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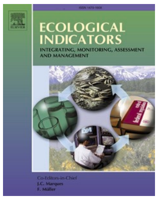

Original Articles

Effectiveness of acoustic indices as indicators of vertebrate biodiversity

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ABSTRACT

Effective monitoring tools are key for tracking biodiversity loss and informing management intervention strategies. Passive acoustic monitoring promises to provide a cheap and effective way to monitor biodiversity across large spatial and temporal scales, however, extracting useful information from long-duration audio recordings still proves challenging. Recently, a range of acoustic indices have been developed, which capture different aspects of the soundscape, and may provide a way to estimate traditional biodiversity measures. Here we investigated the relationship between 13 acoustic indices obtained from passive acoustic monitoring and biodiversity estimates of various vertebrate taxonomic groupings obtained from manual surveys at six sites spanning over 20 degrees of latitude along the Australian east coast. We found a number of individual acoustic indices that correlated well with species richness, Shannon's diversity index, and total individual count estimates obtained from traditional survey methods. Correlations were typically greater for avian and total vertebrate biodiversity than for anuran and non-avian vertebrate biodiversity. Acoustic indices also correlated better with species richness and total individual count than with Shannon's diversity index. Random forest models incorporating multiple acoustic indices provided more accurate predictions than single indices alone. Out of the acoustic indices tested, cluster count, mid-frequency cover and spectral density contributed the greatest predictive ability to models. Our results suggest that models incorporating multiple acoustic indices could be a useful tool for monitoring certain vertebrate groups. Further work is required to understand how site-specific variables can be incorporated into models to improve predictive capabilities and how to improve the monitoring of taxa besides avians, particularly anurans.

1. Introduction

Biodiversity loss is occurring worldwide, and is caused by a variety of factors, including invasive species (Clavero et al., 2009; Doherty et al., 2016), habitat loss (Brooks et al., 2002), and climate change (Pimm, 2009). This loss is severe enough for the current era to be classified as the sixth mass extinction event (Ceballos et al., 2015). Key to understanding and preventing biodiversity loss is effective monitoring, so that species declines can be detected, and the success of interventions and management strategies appropriately evaluated (Schmeller et al., 2015). Given the scale of biodiversity loss, traditional monitoring techniques that rely on manual surveys are unlikely to be sufficient, as they are impractical (expensive and time-consuming) to conduct on large temporal and spatial scales (Darras et al., 2019). Given that many taxa vocalise, emerging technologies such as passive acoustic monitoring may be viable alternatives to traditional surveys and might help facilitate the efficient and effective monitoring of biodiversity at the required scale (Acevedo & Villanueva-Rivera, 2006; Obrist et al., 2010; Sugai et al., 2019).

Recent advances in data storage have allowed the establishment of large-scale acoustic sensor networks, which may be useful for scaling biodiversity monitoring, because acoustic recorders can be deployed at many locations and survey the soundscape (i.e., the collection of sounds within an area) continuously (Digby et al., 2013; Roe et al., 2021). Many

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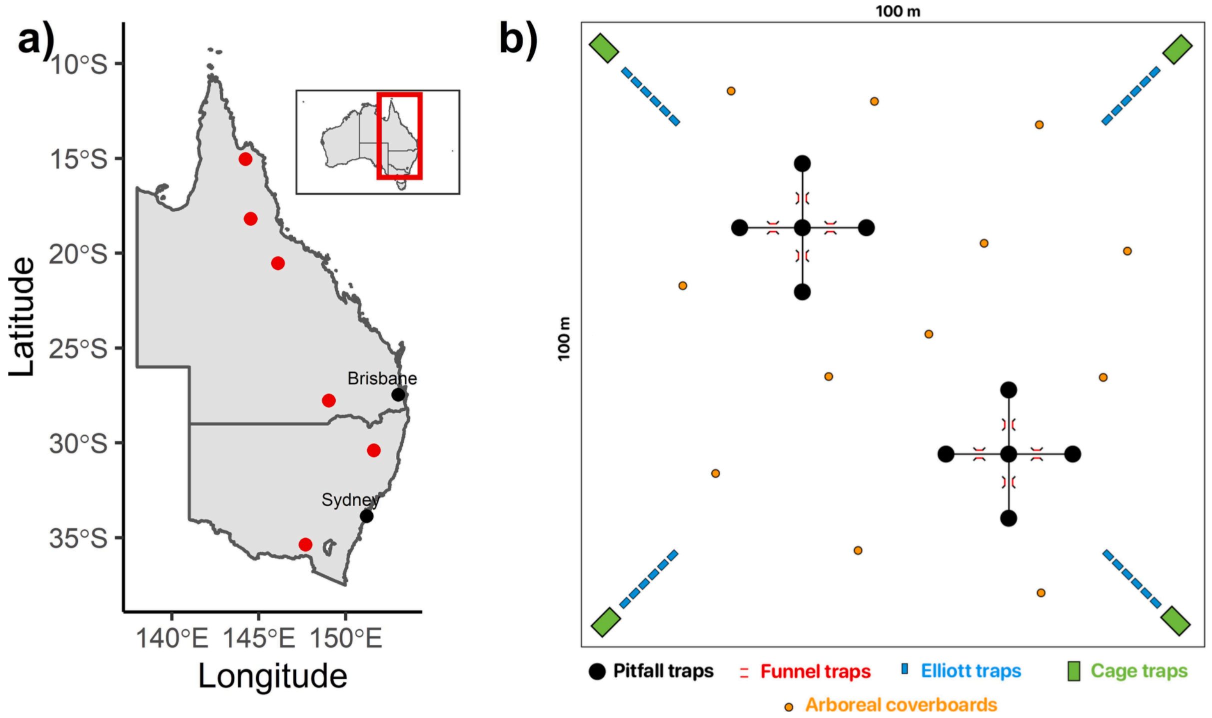

Fig. 1. A) Map showing the locations of the six study locations along the east coast of Australia. b) approximate layout of the vertebrate trapping methods used on each survey plot.

Table 1
Table of study sites, survey dates, and the total number of surveys with seven days of matched vertebrate survey and acoustic data, two sites were not surveyed in spring because they were inaccessible because of high rainfall.

Site name	Survey dates - Trip 1	Survey dates - Trip 2	Total number of matched surveys
Tarcutta	2021–04-29 – 2021–05-06	2021–10-18 – 2021–10-25	8
Duval	2021–04-18 – 2021–04-25	NA	4
Mourachan	2021–05-09 – 2021–05-16	NA	3
Wambiana	2021–07-05 – 2021–07-12	2021–11-09 – 2021–11-16	7
Undara	2021–06-03 – 2021–06-10	2021–09-29 – 2021–10-06	6
Rinyirru	2021–06-14 – 2021–06-21	2021–10-09 – 2021–10-16	7

taxa vocalise and contribute to the soundscape, therefore analysis of these recordings should provide useful estimates of biodiversity through time, allowing the detection of species population trends, including declines (Laiolo, 2010; Obrist et al., 2010; Sugai & Llusia, 2019). However, many barriers still exist to effectively extracting useful data from acoustic recordings for biodiversity monitoring (Gibb et al., 2019). Despite the promise of automated recognition of species from vocalisations, the majority of acoustic analyses still employ manual identification (Sugai et al., 2019), because we lack either the labelled data or the requisite investment to develop deep-learning models of species vocalisations (Bravo Sanchez et al., 2021). While species inventories obtained by manually listening to the audio are useful for estimating biodiversity in small-scale studies, this approach is laborious and does not scale well to large acoustic datasets (Sugai et al., 2019). The solution has often been to sample large acoustic datasets or implement temporal sampling at the time of deployment, however this may reduce species detectability and impact biodiversity estimates (Sugai et al., 2019). Alternative approaches are needed that can take advantage of the large amount of data present in long-term passive recordings, while still providing accurate estimates of biodiversity.

Acoustic indices provide a sum of spectral and temporal information obtained from audio recordings, and they may provide a way to monitor biodiversity without the need to determine species identity (Sueur et al., 2008; Buxton et al., 2018; Towsey et al., 2018). Over the last 15 years, a great number of acoustic indices have been developed (Boelman et al., 2007; Sueur et al., 2008; Sueur et al., 2014; Towsey et al., 2014), most of which aim to capture information about the acoustic diversity of a site (e.g., the range of occupied frequencies, often with the assumption that greater acoustic diversity is, in some way, a function of greater species diversity). While the use of acoustic indices to compare habitats has increased in recent years, results from studies quantifying the ability of acoustic indices to estimate traditional biodiversity measures (i.e., richness, evenness, abundance) at a location are mixed (Mammides et al., 2017; Eldridge et al., 2018; Moreno-Gómez et al., 2019; Retamosa Izaguirre et al., 2021). Typically, the performance of indices has been tested using birds, and using sites that are in close proximity to one another. Therefore, it is uncertain whether any patterns found still hold at large spatial scales. Additionally, the majority of previous work has focused on correlating biodiversity metrics with single acoustic indices, rather than attempting to generate multi-index models (but see Towsey et al., 2014; Buxton et al., 2018). If acoustic indices are to be useful in monitoring programs, then their reliability for providing estimates of the biodiversity of a site needs to be determined, as well as testing which acoustic indices are most informative (Alcocer et al., 2022). Additionally, we need an improved understanding of which taxa can be effectively monitored using acoustic indices (Alcocer et al., 2022). Vertebrate taxa other than birds contribute to the soundscape (e.g., mammals and frogs), yet they were seldom considered in studies employing acoustic indices until relatively recently (see Ferreira et al., 2018; Moreno-Gómez et al., 2019; Boullhesen et al., 2021).

In this study we aimed to test the utility of 13 acoustic indices for monitoring vertebrate biodiversity at a number of sites in the recently deployed Australian Acoustic Observatory (Roe et al., 2021). Specifically, we aimed to test the performance of individual acoustic indices,

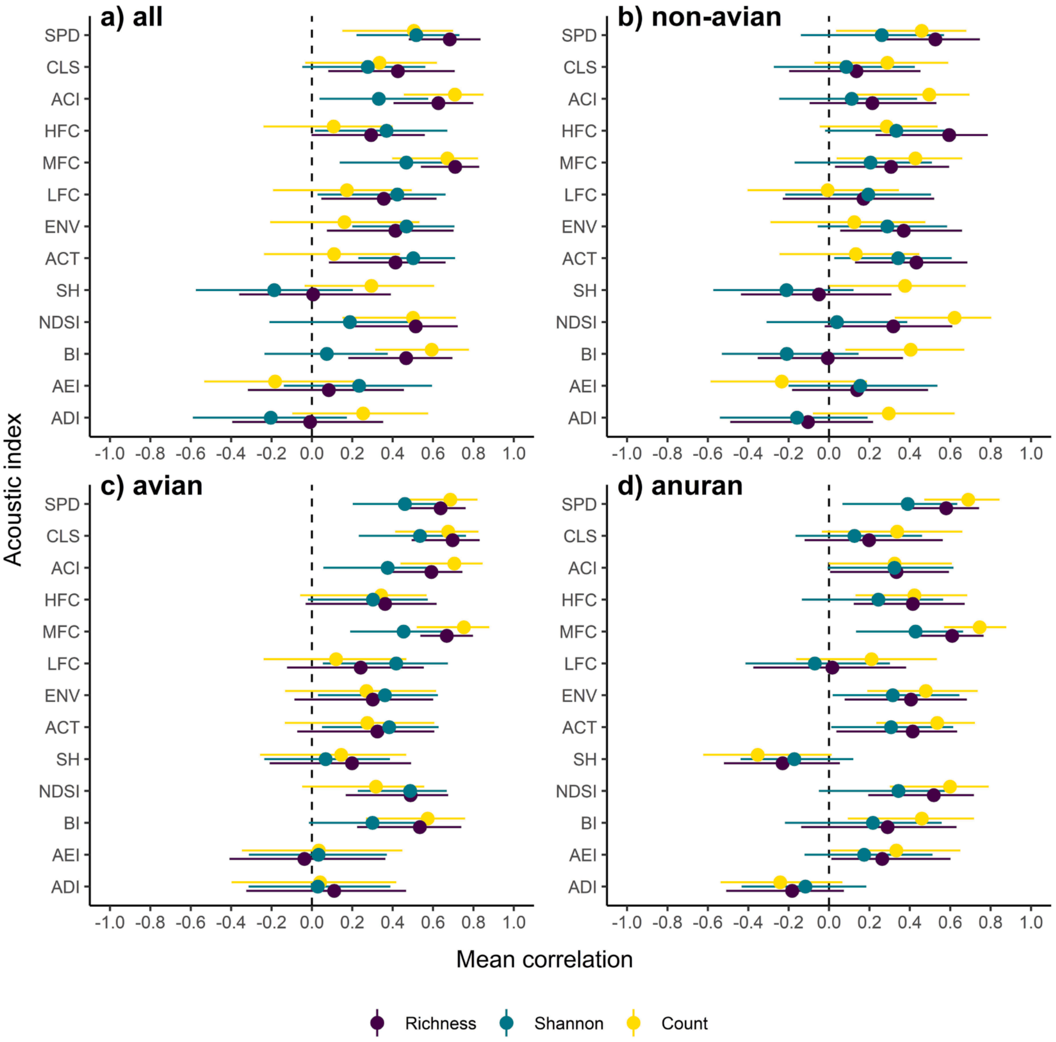

Fig. 2. Bootstrapped Spearman's rank correlation values (±95 % CI) of thirteen acoustic indices and three biodiversity measures (species richness, Shannon's diversity index and total count) for a) all vertebrate taxa, b) all non-avian vertebrate taxa, c) avians, and d) anurans.

and models incorporating multiple acoustic indices, for estimating traditional biodiversity measures of species richness, Shannon's diversity index, and total count, of various vertebrate taxonomic groupings.

2. Methods

2.1. Study sites

We surveyed six sites distributed along the east coast of Australia that form part of the Australian Acoustic Observatory (Roe et al., 2021; Fig. 1a). All six sites were selected to be a similar broad habitat type of open eucalypt woodland. Each site consisted of four 100 × 100 m plots. Plots were arranged in pairs (≥500 m between pairs), and each pair included a wet plot (≤50 m from a body of water) and dry plot (≥50 m from a body of water and ≥ 500 m from the wet plot). When possible, each site was surveyed twice in 2021. Each survey lasted for seven days (excluding setup days), and all four plots within a site were surveyed simultaneously.

2.2. Vertebrate surveys

For each survey plot, a standardized series of survey and trapping methods was used to document the vertebrate fauna (Gibbons & Semlitsch, 1981; Garden et al., 2007; McKnight et al., 2015; Nordberg & Schwarzkopf, 2015). All methods were used continuously for 7 days during each survey period, and methods were consistent across plots. Each plot contained: two drift fences with pit and funnel traps, 12 arboreal cover boards, four cage traps, and 24 Elliot traps (Fig. 1b).

Drift fences (30-cm tall) were + -shaped, with four 10-m arms and five 20-L pitfall traps (one in the center and one at the end of each arm). Additionally, each arm had two funnel traps (18 × 18 × 79 cm; one in the middle of each side of the arm) with an opening on each end (eight funnel traps per fence). To improve capture rates, a "wing" (18 × 30 cm) of fence fabric was placed at a 45° angle to each opening of each funnel trap to guide additional animals into the traps (McKnight et al., 2013). To prevent desiccation and overheating, wet sponges were placed in each funnel and pitfall trap, shade cloths were placed over the funnel traps, and all traps were checked twice daily (in the morning and evening).

Arboreal cover boards consisted of foam mats (50 × 50 × 1 cm) attached to trees by two elastic straps (Nordberg & Schwarzkopf, 2015). They were placed on 12 haphazardly selected trees and checked every morning. They were placed at the start of each survey period and removed at the end.

Cage traps were 66 × 26 × 25 m and were placed in each corner of the plot (~10 m from the corner at a 45° angle to the plot boundaries). Elliot traps were 8 × 9 × 33 cm and were placed in a line (six per line)

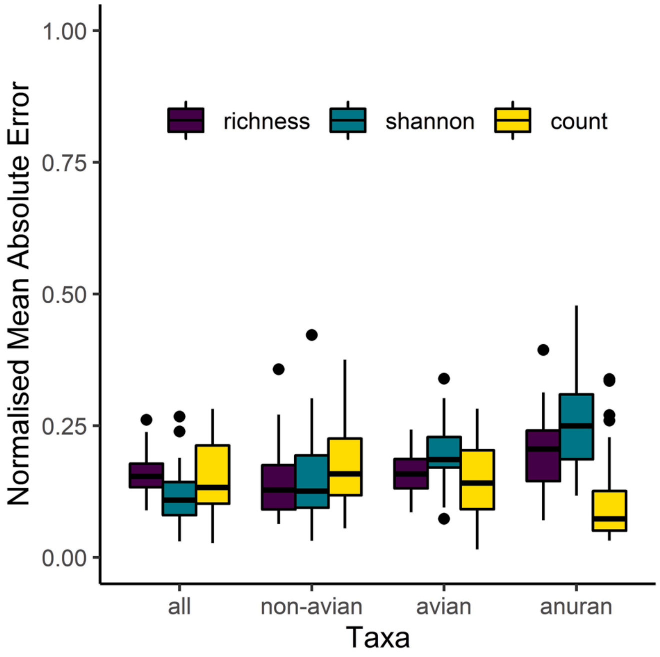

Fig. 3. Normalised mean absolute error of random forest models predicting richness, Shannon's diversity index, and total count of all vertebrates, non-avian vertebrates, avians, and anurans. Values closer to zero indicate better performance while values closer to one indicate worse performance. Performance measured with 10 × 3 cross-validation.

starting in each corner ~ 5 m from the cage trap and ending near the center of the plot (~5 m between each trap). Cage and Elliot traps were baited with bait balls made of peanut butter, oats, and vanilla. Each trap was opened in the evening, checked the following morning, and closed during the day. Baited camera traps were also deployed at each plot; however, we have not reported vertebrate data from cameras here because we were interested in comparing active surveys methods with passive acoustic recordings.

In addition to trapping methods, we conducted a 15-minute area search each morning and night. Searches were conducted by two researchers who recorded any animals that were seen or heard. While researchers stayed within the plots, animals seen or heard off the plots were also noted. Morning searches focused on diurnal bird species, while nocturnal searches used head torches and focused on reptiles, anurans, and nocturnal birds such as owls. During each 7-day survey, researchers rotated among teams and plots to minimize observer bias. Finally, throughout the 7-day surveys, we noted incidental encounters with animals that were seen or heard outside of our 15-minute search periods.

2.3. *Audio surveys*

At each survey plot, audio was continuously recorded using acoustic sensors that are part of the Australian Acoustic Observatory (Roe et al., 2021). Each sensor was fitted with a single microphone mounted 1.2–1.8 m above the ground, recording continuously at a sampling rate of 22.05 kHz in the FLAC file format (FrontierLabs Solar BAR - https://www.frontierlabs.com.au/solar-bar; see Roe et al., 2021 for full details). A total of 5,965 h of audio was recorded across the 6 sites in 2021.

2.4. *Vertebrate diversity measures*

To compare manual survey results with acoustic indices, we split the data into four taxonomic groupings: all vertebrates (containing all observations regardless of taxa or method of detection), anurans (all frogs detected by any method), avians (only birds observed during the morning birding surveys), and non-avian vertebrates (all taxa other than birds detected by any method). The anuran and avian subsets were chosen because both taxa vocalise and are likely to be detected on acoustic recorders (thus directly testing acoustic indices). The remaining two categories were intended to test the possibility that diversity in acoustic species would reflect diversity more generally and, therefore, acoustic indices would be useful for describing the broader vertebrate diversity. For each plot, we calculated species richness (total species observed), Shannon's diversity index (which combines richness and evenness), and the total count of observations for each taxonomic grouping.

2.5. *Acoustic indices*

Thirteen acoustic indices were generated from the audio for the entire 7 days (12:00 on day of first spotlighting survey – 12:00 on the day of last bird survey) at a 1-min resolution using Kaleidoscope Pro (Wildlife Acoustics; version 5.4.1) and QUT Ecoacoustics Audio Analysis Software (Towsey et al., 2020; version 20.11.2.0; Table 2).

Acoustic indices were calculated using their default settings and frequency ranges as they broadly cover the range expected to be affected by the vertebrate groups under study. From Kaleidoscope Pro, both the Acoustic diversity index (ADI) and the Acoustic evenness index (AEI) use 0–11 kHz, with 1 kHz steps, the Bioacoustic index (BI) uses 2–11.025 kHz, the Normalized difference soundscape index (NDSI) uses 1–2 kHz for the anthropophony component and 2–11.025 kHz for the biophony component, and Spectral entropy (SH) uses 0–11.025 kHz. From the QUT Ecoacoustics Audio Analysis Software, the Activity (ACT) and Events per second (EVN) indices use the full 0–11.025 kHz range. The Low-frequency cover (LFC), Mid-frequency cover (MFC), and High-frequency cover (HFC) indices measure the fraction of spectrogram cells exceeding 3 dB in the ranges 1–1000 Hz, 1–8 kHz, and 8–11.025 kHz respectively. The Acoustic complexity index (ACI), Cluster count (CLS), and Spectral peak density (SPD) indices utilise the same frequency band as MFC (i.e., 1–8 kHz; Towsey, 2017).

For comparison with the on-ground vertebrate survey data, we only examined audio data for the dates that corresponded to survey dates. Each acoustic index was aggregated into a weekly value (per plot) by taking the average of all 1-minute values for certain taxa-specific time periods. Initial exploration of using the median instead of the average found very little difference between these two options. For avians, indices were averaged for the day (sunrise-sunset; 3478–5537 min per weekly value). For anurans, indices were averaged for the night (sunset-sunrise; 3959–5614 min). For total vertebrate biodiversity and non-avian vertebrate biodiversity, indices were averaged for the entire 7-day dataset (7437–10080 min). These times were selected based on expected periods of high activity for the different taxonomic groups and have been used in previous studies (Sugai et al., 2019). Any time period that had less than 70 % of the audio available (e.g., due to hardware failure) was removed from the dataset. This resulted in a total of 35 matched, 7-day vertebrate and acoustic survey periods (Table 1).

2.6. *Statistical analyses*

To determine which individual acoustic indices may be useful proxies for vertebrate biodiversity, bootstrap Spearman's rank correlation values (and 95 % CIs) were calculated for each acoustic index and each biodiversity measure (i.e., species richness, Shannon's diversity index, total count) for the four vertebrate taxonomic groupings.

To determine how well multiple acoustic indices predict vertebrate biodiversity, random forest models were fit to each biodiversity measure using all 13 acoustic indices as predictors. Unbiased random forest models were fit using 1000 trees, and 10 × 3 cross validation was used to estimate predictive performance (R version 3.6.1; 'party' version 1.3.7; 'caret' version 6.0.86). Model performance was evaluated on the out-of-bag samples using normalised mean absolute error (MAE; MAE/(maximum – minimum response)). To determine which acoustic indices

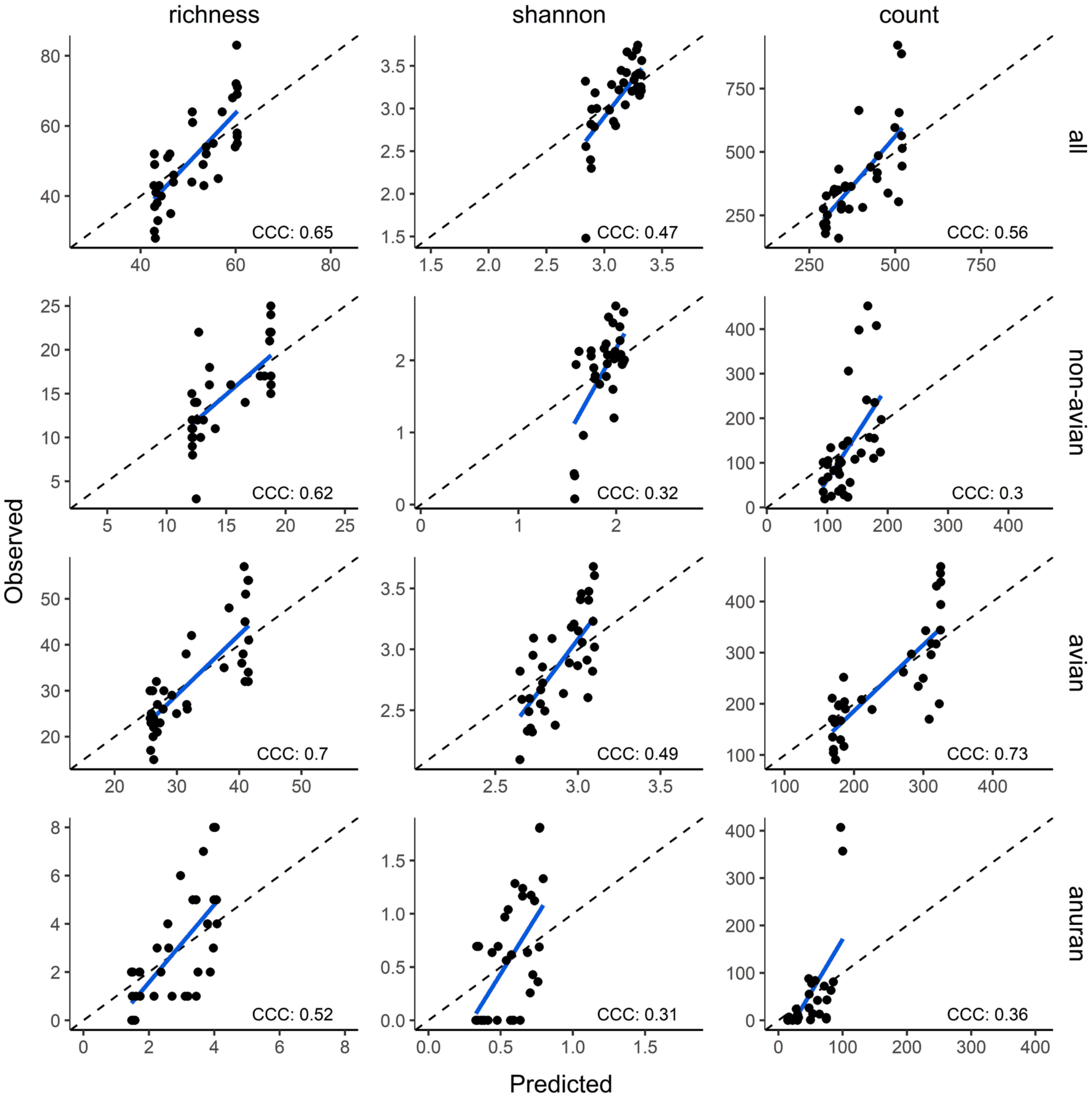

Fig. 4. Comparison of observed biodiversity values and out-of-bag predicted values from each random forest model. The Concordance Correlation Coefficient (CCC) values measure the agreement between data and the 45-degree line (i.e., 1 = perfect concordance).

contributed most to the predictive accuracy of each model, variable importance for each random forest model was calculated using conditional permutation importance (threshold = 0.95) and scaled by the total (null-model) error using the *permimp* package (version 1.0.1).

Given that site-specific environmental characteristics and species composition will influence the soundscape, models for individual sites may perform better than models for all sites (Fuller et al., 2015). So, to determine how well acoustic indices predict avian biodiversity within a single site, site-specific linear mixed effects models (with survey plot as a random effect) were fit using the top three, most important, acoustic indices from the random forest models as predictor variables and avian richness and avian total count as the response variables for the three sites with the most surveys (i.e., >7; Tarcutta, Wambiana, Rinyirru). Models were fit using lme4 (version 1.1.26; Bates et al., 2015) and lmerTest (version 3.1.3; Kuznetsova et al., 2017).

3. Results

3.1. Vertebrate surveys

A total of 327 vertebrate species were found during surveys across all sites. There were 172 avian species detected during bird surveys, and a total 21 anuran species found from all methods. The mean (±SD) number of species found on each survey plot during each seven-day survey period was 50.9 (±12.8) for all vertebrates, 32.4 (±10.9) for avian vertebrates, 2.66 (±2.29) for anuran vertebrates, and 14.9 (±4.96) for non-avian vertebrates.

3.2. Acoustic index correlations

A number of the acoustic indices had moderate to strong correlations ($0.5 \leq r_s \geq 0.8$) with the vertebrate biodiversity measures, particularly

Table 2
List of the 13 acoustic indices generated from the acoustic recordings.

Acronym	Name	Reference
ADI*	Acoustic diversity index	Villanueva-Rivera et al. (2011)
AEI*	Acoustic evenness index	Villanueva-Rivera et al. (2011)
BI*	Bioacoustic index	Boelman et al. (2007)
NDSI*	Normalized difference soundscape index	Kasten et al. (2012)
SH*	Spectral entropy	Sueur et al. (2008)
ACT†	Activity	Towsey (2017)
EVN†	Events per second	Towsey (2017)
LFC†	Low-frequency cover	Towsey (2017)
MFC†	Mid-frequency cover	Towsey (2017)
HFC†	High-frequency cover	Towsey (2017)
ACI†	Acoustic complexity index	Pieretti et al. (2011)
CLS†	Cluster count	Towsey (2017)
SPD†	Spectral peak density	Towsey (2017)

*Indices generated using Kaleidoscope Pro.
†Indices generated with QUT Ecoacoustics Audio Analysis Software.

Table 3
Spearman rank correlation coefficients (r_s) for the best individual acoustic index and random forest model predictions.

Vertebrate Grouping	Biodiversity measure	Individual Acoustic Indices		Random forest
		r_s	Index	r_s
All	richness	0.71	MFC	0.77
	Shannon's	0.52	SPD	0.62
	count	0.71	ACI	0.78
Non-avian	richness	0.59	HFC	0.73
	Shannon's	0.34	ACT	0.47
	count	0.62	NDSI	0.66
Avian	richness	0.7	CLS	0.78
	Shannon's	0.53	CLS	0.72
	count	0.75	MFC	0.8
Anuran	richness	0.61	MFC	0.71
	Shannon's	0.43	MFC	0.59
	count	0.75	MFC	0.76

for avians and all vertebrates, less so for anurans and non-avian vertebrates (Fig. 2). In general, acoustic indices had lower correlations with Shannon's diversity index than with species richness and total count across all vertebrate groupings examined.

For all vertebrates, species richness had the highest correlation (index; mean correlation; 95 % CI) with spectral density (SPD; $r_s = 0.68$; 0.48–0.83) and mid-frequency cover (MFC; $r_s = 0.71$; 0.54–0.83), Shannon's diversity index had the highest correlation with activity (ACT; $r_s = 0.5$; 0.23–0.71) and SPD ($r_s = 0.52$; 0.22–0.73), and total count had the highest correlation with the acoustic complexity index (ACI; $r_s = 0.71$; 0.45–0.85) and MFC ($r_s = 0.67$; 0.4–0.82; Fig. 2a).

For non-avian vertebrates, many of the acoustic indices tested had low correlations approaching zero (Fig. 2b). High-frequency cover (HFC; $r_s = 0.59$; 0.23–0.79) and SPD ($r_s = 0.53$; 0.25–0.75) correlated with species richness, and the normalized difference soundscape index correlated with total count ($r_s = 0.62$; 0.33–0.8).

For avians, MFC, SPD, ACI and cluster count (CLS) had the highest correlations with biodiversity measures (Fig. 2c). Specifically, species richness ($r_s = 0.7$; 0.49–0.83) and Shannon's diversity index ($r_s = 0.53$; 0.23–0.76) had the highest correlation with CLS, and total count had the highest correlation with MFC ($r_s = 0.75$; 0.57–0.88).

For anurans, MFC and SPD had moderate correlations with species richness ($r_s = 0.61$; 0.41–0.77, and $r_s = 0.58$; 0.36–0.74 respectively) and total count ($r_s = 0.75$; 0.57–0.88, and $r_s = 0.69$; 0.47–0.84 respectively), while none of the acoustic indices correlated particularly well with Shannon's diversity index (Fig. 2d).

3.3. Random forest models

Random forest models for all vertebrate groupings examined performed well (i.e., mean normalised MAE < 0.25; Fig. 3). In general, models for anurans had a higher MAE (i.e., worse predictive performance) than the equivalent models for the other vertebrate groupings considered.

Observed vs predicted plots show that, in general, of the three biodiversity measures examined, Shannon's diversity index was most poorly predicted using random forest models combinations of indices (Fig. 4), while species richness was the best. For species richness and total count, models were more accurate at predicting all vertebrates and avians than the other vertebrate groupings we examined. Random forest models had higher spearman rank correlations than the best performing individual acoustic index for all vertebrate groupings and biodiversity measures (Table 3), indicating predictive models using multiple acoustic indices had a stronger relationship with biodiversity measures than individual indices alone.

For all vertebrates, SPD and MFC were the most important acoustic indices for predicting species richness, and MFC and ACI was the most important for total counts. For non-avian vertebrates, only high-frequency cover (HFC) was identified as an important acoustic index for the species richness model. For avians, the most important acoustic indices according to the random forest models were CLS, SPD and MFC for both species richness and total count, with no particular acoustic index the most important for Shannon's diversity index (Fig. 5). For anurans, no single acoustic index was particularly important to model performance, which aligns with random forest models for frogs performing comparatively poorly.

Site-specific, linear, mixed-effects models were fit to data from Tarcutta, Wambiana and Rinyirru (the sites with most sample points) to predict avian species richness and avian total count using cluster count (CLS), spectral density (SPD) and mid-frequency cover (MFC). Observed vs predicted plots for these site-specific models showed that avian species richness and total count were accurately predicted using these three indices (Fig. 6).

4. Discussion

Acoustic monitoring has the potential to be a powerful tool to monitor vertebrate biodiversity at large temporal and spatial scales, but reliable analysis methods, validated with on ground-surveys, are needed to take advantage of large acoustic datasets for ecological monitoring and prediction. We used data from six sites across a large geographic area to examine the relationships among 13 acoustic indices and biodiversity estimates of various vertebrate taxonomic groupings and found a number of individual acoustic indices had moderate to strong correlations with species richness and total count. Despite this, only relatively poor correlations with Shannon's diversity index were observed. Models incorporating multiple acoustic indices outperformed individual indices and predicted species richness of all vertebrates and avians with reasonable accuracy, but they performed relatively poorly for non-avian vertebrates and anurans. Additionally, site-specific models showed strong relationships between acoustic indices and avian species richness and total count, and they suggest that it may be possible to monitor for fine-scale changes at specific sites using acoustic indices.

Previous studies have reported correlations between bird species richness and ADI (Machado et al., 2017; Mammides et al., 2017; Dröge et al., 2021; Retamosa Izaguirre et al., 2021) and AEI (Mammides et al., 2017; Jorge et al., 2018; Dröge et al., 2021). In contrast, we found low correlations between ADI and AEI and our biodiversity measures in this study, highlighting the importance of ground-truthing relationships between acoustic indices and local biodiversity data for a given project. We found that ACI correlated well with total avian count but not richness or Shannon's diversity index, similar to the results of Retamosa

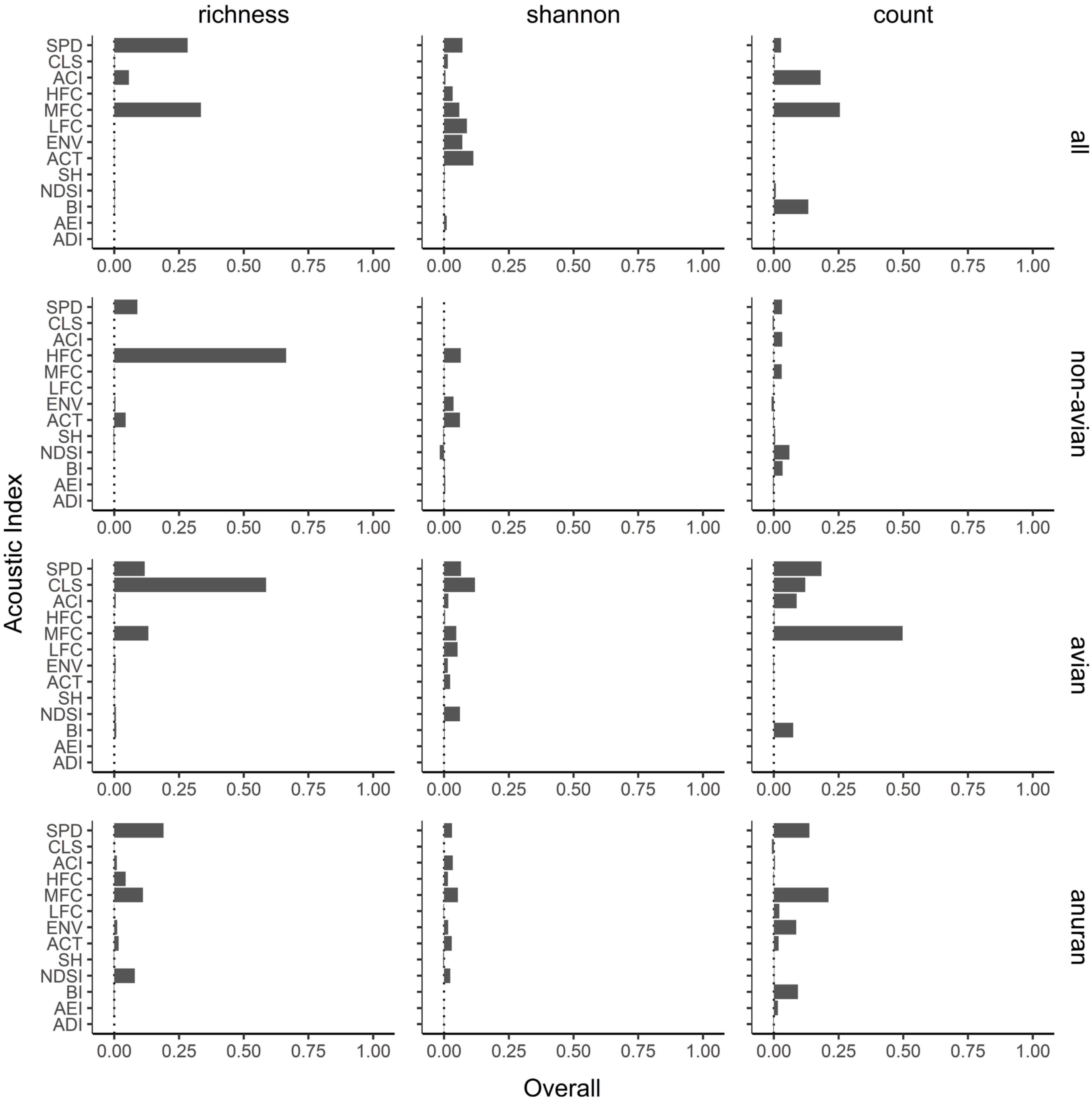

Fig. 5. Variable importance metrics for each random forest model. Values are the mean decrease in accuracy as a proportion of total null-model error from random permutations of each acoustic index (i.e., high values indicate that an index was an important predictor in the model).

Izaguirre and Ramírez-Alán (2018). In general, we did not find strong correlations between many of the commonly used acoustic indices (e.g., ACI, ADI, AEI, NDSI) and species richness. However, in addition to those indices, we also included some less common acoustic indices, three of which were often the indices with the highest single-index correlations and the most important variables in random forest models. Cluster count (CLS), spectral density (SPD), and mid-frequency cover (MFC) were the three best performing acoustic indices for avian biodiversity. All three indices are calculated using the 1–8 kHz frequency range which captures the range occupied by most bird species (Towsey, 2017). Cluster count (CLS) performed best for species richness and Shannon's diversity index, as it measures the number of distinct clusters identified in the middle frequency band, which should increase with the number of unique bird vocalisations within that band, whereas mid-frequency cover was the individual acoustic index with the highest correlation with avian total count, and the most important index from random forest models. This makes sense, as the amount of sound in the middle frequency band should increase with lots of vocalisations from birds, whether they are from the same species, or from many different species. To our knowledge, this is the first time these three acoustic indices have been used to estimate biodiversity and future studies should include these highly promising indices to determine whether they are useful in a broader range of situations and environments.

Acoustic indices were the most useful as proxies for total vertebrate biodiversity and avian biodiversity of a site. Across our survey periods, bird richness contributed on average 62 % of total vertebrate species richness, and the two biodiversity measures correlated strongly (r_s = 0.89). This suggests that despite many other vertebrate taxa not

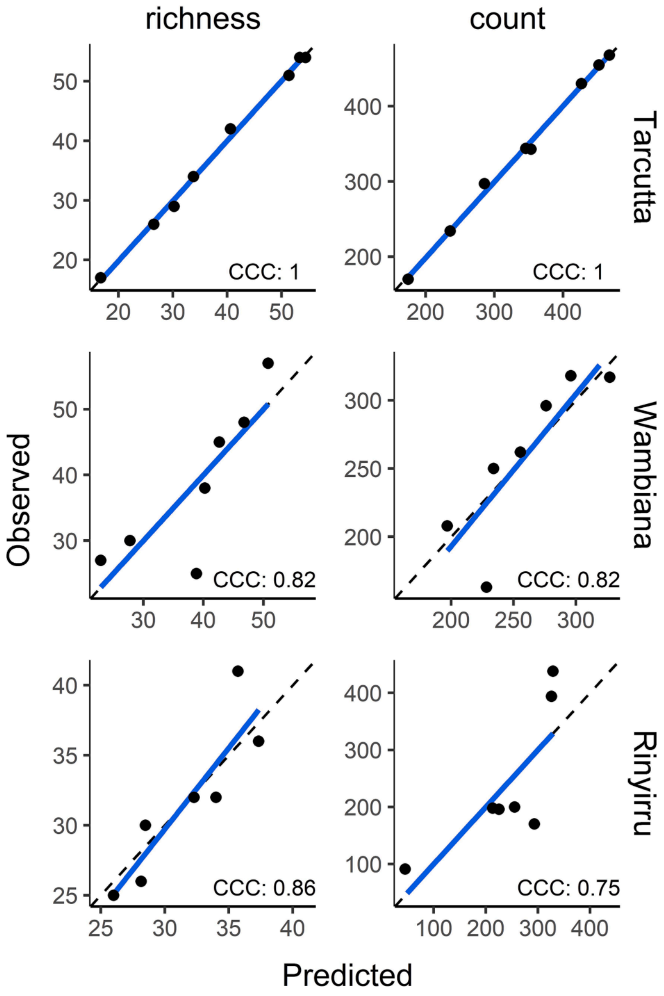

Fig. 6. Comparison of observed biodiversity values (avian species richness and avian total count) and predicted values from each site-specific linear mixed-effects model. The Concordance Correlation Coefficient (CCC) values measure the agreement between data and the 45-degree line (i.e., 1 = perfect concordance).

vocalising and contributing directly to the soundscape, acoustic indices may still act as a reasonable proxy for estimating the total vertebrate biodiversity of a site. This may, however, only be true in environments where birds are the dominant sources of sound. Environments with diverse insect fauna (e.g. tropical environments, or years in which loud taxa such as cicadas are present) may reduce the correlation between acoustic indices and total vertebrate diversity (Eldridge et al., 2018).

To date, there has been very little research using acoustic indices to estimate the biodiversity of anurans. However, previous research has shown that multiple acoustic indices can be reliable predictors of species-level calling behaviour of various frogs at short time-scales (Brodie et al., 2020; Indraswari et al., 2020). In general, acoustic indices performed poorly as proxies for frog biodiversity in this study (i.e., low correlations, poorer performing random forest models). Frogs are known for conspicuous vocalization, so this result is surprising. One likely reason for this poor performance is that, during the week-long surveys, there was typically low or no frog vocalisation. A number of the sites examined are located in tropical savannah environments where frog chorusing activity is initiated by rainfall (Woinarski et al., 1999; Brodie, 2022). Indeed, vocalizations are seasonal for many species of frog, and acoustic indices may not accurately reflect frog diversity unless they coincide with breeding events (for sites where many species breed simultaneously) or cover a long time period (for sites where breeding is staggered among species; McKnight & Ligon, 2016). One previous study on acoustic indices and frog biodiversity found poor correlations between seven acoustic indices and frog richness (Moreno-Gómez et al., 2019). Of those same indices tested here, we also found low correlations, however, the two indices with highest correlations in the present study, MFC and SPD, were not used by Moreno-Gómez et al. (2019). Further study should examine whether acoustic indices may perform well for frogs at appropriate times of the year (e.g., the rainy season or when a breeding pulse is known to have occurred onsite), particularly those indices that worked well for birds (i.e., MFC, CLS and SPD), as they have not been examined before. These indices were calculated using the 1–8 kHz frequency band which also covers most frog vocalisations; however, they could be adjusted to be more specific to frogs, which primarily vocalise below 5 kHz (Loftus-Hills & Johnstone, 1970). The fine-tuning of acoustic indices to certain frequency bands has been shown to improve biodiversity predictions of certain taxonomic groups and warrants further investigation (Metcalf et al., 2021).

Models incorporating multiple indices performed better than any single acoustic index, and in general performed reasonably well at predicting total vertebrate and avian species richness, and avian total count. However, other studies have used multiple acoustic index models to predict biodiversity with mixed results (e.g. Buxton et al., 2018; Retamosa Izaguirre et al., 2021). This may be due to methodological differences used to estimate biodiversity. For example, Buxton et al. (2018) estimated biodiversity from the audio recordings themselves and found random forest models predicted biodiversity accurately, whereas Retamosa Izaguirre et al. (2021) used bird point count surveys, which include both visual and aural detections, and found random forest models predicted biodiversity poorly. Our models still predicted biodiversity measures relatively well for birds and all vertebrates, even when estimating these measures from on-ground field surveys. This difference may occur because these studies used different time-scales. We aggregated acoustic indices into weekly summary indices for comparison with 7-day field surveys, whereas Retamosa Izaguirre et al. (2021) estimated bird diversity from 6-minute point counts, possibly introducing more variability.

The study sites examined here spanned a large latitudinal gradient (>20°), with sites having distinct but overlapping community composition, yet indices performed well for representing vertebrate biodiversity in a number of cases. Most prior studies examining the relationship between acoustic indices and biodiversity have done so using sites spaced much closer together (e.g., Depraetere et al., 2012; Moreno-Gómez et al., 2019; Bradfer-Lawrence et al., 2020). This suggests that acoustic indices may be useful in a wide range of conditions and that large-scale ecological monitoring networks such as the Australian Acoustic Observatory (A2O) could potentially use acoustic indices for rapid estimates of vertebrate biodiversity. However, more work is needed if acoustic indices are to be used to monitor finer scale changes in species richness, such as the loss of a species. Site-specific models showed a much stronger relationship between acoustic indices and avian biodiversity than models using all sites, suggesting that accounting for the unique fauna and environmental characteristics of a site may further strengthen the predictive performance of acoustic indices (Fuller et al., 2015). Accounting for unique site characteristics is potentially possible using acoustic monitoring, as long-term fine-scale temporal data at a variety of sites are available using this method.

5. Conclusions

Biodiversity monitoring techniques that can be used at large temporal and spatial scales are needed to provide the necessary data to detect changes in biodiversity and inform management interventions. The use of acoustic indices promises to provide a rapid way to monitor the biodiversity of terrestrial environments, however, at least initially, they need to be thoroughly tested and ground-truthed using more traditional monitoring methods. Our study found moderate to strong correlations between vertebrate diversity and specific acoustic indices, and especially combinations of acoustic indices, over week-long surveys. Additionally, models combining multiple indices made accurate biodiversity estimates for avians and all vertebrates. Future work should incorporate site-specific environmental variables that may account for some of the variability in the relationship between acoustic indices and biodiversity measures, and thus improve predictive capabilities. Additionally, the effectiveness of using acoustic indices for monitoring taxa beside avians, particularly anurans, requires more examination.

CRediT authorship contribution statement

Slade Allen-Ankins: Methodology, Formal analysis, Data curation, Visualization, Conceptualization, Writing – original draft, Writing – review & editing. **Donald T. McKnight:** Conceptualization, Methodology, Data curation, Writing – original draft, Writing – review & editing. **Eric J. Nordberg:** Conceptualization, Methodology, Writing – review & editing. **Sebastian Hoefer:** Methodology, Data curation, Writing – review & editing. **Paul Roe:** Conceptualization, Writing – review & editing, Funding acquisition. **David M. Watson:** Conceptualization, Writing – review & editing, Funding acquisition. **Paul G. McDonald:** Conceptualization, Writing – review & editing, Funding acquisition. **Richard A. Fuller:** Conceptualization, Writing – review & editing, Funding acquisition. **Lin Schwarzkopf:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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