

Acoustic indices enable the discrimination of temperate forest types and better predict differences in bird species composition than in bird species richness

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ABSTRACT

Acoustic indices have been proposed as a tool to estimate animal biodiversity and abundance, as well as habitat types and vegetation structure. However, recent studies have reported inconsistent relationships between acoustic indices and environmental metrics. In this study, we recorded soundscapes across different forest types and calculated six of the most commonly used acoustic indices to evaluate their effectiveness in predicting bird species richness, bird community composition and temperate forest characteristics.

We observed that bird species richness did not significantly differ between forest types, soil moisture, forest age, the Normalized Difference Vegetation Index (NDVI), the area covered by standing dead trees, or forest protection. In contrast, acoustic indices showed significant differences between forest types, soil moisture levels, forest age, and NDVI. In general, acoustic complexity increased with the progression of forest productivity and moisture, was the lowest in the youngest forests, decreased with increasing NDVI, did not differ between protected and unprotected areas, and was not affected by the amount of standing dead trees. The dissimilarity of the acoustic structure of the environment correlated more strongly with dissimilarity of bird community composition than with bird species richness, but it best explained the differences in forest characteristics obtained from satellite data. These correlations were weak, in contrast to the moderate dependency observed between differences in bird community composition and satellite data describing forest characteristics.

Our study revealed that in temperate forests, soundscape enables discrimination between forest types, based on productivity, moisture, or age. Furthermore, the acoustic structure of the environment better explains differences in characteristics of the forest obtained from satellite data than differences in bird community composition or bird species richness. This suggests that soundscape complexity depends on forest characteristics and is shaped by species richness, community composition, and the abundance of individual bird species. Therefore, the soundscape can serve as an indicator of temperate forest quality and disturbance levels.

1. Introduction

The passive acoustic approach has been proposed as an easy-to-apply, quick, and effective method for estimating animal biodiversity and abundance (Celis-Murillo et al., 2009; Darras et al., 2019; Sugai et al., 2019a; Pérez-Granados and Traba, 2021). This technique comprises two parts: collecting soundscape recordings in the field using autonomous sound recorders and analysing bioacoustic data in the lab (Villanueva-Rivera et al., 2011; Sugai et al., 2019b). With the current

level of technological development, it is now possible to achieve near-continuous recording of soundscapes. However, analysing large acoustic datasets remains a challenge. Manual spectrogram scanning and listening to recordings to detect and identify all vocalizing species are extremely time-consuming tasks and impossible to implement on a large scale (Kulaga and Budka, 2019). While the field of automatic signal detection and classification is rapidly developing, the current widely available tools are still insufficient for estimating overall biodiversity (Priyadarshani et al., 2018). Although biodiversity is essential for

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ecosystems stability and resilience, ensures maintenance of ecological networks and also provides benefits to economy (Singh, 2002; Bisht et al., 2023; Fartyal et al., 2022), it is frequently expensive and time consuming to reliably assess the status of biodiversity. Therefore, acoustic indices, which measure the complexity of entire soundscapes, have been proposed as an automatic and rapid method for approximating biodiversity and abundance without the need for species classification thus minimizing cost and time (Sueur et al., 2008b; Pijanowski et al., 2011b). The use of acoustic indices is based on the assumption that vocalizing animals reflect overall biodiversity and that ecosystems with higher species richness or abundance generate more complex soundscapes than simpler ones (Sueur et al., 2008b, 2014).

Recent studies have shown that the dependencies between acoustic indices and species richness or abundance are not as straightforward as expected and may vary across ecological conditions (Eldridge et al., 2018; Pan et al., 2024). Moreover, applying the same indices in different locations has produced inconsistent results in terms of biodiversity estimation (Buxton et al., 2018; Bateman and Uzal, 2021; Alcocer et al., 2022), with better predictive power observed at higher latitudes. This inconsistency may be due to several factors, including the presence of geophonic and anthropogenic sounds (Hyland et al., 2023), variations in methods for estimating biodiversity and calculating acoustic indices (e.g., Bradfer-Lawrence et al., 2020; Alcocer et al., 2022; Budka et al., 2023) or differences in the complexity of vocalisations among animal species (Catchpole and Slater, 2008). The first two technical limitations can be addressed by filtering out or eliminating recordings polluted by noise and by rigorously standardizing field and analytical methods (Ross et al., 2021; Bradfer-Lawrence et al., 2023). The last factor, however, requires more attention from researchers. Animal biodiversity and abundance increase from the poles to the equator, as do the taxonomic components of biophony (Willig and Presley, 2017). For instance, in higher latitudes, only birds and mammals vocalize, while closer to the equator, the biophony is enriched by additional groups such as amphibians and insects (Robert et al., 2019). Additionally, the evolution of acoustic signals is influenced by the environment (the acoustic adaptation hypothesis (Morton, 1975)) and by acoustic interference from biotic and abiotic sound sources (the acoustic niche partitioning hypothesis (Krause, 1993)). Therefore, differences in acoustic structures among various environments should be expected both at macrogeographic and local scales (Pijanowski et al., 2011a; Do Nascimento et al., 2020). On the other hand, considering acoustic space as a resource that must be shared by all vocalizing animals in an environment, and acknowledging that some species produce simple vocalizations while others produce highly complex ones, we might assume that different species compositions, or numbers of species could generate similar soundscape complexity (Gasc et al., 2015).

Acoustic indices have been applied with varying degrees of effectiveness to predict habitat types and vegetation structure (e.g., Farina and Pieretti, 2014; Fuller et al., 2015; Do Nascimento et al., 2020; Chen et al., 2021). Such studies usually compare habitats that differ significantly from each other, such as open areas versus forests (Gómez et al., 2018; Do Nascimento et al., 2020). However, even in seemingly homogeneous environments, variations in microhabitats can lead to differences in species richness, abundance, and community composition, which should be reflected in soundscape variability. Moreover, the acoustic structure of an environment has been proposed as an indicator of ecosystem quality and condition (Tucker et al., 2014; Gómez et al., 2018). Given the rapid changes in habitats and the need for effective monitoring, it is crucial to identify an indicator capable of distinguishing between subtly different habitats and detecting environmental disturbances at an early stage. The acoustic structure of the environment has emerged as a promising candidate for such an indicator for two reasons: first, it may reflect differences in species richness, community composition and the abundance of vocalizing species across habitats (with more abundant and species-rich ecosystems likely generating more complex acoustic environments); second, according to the acoustic

niche partitioning hypothesis, stable ecosystems are expected to exhibit more even acoustic structures than disturbed ones. Unfortunately, the question of how accurate and precise acoustic indices are in distinguishing between different habitats and the disturbances within them remains open.

In this study, we examined differences in soundscapes between various types of protected and unprotected temperate forests, where birds are the primary source of biological sounds. We assumed that the bird community composition and abundance of individual bird species would vary depending on forest type (Wesolowski et al., 2015). We also expected that these variations would be reflected in the acoustic structure of the environment – more diverse and abundant bird communities should produce more complex soundscapes. Since similar levels of species richness could arise from different bird community compositions, we predicted that acoustic structure similarity between the environments would correlate more strongly with bird community composition than with overall species richness. Ultimately, the main goal of our study was to assess the usefulness of acoustic indices in predicting forest characteristics, bird species richness, and bird community composition in one of the least human-modified lowland temperate forests — the Białowieża Forest.

2. Methods

2.1. Study site

We conducted our study in Białowieża Forest (eastern Poland; central coordinates 52.70°N 23.90°E), a large complex covering approximately 1500 km² of lowland (from 140 to 200 m a.s.l.) temperate, mixed-deciduous forest that has been relatively unchanged by human activity. The Białowieża Forest is characterized by extensive undisturbed areas where natural processes continue, as well as old-growth tree stands, a high proportion of deadwood, and overall high biodiversity (Jaroszewicz et al., 2019). The Białowieża Forest is a UNESCO Biosphere Reserve, protected as a NATURA 2000 area (both as a Special Protection Area for birds and a Special Area for Conservation for habitats), and is part of a transboundary UNESCO World Heritage Site. Around 35% of the Polish part of Białowieża Forest remains under various protection regimes (Białowieża National Park, partly and strictly protected reserves (Czerepko et al., 2021)). The remaining part of the forest is managed by the Polish State Forests, with varying intensities of logging. The climate of the Białowieża Forest can be classified as temperate continental, cool with an Atlantic influence. The average annual temperature is approximately 6.7 °C. The warmest month is July (17.7 °C), and the coldest is January (-4.4 °C). Winter is relatively long, with snow cover lasting for about 85 days per year. The growing season lasts around 205 days, and the average annual precipitation is 637 mm (Boczoń and Salachewicz, 2022). The main sources of biotic sounds are birds (approximately 250 species) that vocalize intensively during the breeding season (from the beginning of April to the middle of June (Wesolowski et al., 2015)). The Białowieża Forest is home to 13 amphibian, 7 reptile, 59 mammal, and 12,000 invertebrate species. Anthropogenic noise is limited to the villages and two main roads crossing the Białowieża Forest.

2.2. Soundscape recording

We randomly selected 83 recording points distributed throughout the Białowieża Forest District (south-eastern part of the Polish Białowieża Forest; 12,500 ha). These recording points were located in both protected (partly and strictly protected reserves; 31 recording points) and unprotected areas (52 recording points; Fig. 1). The distance between neighbouring recording points ranged from approximately 500 m to 1000 m, minimizing the chance of recording the same individual from different points (Winiarska et al., 2024). We deployed 10 Song Meter SM3 autonomous sound recorders (Wildlife Acoustics) equipped

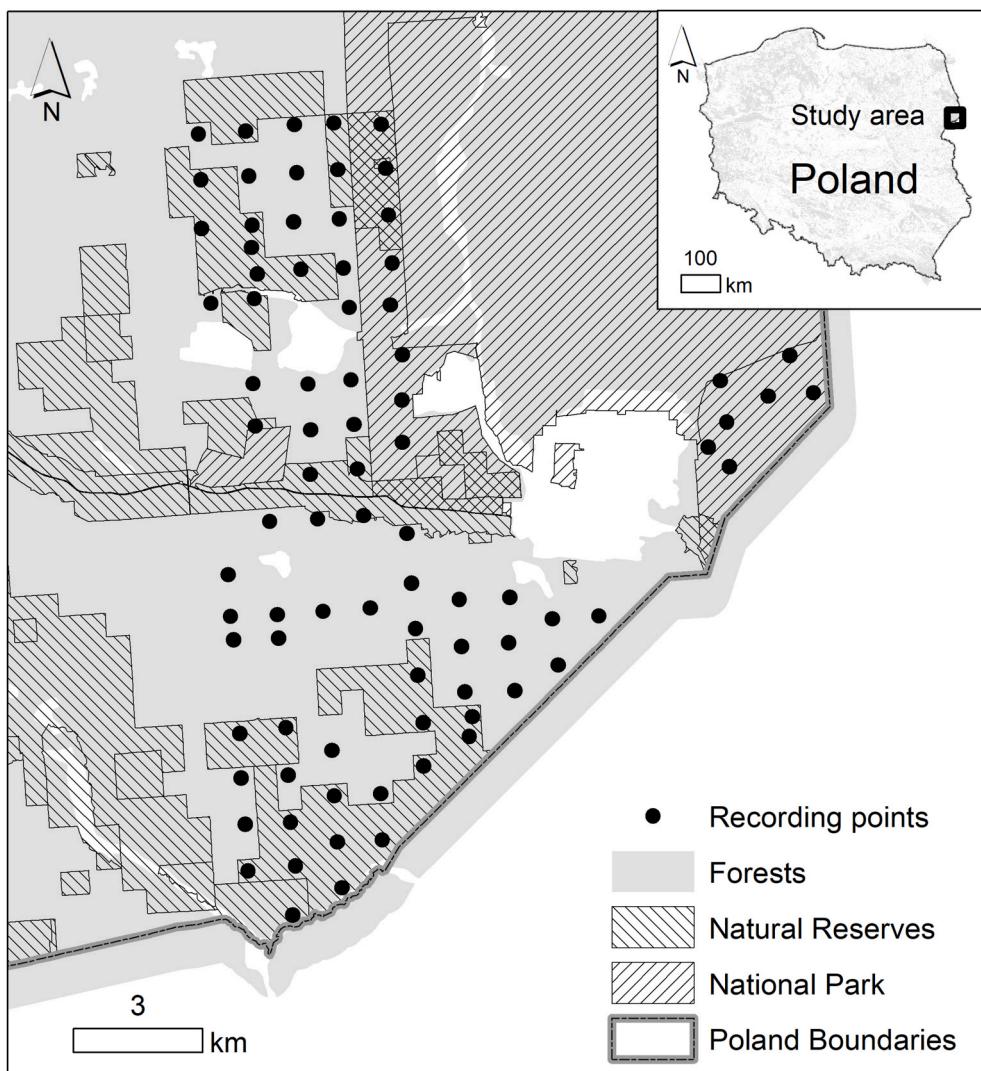


Fig. 1. Distribution of 83 recording points within the study area – The Białowieża Forest.

with SMM-A1 omnidirectional microphones, featuring a sensitivity of -11 ± 4 dB and a signal-to-noise ratio greater than 68 dB. These recorders were mounted on trees approximately 8 m above ground level to capture species singing from both undergrowth and from the tree crowns.

At each recording point, we conducted two recording sessions during the breeding season: an early survey (from April 20 to May 2, 2021) and a late survey (from May 18 to May 26, 2021). Each recording session lasted 6 h, starting 2 h before sunrise and continuing for 4 h after sunrise. Before each recording session, we checked microphones using a VOLT-CRAFT SLC-100 sound level calibrator and applied the same recording settings throughout the study: 48 kHz, 16-bit sampling rate, frequency band filters off, gain 24 dB, and 1-h WAV files. For more detailed methodology, refer to (Budka et al., 2023).

2.3. Forest characteristics

We described basic characteristics of the forest within 100 m around each recording point using two sources of data: Forest Data Bank (<https://www.bdl.lasy.gov.pl/portal/en>) and satellite imagery.

The Forest Data Bank is based on field surveys of the forest and provides information on forest management, condition, and changes (data are updated every 10 years; the last update took place in 2021.). By utilizing this data, we obtained information about the dominant forest

type (ordinal scale, from least to most productive: coniferous, mixed coniferous, mixed broadleaved, broadleaved, streamside), soil moisture (ordinal scale, from driest to wettest: fresh, moist, wet), the age of the dominant forest stand type (ordinal scale, from youngest to oldest: 20-year age classes), and the protection status of the forest (protected or unprotected) (Suppl. Dataset and S1 Figure).

Landsat 8 Level 2 Collection 2 satellite data were obtained through Google Earth Engine (GEE) (Gorelick et al., 2017). The data include atmospherically corrected images processed to orthorectified surface reflectance. Using GEE and quality bands (QA) provided along with the Landsat multispectral images we removed unwanted pixels containing clouds, cloud shadows and fill. After data cleaning, only images acquired on 24th March and May 11, 2021 covered all the study sites with similar and high quality. Then, we calculated Normalized Difference Vegetation Index (NDVI) (Rouse et al., 1973) using the following equation (1):

$$NDVI = \frac{R_{NIR} - R_{RED}}{R_{NIR} + R_{RED}} \quad (1)$$

Where R_{NIR} —reflectance in near-infrared band (band no. 5 in Landsat 8); R_{RED} —reflectance in red band (band no. 4 in Landsat 8).

NDVI is a common index reflecting photosynthetic activity and abundance of plants (Jiang et al., 2006). The calculated NDVI values were denoted as $NDVI_{March}$ and $NDVI_{May}$. These two variables reflected leaf-off and leaf-on conditions, respectively. In addition, we also

calculated total area covered by standing dead trees within the buffers. This was done using aerial orthoimages acquired from Polish Head Office of Geodesy and Cartography via rgugik R package (Dyba and Nowosad, 2021). We used the most up to date orthoimages available – taken on August 13, 2020 with a spatial resolution of 0.25 m. Two compositions, RGB and CIR were used in the study and the total number of tiles was 183. In these images, standing dead trees were easily visible so their boundaries were delimited manually in ArcGIS 10.3. For simplicity, variables acquired from satellite and aerial images are grouped and referred to as satellite data. For more details see Suppl. Dataset and S1 Figure.

2.4. Bird species richness estimation

To estimate bird species richness and community composition at each recording point, we sampled 1 min every 10 min of soundscape recording (36 1-min sound samples per survey per recording point). One-minute sound samples were analysed by three observers (AM, ES, MB) through manual spectrogram scanning and listening to recordings in Raven Pro 1.6.1 software (Window = Hamming, window size = 23.1 ms, Overlap = 75%). For each 1-min sound sample, we compiled a list of vocalizing bird species. Finally, we compiled the list of vocalizing species for a single survey as well as for both surveys at the recording point.

2.5. Acoustic analyses

We divided our 1-h soundscape recordings into 1-min sound samples using the warbleR package (Araya-Salas and Smith-Vidaurre, 2017) and applied band-pass filter (500–10,000 Hz) in Raven Pro 1.6.5 software to focus on the frequency spectrum in which most bird species at our study location vocalize, and to remove background noise. From each 1-h recording, we analysed the first 59 1-min sound samples (the last sound sample was a few milliseconds shorter, so we removed it). Because most bird species in our study area begin singing just before sunrise (Budka et al., 2023), we focused on the time period from 30 min before sunrise to 4 h after sunrise. During a single survey at each recording point, we analysed 265 1-min sound samples. In total, we analysed 43,990 1-min sound samples (83 recording points x 2 surveys x 265 min per survey).

For each 1-min sound sample, we calculated the six most commonly applied bioacoustics indices: Acoustic Complexity Index (ACI), Acoustic Diversity Index (ADI), Acoustic Entropy Index (H), Acoustic Evenness Index (AEI), Acoustic Richness Index (AR) and Bioacoustic Index (BI). The indices were calculated using seewave (Sueur et al., 2008a) and soundecology (Villanueva-Rivera and Pijanowski, 2018) packages in R 4.3.3 software. To better customize the acoustic indices to the specifications of our study area, we modified the calculation settings of the acoustic indices (Table 1).

2.6. Statistics

First, we investigated whether total bird species richness at the recording point depends on environmental variables. We conducted two separate Generalized Linear Mixed Models (GLMMs). The first model included fixed factors obtained from the Forest Data Bank: forest type, soil moisture, forest age, and the protection regime (Species Richness ~ Forest type + Moisture + Age + Protection). In the second model, the fixed factors included satellite data: NDVI measured in March, NDVI measured in May, the proportion of the area covered by standing dead trees, and the protection of the forest (Species Richness ~ NDVI_{March} + NDVI_{May} + Dead trees + Protection). Data were fitted using a Poisson distribution with a log-link function.

Next, we examined whether acoustic indices reflect differences in forest characteristics. Due to outlier values of acoustic indices caused by extreme acoustic events, such as birds singing close to the microphone or wind gusts, we removed 1% of the lowest and 1% of the highest values

Table 1

Description of acoustic indices and their calculation settings used in the study. F_{min} – minimal frequency, F_{max} – maximal frequency, FFT – fast Fourier transformation window size, J – parameter splitting recording into j-subsamples, Thr – threshold, F_{step} – width of frequency band.

Index	Reference	Description	Settings
Acoustic Complexity Index (ACI)	Pieretti et al., (2011)	Calculates the absolute difference in sound amplitude between two adjacent cells within a frequency band relative to the total amplitude within that band. Highest values generate recordings containing complex vocalizations, while low values indicate silence or consistent noise (e.g., cicadas).	F _{min} = 0.5 kHz F _{max} = 10 kHz FFT = 512 J = 5
Acoustic Diversity Index (ADI)	Villanueva-Rivera et al. (2011)	Focuses on the occupancy of signals above a predefined threshold in frequency bins, applies the Shannon index, and measures evenness across frequency bands. Constant noise or silence generates high values, while sounds occupying a single frequency band will be close to 0.	F _{min} = 0.5 kHz F _{max} = 10 kHz Thr = -50 dB F _{step} = 0.5 kHz
Acoustic Entropy Index (H)	Sueur et al. (2008b)	Measures the temporal and spectral entropies of the acoustic signal. A single pure tone will tend toward 0. Occupation of more frequency bins and increased amplitude modulation will tend toward 1. Therefore, more species-rich and abundant communities should generate higher values of the index.	F _{min} = 0.5 kHz F _{max} = 10 kHz FFT = 512
Acoustic Evenness Index (AEI)	Villanueva-Rivera et al. (2011)	Divides the spectrogram into frequency bins, measures, and compares the sound energy within each bin. Equal distribution of sound energy across the bins generates higher values of AEI and indicates a balanced acoustic environment. Energy concentration in a few bands generates lower AEI values and indicates dominance by certain species or sound sources.	F _{min} = 0.5 kHz F _{max} = 10 kHz Thr = -50 dB F _{step} = 0.5 kHz FFT = 512
Acoustic Richness Index (AR)	Depraetere et al. (2012)	Divides the spectrogram into frequency bins and time steps and counts the number of distinct acoustic events in each frequency bin and time step. Higher values of the ARI indicate a rich and diverse soundscape with a high number of acoustic events, generated by more species or individuals.	F _{min} = 0.5 kHz F _{max} = 10 kHz Thr = -50 dB FFT = 512
Bioacoustic Index (BI)	Boelmann et al., (2007)	Measures the area under the log amplitude spectrum curve in the recording. Highest values generate high-amplitude sound across all frequency bands,	F _{min} = 0.5 kHz F _{max} = 10 kHz FFT = 512

(continued on next page)

Table 1 (continued)

Index	Reference	Description	Settings
		while low values indicate silence within the measured frequency range.	

from our dataset. We performed this procedure separately for each index. Subsequently, we conducted separate GLMMs for Forest Data Bank and satellite data. In these models we used the acoustic index calculated for 1-min sound samples as the dependent variable and applied three random effects: recording point ID, survey (early or late), and time of day (minute of recording in the survey). The final models were as follows: (1) for Forest Data Bank: Acoustic Index ~ Protection + Forest type + Moisture + Age + (1|Point ID) + (1|Survey) + (1|Minute); (2) for satellite data: Acoustic Index ~ Protection + NDVI_{March} + NDVI_{May} + Dead trees + (1|Point ID) + (1|Survey) + (1|Minute). Data were fitted by using Gaussian distribution and identity link function (*AR, BI*), Gaussian distribution and log link function (*H*), and gamma distribution and log link function (*ACI, ADI, AEI*).

Finally, we compared five dissimilarity matrices describing differences between recording points in (1) bird species richness, (2) bird community composition, (3) acoustic similarity (median *ACI, ADI, AEI, AR, BI, H* for recording point), forest characteristics obtained from (4) Forest Data Bank (forest type, soil moisture, age class) and (5) satellite data (NDVI_{March}, NDVI_{May}, standing dead trees). To calculate dissimilarity matrices we applied Jaccard similarity index for bird community composition, Euclidean distance for bird species richness, acoustic similarity and satellite data, and Gower's distance for ordinal variables obtained from Forest Data Bank. We compared the matrices using Mantle test with 999 permutations. Statistical analyses and data

visualisation were done in R 4.3.3, using glmmTMB (Brooks et al., 2017), DHARMA (Hartig, 2021), vegan (Oksanen et al., 2022), performance (Lüdecke et al., 2021) and ggplot2 (Wickham, 2016) packages.

3. Results

3.1. Bird species richness in different types of the forest

The average bird species richness at the recording point was 21 ± 3.4 , with values ranging from 15 to 31 (see S1 Table for the list of bird species detected in each recording point). We did not find any significant relationships between bird species richness and the environmental variables obtained from the Forest Data Bank and satellite data (S2 Table). This suggests that bird species richness in our study area was not significantly influenced by factors such as the protection regime, forest type, soil moisture, forest age, NDVI values (measured in March and May), or the area covered by standing dead trees.

3.2. Acoustic indices and forest characteristics

Analysis of data from the Forest Data Bank revealed that acoustic indices varied significantly with forest type, soil moisture, and forest age classes, but not between protected and unprotected areas (S3 Table and Figs. 2–4). Generally, *ACI, AEI* and *BI* were lowest in coniferous forests and increased with forest productivity, while *ADI* and *H* showed the opposite trend, reaching highest values in coniferous forests (S3 Table, Fig. 2). *ACI, AEI*, and *BI* were lowest in fresh forests and highest in wet forests, while *ADI, AR*, and *H* displayed the opposite pattern, with the highest values in fresh forests and the lowest in wet ones (S3 Table, Fig. 3). The relationship between acoustic indices and forest age was less consistent. For example, the lowest values of *ACI* and *BI* were observed

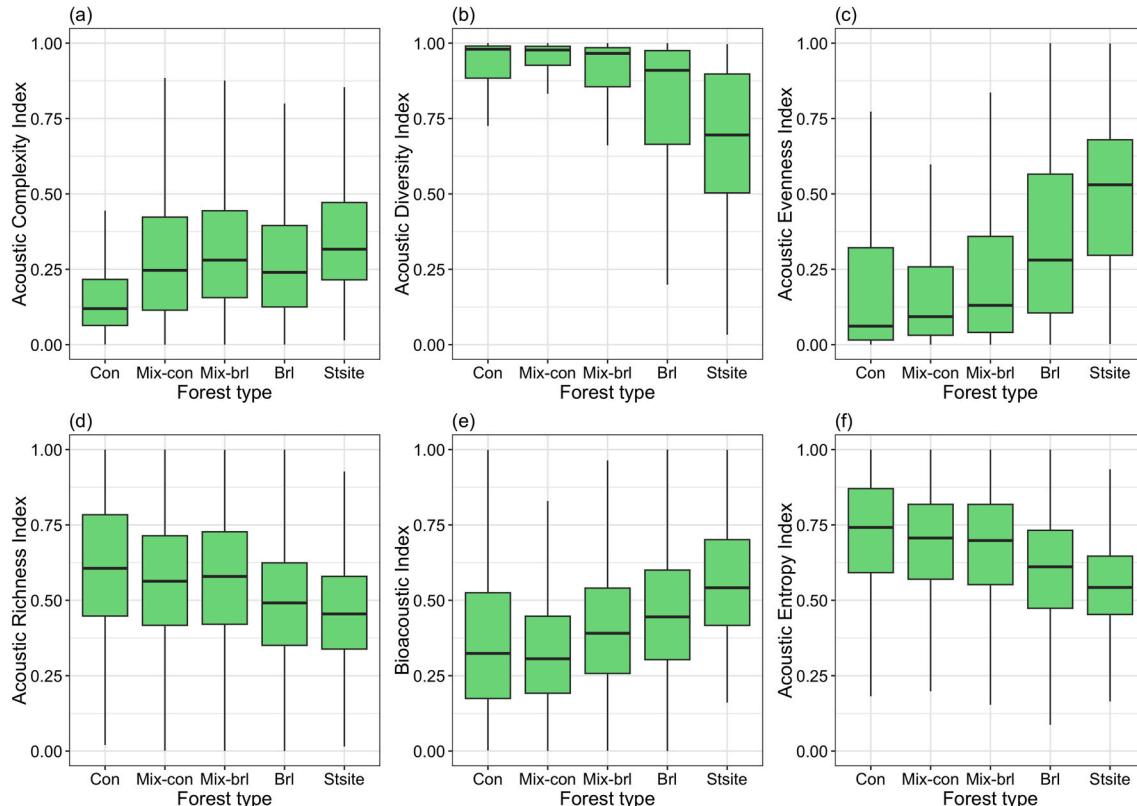


Fig. 2. Differences in standardized values of six bioacoustic indices among forest types. Forest types are ranked from least to most productive. Abbreviations of forest types are as follows: Con – coniferous forest; Mix-con – mixed coniferous forest; Mix-brl – mixed broadleaved forest; Brl – broadleaved forest; Stsite – streamside forest. Graphs show medians, 25–75% quartiles, and the ranges of data. Acoustic indices were calculated based on 43,110 1-min sound samples recorded at 83 recording points during early and late surveys.

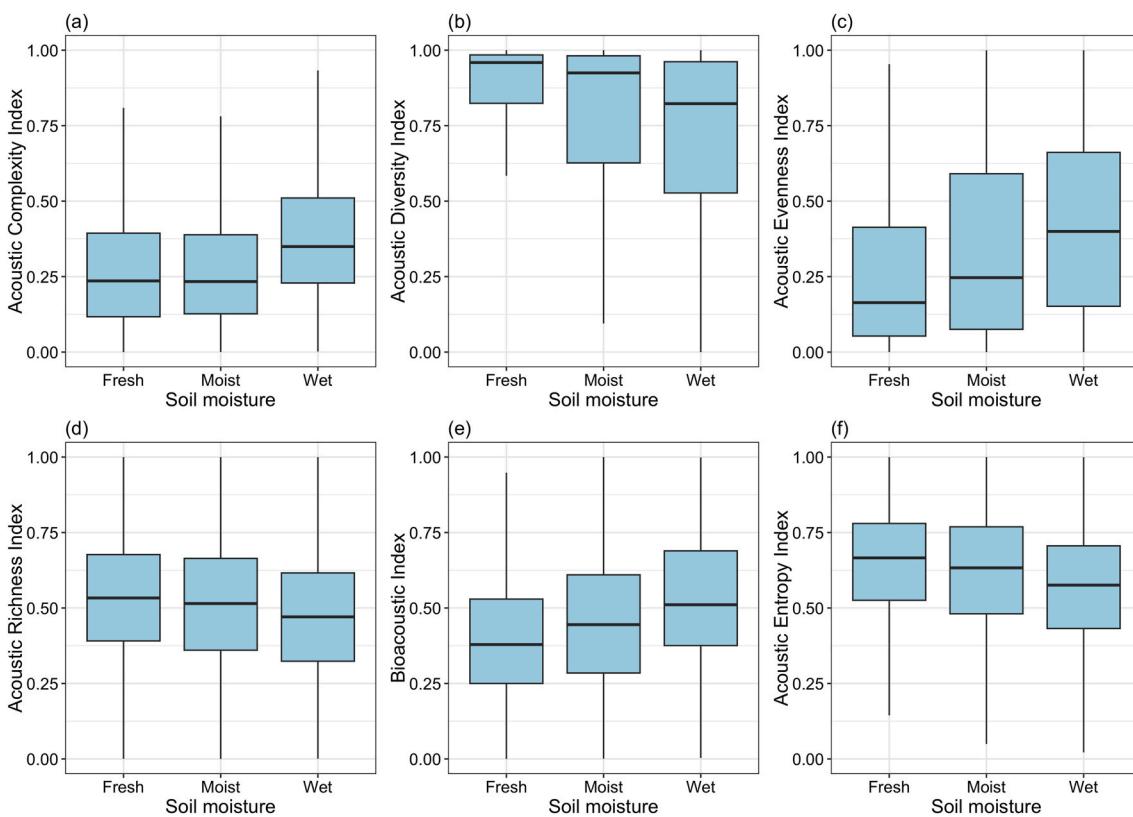


Fig. 3. Differences in standardized values of six bioacoustic indices among soil moisture. Soil moistures are ranked from driest to wettest. Graphs show medians, 25–75% quartiles, and the ranges of data. Acoustic indices were calculated based on 43,110 1-min sound samples recorded at 83 recording points during early and late surveys.

in forests younger than 60 years, while the highest values were observed in forests aged 121–140 years (*BI*) and 141–160 years (*ACI*). *AEI* was lowest in forests aged 41–60 and 141–160 years, but the highest in those aged 121–140 and 161–180 years. In contrast, *ADI*, *AR* and *H* showed an opposite pattern, with the highest values in forests younger than 60 and between 141 and 160 years, and the lowest in forests aged 121–140 and 161–180 years (S3 Table, Fig. 4).

Regarding satellite data, we observed a significant negative relationship between NDVI measured in March and *ACI*, *AEI* and *BI*, and a positive relationship with *ADI*, *AR*, and *H*. NDVI values measured in May correlated negatively and significantly with *ACI* only. None of the acoustic indices differed between protected and unprotected areas, nor were they influenced by the proportion of the area covered by standing dead trees (see S4 Table).

3.3. Acoustic structure, habitat characteristics, bird species richness and bird community composition

The comparison of dissimilarity matrices using the Mantel test revealed that the acoustic structure of the forest, as measured by *ACI*, *ADI*, *AEI*, *AR*, *BI* and *H*, correlated more strongly with bird community composition ($r = 0.13$, $p < 0.01$) than with bird species richness ($r = 0.08$, $p < 0.05$). The strongest correlation was found between acoustic structure and forest characteristics obtained from the satellite data ($r = 0.17$, $p < 0.001$; Table 2; Fig. 5). We also found a weak but significant correlation between the acoustic structure of the forest and differences in forest characteristics described by Forest Data Bank ($r = 0.12$, $p < 0.01$). Moreover, differences in forest characteristics obtained from the satellite data correlated moderately with differences in bird community composition ($r = 0.42$, $p < 0.001$) and weakly with bird species richness ($r = 0.10$, $p < 0.05$; Table 2).

4. Discussion

Our study revealed that bird species richness did not vary significantly with forest type, age, soil moisture, protection regime, area covered by standing dead trees, or NDVI values. These findings are surprising, as bird species richness is often reported to differ across various temperate forest types (e.g., James and Wamer, 1982; Storch et al., 2018; Basile et al., 2021). However, in the primeval forest of Białowieża National Park, bird species richness shows only slight variation between forest types, averaging 32–40 species per study plot (excluding edge plots). Despite this, significant differences in bird community composition and abundance are observed, ranging from 52 pairs/10 ha in coniferous forests to 92 pairs/10 ha in ash-alder forests (Wesolowski et al., 2015). Thus, areas with similar bird species richness can produce different levels of acoustic complexity if their species composition and abundance differ. The question then becomes how much species richness, community composition, and bird abundance contribute to the acoustic indices.

Although no significant relationships were found between bird species richness and forest characteristics, acoustic indices revealed that soundscape complexity increased with forest productivity and soil moisture, and decreased with increasing NDVI. This suggests that soundscape complexity is influenced by not only species richness, but also by species composition and abundance (Zhao et al., 2019). We demonstrated that acoustic structure dissimilarity was more strongly correlated with differences in bird species composition ($r = 0.126$, $p < 0.01$) than with species richness ($r = 0.079$, $p < 0.05$). Although we did not account for bird abundance, previous studies in Białowieża Forest have shown that bird abundance can be nearly twice as high in ash-alder forests compared to coniferous forests (Wesolowski et al., 2015). The significant relationship between acoustic complexity and NDVI suggests that areas with a higher proportion of coniferous trees, heterogeneous

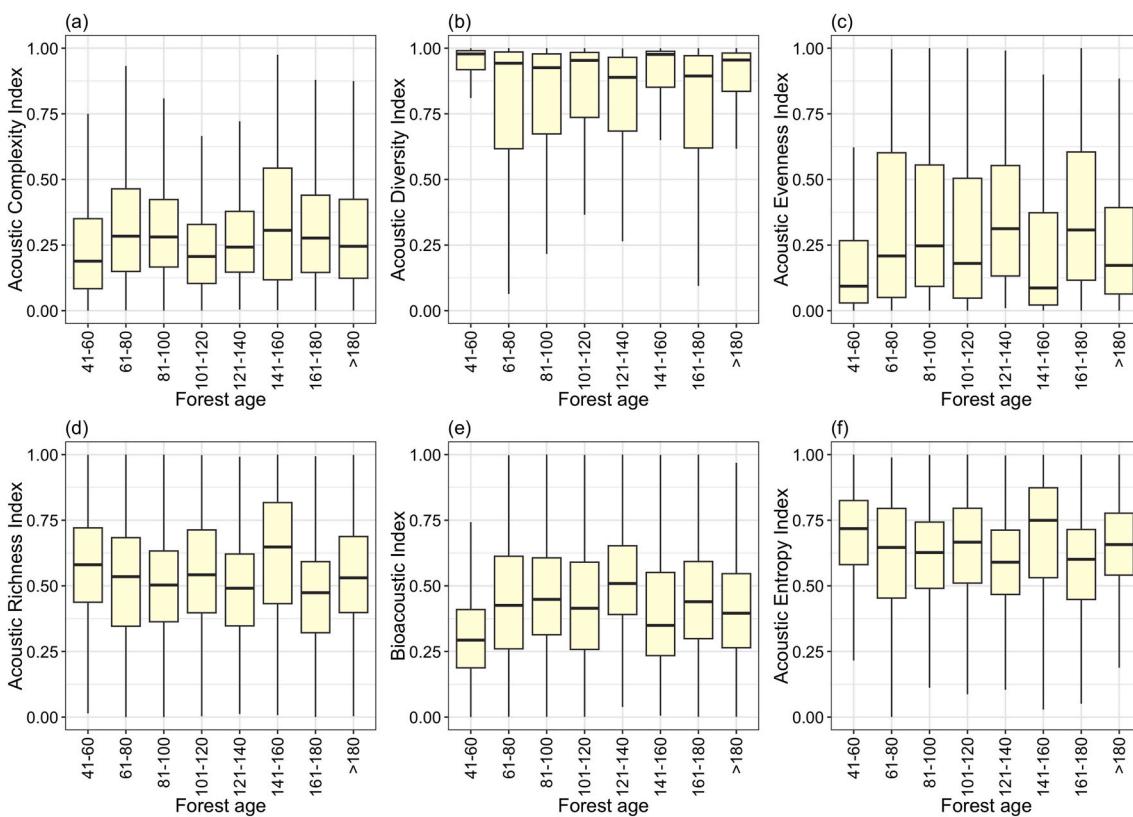


Fig. 4. Differences in standardized values of six bioacoustic indices among the classes of the age of the dominant forest type stand. Graphs show medians, 25–75% quartiles, and the ranges of data. Acoustic indices were calculated based on 43,110 1-min sound samples recorded at 83 recording points during early and late surveys.

Table 2

Results from Mantel test with 999 permutations, comparing dissimilarity matrices of Acoustic indices (ACI, ADI, AEI, AR, BI, H), Forest Bank Data (forest type, soil moisture, forest age), Satellite data (NDVI_{March}, NDVI_{May}, standing dead trees), bird species composition, and bird species richness. Significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

	Acoustic indices	Forest Bank Data	Satellite data	Species composition
Forest Bank Data	0.1181**			
Satellite data	0.1714***	0.2518***		
Species composition	0.1260**	0.1594***	0.4183***	
Species richness	0.0792*	0.0409	0.1011*	0.1606***

forests with canopy gaps, and middle-aged forests tend to have a greater bird species richness and abundance (Klimavičius et al., 2023). Surprisingly, we did not find significant differences in acoustic structure or species richness between protected and unprotected forests. This could be due to the fact that forest management in our study area is quite limited, and the differences between protected and unprotected areas are less pronounced than in regions dominated by intensively managed forests. We expect that comparing intensively managed forests with our study area would yield different results.

The dependencies between acoustic indices and environmental variables have been reported in many studies. For example, BI and ACI were higher in organic than in conventional olive groves (Myers et al., 2019). In Colombia, a combination of acoustic indices distinguished mature forest, secondary growth, and pasture (Gómez et al., 2018). Differences in the Acoustic Richness Index and Acoustic Dissimilarity Index have been found among mature forest, young forest, and forest-cropland

ecotone in France (Depraetere et al., 2012). In Cosa Rican forest, ACI was correlated positively with liana abundance (Hilje et al., 2017). Acoustic indices also correlated moderately with landscape characteristics and ecological condition in Australia, although they poorly predicted forest type (Fuller et al., 2015). In our study, we were able to distinguish subtle forest type classes related to habitat productivity and moisture. However, our study had limitations. We analysed only 530 min of soundscape per recording point across two surveys, and a longer recording period may have stabilized index values and improved predictions (Bradfer-Lawrence et al., 2019). Additionally, we did not remove or filter recordings affected by wind and rain, which may reduce prediction accuracy (Gasc et al., 2015). Moreover, the variation in bird song activity throughout the breeding season may explain the weak or moderate correlations observed. Despite these limitations, our study demonstrates that acoustic indices can be used to discriminate between temperate forest types, and we believe it is possible to create an acoustic profiles of each forest type, which could be used to monitor environmental disturbances.

5. Conclusions

Our study demonstrated that, although bird species richness did not vary significantly between different temperate forest sites, these forest types differ in their acoustic characteristics. Soundscape dissimilarity was more strongly related to bird community composition than bird species richness. Although bird abundance was not analysed, all three factors—species richness, community composition, and abundance—impact soundscape structure and are influenced by habitat characteristics. Therefore, a simple soundscape analysis, without species identification, can be an effective tool for distinguishing between different temperate forest types and assessing changes in their condition.

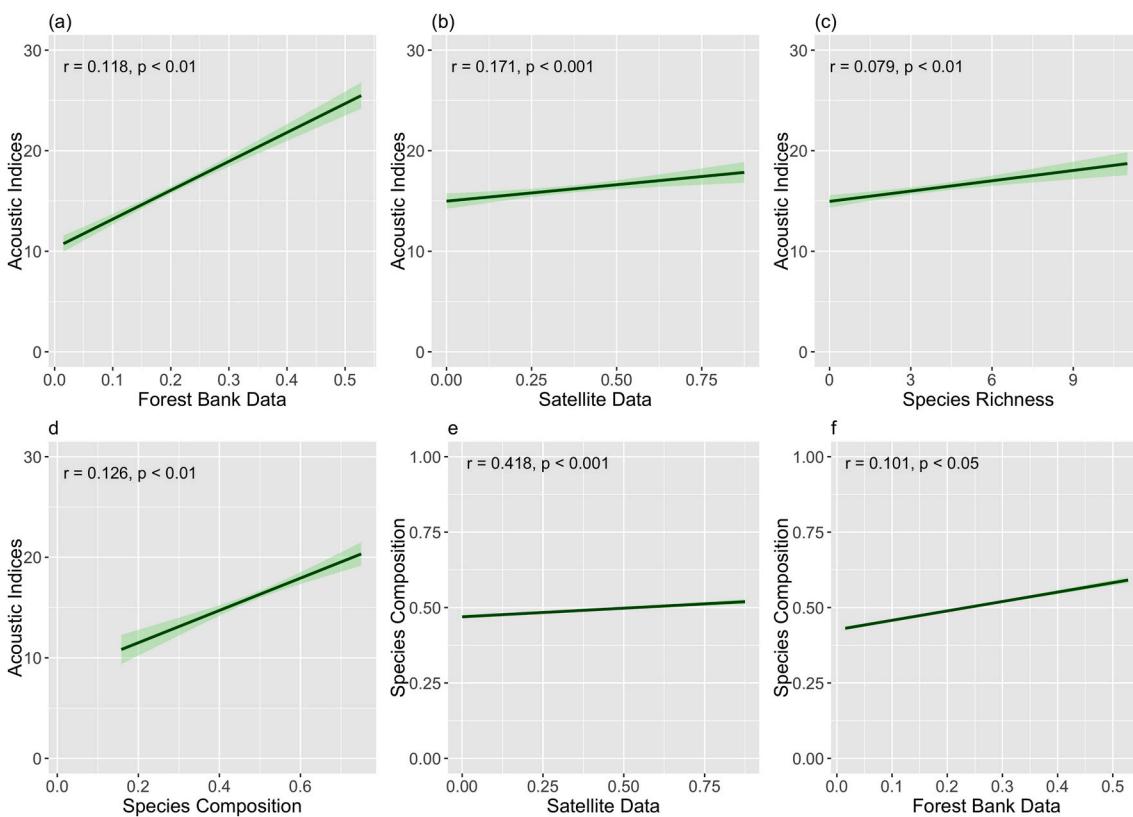


Fig. 5. Differences in dissimilarity matrices between the acoustic structure of the forest and: (a) habitat characteristics obtained from Forest Bank Data, (b) habitat characteristics obtained from satellite data, (c) bird species richness, (d) bird species composition, and bird species composition and: (e) satellite data, (f) Forest Bank Data. Values of Mantel test statistics are given.

CRediT authorship contribution statement

Michał Budka: Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Gustaw Gazda-Szypulski:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis. **Adrianna Muszyńska:** Writing – review & editing, Investigation, Formal analysis. **Emilia Sokołowska:** Writing – review & editing, Investigation, Formal analysis. **Agata Staniewicz:** Writing – review & editing, Validation, Investigation. **Paweł Bogawski:** Writing – review & editing, Visualization, Methodology, Formal analysis.

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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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.indic.2024.100529>.

Data availability

Data used in the study are included in supplementary materials. Soundscape recordings (42 496 one-minute sound samples) will be made available on request.

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