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Acoustic indices estimate breeding bird species richness with daily and seasonally variable effectiveness in lowland temperate Białowieża forest

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ABSTRACT

Acoustic indices have been proposed as rapid and easy to apply tool for biodiversity estimation of vocalising animals without the need for individual species identification. However, inconclusive, or even opposite dependencies between acoustic indices and animal biodiversity found in various studies suggest that their effectiveness is environmentally variable.

Here we examined how three acoustic indices: Bioacoustic Index (BI), Acoustic Complexity Index (ACI) and Acoustic Diversity Index (ADI) predict bird species richness in a species-rich, lowland temperate forest in Europe – the Białowieża Forest. We recorded soundscape in early and late spring at 84 recording points. We analysed 72 1-min sound samples collected per recording point to evaluate how well acoustic indices predict bird species richness from the perspective of a single sound sample, survey and recording point and how they follow the daily pattern of singing activity.

When we compared the values of acoustic indices with the number of bird species detected manually in 1-min sound samples, we found BI to best predict the bird species richness, independently of time in the season but variably across the day, while ACI and ADI showed weaker dependency, variable both seasonally and daily. The correlation between each index and number of bird species was stronger in the early part of the season. Averaged by survey or recording point, the acoustic indices correlated more strongly with the mean compared to the total bird species richness, and provided better estimation of bird biodiversity in the early than the late survey. At the level of the recording point, BI correlated most strongly with mean bird species richness (rho = 0.584), while ADI correlated most strongly with total bird species richness (rho = -0.347). Acoustic indices followed daily bird activity pattern, yet they provided greater values before the peak of the species richness estimated by manual spectrogram scanning and listening to recordings.

In this study acoustic indices correlated moderately to strongly with the bird species richness, providing a useful tool for rapid estimation of bird biodiversity in temperate forests. However, daily and seasonal variation in effectiveness of acoustic indices should be taken into account in the analysis. Using the mean instead of the total number of bird species in comparisons improved the effectiveness of indices but measured different aspects of biodiversity.

1. Introduction

Passive acoustic approaches have been proposed as an alternative to traditional methods of biodiversity assessment and monitoring of terrestrial, marine, and freshwater environments (Todd et al., 2014; Sugai et al., 2019; Desjonquères et al., 2020). This technique should allow for easy and quick collecting of soundscape data in the field and automated data processing in the lab. Indeed, autonomous sound recorders allow for collection of thousands of hours of soundscape recordings in highly standardised way, and their effectiveness in biodiversity estimation is similar to a traditional human-based approach, at least in the case of bird surveys (Darras et al., 2019). However, automatic acoustic data analysis is more challenging than collecting data in the field. Soundscape recordings contain geophysical and anthropogenic noise, which is difficult to separate from biophonic sounds (Pijanowski et al., 2011; Ross et al., 2021). Moreover, biological sounds are extremely variable in complexity, duration, amplitude, and frequency at various levels: between-species, within-species or within-

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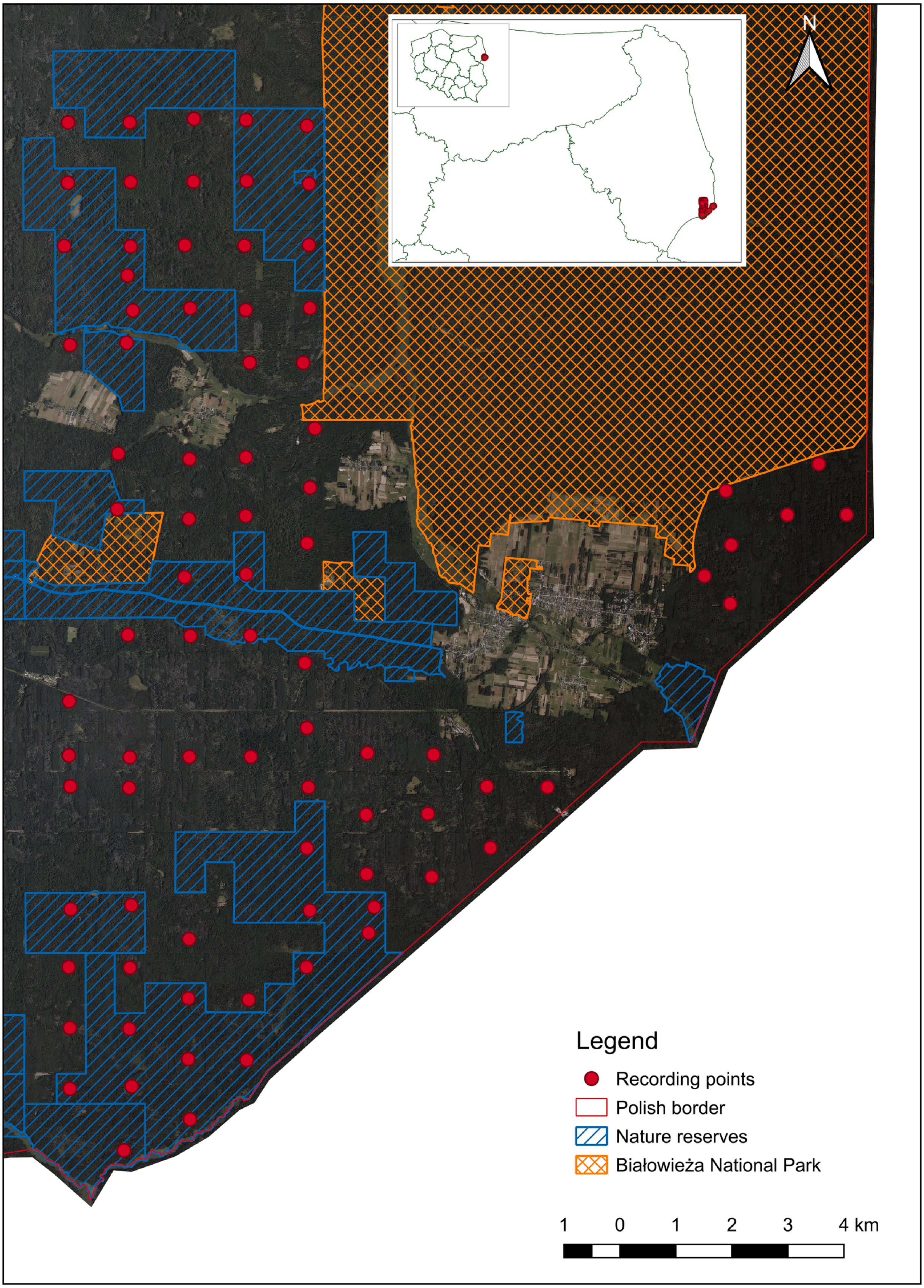

Fig. 1. Distribution of recording points in the Polish part of the Białowieża Forest (Białowieża Forest District).

individual (Catchpole and Slater, 2008). What is more, in nature many individuals of the same or different species vocalise simultaneously, creating endless combinations of possible acoustic events. All these factors make automatic classification of biological sounds from soundscape recordings difficult.

Analysis of soundscape data from the perspective of a single species appears to be the easiest task. Currently it is possible to prepare a well-performing algorithm which will automatically detect the vocalisations of a target species and to use such detections both for behavioural and monitoring purposes (Priyadarshani et al., 2018; Szymański et al., 2021). The challenge arises when the goal of the study is overall biodiversity assessment. The simplest way to obtain species richness from soundscape recordings is manual spectrogram scanning and listening to recordings to identify the vocalising species (Kułaga and Budka, 2019). However, this method is extremely time consuming and difficult to apply, especially in complex environments inhabited by many different vocalising taxa including insects, anurans, birds, and mammals (Ferreira et al., 2018). Therefore, acoustic indices have been proposed as easily applied and rapid measures describing biodiversity of vocalising animals (within-group or α diversity) or comparing dissimilarity between communities inhabiting different areas or their changes over time (between-group or β diversity) without individual species identification (review in: Sueur et al. 2014).

Acoustic indices measure the distribution of energy of acoustic signals in time and/or frequency and assume that, in general, communities with more abundance or higher species richness should produce greater acoustic diversity (Sueur et al., 2008b; Sueur et al. 2014). However, acoustic indices are just mathematical descriptions of acoustic complexity, therefore can be sensitive to other sources of acoustic diversity, such as within- and between-species variation in complexity and intensity of vocalisation, distance between a sound source and microphone, habitat structure or intensity of abiotic sounds (Gasc et al., 2015; Zhao et al., 2019; Ross et al., 2021). Moreover, acoustic indices reflect biodiversity of vocalising animals only, and are unable to catch silent species, while the occasionally vocalising animals affect them very weakly (Gasc et al., 2015; Zhao et al., 2019). Therefore, from a methodological point of view, effectiveness of acoustic indices is evaluated twofold: comparing them with species richness and abundance of only vocalising species recorded in the soundscape (Shamon et al., 2021), or with overall biodiversity and abundance estimated by traditional field surveys (Bradfer-Lawrence et al., 2020). In the second case, two effects—which are difficult to separate—are examined: how biodiversity of vocalising species correlates with overall biodiversity, and how the methods of data collection in the field (recorder vs observer) affect biodiversity estimation.

Recent studies showed that acoustic indices may reflect many biological and ecological characteristics, like species richness, diversity and abundance (Shamon et al., 2021; Alcocer et al., 2022), daily and seasonal changes in vocal activity of animal community (Buxton et al., 2016), or differences in habitat structure (Atemasov and Atemasova, 2019; Shaw et al., 2021). However, inconclusive, or even opposite dependencies between acoustic indices and characteristics of environment have been found. For example, a positive correlation between acoustic indices and bird species richness has been found in some studies when others reported insignificant dependency (review in: Bateman and Uzal 2021). The same acoustic index positively correlated with bird species richness in one study, while in another the dependency was negative (e.g., (Shamon et al., 2021; Bradfer-Lawrence et al., 2020). Moreover, significance of correlation between acoustic indices and bird species richness may change across the day (Dröge et al., 2021) and season (Atemasov and Atemasova, 2019), or vary across different ecological (Eldridge et al., 2018) or sonic conditions (Ross et al., 2021). All these inconsistencies are the result both of huge variability across time and space in vocal behaviour of animal community, which is often difficult to capture in short recording period (Bradfer-Lawrence et al., 2019), but also of various methods applied to examine the effectiveness of acoustic indices. Therefore, methodologically well-grounded studies from different geographical regions, habitats, stages of a season or time of day, and various recording schedules are needed to determine how and in which environmental conditions acoustic indices can be applied successfully for animal biodiversity assessment.

In this study we examined how well acoustic indices predict bird species richness and their spatial and temporal variation in one of the least modified and most species-rich lowland temperate forests in Europe – the Białowieża Forest (Wesołowski, 2007; Wesołowski et al., 2015). From the acoustic point of view, the study site can be characterised by dominant biotic vocalisations generated by birds and marginal effect of anthropogenic noise. Therefore, we assumed that acoustics indices should be unaffected by anthropogenic noise and directly reflect bird biodiversity. Large variety of forest types within the study area should shape spatial diversity of bird communities. We predict that this spatial variation in species composition should also be reflected in acoustic structure of soundscape. Most bird species in Białowieża forest are long- or short-distance migrants, which arrive and breed at different stages of the season (Wesołowski et al., 2015) and show short but noticeable seasonal peaks of vocal activity. The species-specific breeding phenology and daily activity, combined with varying song complexity among species should create seasonal and daily variable patterns of acoustic complexity of soundscape.

We recorded soundscape in early and late spring in each of the 84 recording points and used 1-min sound samples to examine: (1) whether acoustic indices correlate with manually determined breeding bird species richness from the perspective of a single sound sample, survey and recording point; (2) how averaged values of acoustic indices for survey and recording point improve bird species richness estimation; (3) whether acoustic indices reflect changes in daily pattern of bird activity.

2. Methods

2.1. Study site

The study was conducted in Białowieża Forest - one of the least modified lowland forests in Europe, protected as UNESCO Biosphere Reserve (Wesołowski, 2007). Our study area was in the middle of this large (1,450 km^2) forest complex and covered 120 km^2 within the territorial range of the Białowieża Forest District (Fig. 1). The average forest age within Białowieża Forest District is estimated to be 90 years, but forest over 140 years old covers 27 % of the study area. Most of the forest is under extensive management (65 %) while the rest (35 %) is protected in reserves. The dominant tree species are spruce *(Picea abies)*, pine *(Pinus sylvestris)*, common oak *(Quercus robur)*, Norway maple *(Acer platanoides)* and silver birch *(Betula pendula)*. Białowieża Forest is characterised by multi-storey profile of stands, huge variability of forest types, large amount of deadwood and uprooted trees, diverse plant and animal community. The climate is subcontinental, with the mean annual temperature 7.3 °C (from 5.9 °C to 9.2 °C) and precipitation 625 mm (data for the period from 1985 to 2015; Boczoń et al., 2018). Most of the breeding bird species in Białowieża Forest are migrant, with the breeding season ranging from the beginning of April to the end of June, however seasonal peaks in breeding activity are species-specific (Wesołowski et al., 2015).

2.2. Soundscape recording

We recorded soundscape in 84 randomly chosen recording points within the territorial range of Białowieża Forest District (Fig. 1; S1Dataset). The points were located both in protected and unprotected areas. We used ten Song Meter SM3 acoustic recorders (Wildlife Acoustics) with built-in omnidirectional microphones SMM-A1 (sensitivity −11 +/- 4 dB; signal-to-noise ratio greater than 68 dB) calibrated using sound level calibrator (VOLTCRAFT SLC-100). At each point, we left the recorder for one morning, then moved it to another point. We recorded the soundscape in wav file format (16-bit, 48 kHz sampling rate, low and high frequency filters off, gain 24 dB). Each time we placed recorders on the same tree, 8 m above ground, with the microphone directed west. We collected soundscape recordings under normal weather conditions, acceptable for surveying birds by human-observers (no strong wind or heavy rain). Previous studies showed that detection distance of songbird songs by autonomous sound recorders should range between 100 and 150 m (Yip et al., 2017). The distance between neighbouring recording points in our study ranged from 470 m to 1,180 m. Therefore, probability of recording the same individual from different points was marginal.

We recorded soundscape twice at each recording point: during one day in early survey (from April 20 to May 02, 2021) and during one day in late survey (from May 18 to May 26, 2021). These periods correspond to the methodology of common birds monitoring in Poland and enable detection of early and late breeding species. In each recording point we recorded six hours of soundscape: from two hours before sunrise to four hours after sunrise (averaged sunrise time for the study site: April 20 – 05:15; May 18 – 04:23; local time), to detect both diurnal and nocturnal species. All recorders worked correctly, and we did not have gaps in soundscape data.

2.3. Acoustic analysis

In each survey we analysed 36, 1-min sound samples per recording point (1-min every ten min of soundscape recording, first sound sample beginning two hours before sunrise). Sound samples were analysed by manual spectrogram scanning and listening to recordings by three observers (AM, ES, MB; each observer analysed 1/3 of whole dataset) in Raven Pro 1.6.1 software (Cornell Lab of Ornithology) with the following settings: Window = Hamming, window size = 23.1 ms, Overlap = 75 %. In each 1-min sound sample we classified each breeding vocalisation—i.e., songs in songbirds, vocalisations used for mate attraction and territory defence in other birds, such as territorial calls of owls, drumming of woodpeckers—to the species. In this way we obtained lists of bird species recorded in each of the 6,048 1-min sound samples (36 × 1-min sound sample × 84 recording points × 2 surveys per point). All 1-min sound samples used in this study are available in a public data repository at https://doi.org/10.5061/dryad.zcrjdfnhc.

2.4. Acoustic indices

We applied three acoustic indices which are commonly used for bird species richness and abundance estimation. We calculated acoustic indices in Kaleidoscope Pro 5.4.7 software (Wildlife Acoustics).

Bioacoustic Index (BI).

The bioacoustic index measures the area under the log amplitude spectrum curve in the recording and originally has been applied to estimate relative bird abundance and species composition (Boelman et al., 2007). However recent studies showed that BI can be successfully applied to the bird species richness estimation (Fuller et al., 2015; Bradfer-Lawrence et al., 2020). Originally, BI has been calculated for frequency range between 2 and 8 kHz. We adjusted the frequency range of BI to fit the vocalisations of species expected in Białowieża Forest and set minimal frequency (F_{min}) to 500 Hz (which corresponds with calls of pigeons) and maximal frequency (F_{max}) to 10,000 Hz (songs and calls of tits). To balance between accuracy in temporal and spectral resolution we applied FFT (fast Fourier transformation) of 1,024 samples.

Acoustic Complexity Index (ACI).

The acoustic complexity index initially has been applied to measure bird song complexity, however recent studies showed that ACI also correlates with bird biodiversity and abundance (Pieretti et al., 2011). The ACI calculates the absolute difference in sound intensity between two adjacent cells of temporal and frequency matrix, then averages and sums them for the recording (Pieretti et al., 2011). Calculating ACI, we applied the same frequency range as in BI (F_{min} = 500 Hz; F_{max} = 10,000 Hz). To minimise the effect of varying distances between the microphone and singing birds in the soundscape recordings we set the J parameter to 5 s, meaning that before the calculation of final ACI for a recording, the ACI was averaged for each five-seconds subsample and then averaged for whole 1-min sound sample (Fuller et al., 2015).

Acoustic Diversity Index (ADI).

Acoustic diversity index is focused on occupancy of signal above a predefined threshold in frequency bins and applies the Shannon index (Pijanowski et al., 2011; Villanueva-Rivera et al., 2011). The ADI ranges from zero to the natural log of the number of bins (noise or silence across all frequency bins will give high values while complex songs that span a wide range of frequency should generate lower values; Bradfer-Lawrence et al., 2020). In the study we applied frequency ranges for ADI from 500 Hz to 10,000 Hz, 500 Hz frequency step and −50 dB threshold.

2.5. Statistical analysis

First, we examined how acoustic indices (BI, ACI, ADI) predict bird species richness in 1-min sound samples. To do this we constructed three independent generalized linear mixed models (GLMM) in which as a dependent variable we used the acoustic index and as fixed effects: number of bird species detected manually, survey (early or late), time of day (continuous variable). Because effectiveness of acoustic indices may vary depending on time of day or season, we also included 2-ways interactions in the model: number of bird species*survey and number of bird species*time of day. We specified crossed random effect (recording point ID*survey) and fitted the data using normal distribution and identity link function (BI, ACI) or gamma distribution and log link function (ADI). Additionally, to evaluate the strength of dependency between acoustic indices and number of bird species determined by manual spectrogram scanning in each 1-min sound sample we calculated Spearman's rank correlation for the whole dataset, and separately for early and late surveys.

Because increasing the sampling rate should stabilize the index and better correlate with bird species richness (Bradfer-Lawrence et al., 2019), we constructed three additional GLMMs in which as a dependent variable we used mean index for survey (early and late) or recording point. As fixed effects we specified the total or mean number of species detected manually (continuous variable). As total number of bird species per survey or per recording point we defined all bird species detected manually in 36 1-min sound-samples analysed in survey or in 72 1-min sound-samples analysed during early and late survey at recording point, respectively. We calculated the mean number of bird species per survey or per recording point by summing the number of bird species detected in each 1-min sound sample and dividing it by 36 sound samples analysed in a single survey or 72 sound samples analysed in both surveys at recording point, respectively. Models with number of bird species detected during survey also contained survey as a categorical effect, and interaction between number of species and survey and recording point ID as a random effect. To checked which of the predictor—the total number of bird species or the mean number of bird species—explain the acoustic index better, we used corrected Akaike Information Criterion (AIC) and chose the model with lower AIC value (Burnham and Anderson 2002). Additionally, we calculated Spearman's rank correlation between averaged indices and mean and total number of bird species detected manually. We visually checked monotonic relationship between species richness and values of acoustic indices.

To determine how well acoustic indices follow daily changes in bird species richness we calculated Spearman's rank correlation between the number of manually detected bird species and each acoustic index in 1-min sound samples for each survey conducted at recording point separately. In this way we obtained 168 correlation coefficients (84 for early and 84 for late session) for each acoustic index. Then we applied Friedman test for several related samples. Because we analysed strength of dependency as dependent variable, we used absolute values of Spearman's coefficients (BI vs ACI, BI vs ADI, ACI vs ADI). We conducted

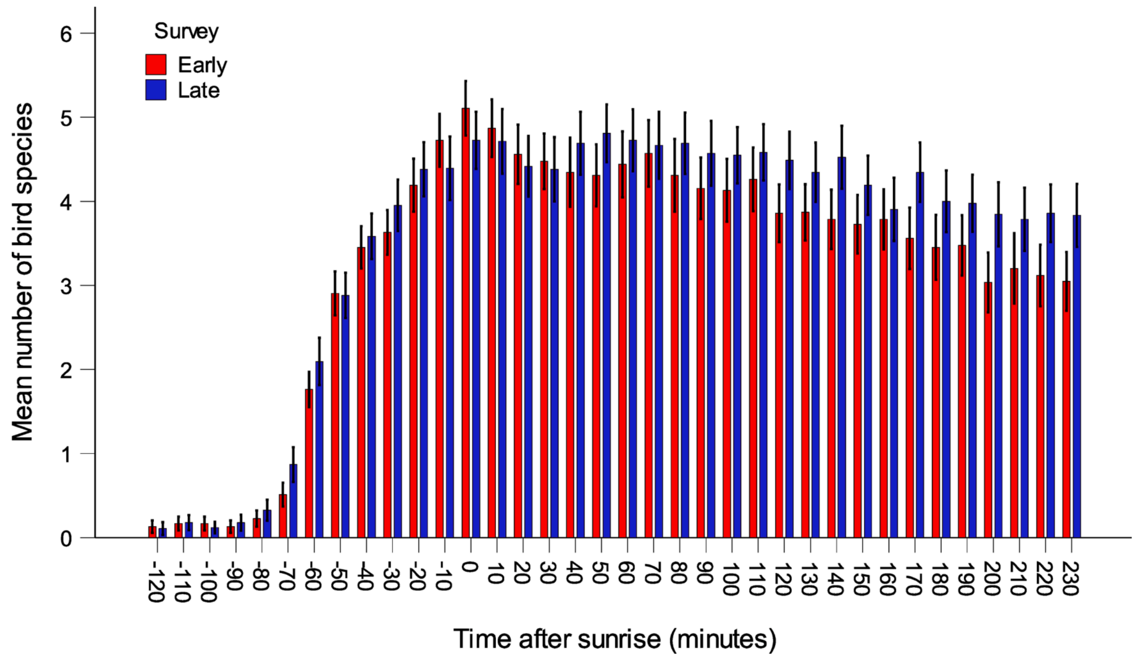

Fig. 2. Daily changes in mean (95% confidence interval levels) number of bird species per recording point detected by manual spectrogram scanning and listening to 1-min sound samples in relation to sunrise. Figure based on total 6,048 1-min sound samples recorded in early (red bars) and late (blue bars) surveys. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Results of GLMM examining how acoustic indices reflect bird species richness, season, and time of day. In the models we used the acoustic index as a dependent variable, and the number of manually detected bird species in 1-min sound sample, survey (early or late), time of day (continuous variable) as fixed factors.

	Coefficient	SE	t	p
	Bioacoustic Index (BI)			
Intercept	30.319	2.725	11.125	<0.001
Number of species	20.892	0.399	52.340	<0.001
Survey [early]	−19.915	3.738	−5.328	<0.001
Time of day	1.778	0.066	27.059	<0.001
Number of species*Season [early]	0.627	0.371	1.690	0.091
Number of species*Time of day	−0.564	0.019	−29.249	<0.001
	Acoustic Complexity Index (ACI)			
Intercept	1456.014	4.997	291.366	<0.001
Number of species	22.024	0.850	25.896	<0.001
Survey [early]	−12.195	6.776	−1.800	0.072
Time of day	2.077	0.140	14.856	<0.001
Number of species*Season [early]	8.008	0.780	10.142	<0.001
Number of species*Time of day	−0.610	0.041	−14.858	<0.001
	Acoustic Diversity Index (ADI)			
Intercept	0.036	1325.897	0.001	0.999
Number of species	−0.012	0.001	−20.441	<0.001
Survey [early]	1.045	1325.897	0.001	0.999
Time of day	−0.001	0.001	−8.217	<0.001
Number of species*Season [early]	0.001	0.001	2.372	<0.05
Number of species*Time of day	0.001	0.001	11.964	<0.001

separate analyses for early and late surveys. To examine which pairs of variables differ significantly from each other we conducted post-hoc pairwise Wilcoxon tests and applied Bonferroni correction for multiple comparisons.

All statistical analyses were conducted by using IBM SPSS Statistics 27 software. All p-values are two tailed. See S3Models for detailed description of statistical analyses.

3. Results

3.1. Avian species richness

Manual spectrogram scanning and listening to 6,048 1-min sound samples allowed 20,591 detections of presence of 65 bird species (see S1Dataset for the full list of detected bird species). On average in a 1-min sound sample we detected 3.40 ± 2.13 species (range from 0 to 11 species). The number of species recorded in a 1-min sound sample was significantly higher (Mann-Whitney test: $Z = -5.370$; $p < 0.001$) in late (3.50 ± 2.15) than early survey (3.26 ± 2.11) and varied across a day, with the highest values observed 10 min after sunrise (4.92 ± 1.54) (Fig. 2). The correlation between the total number of species recorded at recording point in survey and the maximal number of species detected during 1-min sound sample with the highest number of species was moderate and significant (rho = 0.666, $p < 0.001$). The most common species, the Common chaffinch *(Fringilla coelebs)* was observed in 47 % of 1-min sound samples, nine species were observed in more than 10 % and 26 in more than 1 % of 1-min sound samples (S2Figure).

3.2. Acoustic indices and bird species richness in 1-min sound samples

All acoustic indices predicted bird species richness in 1-min sound

Table 2
Spearman's rank correlation coefficients between acoustic indices and bird species richness. The correlation was calculated separately for early and late recording session. The *** indicates $p < 0.001$, **<0.01, *<0.05.

	BI	ACI	ADI
Mean recording point	0.584**	0.457*	−0.557**
Total recording point	0.330**	0.234*	−0.347**
Mean early survey	0.602***	0.512***	−0.456***
Total early survey	0.443***	0.333***	−0.325**
Mean late survey	0.228*	0.166	−0.328**
Total late survey	0.053	0.131	−0.199
1-min early survey	0.683***	0.621***	−0.549***
1-min late survey	0.514***	0.446***	−0.513***
1-min early and late survey	0,600**	0,530**	−0,538**

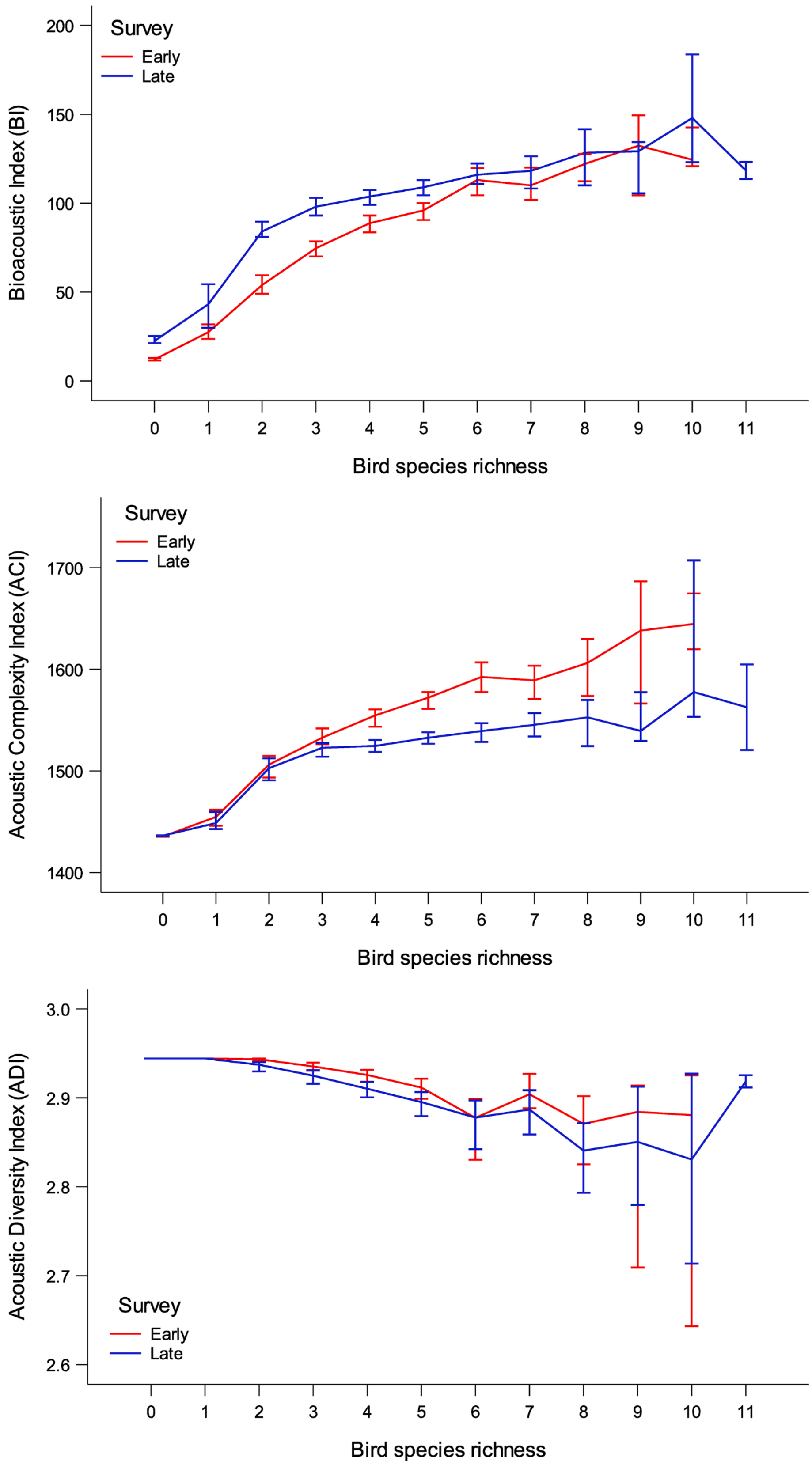

Fig. 3. Relationship between Bioacoustic index (BI), Acoustic Complexity Index (ACI), Acoustic Diversity Index (ADI) and bird species richness in 1-min sound samples calculated separately for the early (blue) and late (red) survey. Median values and 95% confidence interval levels are given. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Results of GLMM examining how acoustic indices predict mean and total number of bird species detected in early and late survey. In the case of each index, the best fitted model contained the mean rather than the total number of bird species.

	Coefficient	SE	t	p
	Bioacoustic Index (BI)			
Intercept	83.442	9.064	9.206	<0.001
Mean number of species	3.105	2.468	1.258	0.210
Survey [early]	−59.444	11.915	−4.989	<0.001
Mean number of species*Season [early]	12.515	3.401	3.680	<0.001
	Acoustic Complexity Index (ACI)			
Intercept	1511.641	17.188	87.949	<0.001
Mean number of species	4.108	4.692	0.876	0.383
Survey [early]	−59.716	23.129	−2.582	<0.05
Mean number of species*Season [early]	22.442	6.579	3.411	<0.001
	Acoustic Diversity Index (ADI)			
Intercept	1.068	0.011	99.187	<0.001
Mean number of species	−0.006	0.003	−2.092	<0.05
Survey [early]	0.018	0.014	1.225	0.222
Mean number of species*Season [early]	−0.003	0.004	−0.790	0.431

Table 4
Results of GLMM examining how acoustic indices predict mean and total number of species detected at recording point. In the case of each index, the best fitted model contained the mean rather than the total number of bird species.

	Coefficient	SE	t	p
	Bioacoustic Index (BI)			
Intercept	27.611	9.381	2.943	<0.01
Mean number of species	16.771	2.699	6.213	<0.001
	Acoustic Complexity Index (ACI)			
Intercept	1463.987	16.037	91.286	0,000
Mean number of species	20.088	4.615	4.353	<0.001
	Acoustic Diversity Index (ADI)			
Intercept	1.098	0.010	107.570	<0.001
Mean number of species	−0.014	0.003	−4.793	<0.001

samples and differed significantly with time of day. Only BI was significantly lower during the early than the late survey. We also found that all indices predicted bird species richness differently depending on time of day, while ACI and ADI also predicted bird species richness differently in early and late survey (Table 1). We found consistent correlation pattern between number of manually detected bird species in 1-min sound samples and acoustics indices. Independently of survey, we observed moderate or strong significant positive correlation between bird species richness and BI and ACI and negative correlation between bird species richness and ADI. The correlations were stronger in the early than in the late survey (Table 2, Fig. 3).

3.3. Averaged acoustic indices for survey and recording point

All GLMMs with averaged acoustic indices for survey contained mean number of species detected in 1-min sound samples instead of the total number of species detected during the survey (Table 3). However, only ADI correlated significantly with the mean number of species, did not differ between early and late survey and explained the mean number of species independently of time in the season. In the case of BI and ACI we found significantly lower values of indices in early compared to late survey and significant interaction between survey and the mean number of species, meaning that BI and ACI predicted mean species richness differently in early and late survey but failed to predict it when both surveys are analyzed together (Table 3) (Table 4).

Spearman's rank correlation analysis also revealed that averaged acoustic indices for single survey or both surveys at recording point correlated more strongly with the mean number of bird species than with the total number of bird species. The correlations were stronger in early than in late survey (Table 2). When looking at the recording point, the averaged acoustic indices were also better at predicting the mean number of species than the total number of species (Table 2). The Spearman's rank correlation coefficient between the mean and the total number of bird species recorded at point was significant and moderate ($r = 0.552$; $p < 0.001$).

3.4. Acoustic indices and daily vocal activity

Friedman tests showed that acoustic indices reflected daily changes in bird species richness differently in the early ($X^2 = 58.167$, $df = 2$, $p < 0.001$) and late surveys ($X^2 = 12.198$, $df = 2$, $p = 0.002$) (Fig. 4). During the early survey BI (mean rho = 0.60, SD = 0.112) described daily changes in bird species richness significantly better than ADI (mean rho = 0.45, SD = 0.154; Wilcoxon test: Z = -6.987, $p < 0.001$) and ACI (mean rho = 0.57, SD = 0.142; Wilcoxon test: Z = -2.738, $p = 0.006$), while ACI was better than ADI (Wilcoxon test: Z = -5.131, $p < 0.001$). In the late survey the BI (mean rho = 0.52, SD = 0.158) described daily changes in bird species richness significantly better than ADI (mean rho = 0.46, SD = 0.163 Wilcoxon test: Z = -3.240, $p < 0.001$) but not better than ACI (mean rho = 0.49, SD = 0.169; Wilcoxon test: Z = -2.481, $p < 0.013$). The effectiveness of ACI and ADI in estimating daily changes in bird species richness did not differ significantly (Wilcoxon test: Z = -2.232, $p = 0.026$; insignificant after Bonferroni correction).

4. Discussion

Our study showed that BI, ACI and ADI correlate with moderate strength (rho ranged from 0.446 to 0.683) with temperate forest bird species richness detected on 1-min sound samples. The BI correlated with bird species richness the best, independently of the time in season, while ACI and ADI showed weaker correlation with additional seasonal variation. The correlation between the number of bird species detected manually in sound samples and each index was lower in the late than in the early survey. Moreover, similarly to other studies (e.g., Villanueva-Rivera et al., 2011; Fuller et al., 2015), all acoustic indices reflected daily changes in the number of vocalizing species, but the BI performed the best. It is worth noting that the highest value of each index was observed 20–40 min before the time in which we manually detected the greatest number of bird species in 1-min sound sample, suggesting that indices are affected more by the number of singing individuals than the number of singing species, or that some early singing species affect indices more than others (Gasc et al., 2015; Buxton et al., 2016). Both explanations are possible, since acoustic indices describe complexity of soundscape, therefore more species or individuals vocalizing in the same sound sample (i.e. general higher abundance of sounds) should generate more complex soundscape, and greater index value (Sueur et al., 2008a; Fuller et al., 2015).

Many studies reported positive correlations between bird species richness and BI and ACI (e.g., (Boelman et al., 2007; Hilje et al., 2017; Eldridge et al., 2018) and negative between bird species richness and ADI (e.g., Eldridge et al., 2018; Bradfer-Lawrence et al., 2020), however strength of correlation varied considerably between the studies and locations (e.g., Bateman and Uzal 2021). Sound samples contain various numbers of songs produced by different number of individuals belonging to various species. Birds show considerable within-individual, between-individuals and between-species variation in song complexity (review in: Catchpole and Slater, 2008). In consequence, different species, individuals or even the same individual singing different song types will generate various complexities of soundscape. Therefore, we should not expect extremely strong correlation between number of vocalizing species and acoustic indices but consider acoustic indices as an approximation of species richness (Alcocer et al., 2022).

Our results showed that effectiveness of acoustic indices in bird species richness estimation varies daily (BI, ACI, ADI) and seasonally

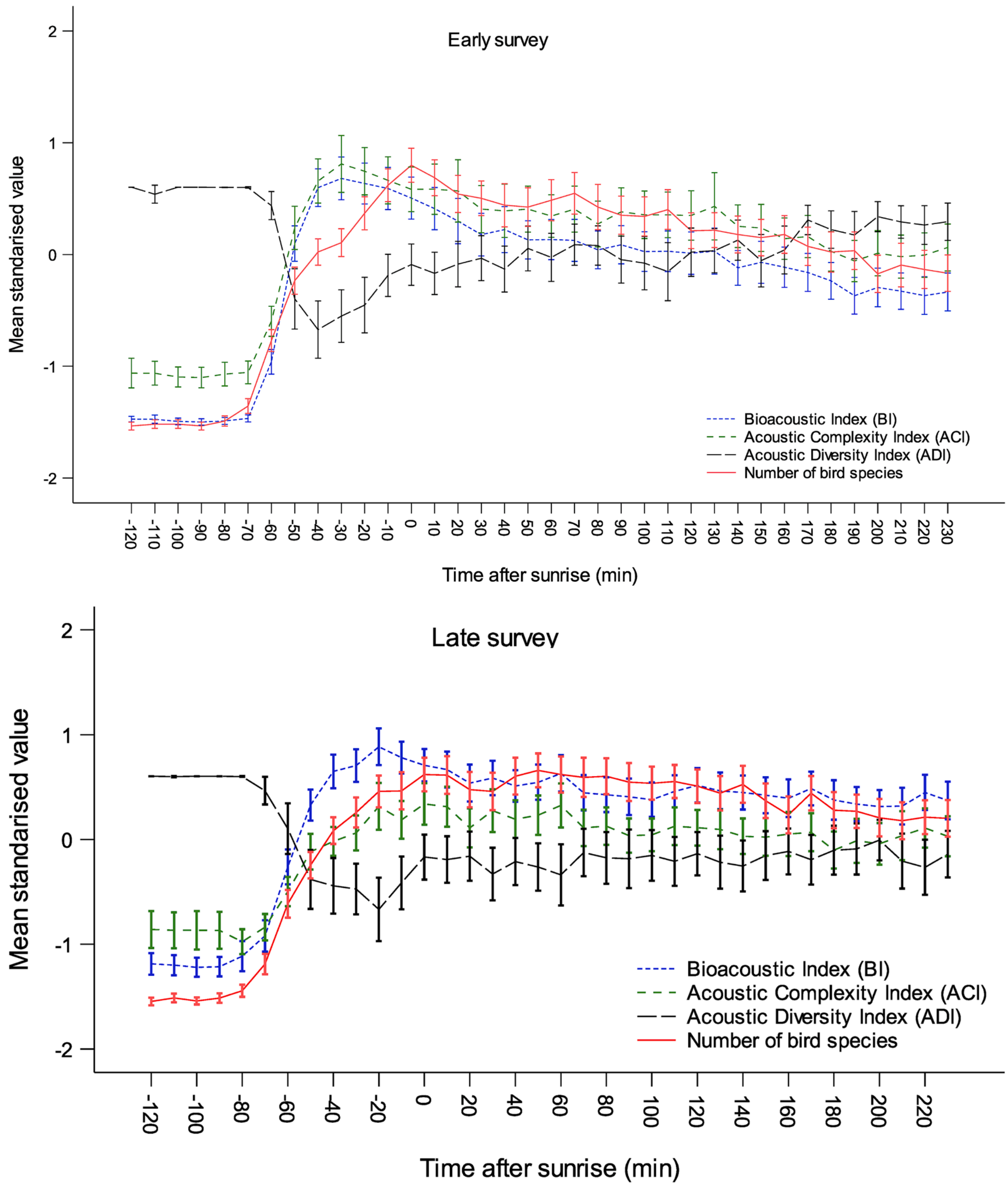

Fig. 4. Daily changes in standardised acoustic indices (BI, ACI, ADI) and bird species richness during early and late survey. Mean values ± 95 % confidence interval levels are given. Both in early and late survey BI reflects bird species richness significantly better than ACI and ADI.

(ACI and ADI) even in the same study site and at relatively short intervals between surveys. We suggest that such pattern is related to different species composition singing at different times of day (daily singing activity pattern is species-specific; (Thomas et al., 2002)), species-specific phenology of breeding in temperate regions (various species breed and sing in different times of year; (Dunn and Møller, 2014)) and species-specific effects of produced sound on the acoustic indices (Gasc et al., 2015; Zhao et al., 2019; Shamon et al., 2021). Therefore, before using acoustic indices for bird species richness estimation and its changes we recommend evaluating them not only within a study site (Bateman and Uzal, 2021) but also over the day and season in order to avoid misleading results.

The 1-min sound samples analysed from the recording points are random acoustic events characterized by high variation. Therefore, averaging many such events should stabilize variation of an acoustic index, leading to a more accurate prediction of bird species richness (Bradfer-Lawrence et al., 2019). When we averaged the acoustic indices for survey (36 × 1-min sound sample) or recording point (72 × 1-min sound sample) and compared them to the total or the mean number of bird species detected manually, we observed a decrease of correlation with all indices, or even insignificant correlations in some comparisons in late survey. Moreover, correlation was stronger when the mean instead of the total number of bird species was used in the comparison. Finally, the mean bird species richness at recording point correlated most strongly with BI (rho = 0.584), while the total bird species richness with ADI (rho = 0.-347). These two measures of bird biodiversity are used in various studies to evaluate the effectiveness of acoustic indices even though they describe different aspects of biodiversity: how stable is the number of species singing at the same time (BI) vs how high is the total biodiversity (ADI). We found moderate Pearson correlation coefficient between the mean and the total number of bird species recorded at point, thus studies including total and mean number of species should be compared with great care.

Regardless of using the total or mean number of bird species detected at recording point, we found moderate to strong correlations with acoustic indices, which is rare in ecological studies. Usually the average effect size measured by Pearson correlation ranges between $r = 0.180$ and 0.193 (Møller and Jennions, 2002). Our results are similar to those obtained for other temperate locations (Eldridge et al., 2018), suggesting that high correlations between acoustic indices and bird species richness could be specific to environments, where anthropogenic noise is low and birds are the main source of biophonic sounds, while vocalisations by other animals such as insects, mammals or amphibians are extremely rare. However, to make more general conclusions we still need comparable studies showing how acoustic indices works under various environmental conditions.

Studies evaluating usefulness of acoustic indices in estimating species richness applied various methodological approaches and effort, used different sound sample duration or recorded at various times of day (e.g., (Eldridge et al., 2018; Jorge et al., 2018; Bradfer-Lawrence et al., 2020; Dröge et al., 2021), making direct studies comparisons difficult. Here we examined directly how acoustic indices reflect vocalizing bird species richness obtained by manual spectrogram scanning and listening to the same recordings for which acoustic indices were calculated. Moreover, we analysed sound samples from two hours before to four hours after sunrise, which should allow us to capture virtually all bird species vocalizing during the recording day. Such approach enables us to evaluate effectiveness of acoustic indices only, and eliminate potential biases related to various methodological approaches applied to measure bird species richness in the field (e.g., skills of field observers, weather conditions, time effort, time of day and season when surveys are conducted). The key limitation of our study is that we did not measure species abundance. Therefore, we are not able to separate the effect of species richness and species abundance on the acoustic indices.

5. Conclusions

We demonstrated that acoustic indices correlate moderately to strongly with the bird species richness and can be used as a tool for rapid estimation of bird biodiversity in temperate forests. This can be applied to a single sound sample, as well as survey or recording point. However, effectiveness of acoustic indices in bird biodiversity estimation varied daily and seasonally, which should be included in studies applying acoustic indices to bird biodiversity estimation. Using the mean rather than the total number of bird species in the comparisons improved the effectiveness of indices, however these two variables measured different aspects of biodiversity. Analysis of daily patterns showed that acoustic indices followed bird singing activity, however provided greater values before the peak of the species richness estimated by manual spectrogram scanning and listening to recordings. Results of the study suggests that rapid bird species richness estimation is possible by acoustic indices in temperate forests. However more detailed studies are needed to examine how bird abundance and phylogenetic diversity affect acoustic indices.

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.

Data availability

Dataset is included as a supplementary material. Original recordings of 1-min sound samples are available at: https://doi.org/10.5061/dryad.zcrjdfnhc

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110027.

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