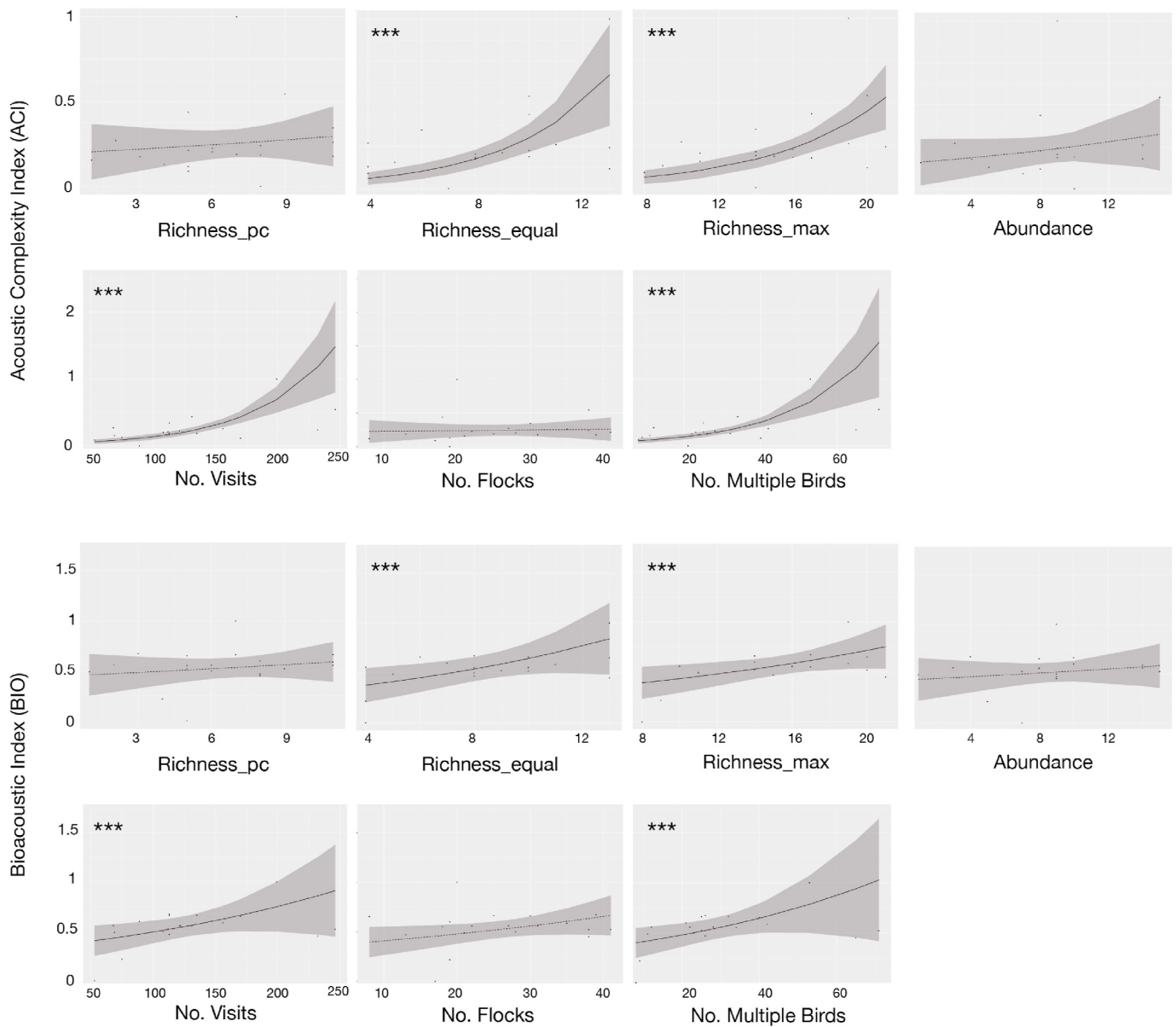


Fig. 5. The response of the ACI and BIO acoustic indices bird assemblage and activity metrics. Solid lines indicate a significant relationship, dashed lines indicate non-significance, shaded areas indicate 95 % confidence interval.

Table 2

Models results of all models testing one acoustic index as the dependent variable, and one bird assemblage metric as the independent variable (all models also included vegetation PCs 1 and 2). Each row is a set of seven models, and each column is the bird assemblage metric used as the independent variable. Models can be compared row-wise by their $\Delta AICc$ and Akaike weights (w_i). Models with a significant response to the bird metric are bolded.

Acoustic Index	Richness_pc	Richness_equal	Richness_max	Abundance	No. Occurrences	No. Flocks	No. Multiple Birds
ACI	22.78	9.43	15.84	22.14	2.14	19.75	0
w_i	0	0.01	0	0	0.25	0	0.74
ADI	7.11	4.39	5.43	6.74	5.14	0	4.26
w_i	0.02	0.08	0.05	0.02	0.05	0.7	0.08
BIO	7.52	3.14	0.23	7.95	3.99	0	3.36
w_i	0.01	0.08	0.36	0.01	0.06	0.41	0.08
EVE	5.39	2.69	1.29	1.46	1.77	0	0.65
w_i	0.02	0.07	0.15	0.14	0.12	0.29	0.21
H	25.64	22.19	22.49	24.96	23.29	0	22.46
w_i	0	0	0	0	0	1	0
NDSI	1.5	0.33	0.89	1.55	0.63	3.28	0
w_i	0.11	0.19	0.15	0.11	0.17	0.04	0.23

frequency noise typical of wind or machinery) accounted for the autocorrelation in NDSI models. This variable also greatly improved the AICc of the other five NDSI models, so it was included in all NDSI models (Appendix F). For full discussion of spatial autocorrelation of acoustic indices, see Appendix G.

4. Discussion

4.1. Bird richness: point count versus bioacoustic identification

This is the first winter study to apply a combined bioacoustic and ecoacoustic monitoring approach, and compare it to traditional point count surveys. Bird identifications from acoustic recordings yielded significantly higher bird richness, although only when the sampling effort was greater than that of point counts. This is partially due to an increase in sampling effort, but an increase in sampling effort is feasible for acoustic monitoring (by simply reviewing more files in the lab—an addition of minutes), however point counts would require multiple field visits (and therefore an addition of hours or days). Both bioacoustic metrics of bird richness (40 and 200 min) showed significant relationships to the Structural Heterogeneity axis, while point count richness did not. This suggests that although richness_equal and richness_pc were not statistically different, they were different enough for bioacoustic richness to serve as a better metric than point counts for revealing relationships between bird richness and forest structure. Both bioacoustic richness values were also significantly related to ACI and BIO indices, while point count richness was not (Fig. 5, Table 2), suggesting that bioacoustic richness values are better ground-truth metrics with which to test acoustic indices as proxies for bird richness. Currently point count surveys are the industry standard for ground-truthing acoustic indices, however our results indicate that if we had relied solely on point count data, we would have concluded that there was no relationship between any acoustic index and bird richness when there was in fact a strong, positive relationship that the winter point counts did not capture. Other studies combining bioacoustic and ecoacoustic approaches exist, although not in winter and not using the new metrics outlined in our study, which have shown similar positive findings between bioacoustic identifications and acoustic indices (Eldridge et al., 2018; Deichmann et al., 2017; Ferreira et al., 2018; Towsey et al., 2014; Depaetere et al., 2012). Our results provide strong evidence that the point count method is disadvantageous in winter when bioacoustics monitoring is available as an alternative. In spring, 20 min point counts have been shown to be efficient for estimating species richness (Fuller and Langslow, 1984; Hutto et al., 1986; Bibby et al., 2000; Sorace et al., 2000), but our results suggest that in winter, even doubling that survey time to two 20-min surveys is insufficient.

Other studies comparing point counts to acoustic recordings found either similar outcomes between methods (Alquezar and Machado, 2015; Castro et al., 2019; Celis-Murillo et al., 2012; Darras et al., 2018; Klingbeil and Willig, 2015; McGuire et al., 2011; Van Wilgenburg et al., 2017; Yip et al., 2017) or that recorders outperformed humans (Borker et al., 2015; Digby et al., 2013; Haselmayer and Quinn, 2000; Hutto and Stutzman, 2009; Klingbeil and Willig, 2015; Tegeler et al., 2012; Venier et al., 2012; Zwart et al., 2014). The differences between study outcomes depend on factors such as distance from recorder, recorder type, species of interest, vegetation density, habitat type, climatic zone and if detection probabilities were calculated and standardised. These studies were not conducted in winter, however, and they noted that it is difficult to directly compare sampling methods, all factors considered. Numeric species richness may be greater from one method, but the species compositions of birds identified between methods are not directly comparable (Celis-Murillo et al., 2009; Haselmayer and Quinn, 2000; Leach et al., 2016), which we also observed in our data. Further, some acoustic datasets have hidden costs of time-consuming data cleaning (rain, wind, etc.), however improvements in automated file processing are rapidly advancing (e.g. Oliver et al., 2018; Huanapaza Hilasaca

et al., 2021) and minimizing this disadvantage.

Our results provide evidence that bioacoustic monitoring performs well as a method for estimating resident bird richness, activity and habitat selection during winter in a heterogeneous boreal forest landscape.

4.2. Response of bird assemblage and activity to forest structure

Richness and abundance metrics derived from point counts showed no response to either vegetation structure PC, highlighting the difficulty in relying on winter point count surveys to yield useful assemblage data. However, bird activity metrics that leverage the advantages of long-term acoustic recordings can be created: No. Occurrences, No. Flocks and No. Multiple Birds. All three activity metrics are theoretical indicators of habitat quality: the number of vocalisation events (by individuals, flocks or multiple birds) increases the more time species spend in a given habitat, due to provisioning of food, shelter from low temperatures, precipitation and wind, or protection from the sight of predators. Therefore, cumulative counts observations of individuals, mixed-species flocks or multiple individuals calling within the same minute should each increase with higher habitat quality. Interestingly, this was confirmed for No. Occurrences and No. Multiple Birds, as they both showed clear positive significant responses to increased structural heterogeneity (Fig. 4), but No. Flocks did not have a significant relationship to either vegetation PC. One explanation for this is that there are different mix-species flocking events each with different structural requirements for food provisioning. For example, multiple tit species, nuthatches, goldcrests, treecreepers and sometimes lesser spotted woodpeckers flock together and primarily eat canopy insects; redpolls and siskins flock together and prefer small seeds from e.g. alder trees; crossbill flocks feed on conifer seeds; and waxwing flocks prefer fruits. Each of these species were observed in our flocking events, but the No. Flocks metric did not distinguish between them; multiple signals were thus collapsed into one, potentially explaining a flatter response to either structural PC, particularly the Structural Heterogeneity axis.

No bird assemblage metrics showed a significant response to the Deadwood Volume axis (Figs. 3 and 4), although bird richness has been shown to increase with deadwood volume in previous research (Bouvet et al., 2016; Cadieux and Drapeau, 2017; Reise et al., 2019; Zan et al., 2017). These studies, however, were conducted in spring, and often contained a gradient of deadwood much larger than what was available in our sites. These studies captured maximum deadwood volumes up to 370 m³/ha, while our sites contained from 0 to 40 m³/ha of standing or downed deadwood, with the exception of one site.

4.3. Response of acoustic indices to bird metrics

Our results suggest that the ACI and BIO indices can serve as proxies for winter bird richness and activity in a boreal forest. This is consistent with research in other seasons and climatic zones that found relationships between these indices and species richness (Dröge et al., 2021; Eldridge et al., 2018; Towsey et al., 2014), abundance (Boelman et al., 2007; Bradfer-Lawrence et al., 2020) and activity (Fairbrass et al., 2017; Pieretti et al., 2011). ACI and BIO were both significantly driven by the same bird metrics: Richness_equal, Richness_max, No. Occurrences and No. Multiple Birds, although ACI was most strongly linked to No. Multiple Birds and BIO was most strongly linked to Richness_max (Table 2). The ACI was also susceptible to spatial autocorrelation, while BIO was not. The ACI, which is an additive index designed to reflect rapid variations in frequency and intensity typical of birdsong, may be more sensitive to the addition of vocalising species to the soundscape, either in a 1-min file (No. Multiple Birds) or across the entire recording period (No. Occurrences). This is supported by *wi* values across all ACI models, which indicate that No. Multiple Birds and No. Occurrences would be the ACI's strongest predictors if this study were to be repeated many times (Table 2). Gasc et al., (2015) have also demonstrated the ACI to be

sensitive to the addition of another species, and even more so when songs from different species do not overlap within the song file.

Compared to the ACI, BIO is a more generalized index that increases with increasing biophony; it responds not only to complex birdsong but also blanket noise such as insect stridulations. It computes the area under the curve of high amplitude signals across all frequency bands relative to the band with the lowest amplitude. Although the *wi* values for BIO models indicate that the relative strengths of the four significant bird metrics differ in their probabilities of being the best-fitting model (Table 2, bolded), they all share some percentage of the Akaike weight, making BIO the index that best reflects multiple aspects of bird assemblage and activity simultaneously. Overall, ACI and BIO are promising indices as winter monitoring proxies, but multi-year studies are needed to assess the degree to which these results replicate interannually with different temperature fluctuations, wind events and levels of rain- and snowfall. This is particularly relevant because bird activity is known to vary with environmental conditions (Oliver et al., 2018), and in our study the 2020 winter was unusually warm, with very little snow.

ADI, EVE, H and NDSI were not significantly predicted by any bird metric, unlike some studies that found these indices reflected bird richness well (Jorge et al., 2018; Machado et al., 2017; Mammides et al., 2017). This is likely due to seasonality; past studies were conducted in spring, and our data was collected in winter when there is a drastically lower bird vocalisation frequency. Krause et al. (2011) found that soundscapes in a temperate montane evergreen forest were quietest in winter and lacked biophony compared to all other seasons. Of our 200 recordings reviewed per site, 55 % did not contain any bird vocalisations, meaning over half of the acoustic index values that comprised our index means were reflecting non-bird sounds (likely silence or wind). Further, ADI and H are indices that similarly quantify spectral entropy, and EVE quantifies how evenly sound signals are distributed across twelve frequency bands. These three indices excel at reflecting coarse differences in large-scale acoustic activity, for example between different times of day (dawn chorus vs. night), or between distinctly different habitats (mature oak forest, secondary forest, wetland, plantation, etc.). It is unlikely that they were able to distinguish between sites of the same habitat type during the same time of day, at least when over half the files did not contain bird vocalisations. The ACI and BIO indices are more robust for monitoring across seasons (BIO's robustness has also been demonstrated across temperate and tropical climatic zones (Eldridge et al., 2018)), while the ADI, EVE, H and NDSI indices are likely only useful when bird vocalisations dominate the soundscape and the higher frequency of vocalisations increase the performance of these indices (Zhao et al., 2019).

5. Conclusion

To our knowledge, this is the first study of its kind using acoustic monitoring for resident bird assemblages in the winter season. Acoustic monitoring was a superior method to point counts for determining species richness, particularly if resources allow for bioacoustic identification effort greater than 40 min per site (in our case, 200 1-min files per site). Automated monitoring allows for more distributed sampling effort across time, and less detectability bias. The bioacoustic approach is additionally useful because it yields new metrics about bird activity that have direct links to structural complexity, which can serve as indicators of habitat quality. On the contrary, 40-min point count richness and abundance showed no link to habitat quality, demonstrating the relative ineffectiveness of point counts compared to the spring season.

The ecoacoustic approach of acoustic index computation also proved useful: the ACI and BIO indices showed significant relationships to almost all bird assemblage metrics, indicating they could serve as proxies for bird richness and activity that reflect differences in habitat quality. No relationship was found between point count metrics (richness and abundance) and acoustic indices, further indicating that point counts are not a sufficient 'ground truth' of ecoacoustic indices for

winter monitoring schemes, compared to the greater potential data available in acoustic recordings. Acoustic monitoring, in the form of bioacoustic and ecoacoustic data, can provide new insights about winter behaviour that can allow for more efficient monitoring and inference about habitat choice, improving our ability to identify forest patches important for birds in winter.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank our two reviewers for their valuable contributions to the manuscript. We also thank Johannes Penner for his supervision of RH and general feedback, Dariusz Graszka-Petrykowski for aural identifications, Ricardo J. Abraham for assisting us in recorder installation fieldwork and the ConFoBi RTG for manuscript feedback. We are grateful to Färna Ecopark for access to the sites and Stefan Toterud for providing inventory data for site selection.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.indic.2021.100141>.

Author contributions

TS, GM, AR, MHir, MHed and SE designed the study and collected acoustic data. GM conducted point counts, AS conducted the vegetation survey. TS and RH processed and analysed the data. TS, RH and GM wrote the first draft of the manuscript, and all authors contributed to subsequent drafts. GM and TS provided funds and materials to support this research.

Funding

This study was supported by the Research Training Group ConFoBi (GRK 2123/1 TPX), funded by the German Research Association (DFG). This work was also funded by the Faculty of Forest Sciences, Swedish University of Agricultural Sciences SLU.

References

- Alquezar, R.D., Machado, R.B., 2015. Comparisons between autonomous acoustic recordings and avian point counts in open woodland savanna. *Wilson J. Ornithol.* 127 (4), 712–723. <https://doi.org/10.1676/14-104.1>.
- Barbe, L., Morel, R., Rantier, Y., Lebas, J.-F., Butet, A., 2018. Bird communities of a temperate forest: spatio-temporal partitioning between resident and migratory species. *J. Ornithol.* 159 (2), 457–469. <https://doi.org/10.1007/s10336-017-1523-y>.
- Beauducel, F., 2020. SUNRISE: Sunrise and Sunset Times. MATLAB [Windows], Version 1.4.1.
- Ben-Shachar, M., Ludecke, D., Makowski, D., 2020. Effectsize: estimation of effect size indices and standardized parameters. *J. Open Sourc. Softw.* 5 (56), 2815. <https://doi.org/10.21105/joss.02815>.
- Bibby, C.J., Burgess, N.D., Hill, D.A., 2000. *Bird Census Techniques*, second ed. Academic Press, San Diego, Calif.
- Blicharska, M., Baxter, P.W.J., Mikusiński, G., 2014. Practical implementation of species' recovery plans – lessons from the White-backed. *Woodpecker Action Plan Sweden* 91, 21.
- Boelman, N.T., Asner, G.P., Hart, P.J., Martin, R.E., 2007. Multi-trophic invasion resistance in Hawaii: bioacoustics, field surveys, and airborne remote sensing. *Ecol. Appl.* 17 (8), 2137–2144. <https://doi.org/10.1890/07-0004.1>.
- Borcard, D., Gillet, F., Legendre, P., 2011. Ordination in reduced space. In: Borcard, D., Gillet, F., Legendre, P. (Eds.), *Numerical Ecology with R*, first ed. Springer-Verlag, New York.
- Borker, A., Halbert, P., Mckown, M., Tershry, B., Croll, D., 2015. A comparison of automated and traditional monitoring techniques for marbled murrelets using passive acoustic sensors. *Wildlife Soc. Bull.* 39 (4), 813–818.

- Bouvet, A., Paillet, Y., Archaux, F., Tillon, L., Denis, P., Gilg, O., Gosselin, F., 2016. Effects of forest structure, management and landscape on bird and bat communities. *Environ. Conserv.* 1, 1–13. <https://doi.org/10.1017/S0376892915000363>.
- Bradford-Lawrence, T., Bunnefeld, N., Gardner, N., Willis, S.G., Dent, D.H., 2020. Rapid assessment of avian species richness and abundance using acoustic indices. *Ecol. Indic.* 115, 106400. <https://doi.org/10.1016/j.ecolind.2020.106400>.
- Bradford-Lawrence, T., Gardner, N., Bunnefeld, N., Bradbury, L., Marsland, S., Dent, D.H., 2019. Guidelines for the use of acoustic indices in environmental research. *Methods Ecol. Evol.* 10 (10), 1796–1807. <https://doi.org/10.1111/2041-210X.13254>.
- Brewer, R., 1978. A comparison of three methods of estimating winter bird populations. *Bird-Banding* 49 (3), 252–261. <https://doi.org/10.2307/4512367>.
- Brooks, M., Kristensen, K., van Benthem, K., Magnusson, A., Berg, C., Nielsen, A., et al., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 9 (2), 378–400.
- Burnham, K.P., Anderson, D.R., 1998. Practical use of the information-theoretic approach. In: Burnham, K.P., Anderson, D.R. (Eds.), *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer, pp. 75–117. https://doi.org/10.1007/978-1-4757-2917-7_3.
- Cadioux, P., Drapeau, P., 2017. Are old boreal forests a safe bet for the conservation of the avifauna associated with decayed wood in eastern Canada? *For. Ecol. Manag.* 385, 127–139. <https://doi.org/10.1016/j.foreco.2016.11.024>.
- Castro, I., Rosa, A.D., Priyadarshani, N., Bradbury, L., Marsland, S., 2019. Experimental test of birdcall detection by autonomous recorder units and by human observers using broadcast. *Ecol. Evol.* 9 (5), 2376–2397. <https://doi.org/10.1002/ece3.4775>.
- Celis-Murillo, A., Deppe, J., Allen, M., 2009. Using soundscape recordings to estimate bird species abundance, richness, and composition. *J. Field Ornithol.* 80 (1), 64–78. <https://doi.org/10.1111/j.1557-9263.2009.00206.x>.
- Celis-Murillo, A., Deppe, J.L., Ward, M.P., 2012. Effectiveness and utility of acoustic recordings for surveying tropical birds. *J. Field Ornithol.* 83 (2), 166–179. <https://doi.org/10.1111/j.1557-9263.2012.00366.x>.
- Darras, K., Batáry, P., Furnas, B., Celis-Murillo, A., Van Wilgenburg, S.L., Mulyani, Y.A., Tschamtk, T., 2018. Comparing the sampling performance of sound recorders versus point counts in bird surveys: a meta-analysis. *J. Appl. Ecol.* 55 (6), 2575–2586. <https://doi.org/10.1111/1365-2664.13229>.
- Deichmann, J., Hernandez-Serna, A., Delgado, J., Campos-Cerqueira, M., Aide, T., 2017. Soundscape analysis and acoustic monitoring document impacts of natural gas exploration on biodiversity in a tropical forest. *Ecol. Indic.* 74, 39–48. <https://doi.org/10.1016/j.ecolind.2016.11.002>.
- Depaertere, M., Pavoine, S., Jiguet, F., Gasc, A., Duvail, S., Sueur, J., 2012. Monitoring animal diversity using acoustic indices: implementation in a temperate woodland. *Ecol. Indic.* 13 (1), 46–54. <https://doi.org/10.1016/j.ecolind.2011.05.006>.
- Digby, A., Towsey, M., Bell, B.D., Teal, P.D., 2013. A practical comparison of manual and autonomous methods for acoustic monitoring. *Methods Ecol. Evol.* 4 (7), 675–683. <https://doi.org/10.1111/2041-210X.12060>.
- Dröge, S., Martin, D.A., Andrianomantsoa, R., Burivalova, Z., Fulgence, T.R., Osen, K., Rakotomalala, E., Schwab, D., Wurz, A., Richter, T., Kreft, H., 2021. Listening to a changing landscape: acoustic indices reflect bird species richness and plot-scale vegetation structure across different land-use types in north-eastern Madagascar. *Ecol. Indic.* 120, 106929. <https://doi.org/10.1016/j.ecolind.2020.106929>.
- Eaton, J., Bateman, D., Hauberg, S., Wehbring, R., 2020. GNU Octave. Version 5.2.0 [Windows].
- Eggers, S., Low, M., 2014. Differential demographic responses of sympatric Parids to vegetation management in boreal forest. *For. Ecol. Manag.* 319, 169–175. <https://doi.org/10.1016/j.foreco.2014.02.019>.
- Eldridge, A., Guyot, P., Moscoso, P., Johnston, A., Eyre-Walker, Y., Peck, M., 2018. Sounding out ecoacoustic metrics: avian species richness is predicted by acoustic indices in temperate but not tropical habitats. *Ecol. Indic.* 95, 939–952. <https://doi.org/10.1016/j.ecolind.2018.06.012>.
- Fairbrass, A.J., Rennert, P., Williams, C., Titheridge, H., Jones, K.E., 2017. Biases of acoustic indices measuring biodiversity in urban areas. *Ecol. Indic.* 83, 169–177. <https://doi.org/10.1016/j.ecolind.2017.07.064>.
- Ferreira, L.M., Sousa-Lima, R.S., Oliveira, E.G., Lopes, L.C., Brito, M.R., Baumgarten, J., Rodrigues, F.H., 2018. What do insects, anurans, birds, and mammals have to say about soundscape indices in a tropical savanna. *J. Ecoacoustics* 2 (1), 1. <https://doi.org/10.22261/jea.pv6yz.1>.
- Forsman, J.T., Mönkkönen, M., 2003. The role of climate in limiting European resident bird populations. *J. Biogeogr.* 30 (1), 55–70. <https://doi.org/10.1046/j.1365-2699.2003.00812.x>.
- Fuller, R.J., Langslow, D.R., 1984. Estimating numbers of birds by point counts: how long should counts last? *Hous. Theor. Soc.* 31 (3), 195–202.
- Gasc, A., Pavoine, S., Lellouch, L., Sueur, J., 2015. Acoustic indices for biodiversity assessments: analyses of bias based on simulated bird assemblages and recommendations for field surveys. *Biol. Conserv.* 191, 306–312. <https://doi.org/10.1016/j.biocon.2015.06.018>.
- Gasc, A., Sueur, J., Jiguet, F., Devictor, V., Grandcolas, P., Burrow, C., Depaertere, M., Pavoine, S., 2013. Assessing biodiversity with sound: do acoustic diversity indices reflect phylogenetic and functional diversities of bird communities? *Ecol. Indic.* 25, 279–287. <https://doi.org/10.1016/j.ecolind.2012.10.009>.
- Gasc, A., Francomano, D., Dunning, J.B., Pijanowski, B.C., 2017. Future directions for soundscape ecology: the importance of ornithological contributions. *Auk* 134 (1), 215–228. <https://doi.org/10.1642/AUK-16-124.1>.
- Hartig, F., 2020. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.3.3.0. <https://CRAN.R-project.org/package=DHARMA>.
- Haselmayer, J., Quinn, J.S., 2000. A comparison of point counts and sound recording as bird survey methods in amazonian southeast Peru. *Condor* 102 (4), 887–893. <https://doi.org/10.1093/condor/102.4.887>.
- Helle, P., Järvinen, O., 1986. Population trends of north Finnish land birds in relation to their habitat selection and changes in forest structure. *Oikos* 46 (1), 107–115. <https://doi.org/10.2307/3565386>.
- Huancapaza Hilarasa, L.M., Gaspar, L.P., Ribeiro, M.C., Minghim, R., 2021. Visualization and categorization of ecological acoustic events based on discriminant features. *Ecol. Indic.* 107316. <https://doi.org/10.1016/j.ecolind.2020.107316>.
- Hurvich, C.M., Tsai, C.-L., 1989. Regression and time series model selection in small samples. *Biometrika* 76 (2), 297–307. <https://doi.org/10.1093/biomet/76.2.297>.
- Hutto, R.L., Stutzman, R.J., 2009. Humans versus autonomous recording units: a comparison of point-count results. *J. Field Ornithol.* 80 (4), 387–398. <https://doi.org/10.1111/j.1557-9263.2009.00245.x>.
- Hutto, R.L., Plattsch, S.M., Hendricks, P., 1986. A fixed-radius point count method for nonbreeding and breeding season use. *Auk* 103 (3), 593–602.
- Jolliffe, I., 2002. *Principal Component Analysis*. Springer Science + Business Media, New York, pp. 111–149.
- Jorge, F.C., Machado, C.G., da Cunha Nogueira, S.S., Nogueira-Filho, S.L.G., 2018. The effectiveness of acoustic indices for forest monitoring in Atlantic rainforest fragments. *Ecol. Indic.* 91, 71–76. <https://doi.org/10.1016/j.ecolind.2018.04.001>.
- Kasten, E.P., Gage, S.H., Fox, J., Joo, W., 2012. The remote environmental assessment laboratory's acoustic library: an archive for studying soundscape ecology. *Ecol. Inf.* 12, 50–67. <https://doi.org/10.1016/j.ecoinf.2012.08.001>.
- Klein, J., Thor, G., Low, M., Sjögren, J., Lindberg, E., Eggers, S., 2020. What is good for birds is not always good for lichens: interactions between forest structure and species richness in managed boreal forests. *For. Ecol. Manag.* 473, 118327. <https://doi.org/10.1016/j.foreco.2020.118327>.
- Klingbeil, B.T., Willig, M.R., 2015. Bird biodiversity assessments in temperate forest: the value of point count versus acoustic monitoring protocols. *PeerJ* 3, e973. <https://doi.org/10.7717/peerj.973>.
- Krause, B., Gage, S.H., Joo, W., 2011. Measuring and interpreting the temporal variability in the soundscape at four places in Sequoia National Park. *Landscape Ecol.* 26 (9), 1247. <https://doi.org/10.1007/s10980-011-9639-6>.
- Leach, E.C., Burwell, C.J., Ashton, L.A., Jones, D.N., Kitching, R.L., 2016. Comparison of point counts and automated acoustic monitoring: detecting birds in a rainforest biodiversity survey. *Emu* 116 (3), 305–309. <https://doi.org/10.1071/MU15097>.
- Machado, R.B., Aguiar, L., Jones, G., 2017. Do acoustic indices reflect the characteristics of bird communities in the savannas of Central Brazil? *Landscape Urban Plann.* 162, 36–43. <https://doi.org/10.1016/j.landurbplan.2017.01.014>.
- Mammides, C., Goodale, E., Dayananda, S.K., Kang, L., Chen, J., 2017. Do acoustic indices correlate with bird diversity? Insights from two biodiverse regions in Yunnan Province, south China. *Ecol. Indic.* 82, 470–477. <https://doi.org/10.1016/j.ecolind.2017.07.017>.
- McGuire, A., Johnston, G., Kleindorfer, S., 2011. Comparison of survey methods for detection of the elusive Western Whipbird, *Psophodes nigrogularis*, with notes on its distribution. *South Aust. Ornithol.* 37.
- Mullet, T.C., Gage, S.H., Morton, J.M., Huettmann, F., 2016. Temporal and spatial variation of a winter soundscape in south-central Alaska. *Landscape Ecol.* 31 (5), 1117–1137. <https://doi.org/10.1007/s10980-015-0323-0>.
- Oettel, J., Lapin, K., 2021. Linking forest management and biodiversity indicators to strengthen sustainable forest management in Europe. *Ecol. Indic.* 122, 107275. <https://doi.org/10.1016/j.ecolind.2020.107275>.
- Oliver, R.Y., Ellis, D.P.W., Chmura, H.E., Krause, J.S., Pérez, J.H., Sweet, S.K., Gough, L., Wingfield, J.C., Boelman, N.T., 2018. Eavesdropping on the Arctic: automated bioacoustic reveal dynamics in songbird breeding phenology. *Sci. Adv.* 4 (6). <https://doi.org/10.1126/sciadv.aag1084>.
- Peterjohn, B.G., Sauer, J.R., 1994. Population trends of woodland birds from the north American breeding bird survey. *Wildl. Soc. Bull.* 22 (2), 155–164, 1973–2006.
- Pieretti, N., Farina, A., Morri, D., 2011. A new methodology to infer the singing activity of an avian community: the Acoustic Complexity Index (ACI). *Ecol. Indic.* 11 (3), 868–873. <https://doi.org/10.1016/j.ecolind.2010.11.005>.
- R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Reise, J., Kulkula, F., Flade, M., Winter, S., 2019. Characterising the richness and diversity of forest bird species using National Forest Inventory data in Germany. *For. Ecol. Manag.* 432, 799–811. <https://doi.org/10.1016/j.foreco.2018.10.012>.
- Roberge, J.-M., Angelstam, P., 2006. Indicator species among resident forest birds – a cross-regional evaluation in northern Europe. *Biol. Conserv.* 130 (1), 134–147. <https://doi.org/10.1016/j.biocon.2005.12.008>.
- Roberge, J.-M., Angelstam, P., Villard, M.-A., 2008. Specialised woodpeckers and naturalness in hemiboreal forests – deriving quantitative targets for conservation planning. *Biol. Conserv.* 141 (4), 997–1012. <https://doi.org/10.1016/j.biocon.2008.01.010>.
- Sueur, J., Farina, A., 2015. Ecoacoustics: the ecological investigation and interpretation of environmental sound. *Biosemiotics* 8, 493–502. <https://doi.org/10.1007/s12304-015-9248-x>.
- Shaw, T., Müller, S., Scherer-Lorenzen, M., 2021. Slope does not affect autonomous recorder detection shape: considerations for acoustic monitoring in forested landscapes. *Bioacoustics*. <https://doi.org/10.1080/09524622.2021.1925590> (in press).
- Sorace, A., Gustin, M., Calvario, E., Ianniello, L., Sarrocco, S., Carere, C., 2000. Assessing bird communities by point counts: repeated sessions and their duration. *Acta Ornithol. (Warsaw)* 35 (2), 197–202. <https://doi.org/10.3161/068.035.0213>.

- Storch, F., Dormann, C.F., Bauhus, J., 2018. Quantifying forest structural diversity based on large-scale inventory data: a new approach to support biodiversity monitoring. *For. Ecosyst.* 5 (1), 34. <https://doi.org/10.1186/s40663-018-0151-1>.
- Stowell, D., Sueur, J., 2020. Ecoacoustics: acoustic sensing for biodiversity monitoring at scale. *Rem. Sens. Ecol. Conserv.* 6 (3), 217–219. <https://doi.org/10.1002/rse2.174>.
- Sueur, J., Pavoine, S., Hamerlynck, O., Duvail, S., 2008. Rapid acoustic survey for biodiversity appraisal. *PloS One* 3 (12), e4065. <https://doi.org/10.1371/journal.pone.0004065>.
- Tegeler, A.K., Morrison, M.L., Szewczak, J.M., 2012. Using extended-duration audio recordings to survey avian species. *Wildl. Soc. Bull.* 36 (1), 21–29. <https://doi.org/10.1002/wsb.112>.
- Towsey, M., Wimmer, J., Williamson, I., Roe, P., 2014. The use of acoustic indices to determine avian species richness in audio-recordings of the environment. *Ecol. Inf.* 21, 110–119. <https://doi.org/10.1016/j.ecoinf.2013.11.007>.
- Towsey, M., 2020. *Ecoacoustics Audio Analysis Software. Version 20.6.0.208*. QUT Ecoacoustics Research Group, Brisbane, Australia [Windows].
- Turcotte, Y., Desrochers, A., 2005. Landscape-dependent distribution of northern forest birds in winter. *Ecography* 28, 129–140. <https://doi.org/10.1111/j.0906-7590.2005.04047.x>.
- Van Wilgenburg, S., Sólmos, P., Kardynal, K., Frey, M., 2017. Paired sampling standardizes point count data from humans and acoustic recorders. *Avian Conserv. Ecol.* 12 (1) <https://doi.org/10.5751/ACE-00975-120113>.
- Venier, L.A., Holmes, S.B., Holborn, G.W., McIlwrack, K.A., Brown, G., 2012. Evaluation of an automated recording device for monitoring forest birds. *Wildl. Soc. Bull.* 36 (1), 30–39. <https://doi.org/10.1002/wsb.88>.
- Villanueva-Rivera, L.J., Pijanowski, B.C., Doucette, J., Pekin, B., 2011. A primer of acoustic analysis for landscape ecologists. *Landsc. Ecol.* 26 (9), 1233–1246. <https://doi.org/10.1007/s10980-011-9636-9>.
- Villanueva-Rivera, L., Pijanowski, B., 2018. Soundecology: Soundscape Ecology. R package version 1.3.3. <https://CRAN.R-project.org/package=soundecology>.
- Wesołowski, T., Fuller, R.J., Flade, M., 2018. Temperate forests. In: Mikusinski, G., Roberge, J.-M., Fuller, R.J. (Eds.), *Ecology and Conservation of Forest Birds*, vols. 253–317. Cambridge University Press.
- Wickham, H., Francois, R., Henry, L., Muller, Kirill, 2020. Dplyr: A Grammar Of Data Manipulation. R Package Version 1.0.0. <https://CRAN.R-project.org/package=dplyr>.
- Wolfgang, A., Haines, A., 2016. Testing automated call-recognition software for winter bird vocalizations. *Northeast. Nat.* 23 (2), 249–258.
- Yip, D., Leston, L., Bayne, E., Sólmos, P., Grover, A., 2017. Experimentally derived detection distances from audio recordings and human observers enable integrated analysis of point count data. *Avian Conserv. Ecol.* 12 (1) <https://doi.org/10.5751/ACE-00997-120111>.
- Zan, L.R.D., Gasperis, S. R. de, Fiore, L., Battisti, C., Carpaneto, G.M., 2017. The importance of dead wood for hole-nesting birds: a two years study in three beech forests of central Italy. *Israel J. Ecol. Evol.* 63 (1), 19–27. <https://doi.org/10.1080/15659801.2016.1191168>.
- Zhao, Z., Xu, Z., Bellisario, K., Zeng, R., Li, N., Zhou, W., Pijanowski, B.C., 2019. How well do acoustic indices measure biodiversity? Computational experiments to determine effect of sound unit shape, vocalization intensity, and frequency of vocalization occurrence on performance of acoustic indices. *Ecol. Indic.* 107, 105588. <https://doi.org/10.1016/j.ecolind.2019.105588>.
- Zwart, M.C., Baker, A., McGowan, P.J.K., Whittingham, M.J., 2014. The use of automated bioacoustic recorders to replace human wildlife surveys: an example using nightjars. *PloS One* 9 (7), e102770. <https://doi.org/10.1371/journal.pone.0102770>.