Ecological Informatics 92 (2025) 103493

Contents lists available at ScienceDirect

Ecological Informatics

journal homepage: www.elsevier.com/locate/ecolinf

The effectiveness of ecoacoustic indices in representing bird species richness relies on technical parameters

Rosanne J. Michielsen [a], Dominika Koprowska [a], Grzegorz Mikusiński [b,a], Michał Walesiak [a], Marcin Zegarek [a], Michał Żmihorski [a], Michał Budka [c,*]

[a] Mammal Research Institute Polish Academy of Sciences, ul. Stoczek 1, 17-230, Białowieża, Poland
[b] School for Forest Management, Swedish University of Agricultural Sciences, Skinnskatteberg, Sweden
[c] Department of Behavioural Ecology, Adam Mickiewicz University in Poznań, Uniwersytetu Poznańskiego 6, 61614 Poznań, Poland

A R T I C L E I N F O

Keywords:
Acoustic complexity index
Bioacoustic index
FFT window length
Forest disturbance
Frequency range
Sound ecology
Sampling rate

A B S T R A C T

Ecoacoustic indices have been proposed as proxies for diversity measures such as species richness, however, their effectiveness remains a subject of ongoing debate. We examined how variation in recording sampling rate and computational parameters influences the strength of the relationship between bird species richness and two widely used ecoacoustic indices: the Bioacoustic Index (BI) and the Acoustic Complexity Index (ACI).

We analyzed 5844 one-minute soundscape recordings from the Białowieża Primeval Forest (Poland), down-sampling them from 192 kHz to 96, 48, and 24 kHz. The ACI and BI were calculated for each recording sampling rate using different configuration settings: seven Fast Fourier Transform (FFT) window lengths and two frequency range settings. We then related bird species richness to the ACI and BI across all combinations of FFT window length, sampling rate, and frequency range.

We demonstrated that the relationship between species richness and ecoacoustic indices ranged from significantly positive to significantly negative, depending on the technical parameters applied, with a stronger effect observed for the ACI than for the BI. For both indices, adjusting the analysis frequency range to match the frequency range of bird vocalizations in our study area strengthened the relationship compared to the default settings, and the influence of technical parameters varied among habitats.

In conclusion, the effectiveness of the ACI and the BI in representing bird species richness relies on technical parameters. When calculating ecoacoustic indices, particularly the ACI, we recommend adjusting the FFT window length to match the sampling rate of the recordings and the local ecoacoustic conditions. Furthermore, other calculation settings, such as the analysis frequency range, should be adjusted to the vocalisation characteristics of the studies taxa. Finally, we advise against using the ACI and BI without prior testing of their suitability to reflect local biodiversity measures.

1. Introduction

With the increasing availability and use of autonomous recording units, acoustic biodiversity monitoring can now cover vast areas and extended time periods (Darras et al., 2025). This facilitates the identification of biodiversity hotspots and enables the detection of rare and elusive species (e.g., Robert et al., 2015; Schroeder and McRae, 2020). However, autonomous recording units generate vast amounts of data, even in small-scale studies, making manual classification impractical. Therefore, (semi-) automatic methods are required for signal detection and classification or for measuring the overall acoustic complexity of recordings. For the second task, ecoacoustic indices have been proposed as tools that can be particularly useful for representing measures of diversity (Alcocer et al., 2022). Ecoacoustic indices describe the distribution of acoustic energy across time and frequency within a recording (Sueur et al., 2014). This method generally assumes that communities with greater richness, diversity, and abundance of vocalizing species produce more complex soundscapes (Gasc et al., 2013; Sueur et al., 2008b). Therefore, soundscape diversity, as measured by ecoacoustic indices, can be used as an indicator of biodiversity (Pijanowski et al., 2011a, 2011b).

Many studies have explored the relationships between ecoacoustic

* Corresponding author.
E-mail address: m.budka@amu.edu.pl (M. Budka).

https://doi.org/10.1016/j.ecoinf.2025.103493
Received 15 April 2025; Received in revised form 23 October 2025; Accepted 23 October 2025
Available online 25 October 2025
1574-9541/

indices and species diversity measures, such as (vocalizing) species richness (Budka et al., 2023; Depraetere et al., 2012; Diaz et al., 2023; Shaw et al., 2021), often reporting inconsistent results (Alcocer et al., 2022; Bateman and Uzal, 2022). Moreover, various methodologies have been applied across studies—ranging from different methods used to estimate animal diversity (e.g., field surveys versus species detected in recordings; (Allen-Ankins et al., 2023; Diaz et al., 2023)), through the sampling rate of field recordings (Fairbrass et al., 2017; Pieretti et al., 2011), to differences in the calculation settings of ecoacoustic indices (Boelman et al., 2007; Budka et al., 2024; Diaz et al., 2023). Hence, it is difficult at this stage of knowledge to determine whether the contrasting results regarding the relationships between ecoacoustic indices and species richness reflect real ecological differences or are merely artefacts of differing methodological approaches.

The results obtained from the application of ecoacoustic indices depend on the recording sampling rate and the settings used in their calculation (Bradfer-Lawrence et al., 2024; Kemp et al., 2025; MacPhail et al., 2024). The sampling rate of a recording determines how many samples of the acoustic signal are taken per second and consequently sets the maximum frequency that can be recorded, which is half of the sampling rate (the Nyquist frequency). In the Short-Time Fourier Transform (STFT) method, the Fast Fourier Transform (FFT) window length (hereafter referred to as 'FFT window length'), along with the frame size, window type and degree of overlap, determines how sound is represented in both the temporal and spectral domains and acts as a trade-off between temporal and spectral resolution (Allen and Rabiner, 1977; Cooley and Tukey, 1965). The frequency range used to calculate the ecoacoustic index also influences its value, depending on whether the entire range or a limited frequency band is selected (e.g., to match the frequency range of the vocalizations produced by animals in the studied location; Boelman et al., 2007; Budka et al., 2023; Diaz et al., 2023; Metcalf et al., 2021). Hence, the recording's sampling rate, FFT window length, and the frequency range applied in the analysis influence the ecoacoustic index outcome (Fig. 1). As a result, the association between the indices and species richness (i.e., of vocalizing species) may be affected by both the sampling rate of recording and the computational settings used. However, sampling rates vary greatly across studies (Darras et al., 2025) and consequently, the applied FFT window length and frequency range settings may not be the optimal settings for associating the indices with species richness. Therefore, employing different sampling rates without appropriate adjustment of the settings may weaken the presumed relationship between the index value and species richness and consequently bias the ecological interpretation of the index value. Hence, to fully understand the association between ecoacoustic indices and (vocalizing) species richness, it is essential to examine the combined effects of these technical parameters (i.e., recording sampling rate, the FFT window length and the frequency band limitation) on the direction and strength of the richness-index relationship.

In this study, we examined whether different combinations of computational parameters affect the association of bird species richness with two commonly used ecoacoustic indices: the Bioacoustic Index (BI) and the Acoustic Complexity Index (ACI). Both indices have recently been reviewed in key meta-analyses, without considering how recording sampling rates or the parameters used to calculate them affect the

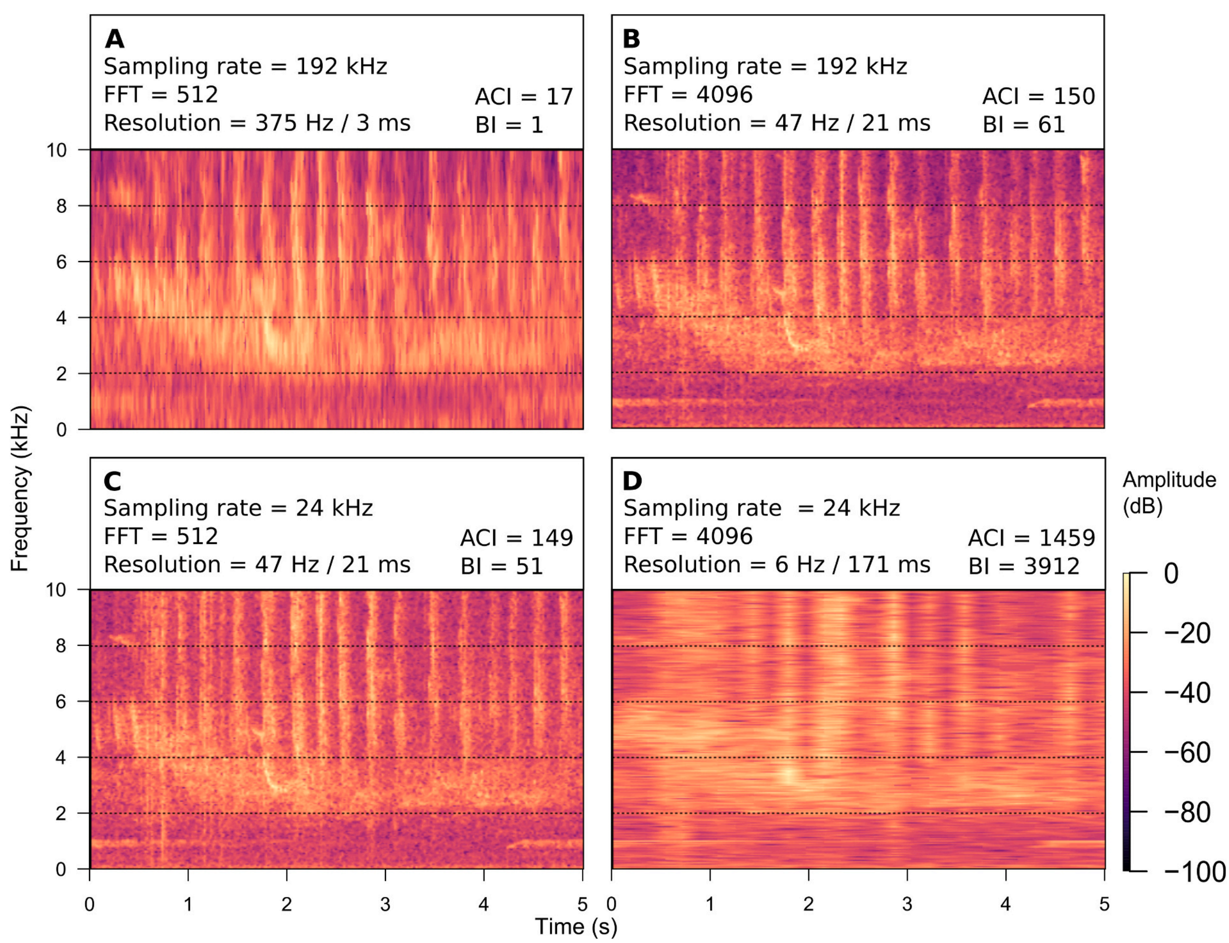

Fig. 1. A comparison of spectrograms visualizing soundscape complexity, measured using the ACI and the BI, calculated for the same recording at two different sampling rates (recorded at 192 kHz/16 bit; A and B; downsampled to 24 kHz/16 bit; C and D), generated with two different FFT window lengths (512: A and C; 4096: B and D) and a frequency range limited to 0.5–10 kHz.

direction and strength of the relationship between index value and ecological characteristics (e.g., Alcocer et al., 2022; Allen-Ankins et al., 2023; Bateman and Uzal, 2022). The BI quantifies the amount of acoustic energy within the frequency range that predominantly contains biophony (as opposed to anthropophony). It calculates the area under the log amplitude spectrum curve (in dB*kHz, with the minimum dB level set to zero; Boelman et al., 2007). The ACI quantifies the complexity of soundscapes by measuring the variation in acoustic patterns across a specified frequency range (i.e., it calculates the absolute difference in amplitude between two adjacent time samples within a frequency bin, relative to the total amplitude; Farina, 2025; Pieretti et al., 2011). Both indices are often used in ecoacoustic studies and interpreted as proxies for species richness (e.g., Bradfer-Lawrence et al., 2020; McGrann et al., 2022; Rajan et al., 2019).

Here, we recorded the soundscape across four habitat types in a temperate forest and nearby farmland, calculated various variants of the BI and ACI using different technical parameters for one-minute sound samples, and analyzed their relationship with bird species richness, which was determined through manual classification of the same recordings. In addition, we assessed the correlations among parameter-derived variants of the two indices calculated from the same recordings to determine whether changes in calculation parameters merely shift index values or also alter the relationships between the indices.

We hypothesize that for both the BI and the ACI, technical parameters will alter the temporal and spectral resolution of sound analysis, thereby affecting index values and, more importantly, modifying the strength and direction of their relationship with bird species richness. In addition, we expect that the technical parameters will affect the correlations between the indices calculated from the same recording using different parameter settings, thereby preventing interchangeable use of different index variants without consequences for their ecological interpretation. Finally, we expect that adjusting the calculation settings of ecoacoustic indices to local acoustic conditions will enhance their effectiveness in representing bird species richness compared to the default settings commonly applied in ecoacoustic studies.

2. Methods

2.1. Study area and site selection

The study was conducted in the Białowieża Primeval Forest, a forest complex spanning Poland and Belarus, covering 150,582 ha, of which 41 % lies in Poland. Due to various levels of forest management across forest stands, nature protection (UNESCO The World Heritage Committee, 2012; Puszcza Białowieska, PLC200004) and disturbance intensities, the forest landscape is best described as a mosaic of different forest environments with generally a high level of naturalness (Jaroszewicz et al., 2019).

In 2022 and 2023, 200 sites were selected in four forest habitat-classes and in farmland adjacent to the forest. The forest habitats covered the majority of the habitats that emerged after the most recent bark-beetle outbreak (*Ips typographus*; 2012–2019; Kamińska et al., 2021): spruce stands unaffected by the outbreak, spruce stands heavily affected by the outbreak and left for natural regeneration, spruce stands heavily affected by outbreak and logged, background forest stands (detailed description of habitats and the sample size given in S1.1). Each site was located at least 50 m from the road, at least 200 m away from other sites (with two exceptions in 2022, where two pairs of points were 160 and 177 m from each other) and surrounded by the target habitat as much as was feasible at the specific location (e.g., in a few cases, the site bordered the target habitat instead of being surrounded by it, due to a fence). As most roads in our study area were infrequently used unpaved forest roads restricted from public access, our choice of a 50-m buffer was linked to the road's influence on the forest structure rather than the direct impact of traffic on the bird community. Sites were selected randomly, with some adjustments based on field observations (a more detailed description of the site selection methods can be found in S1.1).

2.2. Sound recordings and analyses

At each site two sampling rounds were conducted: one in April and the second in May–June (i.e., the birds' breeding season) of either 2022 or 2023 (Table S2). In a few cases, due to technical problems, sessions at some sites were repeated within sixteen days of the original sampling date ($n = 14$) and five points were later removed due to insufficient data or distortion, leading to $n = 390$ in total (Table S2). Each round lasted two days and during each day we recorded the soundscape from 1 h before to 3 h after sunrise (i.e., during the dawn chorus, when most songbirds are vocally active, providing the best representation of bird species richness). Recordings were made for one minute every 20 min, and every 10 min during the first hour after sunrise, using a 192 kHz /16-bit bandwidth (AudioMoth 1.2.0/LunaMoth 1.1.0, firmware version 1.7.1, medium gain, deployed at 2 m height on a tree trunk). This resulted in fifteen one-minute recordings per site per round, minus six recordings that were not classified due to technical problems, totalling 5844 recordings and encompassing almost 100 h of recording time).

Species richness for each recording was determined by a single ornithologist who classified all audible bird species in each one-minute recording. Each recording was played once or twice, depending on the level of background noise (e.g., quality reduced due to noise generated by the recorder, wind or traffic). Playback was conducted using Windows Media Player at maximum volume to enhance the audibility of distant or faint bird calls, and recordings were listened to through JBL TUNE 510BT or JBL WAVE BEAM headphones.

Each recording was down-sampled from 192 kHz to 96 kHz, 48 kHz, and 24 kHz, using the R packages seewave, tuneR, doParallel and foreach (Ligges et al., 2023; Microsoft Corporation, Weston, S, 2022a; Microsoft Corporation, Weston, S, 2022b; Sueur et al., 2008a). Subsequently, the ACI and BI were calculated for each variant of all recordings using the soundecology package (Villanueva-Rivera and Pijanowski, 2018).

A total of 14 variants of the ACI and the BI were calculated for each sampling rate. In the first step, we applied the default settings provided by the soundecology package for the frequency range limitation of ACI (Minfreq = 0 kHz, Maxfreq = Nyquist) and BI (Minfreq = 2 kHz, Maxfreq = 8 kHz). In the next step, we restricted the frequency range to 0.5–10.0 kHz, an ecologically relevant bandwidth, as most bird species in Białowieża Forest vocalize within this range (i.e., pigeons at the lower end, 0.5 kHz, and tits and Regulidae at the higher end, 10 kHz; Budka et al., 2023). In both steps, we applied seven different FFT window lengths (64, 128, 256, 512, 1024, 2048 and 4096), keeping the AIC *j* parameter constant at 5 s (i.e., the complexity of the soundscape is assessed in time windows of 5 s and then averaged for the entire one-minute recording; Pieretti et al., 2011). For three combinations of technical parameters (i.e., a sampling rate of 96 kHz in combination with an FFT window length of 64 or a sampling rate of 192 kHz and an FFT window length of 64 and 128, all with an adjusted frequency range; i.e., 0.5 to 10 kHz), the ACI could not be calculated because the FFT window length was too short relative to the sampling rate. These combinations were therefore excluded from the analyses. In total, 53 and 56 variants of the ACI and the BI were calculated, respectively.

The analyses were divided into three parts. In the first part, to assess how FFT window length and sampling rate affected the relationship between ACI and BI and species richness, we created linear mixed-effects models for each variant of the indices (i.e., calculated for each combination of FFT, sampling rate, and frequency range). In these models, the scaled ACI and BI (mean = 0, SD = 1 for each combination of FFT and sampling rate) were modelled as a function of species richness, with location ID and the date-time as random effects (lme4 package; Bates et al., 2015). The model formula was therefore: richness ~ index + (1|location ID) + (1|date time). We extracted the model estimates for richness (mean and 95 % CI) using the lmerTest package (Kuznetsova et al., 2017).

In the second part of the analyses, to assess how technical parameters influenced the richness-index relationship of ACI and BI in different habitats, we created linear mixed-effects models for each variant of each index, as in the first part. However, here we included habitat as an interaction with species richness. The model formula was therefore: richness ~ index * habitat + (1|location ID) + (1|date time). We then extracted the estimates for richness in each habitat (mean and 95 % CI) using sim_slopes function from the interactions package (Long, 2024).

To evaluate the model performance, we calculated the marginal and the conditional R^2 (hereafter R^2_m and R^2_c, respectively) for each model using the r.squaredGLMM-function from the MuMIn-package (Bartoń, 2025). In addition, we calculated the correlation between predicted and true species richness for each model. Finally, we performed a 10-fold cross-validation on each model using the cv-function from the cv package (Fox and Monette, 2023), to calculate the mean squared error (MSE) and the root mean squared error (RMSE) of each model, with RMSE providing the mean error in the same units as the response variable (i.e., species richness; Hodson, 2022).

In the third part of the analyses, to assess how technical parameters affected the correlation between the ACI and BI, we calculated Pearson correlations for all variants of these indices. All analyses were conducted in R version 4.4.1 (R Core Team, 2024). Data processing (i.e., preparing the data for the analysis) was performed using the tidyverse (Wickham et al., 2019), and data visualization was carried out with ggplot2 (Wickham, 2016), ggstance (for vertical dodging of points and error bars using position_dodgev; Henry et al., 2024), and corrplot (for visualizing the correlation matrix; Wei and Simko, 2024).

3. Results

The richness-index relationship of the ACI and BI ranged from significantly positive to significantly negative, depending on the recording's sampling rate and the FFT window length (Fig. 2). The effect of sampling rate and window length on the relationship between the ecoacoustic index and species richness appeared to be stronger for the ACI than for the BI. For each index, the adjusting the frequency range resulted in a stronger richness-index relationship (both for positive and negative correlations) compared to the default settings.

For the ACI, at a sampling rate of 24 kHz, the richness-index relationship was significantly positive, except for FFT = 128 and 64, for which the relationship was non-significant and negative, respectively. At higher sampling rates, more settings produced non-significant or even negative associations. For 192 kHz, the default settings did not result in a significantly positive relationships at all, and the adjusted frequency range produced a positive relationship only at FFT = 2048 and 4096 (see Table S3.1 for the technical parameters and model output).

Regarding the BI, at sampling rates of 24 kHz and 48 kHz, all tested window lengths and frequency ranges produced a positive richness-index relationship. At 96 kHz, FFT = 64 resulted in a negative relationship for the default frequency range and a non-significant relationship for the adjusted frequency range. At higher sampling rates, more settings produced non-significant or even negative associations, but larger window lengths consistently yielded significantly positive relationships. The adjusted frequency range resulted in more significantly positive associations than the default settings (see Table S3.1 for the technical parameters and model output).

When forest habitats were assessed separately, the effects of the technical parameters on the relationship between the two acoustic indices (ACI and BI) and species richness varied across habitats. These relationships were generally strongest when the frequency range was adjusted (Figs. 3 and 4). For the ACI, most richness-index relationships were non-significant. However, logged spruce stands showed relatively many significantly positive relationships compared to other habitats. Farmland habitats displayed a distinct pattern: the richness-index relationships were significantly negative at larger FFT window lengths compared to those observed in forest habitats. For the BI, adjusting the frequency range resulted in significantly positive associations for most habitats and for most combinations of FFT and sampling rates. Farmland again deviated from this general pattern: most richness-index relationships were non-significant, and at high sampling rates (i.e., 96 kHz and 192 kHz), some smaller FFT window lengths even produced significantly negative associations (see Table S3.2 for the technical parameters and

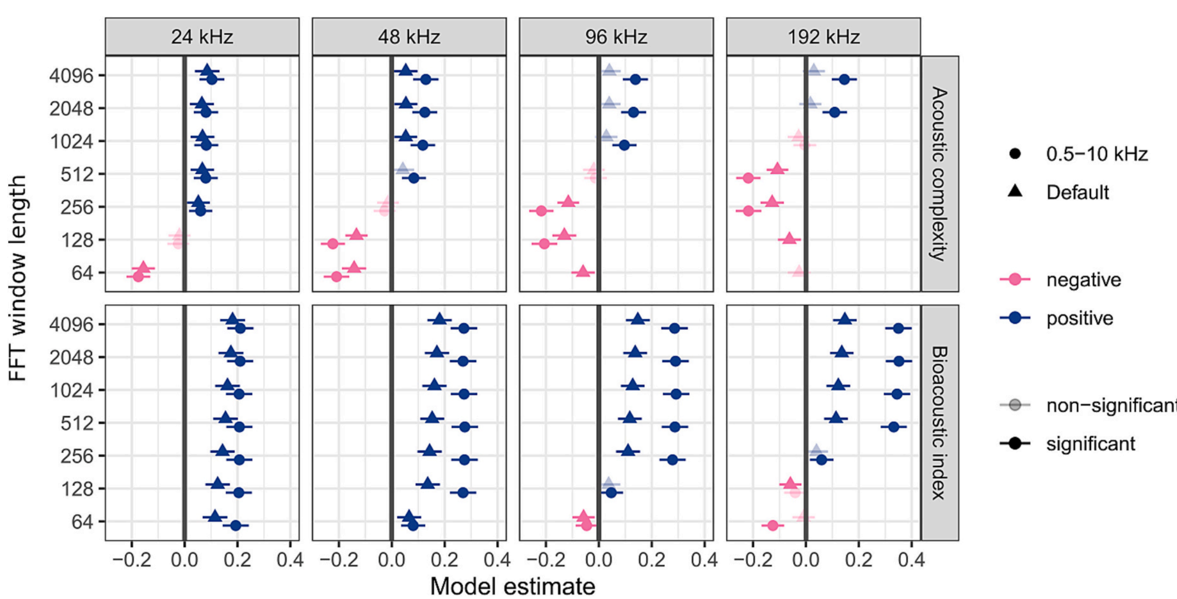

Fig. 2. Richness-index relationships of the scaled values of ACI and BI (scaled to mean = 0, SD = 1; mean model estimates with 95 % CI), as estimated by mixed effect models, for different combinations of sampling rates (24, 48, 96, or 192 kHz), FFT window lengths (64, 128, 256, 512, 1024, 2048, or 4096) and frequency ranges (0.5–10 kHz, indicated with circles; and the default frequency ranges, i.e., 0 kHz–Nyquist frequency for ACI and 2–8 kHz for BI, indicated with triangles). The vertical solid line indicates no effect, positive effects (right) are shown in blue, negative effects (left) in pink, and non-significant responses ($p > 0.05$) are shown as transparent. Points are vertically dodged to avoid overlapping. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

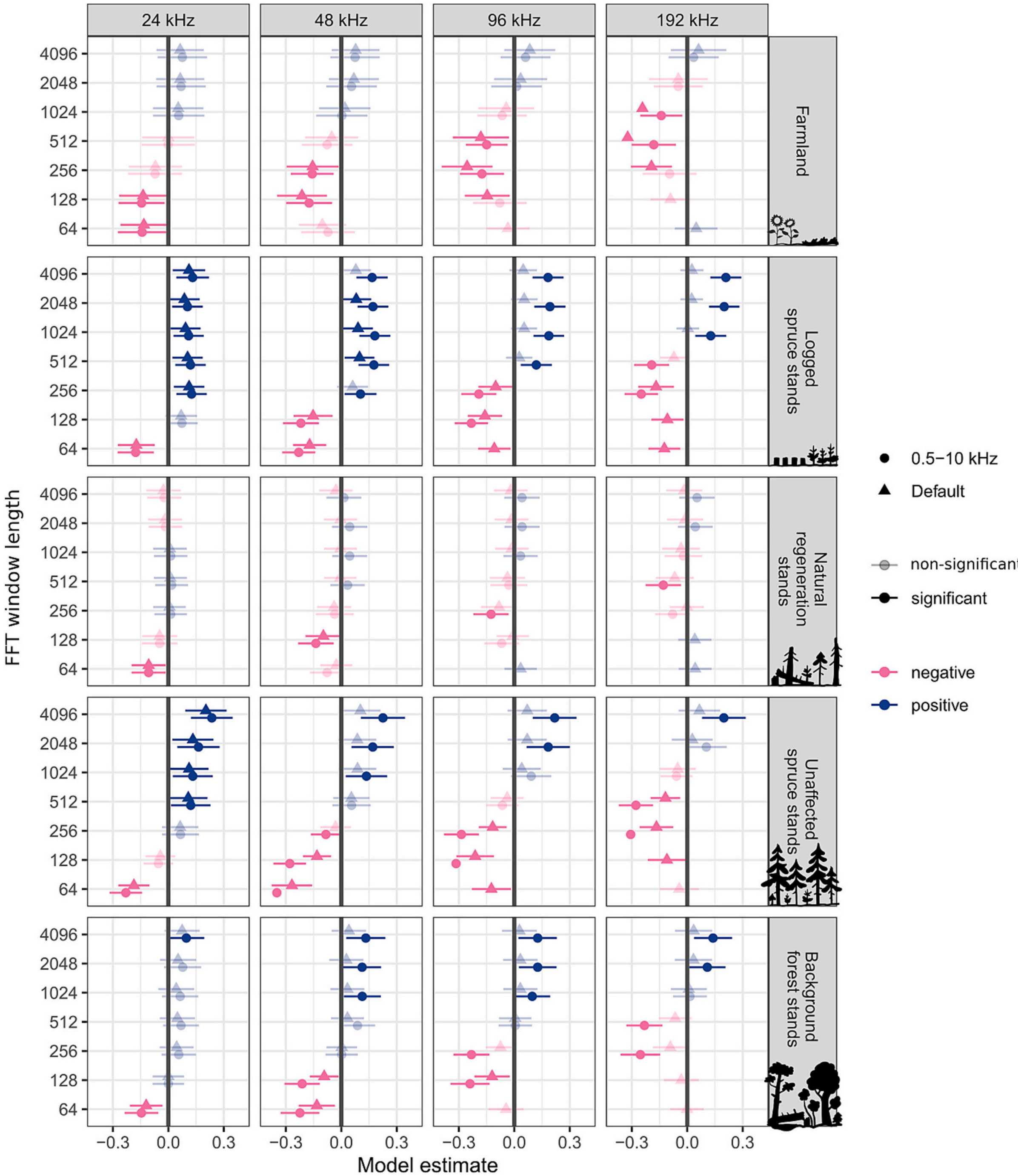

Fig. 3. The richness-index relationships of scaled values of ACI (scaled to mean = 0, SD = 1; mean model estimates with 95 % CI), as estimated by mixed effect models, for different combinations of sampling rates (24, 48, 96, or 192 kHz), FFT window lengths (64, 128, 256, 512, 1024, 2048, or 4096) and frequency ranges (0.5–10 kHz indicated with circles; default frequency range, i.e., 0 kHz–Nyquist frequency, indicated with triangles) in four forest habitats and the adjacent farmland. The vertical solid line indicates no effect; positive effects (right) are shown in blue, negative effects (left) in pink, and non-significant responses ($p > 0.05$) are shown as transparent. Points are vertically dodged, to avoid overlapping. Habitat icons were created by Tomek Samojlik. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

model output).

Most variants of the ecoacoustic indices were positively correlated with each other (Fig. 5). However, ACI variants calculated with small FFT window lengths were negatively correlated with all BI variants, except for a near-zero correlation with the BI calculated using FFT window length of 64 and a sampling rate of 192 kHz. Additionally, ACI variants calculated using small FFT window lengths were negatively correlated with ACI variants calculated using large FFT window lengths. This pattern was more pronounced at high sampling rates. When default settings were used, the correlations between ACI and BI —both positive and negative—were weaker.

4. Discussion

Our results demonstrate that the relationship between bird species richness and the ecoacoustic indices analyzed here—the ACI and BI—, as well as the correlation between these indices for the same recording, strongly depends on the recording's sampling rate and the calculation

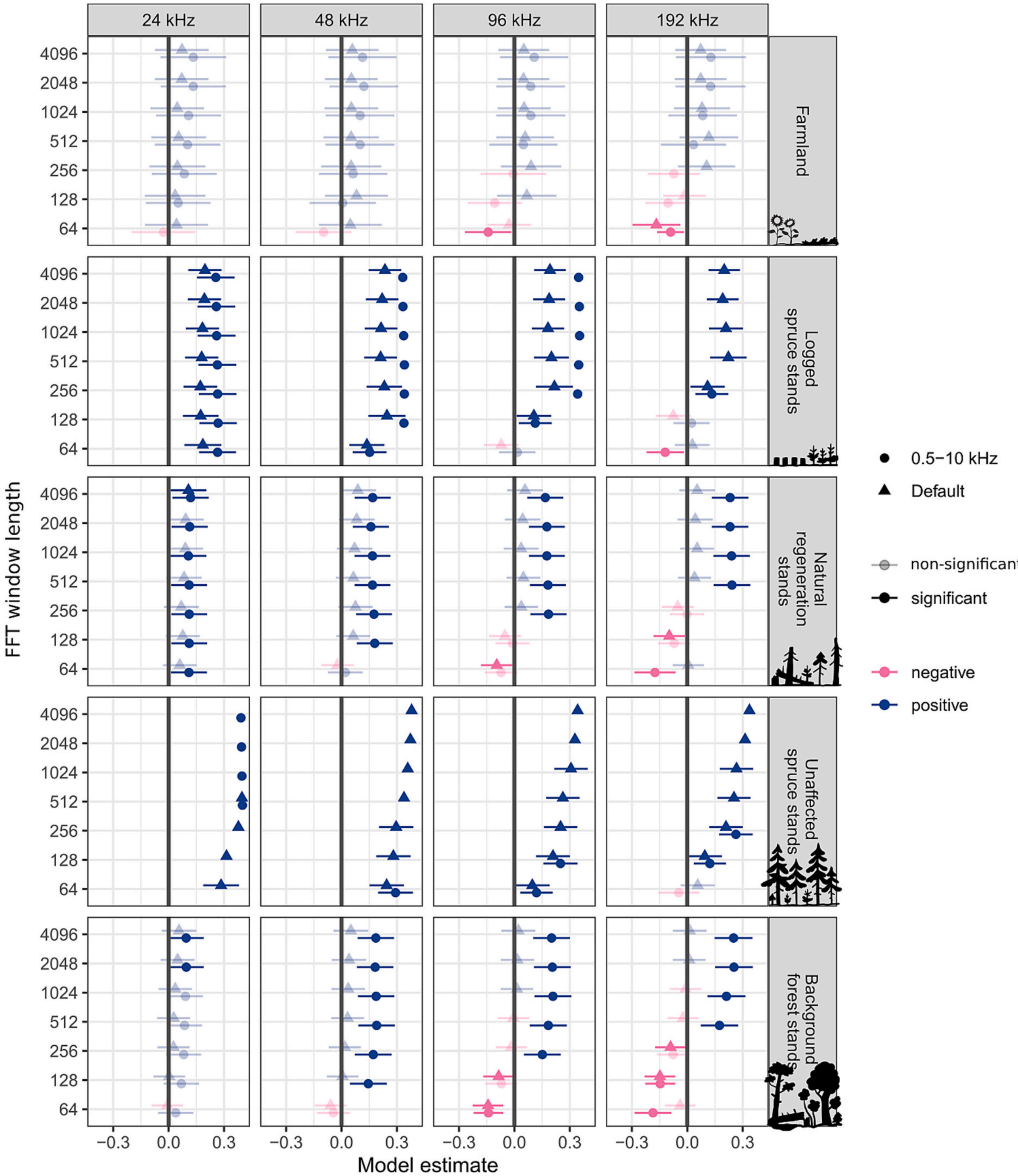

Fig. 4. The richness-index relationships of scaled values of BI (scaled to mean = 0, SD = 1; mean model estimates with 95 % CI), as estimated by mixed effect models, for different combinations of sampling rates (24, 48, 96, or 192 kHz), FFT window lengths (64, 128, 256, 512, 1024, 2048, or 4096) and frequency ranges (0.5–10 kHz, indicated with circles; default frequency range, i.e., 2–8 kHz, indicated with triangles) in four forest habitats and the adjacent farmland. The vertical solid line indicates no effect, positive effects (right) are shown in blue, negative effects (left) in pink, and non-significant responses ($p > 0.05$) are indicated as transparent. Points are vertically dodged, to avoid overlapping. Habitat icons were created by Tomek Samojlik. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

settings, including the FFT window length and the frequency range. For the same set of recordings, different technical parameters can cause the index-index correlation and the richness-index relationship to shift from significantly positive to significantly negative. This means that ecosystems with a complex soundscape and a high species richness could get a lower acoustic complexity index value compared to ecosystems with a less complex soundscape and a lower species richness, merely due to the combination of technical parameters. Therefore, calculation settings should be applied carefully when using these indices as proxies for species richness. Adjusting the calculation settings of ecoacoustic indices (i.e., limiting the frequency range and modifying the FFT window length) enhanced their effectiveness in representing bird species richness, confirming the hypotheses proposed in the introduction. Technical parameters considerably affect the relationship between the ACI and BI and the bird species richness, and appropriate adjustments of the calculation settings improve their performance. Between the two indices, the BI proved to be more robust to changes in sampling rate and FFT window length than ACI. Interestingly, the strength of the

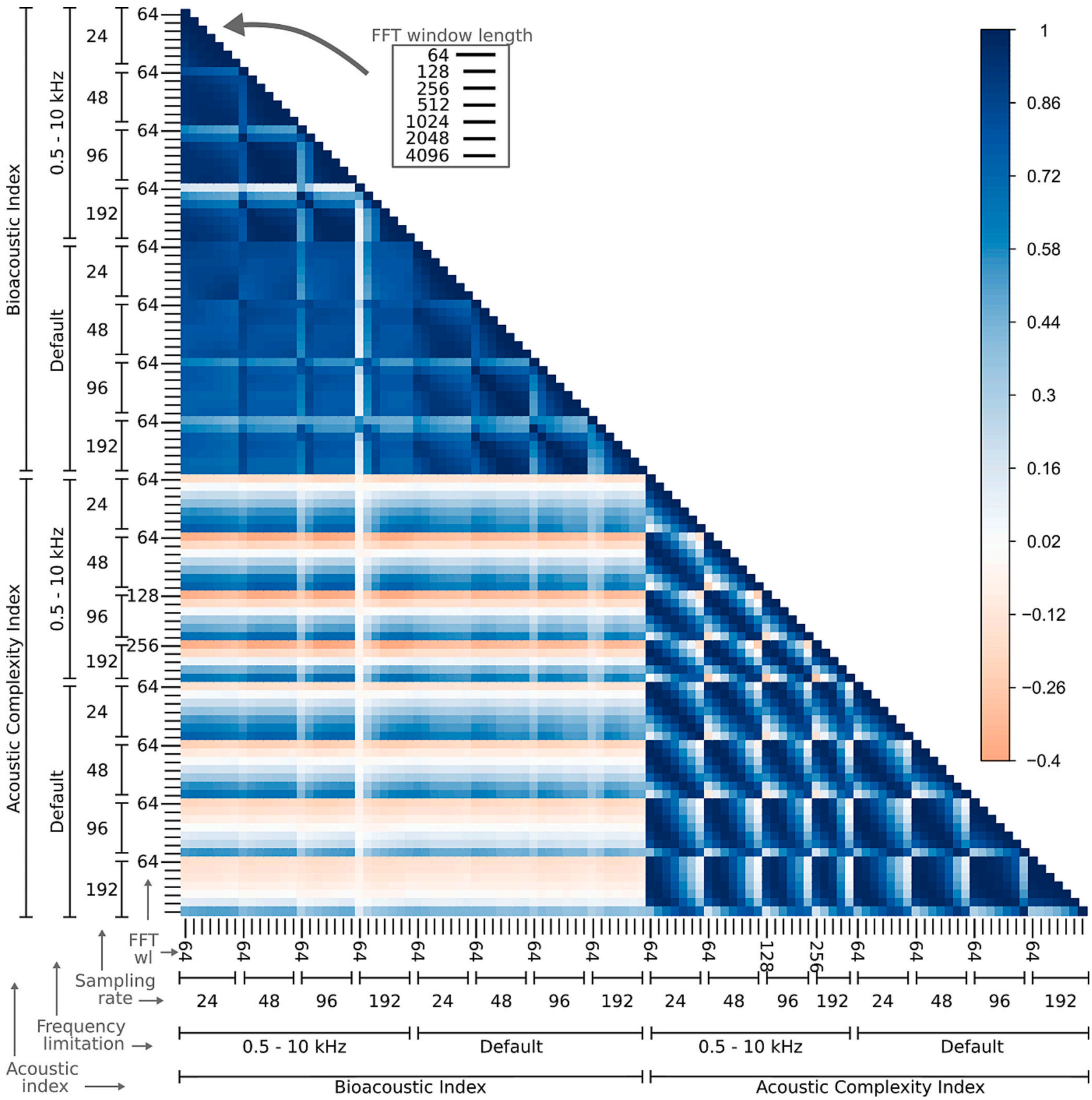

Fig. 5. Correlation matrix showing Pearson correlation coefficients among all variants of the ACI and BI, calculated for two frequency range limitation settings, four different sampling rates and seven different FFT window lengths (FFT wl). To improve the readability of the figure axes, not all FFT window lengths are shown. Instead, an enlarged fragment of the axes is shown to indicate the order at which the FFT window lengths occur.

association between ecoacoustic indices and bird species richness, as well as the effect of technical parameters on this relationship, also depended on habitat type, indicating the uneven effectiveness of acoustic indices in predicting species richness across habitats, even within the same study site. These results have important implications for the application and interpretation of these ecoacoustic indices. In the following discussion, we explore how these factors may influence the outcomes of studies using these indices and provide practical recommendations that, in our opinion, can greatly enhance the effectiveness of the ACI and the BI.

Across ecosystems and biomes, distinct sampling rates are used to capture the soundscapes (Darras et al., 2025), as the sampling rate must be tailored to the studied species, taxa, or soundscape —it should be at least twice the maximum frequency of the target sounds, according to the Nyquist-Shannon Sampling Theorem (Shannon, 1948; Sugai et al., 2020). When applying the BI and ACI as proxies for bird species richness, particularly the ACI, we demonstrated that different sampling rates require specific FFT window length settings to maintain a consistent richness-index relationship. Originally, the ACI was calculated using recordings with a sampling rate of 22.05 kHz and an FFT window length of 512, resulting in a temporal resolution of 0.023 s and a spectral resolution of 43 Hz (Pieretti et al., 2011). Currently, a 48 kHz sampling rate is commonly used for monitoring bird species richness (e.g., Farina and Mullet, 2025; Jorge et al., 2018; Mueller et al., 2024), often combined with an FFT window length of 512—the default setting in the *soundecology* R-package (Villanueva-Rivera and Pijanowski, 2018). In our study, this combination of parameters still produced a positive richness-index relationship, despite the resulting resolution of 0.011 s per 94 Hz differing from the initially assumed values. Therefore, with these parameters, the ACI likely still reflects bird species richness appropriately. However, higher sampling rates may be required when monitoring birds alongside other taxa, such as bats. This was the reason why we recorded at 192 kHz sampling rate in this study and why, for example, Fairbrass et al. (2017) used 96 kHz sampling rate in their work. Applying small FFT window length (like the default of 512 in the ACI calculation) to high sampling rate recordings (e.g., 192 kHz) may render the ACI to a misleading proxy for bird species richness due to the resulting high temporal (0.003 s) but low spectral (375 Hz) resolution. Indeed, a study combining a high sampling rate (192 kHz) with a small FFT window length (512) reported a negative association between bird species richness and the ACI (Shamon et al., 2021). According to our findings, such a combination of sampling rate and FFT window length is not optimal for reflecting bird species richness and fails to capture the soundscape complexity that the index was originally designed to measure. Given the growing popularity of ecoacoustic indices in ecological studies, it is important to recognize this limitation of the ACI. Moreover, generalizing the effectiveness of ecoacoustic indices—particularly the ACI—based on studies using different sampling rates and calculation settings (Alcocer et al., 2022; Bateman and Uzal, 2022) may lead to misleading conclusions. Another issue is the lack of implementation of a background filter on the Discrete Fourier Transform, which removes all frequency components below a certain amplitudes threshold in the spectrogram (Farina, 2025; Farina et al., 2021).

Hence, when calculating ecoacoustic indices, particularly the ACI, we recommend adjusting the FFT window length to match the recording's sampling rate to maintain the index's relationship with species richness. In general, higher sampling rates require proportionally larger FFT window lengths to achieve comparable temporal and spectral resolution in sound analysis. As explained above, the ACI was originally calculated using a 512-point FFT window length for recordings at 22.05 kHz (Pieretti et al., 2011); therefore, a sampling rate of 192 kHz would require an FFT window length of approximately 4096 to achieve comparable temporal and spectral resolution, as confirmed by our results. Additionally, the combination of recording sampling rate and FFT window length allows adjustment of the soundscape analysis resolution to the acoustic characteristics of the studied animal assemblage. Increasing the FFT window length improves the spectral resolution but reduces the temporal resolution, which can be appropriate for communities where most species produce long, narrow-band vocalizations. Conversely, decreasing the FFT window length may be more suitable for vocalizations with short, wide-band frequency elements.

In addition, we recommend adjusting the calculation settings to align with local ecological and, in particular, acoustic conditions. First, in line with previous studies, we advise tailoring the frequency range used in the index calculation to the frequency band of focal animal vocalizations in the study area (Metcalf et al., 2021). As we have shown, this adjustment strengthens the association with species richness, and by excluding low frequencies, helps minimize the effects of background noise and recorder's self-noise. Second, we observed that the association between the tested indices and bird species richness varied among habitats. This suggests that identical technical parameters may produce different richness-index relationships across habitats due to habitat-driven variations in bird song characteristics (Morton, 1975), species composition, and soundscape phenology (Budka et al., 2023).

Moreover, in our study the richness-index relationships obtained for farmland differed remarkably for both indices, suggesting that the farmland soundscape itself differs substantially from forest soundscapes due to, for example, distinct geophony characteristics and higher human presence and anthropophony (for a more detailed explanation and the NDSI, see S4). In addition, the high complexity of the songs of species forming the assemblages and the primary nature of the Białowieża Primeval Forest may have amplified differences in acoustic complexity between habitats, particularly between forest and farmland. In forest, the high number of vocalizing species within a small area must efficiently share the common acoustic environment (Krause, 1993). Therefore, we strongly advise against using the ACI and BI without first testing of their suitability to reflect local components of diversity. We recommend calculating these components (e.g., species richness) based on direct observations, such as manual classification for at least a subset of recordings, and testing various FFT window lengths to identify the optimal calculation settings. Adjusting the calculation settings to the local ecosystem will enhance the ability of the index to represent the diversity components within the study area and may facilitate the comparability of the indices across studies and regions.

In addition to the importance to disentangling ecological effects from the influence of technical parameters, which are the primary focus of this study, the interpretation of ecoacoustic indices as proxies for bird species richness should be approached with caution. Although richness-index relationships reported here were significant, the proportion of index variance explained by species richness was relatively limited, as indicated by the low R^2_m values obtained for the models. Most of the variation was instead attributable to random effects, namely recording location and time of recording (Table S3.1 and S3.2). This suggests that, in near-natural temperate forests, the acoustic indices analyzed here reflect the overall acoustic environment at the recording point, shaped not only by species richness but also by species composition, the abundance of individual species, and their population densities. Consequently, ecoacoustic indices should be interpreted cautiously when used as proxies for bird species richness.

4.1. Conclusions and practical recommendations

We conclude that the effectiveness of the ACI and the BI in representing bird species richness depends on technical parameters. Any default settings in the software should therefore be regarded as a simplification rather than a standard. When calculating ecoacoustic indices, particularly the ACI, we recommend adjusting the FFT window length to match the sampling rate of the recordings. In general, higher sampling rates require proportionally larger FFT window lengths to achieve comparable temporal and spectral resolution in sound analysis. The combination of the recording sampling rate and the chosen FFT window length, together with other calculation settings, allows the temporal and spectral resolution of the analysis to be tailored to the local ecological and acoustic characteristics of the vocalizing animal assemblages. An alternative is to use an index that does not require the specifying the FFT window length and is not affected by the sampling rate (e.g., the ADI, or its corrected version: the FADI; Villanueva-Rivera et al., 2011; Xu et al., 2023). Moreover, we strongly advise estimating diversity components (e.g., species richness) based on direct observations, such as manual classification, for at least a subset of recordings and testing various FFT window lengths to determine the optimal calculation settings.

CRediT authorship contribution statement

Rosanne J. Michielsen: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Dominika Koprowska:** Resources, Project administration, Investigation, Data curation. **Grzegorz Mikusiński:** Writing – review & editing, Supervision. **Michał Walesiak:** Writing – review & editing, Methodology, Data curation. **Marcin Zegarek:** Resources, Methodology. **Michał Żmihorski:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Michał Budka:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Conceptualization.

Ethics statement

This study was conducted following Polish law and with the necessary permissions from Białowieża National Park (Permit received on 14th of February 2022, case number: PN.51.09.2022).

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used chatGPT in order to improve the language and readability of the manuscript. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Funding

This research was funded in whole by National Science Centre, Poland (grant number: 2020/39/B/NZ8/03175). For the purpose of Open Access, the author has applied a CC-BY public copyright licence to any Author Accepted Manuscript (AAM) version arising from this submission.

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 are grateful to Taylor Shaw for her advice regarding soundscape analyses and to Doriane Hagnier, Rik Nienhuis, Flora van Eupen, Ewa Komar, Ireneusz Ruczyński and Beata Bramorska for their help with installing the recorders in the forest. We thank Tomasz Samojlik for creating the forest icons and Alexandra Elbakyan for supporting this study. We also acknowledge Białowieża National Park for granting us access to conduct research in this precious forest. Finally, we thank the anonymous reviewers for their suggestions which helped improve the manuscript.

Data availability

The replication data can be accessed via: Michielsen et al., 2025 and the R scripts can be obtained here: https://github.com/R00s90/Acoustic-indices-and-bird-species-richness.

References

Alcocer, I., Lima, H., Sugai, L.S.M., Llusia, D., 2022. Acoustic indices as proxies for biodiversity: a meta-analysis. Biol. Rev. 97, 2209–2236. https://doi.org/10.1111/brv.12890.

Allen, J.B., Rabiner, L.R., 1977. A unified approach to short-time Fourier analysis and synthesis. Proc. IEEE 65, 1558–1564. https://doi.org/10.1109/PROC.1977.10770.

Allen-Ankins, S., McKnight, D.T., Nordberg, E.J., Hoefer, S., Roe, P., Watson, D.M., McDonald, P.G., Fuller, R.A., Schwarzkopf, L., 2023. Effectiveness of acoustic indices as indicators of vertebrate biodiversity. Ecol. Indic. 147, 109937. https://doi.org/10.1016/j.ecolind.2023.109937.

Bartoń, K., 2025. MuMIn: Multi-Model Inference. Contributed Packages, CRAN. https://doi.org/10.32614/CRAN.package.MuMIn.

Bateman, J., Uzal, A., 2022. The relationship between the acoustic complexity index and avian species richness and diversity: a review. Bioacoustics 31, 614–627. https://doi.org/10.1080/09524622.2021.2010598.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

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, 2137–2144. https://doi.org/10.1890/07-0004.1.

Bradfer-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.

Bradfer-Lawrence, T., Duthie, B., Abrahams, C., Adam, M., Barnett, R.J., Beeston, A., Darby, J., Dell, B., Gardner, N., Gasc, A., Heath, B., Howells, N., Janson, M., Kyoseva, M.V., Luypaert, T., Metcalf, O.C., Nousek-McGregor, A.E., Poznansky, F., Ross, S.R.P.J., Sethi, S., Smyth, S., Waddell, E., Froidevaux, J.S.P., 2024. The acoustic index user's guide: a practical manual for defining, generating and understanding current and future acoustic indices. Methods Ecol. Evol. 2024, 1–11. https://doi.org/10.1111/2041-210X.14357.

Budka, M., Sokołowska, E., Muszyńska, A., Staniewicz, A., 2023. Acoustic indices estimate breeding bird species richness with daily and seasonally variable effectiveness in lowland temperate Białowieża forest. Ecol. Indic. 148. https://doi.org/10.1016/j.ecolind.2023.110027.

Budka, M., Gazda-Szypulski, G., Muszyńska, A., Sokołowska, E., Staniewicz, A., Bogawski, P., 2024. Acoustic indices enable the discrimination of temperate forest types and better predict differences in bird species composition than in bird species richness. Environ. Sustain. Indic. 24. https://doi.org/10.1016/j.indic.2024.100529.

Cooley, J.W., Tukey, J.W., 1965. An algorithm for the machine calculation of complex Fourier series. Math. Comput. 19, 297. https://doi.org/10.2307/2003354.

Darras, K.F.A., Rountree, R.A., Van Wilgenburg, S.L., Cord, A.F., Pitz, F., Chen, Y., Dong, L., Rocquencourt, A., Desjonquères, C., Diaz, P.M., Lin, T., Turco, T., Emmerson, L., Bradfer-Lawrence, T., Gasc, A., Marley, S., Salton, M., Schillé, L., Wensveen, P.J., Wu, S., Acero-Murcia, A.C., Acevedo-Charry, O., Adam, M., Aguzzi, J., Akoglu, I., Amorim, M.C.P., Anders, M., André, M., Antonelli, A., Do Nascimento, L.A., Appel, G., Archer, S., Astaras, C., Atemasov, A., Atkinson, J., Attia, J., Baltag, E., Barbaro, L., Basan, F., Batist, C., Baumgarten, J.E., Bayle Sempere, J.T., Bellisario, K., David, A. Ben, Berger-Tal, O., Bertucci, F., Betts, M.G., Bhalla, I.S., Bicudo, T., Bolgan, M., Bombaci, S., Bota, G., Boullhesen, M., Briers, R. A., Buchan, S., Budka, M., Burchard, K., Buscaino, G., Calvente, A., Campos-Cerqueira, M., Gonçalves, M.I.C., Ceraulo, M., Cerezo-Araujo, M., Cerwén, G., Chaskda, A.A., Chistopolova, M., Clark, C.W., Cox, K.D., Cretois, B., Czarnecki, C., da Silva, L.P., da Silva, W., De Clippele, L.H., de la Haye, D., de Oliveira Tissiani, A.S., de Zwaan, D., Degano, M.E., Deichmann, J., del Rio, J., Devenish, C., Díaz-Delgado, R., Diniz, P., Oliveira-Júnior, D.D., Dorigo, T., Dröge, S., Duarte, M., Duarte, A., Dunleavy, K., Dziak, R., Elise, S., Enari, H., Enari, H.S., Erbs, F., Eriksson, B.K., Ertör-Akyazi, P., Ferrari, N.C., Ferreira, L., Fleishman, A.B., Fonseca, P.J., Freitas, B., Friedman, N.R., Froidevaux, J.S.P., Gogoleva, S., Gonzaga, C., Correa, J.M.G., Goodale, E., Gottesman, B., Grass, I., Greenhalgh, J., Gregoire, J., Haché, S., Hagge, J., Halliday, W., Hammer, A., Hanf-Dressler, T., Haupert, S., Haver, S., Heath, B., Hending, D., Hernandez-Blanco, J., Higgs, D., Hiller, T., Huang, J.C., Hutchinson, K.L., Hyacinthe, C., Ieronymidou, C., Iniunam, I. A., Jackson, J., Jacot, A., Jahn, O., Juanes, F., Kanes, K.S.J., Kenchington, E., Kepfer-Rojas, S., Kitzes, J., Kusuminda, T., Lehnardt, Y., Lei, J., Leitman, P., León, J., Li, D., Lima-Santos, C.S., Lloyd, K.J., Looby, A., López-Baucells, A., López-Bosch, D., Louth-Robins, T., Maeda, T., Malige, F., Mammides, C., Marcacci, G., Markolf, M., Marques, M.I., Martin, C.W., Martin, D.A., Martin, K., McArthur, E., McKown, M., McLeod, L.J.T., Médoc, V., Metcalf, O., Meyer, C.F.J., Mikusinski, G., Miller, B., Monteiro, J., Mooney, T.A., Moreira, S., Sugai, L.S.M., Morris, D., Müller, S., Muñoz-Duque, S., Murchy, K.A., Nagelkerken, I., Mas, M., Nouioua, R., Ocampo-Ariza, C., Olden, J.D., Oppel, S., Osiecka, A.N., Papale, E., Parsons, M., Pashkevich, M., Patris, J., Marques, J.P., Pérez-Granados, C., Piatti, L., Pichorim, M., Pine, M.K., Pinheiro, T., Pradervand, J., Quinn, J., Quintella, B., Radford, C., Raick, X., Rainho, A., Ramalho, E., Ramesh, V., Rétaux, S., Reynolds, L.K., Riede, K., Rimmer, T., Ríos, N., Rocha, R., Rocha, L., Roe, P., Ross, S.R.P.-J., Rosten, C.M., Ryan, J., Salustio-Gomes, C., Samarra, F.I.P., Samartzis, P., Santos, J., Sattler, T., Scharffenberg, K., Schoeman, R.P., Schuchmann, K., Sebastián-González, E., Seibold, S., Sethi, S., Shabangu, F.W., Shaw, T., Shen, X., Singer, D., Širović, A., Slater, M., Spriel, B., Stanley, J., Sueur, J., da Cunha Tavares, V., Thomisch, K., Thorn, S., Tong, J., Torrent, L., Traba, J., Tremblay, J.A., Trevelin, L., Tseng, S., Tuanmu, M., Valverde, M., Vernasco, B., Vieira, M., da Paz, R.V., Ward, M., Watson, M., Weldy, M.J., Wiel, J., Willie, J., Wood, H., Xu, J., Zhou, W., Li, S., Sousa-Lima, R., Wanger, T.C., 2025. Worldwide soundscapes: a synthesis of passive acoustic monitoring across realms. Glob. Ecol. Biogeogr. 34. https://doi.org/10.1111/geb.70021.

Depraetere, 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, 46–54. https://doi.org/10.1016/j.ecolind.2011.05.006.

Diaz, S.D.U., Gan, J.L., Tapang, G.A., 2023. Acoustic indices as proxies for bird species richness in an urban green space in metro Manila. PLoS One 18, e0289001. https://doi.org/10.1371/journal.pone.0289001.

Fairbrass, A.J., Rennett, 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.

Farina, A., 2025. The acoustic complexity index (ACI): theoretical foundations, applied perspectives and semantics. Oikos 2025, 1–17. https://doi.org/10.1111/oik.10760.

Farina, A., Mullet, T.C., 2025. The Sonoscape of a rural town in the Mediterranean region: a case study of Fivizzano. Acoustics 7, 23. https://doi.org/10.3390/acoustics7020023.

Farina, A., Mullet, T.C., Bazarbayeva, T.A., Tazhibayeva, T., Bulatova, D., Li, P., 2021. Perspectives on the ecological role of geophysical sounds. Front. Ecol. Evol. 9, 1–11. https://doi.org/10.3389/fevo.2021.748398.

Fox, J., Monette, G., 2023. cv: Cross-Validating Regression Models. CRAN: Contributed Packages. https://doi.org/10.32614/CRAN.package.cv.

Gasc, A., Sueur, J., Jiguet, F., Devictor, V., Grandcolas, P., Burrow, C., Depraetere, 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.

Henry, L., Wickham, H., Chang, W., 2024. ggstance: Horizontal "ggplot2" Components. R package version 0 (3), 7.
Hodson, T.O., 2022. Root-mean-square error (RMSE) or mean absolute error (MAE): when to use them or not. Geosci. Model Dev. 15, 5481–5487. https://doi.org/10.5194/gmd-15-5481-2022.
Jaroszewicz, B., Cholewińska, O., Gutowski, J.M., Samojlik, T., Zimny, M., Latałowa, M., 2019. Białowieza forest-a relic of the high naturalness of European forests. Forests 10, 1–28. https://doi.org/10.3390/f10100849.
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.
Kamińska, A., Lisiewicz, M., Kraszewski, B., Stereńczak, K., 2021. Mass outbreaks and factors related to the spatial dynamics of spruce bark beetle (Ips typographus) dieback considering diverse management regimes in the Białowieża forest. For. Ecol. Manag. 498. https://doi.org/10.1016/j.foreco.2021.119530.
Kemp, J., Azofeifa-Solano, J.C., Barneche, D.R., Brooker, R., Arévalo, J.E., Erbe, C., Parsons, M., 2025. Impact of acoustic index parameters on soundscape comparisons. Methods Ecol. Evol. 16, 872–885. https://doi.org/10.1111/2041-210X.70007.
Krause, B., 1993. The niche hypothesis. Soundscape Newsl. 06, 1–5.
Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. J. Stat. Softw. 82, 1–26. https://doi.org/10.18637/JSS.V082.I13.
Ligges, U., Krey, S., Mersmann, O., Schnackenberg, S., 2023. tuneR: analysis of music and speech.
Long, J.A., 2024. Interactions: comprehensive, user-friendly toolkit for probing Interactions. https://doi.org/10.32614/CRAN.package.interactions.
MacPhail, A.G., Yip, D.A., Knight, E.C., Hedley, R., Knaggs, M., Shonfield, J., Upham-Mills, E., Bayne, E.M., 2024. Audio data compression affects acoustic indices and reduces detections of birds by human listening and automated recognisers. Bioacoustics 33, 74–90. https://doi.org/10.1080/09524622.2023.2290718.
McGrann, M.C., Wagner, B., Klauer, M., Kaphan, K., Meyer, E., Furnas, B.J., 2022. Using an acoustic complexity index to help monitor climate change effects on avian diversity. Ecol. Indic. 142, 109271. https://doi.org/10.1016/j.ecolind.2022.109271.
Metcalf, O.C., Barlow, J., Devenish, C., Marsden, S., Berenguer, E., Lees, A.C., 2021. Acoustic indices perform better when applied at ecologically meaningful time and frequency scales. Methods Ecol. Evol. 12, 421–431. https://doi.org/10.1111/2041-210X.13521.
Microsoft Corporation, Weston, S, 2022a. doParallel: Foreach Parallel Adaptor for the "parallel" Package (R package version 1.0.17).
Microsoft Corporation, Weston, S, 2022b. foreach: Provides Foreach Looping Construct (R package version 1.5.2).
Morton, E.S., 1975. Ecological sources of selection on avian sounds. Am. Nat. 109, 17–34. https://doi.org/10.1086/282971.
Mueller, S., Jahn, O., Jung, K., Mitesser, O., Ammer, C., Böhm, S., Ehbrecht, M., Farina, A., Renner, S.C., Pieretti, N., Schall, P., Tschapka, M., Wells, K., Scherer-Lorenzen, M., 2024. Temporal dynamics of acoustic diversity in managed forests. Front. Ecol. Evol. 12, 1392882. https://doi.org/10.3389/fevo.2024.1392882.
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, 868–873. https://doi.org/10.1016/j.ecolind.2010.11.005.
Pijanowski, B.C., Farina, A., Gage, S.H., Dumyahn, S.L., Krause, B.L., 2011a. What is soundscape ecology? An introduction and overview of an emerging new science. Landsc. Ecol. 26, 1213–1232. https://doi.org/10.1007/s10980-011-9600-8.
Pijanowski, B.C., Villanueva-Rivera, L.J., Dumyahn, S.L., Farina, A., Krause, B.L., Napoletano, B.M., Gage, S.H., Pieretti, N., 2011b. Soundscape ecology: the science of sound in the landscape. Bioscience 61, 203–216. https://doi.org/10.1525/bio.2011.61.3.6.
R Core Team, 2024. R: a language and environment for statistical computing. R version 4 (4), 1.
Rajan, S.C., Athira, K., Jaishanker, R., Sooraj, N.P., Sarojkumar, V., 2019. Rapid assessment of biodiversity using acoustic indices. Biodivers. Conserv. 28, 2371–2383. https://doi.org/10.1007/s10531-018-1673-0.
Robert, K., Jones, D.O.B., Tyler, P.A., Van Rooij, D., Huvenne, V.A.I., 2015. Finding the hotspots within a biodiversity hotspot: fine-scale biological predictions within a submarine canyon using high-resolution acoustic mapping techniques. Mar. Ecol. 36, 1256–1276. https://doi.org/10.1111/maec.12228.
Schroeder, K.M., McRae, S.B., 2020. Automated auditory detection of a rare, secretive marsh bird with infrequent and acoustically indistinct vocalizations. Ibis 162, 1033–1046. https://doi.org/10.1111/ibi.12805.
Shamon, H., Paraskevopoulou, Z., Kitzes, J., Card, E., Deichmann, J.L., Boyce, A.J., McShea, W.J., 2021. Using ecoacoustics metrices to track grassland bird richness across landscape gradients. Ecol. Indic. 120, 106928. https://doi.org/10.1016/j.ecolind.2020.106928.
Shannon, C.E., 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27, 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x.
Shaw, T., Hedes, R., Sandstrom, A., Ruete, A., Hiron, M., Hedblom, M., Eggers, S., Mikusiński, G., 2021. Hybrid bioacoustic and ecoacoustic analyses provide new links between bird assemblages and habitat quality in a winter boreal forest. Environ. Sustain. Indic. 11. https://doi.org/10.1016/j.indic.2021.100141.
Sueur, J., Aubin, T., Simonis, C., 2008a. Seewave, a free modular tool for sound analysis and synthesis. Bioacoustics 18, 213–226. https://doi.org/10.1080/09524622.2008.9753600.
Sueur, J., Pavoine, S., Hamerlynck, O., Duvail, S., 2008b. Rapid acoustic survey for biodiversity appraisal. PLoS One 3, e4065. https://doi.org/10.1371/journal.pone.0004065.
Sueur, J., Farina, A., Gasc, A., Pieretti, N., Pavoine, S., 2014. Acoustic indices for biodiversity assessment and landscape investigation. Acta Acust. united with Acust. 100, 772–781. https://doi.org/10.3813/AAA.918757.
Sugai, L.S.M., Desjonquères, C., Silva, T.S.F., Llusia, D., 2020. A roadmap for survey designs in terrestrial acoustic monitoring. Remote Sens. Ecol. Conserv. 6, 220–235. https://doi.org/10.1002/rse2.131.
UNESCO The World Heritage Committee, 2012. Bialowieza Forest World Heritage Site (33bis).
Villanueva-Rivera, L.J., Pijanowski, B.C., 2018. soundecology: soundscape ecology.
Villanueva-Rivera, L.J., Pijanowski, B.C., Doucette, J., Pekin, B., 2011. A primer of acoustic analysis for landscape ecologists. Landsc. Ecol. 26, 1233–1246. https://doi.org/10.1007/s10980-011-9636-9.
Wei, T., Simko, V., 2024. R package "corrplot": visualization of a correlation matrix (version 0.95) [software].
Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.
Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the tidyverse. J. Open Source Softw. 4, 1686. https://doi.org/10.21105/joss.01686.
Xu, Z., Yong Chen, L., Pijanowski, B.C., Zhao, Z., 2023. A frequency-dependent acoustic diversity index: a revision to a classic acoustic index for soundscape ecological research. Ecol. Indic. 155, 110940. https://doi.org/10.1016/j.ecolind.2023.110940.