**Title: Using acoustic indices to monitor vertebrate biodiversity**

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**Abstract**

**Introduction**

Biodiversity loss is occurring worldwide due to multiple factors, including invasive species (Clavero *et al.*, 2009; Doherty *et al.*, 2016), habitat loss (Brooks *et al.*, 2002), and climate change (Pimm, 2009), with many recognizing the current situation as the sixth mass extinction event (Ceballos *et al.*, 2015). Key to understanding and preventing this biodiversity loss is effective monitoring such 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 expensive and time-consuming to conduct on large temporal and spatial scales (Darras *et al.*, 2019). Emerging technologies such as passive acoustic monitoring may be a viable alternative to traditional surveys that overcome this problem (Acevedo & Villanueva-Rivera, 2006; Obrist *et al.*, 2010; Sugai *et al.*, 2019).

Due to recent advances in storage and battery capacity, large-scale acoustic sensor networks may be useful for scaling biodiversity monitoring as acoustic recorders can be deployed at many locations and survey the soundscape continuously (Digby *et al.*, 2013; Roe *et al.*, 2021). Many taxa vocalise and contribute to the soundscape, therefore analysis of these recordings should provide useful estimates of biodiversity through time, thus allowing the detection of species declines. However, many challenges still exist as to how useful data can be effectively extracted from acoustic recordings for biodiversity monitoring (Gibb *et al.*, 2019). Despite the promise of automated recognition of species vocalisations, the majority of acoustic analyses still employ manual identification (Sugai *et al.*, 2019), due to the lack of data required to develop deep-learning models of species vocalisations. While species inventories obtained by manually listening to the audio are useful for estimating biodiversity in small scale studies, this approach does not scale well to large acoustic datasets or make use of the continuous data available from passive acoustic monitoring. 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 are summaries of acoustic recordings that capture information about soundscapes without the need to determine species identity, and provide a way to monitor biodiversity from acoustic recordings (Buxton *et al.*, 2018). Over the last 15 years, a great number of acoustic indices have been developed (Boelman *et al.*, 2007; Sueur *et al.*, 2014), most of which aim to capture information about the acoustic diversity of a site, with greater acoustic diversity the supposed result of greater species diversity. While the use of acoustic indices to compare habitats has increased in recent years, the ability of acoustic indices to estimate traditional biodiversity measures of a location is mixed (Mammides *et al.*, 2017; Eldridge *et al.*, 2018; Moreno-Gómez *et al.*, 2019; Retamosa Izaguirre *et al.*, 2021), and has predominately been tested using only birds and with study sites located in close proximity. Additionally, the majority of previous work has focused on correlations with single acoustic indices rather than multi-index models (but see Buxton *et al.*, 2018). If acoustic indices are to be useful in monitoring programs then their ability to provide reliable estimates of the biodiversity of a site needs to be tested, as well as which taxa it works best for and which acoustic indices are most informative.

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 individual acoustic indices as well as models containing multiple acoustic indices for estimating the traditional biodiversity measures of species richness, Shannon’s diversity, and total count of different vertebrate taxonomic groupings.

**Methods**

*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; Figure 1). Each site contained four 100 x 100 m plots. Plots were arranged in pairs (500–5000 m between pairs), and each pair contained a wet plot (≤50 m from a body of water) and dry plot (≥50 m from a body of water and (500–5000 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.

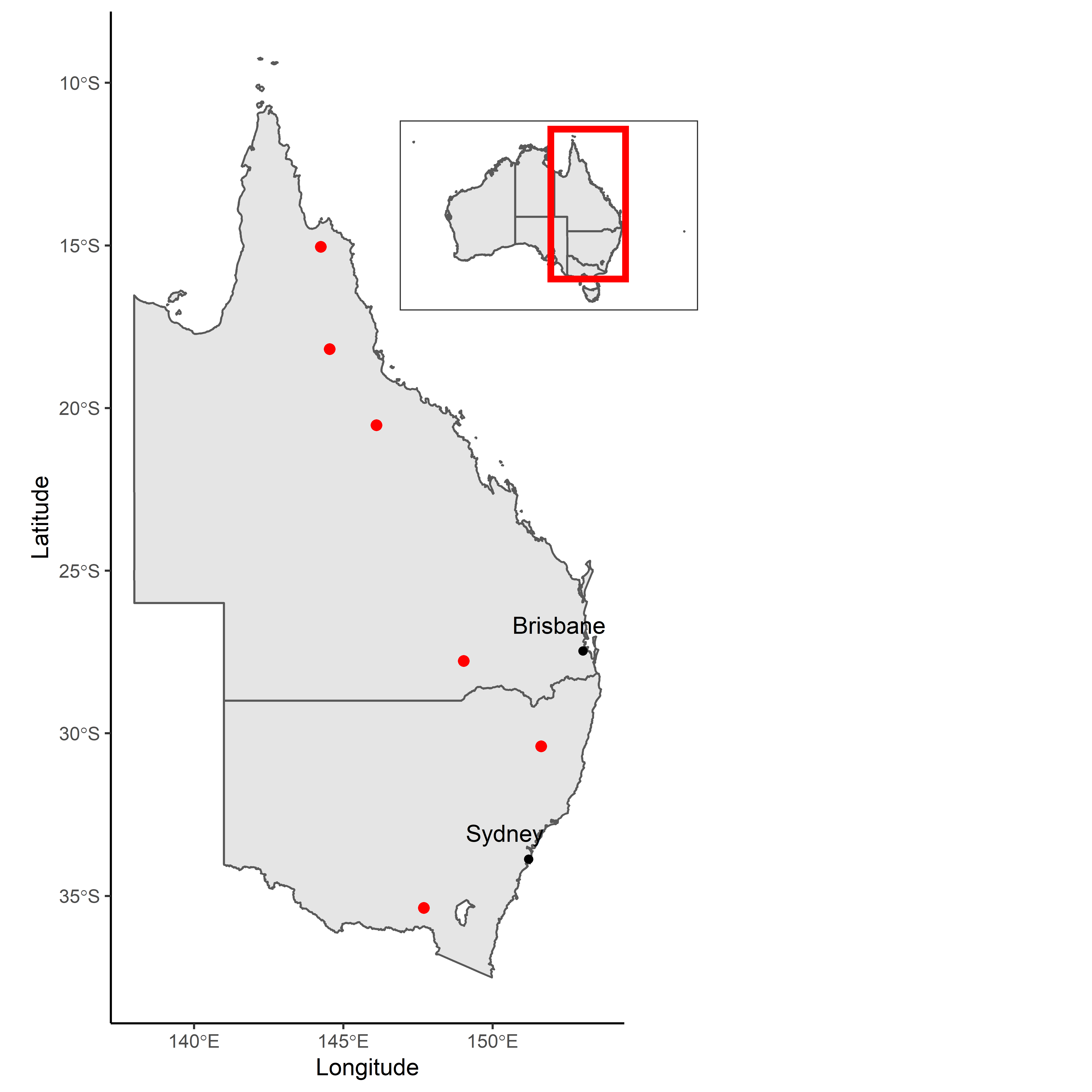


Figure . Map of the six study locations. Each location had 4 plots.

Table . Table of study sites, survey dates, and the total number of surveys with seven days of matched vertebrate survey and acoustic data.

|  |  |  |  |
| --- | --- | --- | --- |
| 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 |

*Vertebrate surveys*

For each survey plot, a standardized series of survey and trapping methods to document the vertebrate fauna present was used. All methods were used continuously for 7 days during each survey period and methods were consistent across plots. Each plot contained: two drift fences, 12 arboreal cover boards, four cage traps, and 24 Elliot traps (Figure 2).

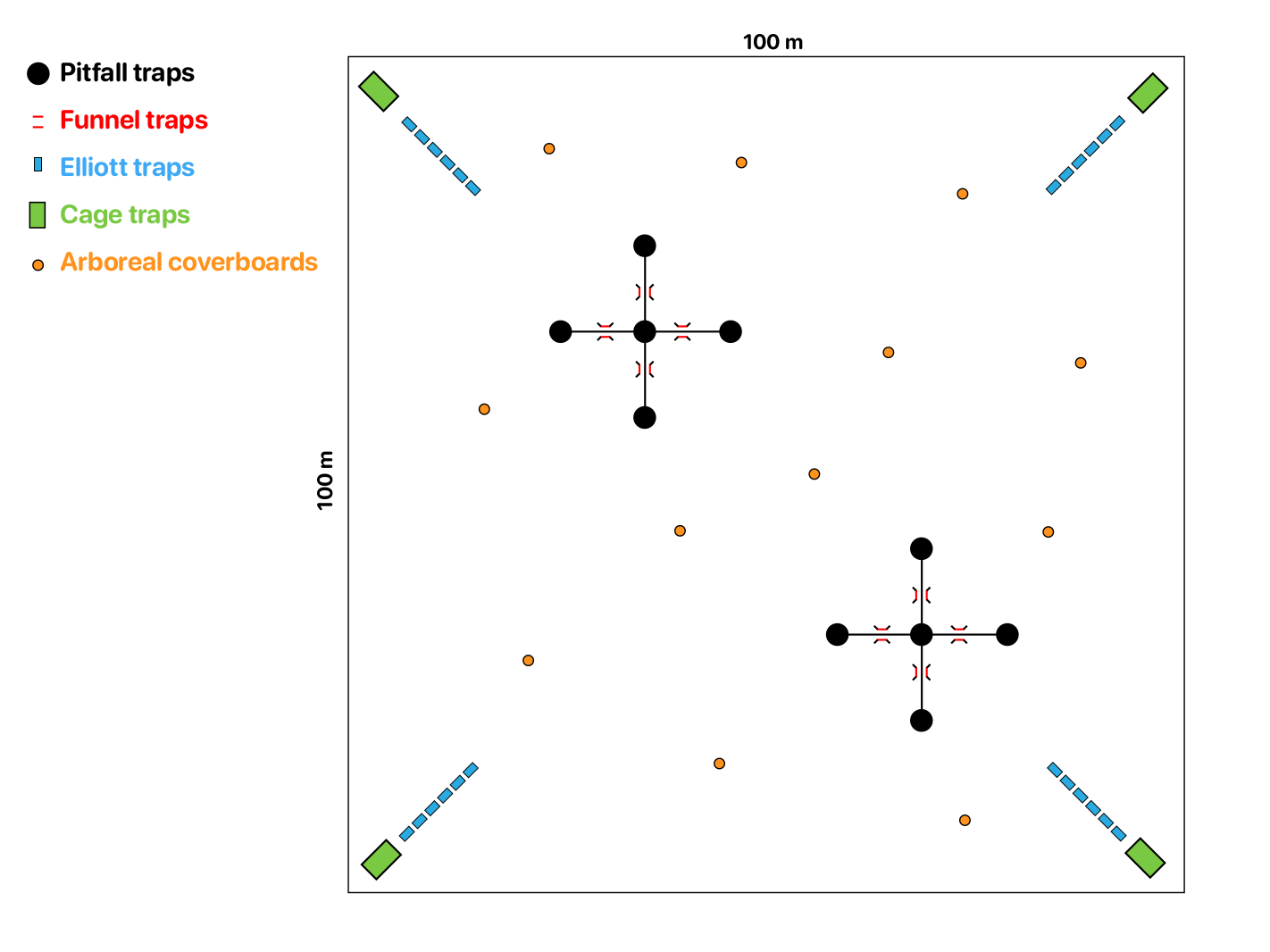


Figure . Approximate layout of the vertebrate trapping methods use on each survey plot.

Drift fences (30 cm tall) were X-shaped, with four 10-m long arms and five 20-L pitfall traps (one in the center and one at the end of each arm). Additionally, each arm contained two funnel traps (18 x 18 x 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 x 50 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 traps, 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 x 50 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 x 26 x 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 x 9 x 33 cm and were placed in a line (six per line) 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. Camera traps were also deployed at each plot, however vertebrate data from them have not been included here.

In addition to trapping methods, we conducted visual and auditory searches each morning and night. During the searches, two researchers meandered through the plots for 15min recording 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 birds, while nocturnal searches used head torches and focused on reptiles and amphibians. 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.

*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 is fitted with a single microphone mounted 1.2-1.8m above the ground, recording continuously at a sampling rate of 22.05kHz in the FLAC file format (FrontierLabs - https://www.frontierlabs.com.au/solar-bar; see Roe *et al.*, 2021 for full details). A total of xx hours of audio was recorded across the 6 sites during 2021.

*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), frogs (all frogs detected by any method), birds (only birds observed during the morning birding surveys), and non-avian vertebrates (all taxa other than birds detected by any method). The frogs and birds 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 be reflective of 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 (which combines richness and evenness), and the total count of observations for each taxonomic grouping.

*Acoustic indices*

Thirteen acoustic indices were generated from the audio for the entire 7 days (12pm on day of first spotlighting survey – 12pm 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 . List of the 13 acoustic indices generated from the acoustic recordings.

|  |  |
| --- | --- |
| Acoustic Index | Description |
| 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) |
| SPT† | Spectral peak density (Towsey, 2017) |

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

For comparison with the on-ground vertebrate survey data, each acoustic index was aggregated into a weekly value by taking the average of all 1-minute values for certain taxa-specific time periods. For birds, indices were averaged for the daytime (6am-6pm). For frogs, indices were averaged for the nighttime (6pm-6am). For total vertebrate biodiversity and non-avian vertebrate biodiversity, indices were averaged for the entire 7-day dataset. 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 survey and acoustic survey periods (Table 1).

*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, 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 x 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 normalized RMSE (RMSE/(maximum – minimum response)), scatter index (RMSE/mean response), and R-squared. To determine which acoustic indices 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).

Additionally, to determine how well acoustic indices may predict 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 and bird biodiversity estimates for the three sites with the most surveys (i.e. >7; Tarcutta, Wambiana, Rinyirru).

**Results**

*Acoustic index correlations*

A number of the acoustic indices tested had moderate to strong correlations (0.5 ≤ rs ≥ 0.8) with the vertebrate biodiversity measures, particularly for birds and all vertebrates, less so for frogs and non-avian vertebrates (Figure 3). In general, acoustic indices had lower correlations with Shannon’s diversity than species richness and total count across all vertebrate groupings examined.

For all vertebrates, species richness had the highest correlation with spectral density (SPD; rs = 0.68) and mid-frequency cover (MFC; rs = 0.67), Shannon’s diversity had the highest correlation with activity (ACT; rs = 0.55), and total count had the highest correlation with the acoustic complexity index (ACI; rs = 0.71) and MFC (rs = 0.69; Figure 3a).

For non-avian vertebrates, many of the acoustic indices tested had low correlations that were not different from zero (Figure 3b). High-frequency cover (HFC; rs = 0.59) and SDP (rs = 0.53) correlated with species richness, and the normalized difference soundscape index correlated with total count (rs = 0.59).

For birds, MFC, SPD, ACI and cluster count (CLS) had the highest correlations with vertebrate biodiversity measures (Figure 3c). Specifically, species richness (rs = 0.7) and Shannon’s diversity (rs = 0.62) had the highest correlation with CLS, and total count had the highest correlation with MFC (rs = 0.77).

For frogs, MFC and SPD had moderate correlations with species richness (rs = 0.53 and rs = 0.56 respectively) and total count (rs = 0.66 and rs = 0.66 respectively), while none of the acoustic indices correlated particularly well with Shannon’s diversity (Figure 3d).

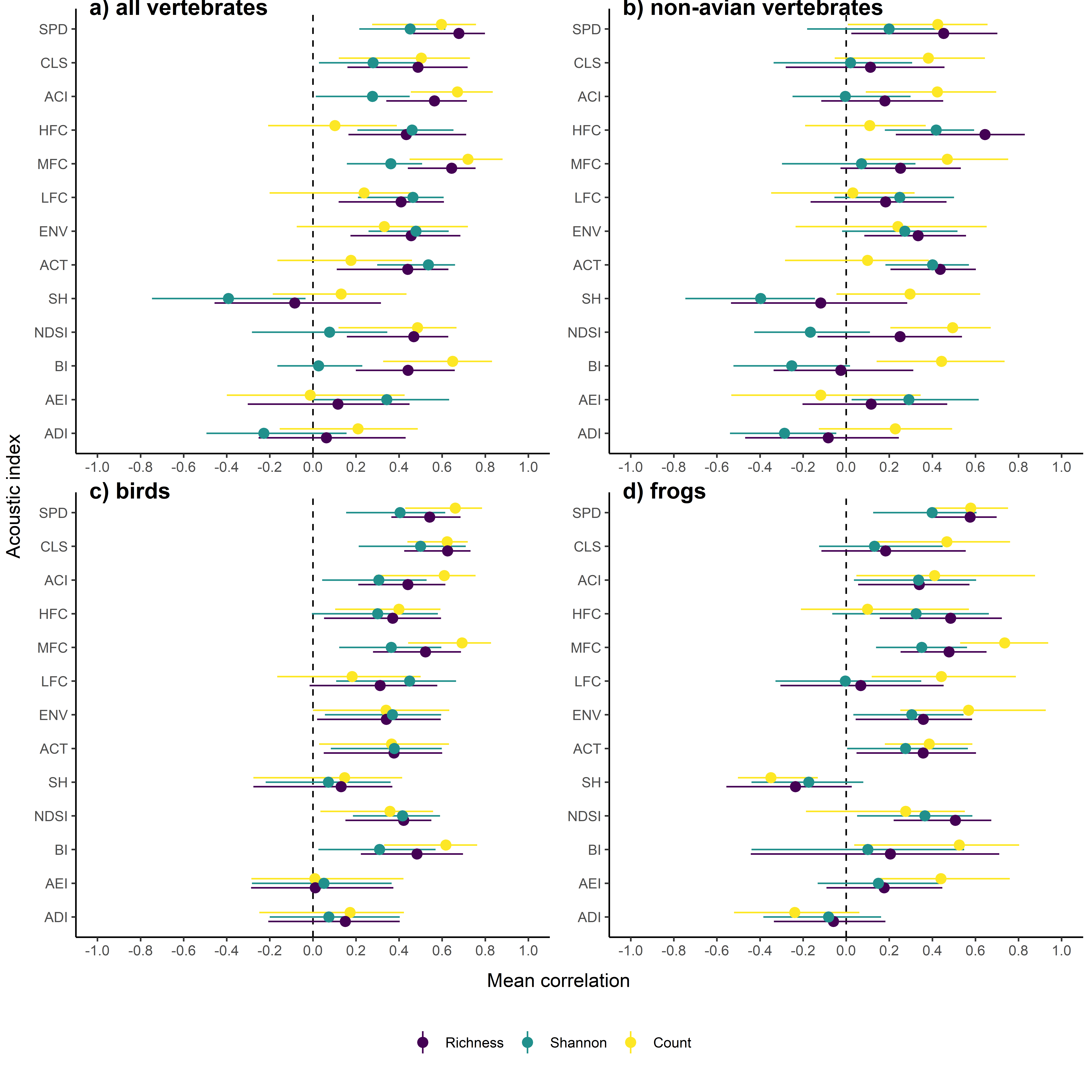


Figure . Bootstrap Spearman’s rank correlation values (±95% CI) of thirteen acoustic indices and three biodiversity measures (species richness, Shannon’s diversity and total count) for a) all vertebrate taxa, b) all non-avian vertebrate taxa, c) birds, and d) frogs.

*Random forest models*

Random forest models for all vertebrate groupings examined, except for frogs, performed well (i.e. low normalised RMSE and scatter index, high R squared; Figure 4). In general, models for frogs had a higher RMSE, higher scatter index, and lower R2 than the equivalent models for the other vertebrate groupings considered (Figure 4). Despite only slightly higher normalised RMSE than models for the other vertebrate groupings, random forest models for frogs had a very high scatter index, particularly for total count (Figure 4b). This is likely due to the high number of survey plots with zero frogs found (n = XX).

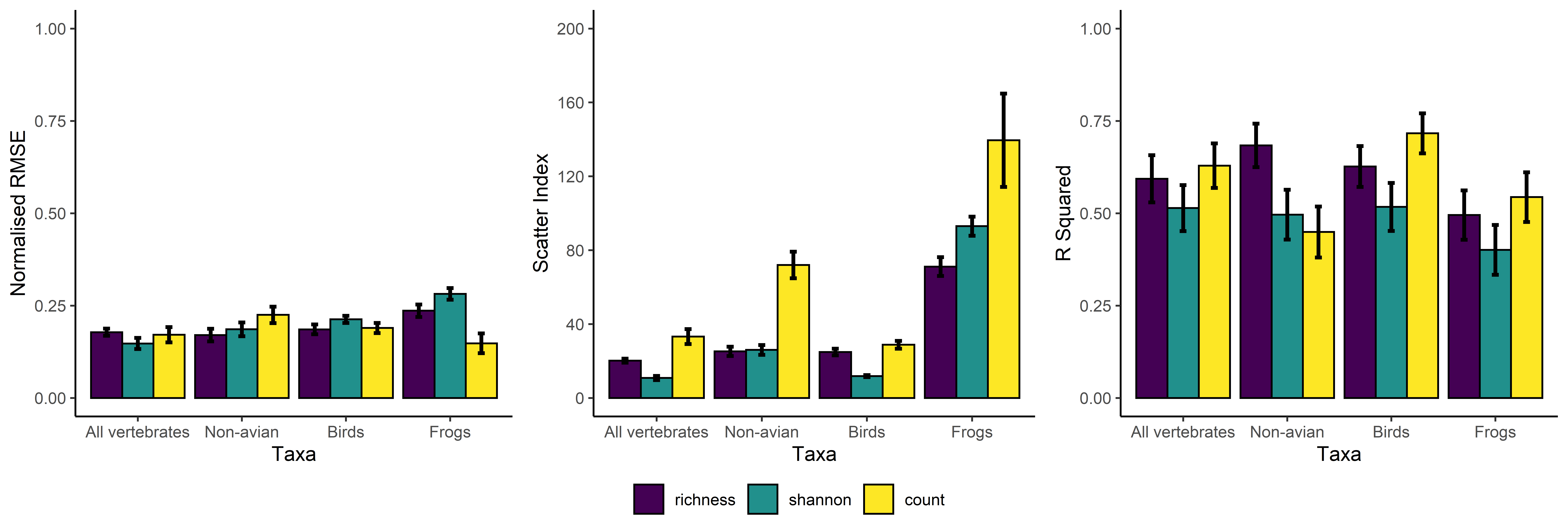


Figure . Mean (±SE) performance of random forest models predicting richness, Shannon’s diversity, and total count of all vertebrates, non-avian vertebrates, birds, and frogs. Performance measured with 10 x 3 cross-validation.

Observed vs predicted plots show that, in general, random forest models were poorest at predicting Shannon’s diversity out of the three biodiversity measures examined (Figure 5), while species richness was predicted best. For species richness and total count, models were more accurate at predicting all vertebrates and birds than the other vertebrate groupings examined. Random forest models performed better than individual indices, with higher spearman rank correlations for all vertebrate groupings and biodiversity measures (Table 3).

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

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Vertebrate Grouping | Biodiversity measure | Individual Acoustic Indices | | Random forest |
| rs | Index | rs |
| All | richness | 0.68 | SPD | 0.76 |
| shannon | 0.55 | ACT | 0.63 |
| count | 0.71 | ACI | 0.81 |
| Non-avian | richness | 0.59 | HFC | 0.72 |
| shannon | 0.44 | HFC | 0.6 |
| count | 0.59 | NDSI | 0.64 |
| Birds | richness | 0.7 | CLS | 0.77 |
| shannon | 0.62 | CLS | 0.71 |
| count | 0.77 | MFC | 0.81 |
| Frogs | richness | 0.56 | SPD | 0.68 |
| shannon | 0.37 | SPD | 0.52 |
| count | 0.66 | SPD | 0.71 |

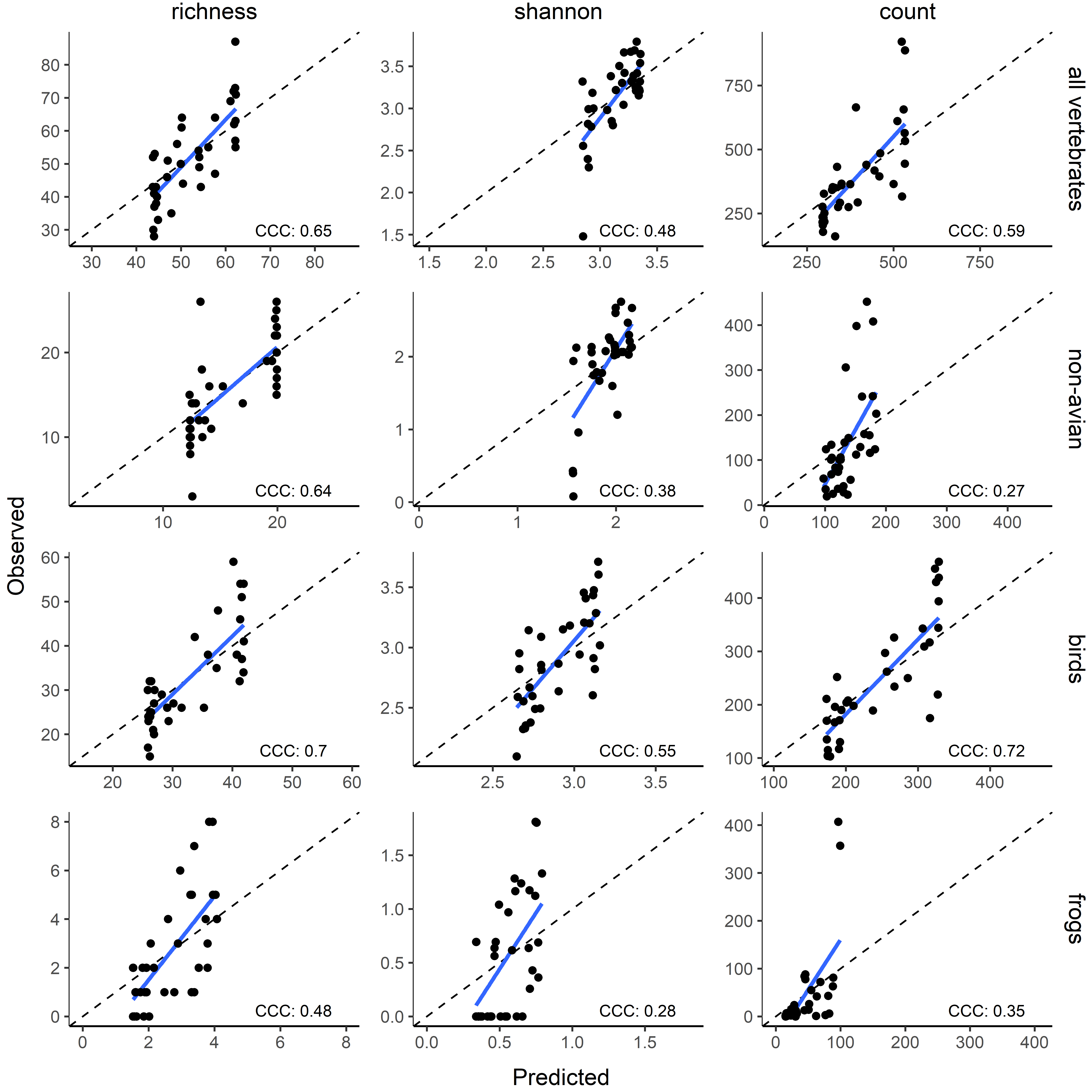


Figure . Comparison of observed biodiversity values and out-of-bag predicted values from each random forest model. The Concordance Correlation Coefficient (CCC) values measure how far the data deviates from the 45 degree line (i.e. perfect prediction).

For all vertebrates, SPD and MFC were the most important acoustic indices for species richness and MFC for total count. (For non-avian vertebrates, only high-frequency cover (HFC) was identified as an important acoustic index for the species richness model.) For birds, the most important acoustic indices to the random forest models were cluster count (CLS) for both species richness and Shannon’s diversity, and mid-frequency cover (MFC) for total count (Figure 6). (For frogs, no single acoustic index was particularly important to model performance, which aligns with random forest models for frogs performing comparatively poorly.)

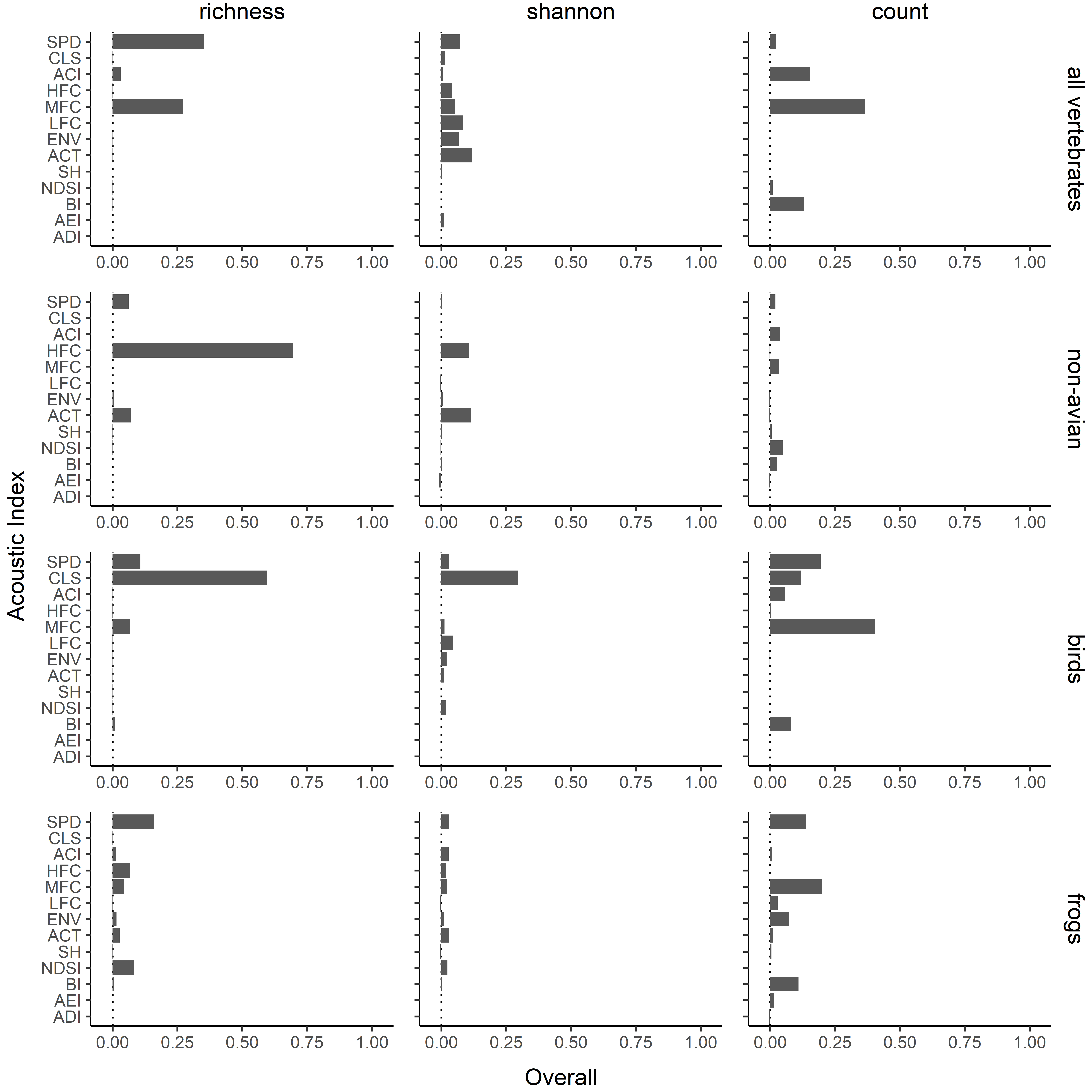


Figure . Variable importance metrics for each random forest model. Values are the mean decrease in accuracy as a proportion of total null-model error from random permutations of each acoustic index.

Site-specific linear mixed-effects models were fit to data from Tarcutta, Wambiana and Rinyirru to predict bird species richness and bird total count using cluster count (CLS), spectral density (SPD) and mid-frequency cover (MFC).

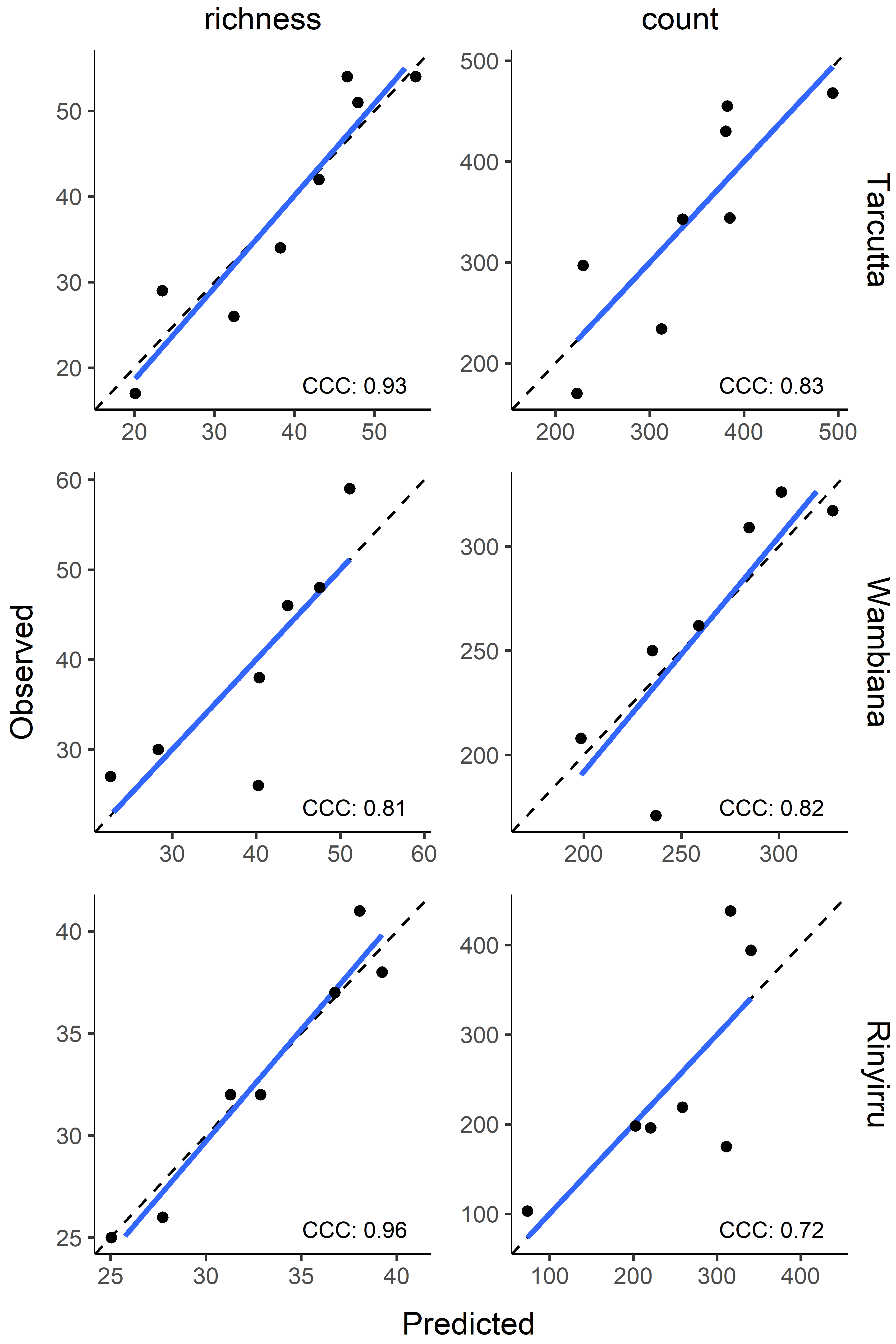
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Figure . Comparison of observed biodiversity values (richness and count) and predicted values from each site-specific linear mixed-effects model. The Concordance Correlation Coefficient (CCC) values measure how far the data deviates from the 45 degree line (i.e. perfect prediction).

**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 that have been validated with on ground-surveys are needed to take advantage of large acoustic datasets. We examined the relationship between 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, but had comparatively poor correlations with Shannon’s diversity. Models incorporating multiple acoustic indices outperformed individual indices and were able to predict species richness of all vertebrates and birds with reasonable accuracy, but performed relatively poorly for non-avian vertebrates and frogs. Additionally, site-specific models showed strong relationships between acoustic indices and the species richness and total count of birds, and suggest that it may be possible to monitor for fine-scale changes 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. We found that ACI correlated well with total bird count but not richness and Shannon’s diversity, similar to the results of Retamosa Izaguirre and Ramírez-Alán (2018). In general, we did not find strong correlations between many of the commonly used acoustic indices (i.e. ACI, ADI, AEI, NDSI) and species richness. However, in addition to those indices, we also included some acoustic indices that are not often used, 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 bird biodiversity. All three indices are calculated using the 1-8 kHz frequency range which captures the frequency range occupied by most bird species (Towsey, 2017). Cluster count (CLS) performed best for species richness and Shannon’s diversity 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 the middle frequency band. Whereas mid-frequency cover was the individual acoustic index with the highest correlation with bird total count and the most important index from random forest models. This makes sense as it 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 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 bird 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 (rs = 0.89). This suggests that despite many other vertebrate taxa not vocalising and directly contributing to the soundscape, acoustic indices may still act as a reasonable proxy for estimating the total vertebrate biodiversity of a site. However, this may only be true in environments where birds are the dominant sources of sound in the environment. Environments with diverse insect fauna (e.g. tropical environments) may reduce the correlation between acoustic indices and total vertebrate diversity (Eldridge *et al.*, 2018).

To date there has been very little research on using acoustic indices to estimate the biodiversity of frogs. 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). As a vertebrate taxa known for conspicuous vocalization this result is surprising. One likely reason for this poor performance is that a large number of surveys found low or no frog diversity during the week long surveys. A number of the sites examined are located in tropical savannah environments where frog chorusing activity is strongly associated with rainfall events (Woinarski *et al.*, 1999). 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), particularly those indices that worked well for birds as they have not been examined before, and most frog vocalisations also occupy the same 1-8 kHz frequency band as birds.

Models incorporating multiple indices performed better than any single acoustic index, and in general performed reasonably well at predicting total vertebrate and bird species richness and bird 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 down 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 to predict biodiversity accurately, whereas Retamosa Izaguirre *et al.* (2021) used bird point count surveys which includes both visual and aural detections and found random forest models to predict 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 be down to the time-scale used. We have 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.

The study sites examined here spanned a large latitudinal gradient (>20 degrees), with sites having distinct communities? 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 much closer in space (e.g. refs). 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) can utilise acoustic indices for rapid estimates of vertebrate biodiversity. However, more work is needed if acoustic indices are to be used to monitor for 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 biodiversity, suggesting that accounting for the unique fauna and environment characteristics of a site may further strengthen the predictive performance of acoustic indices.

**Conclusion**

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 they need to be thoroughly tested and ground-truthed in comparison to traditional monitoring methods. Our study found moderate to strong correlations between vertebrate diversity and specific acoustic indices during week long surveys. Additionally, models combining multiple indices were able to predict biodiversity estimates of birds and all vertebrates. Future work…

**Supporting Information**

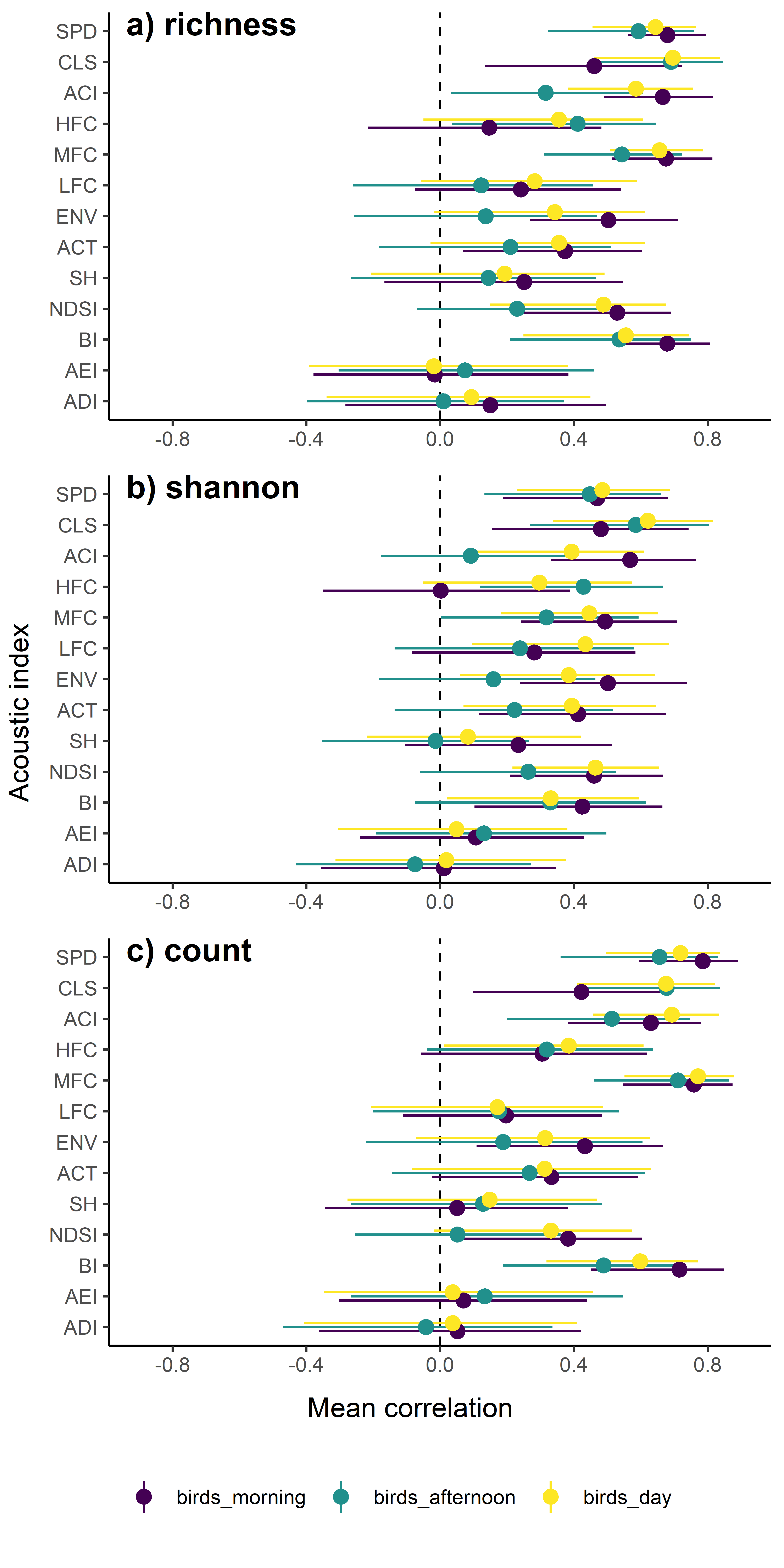


Figure S . Bootstrap Spearman’s rank correlation values (±95% CI) of thirteen acoustic indices and a) species richness, b) Shannon’s diversity and c) total count of birds using acoustic indices calculated from morning recordings (6am-9am; purple), afternoon recordings (3pm-6pm; green) and day recordings (6am-6pm; yellow).

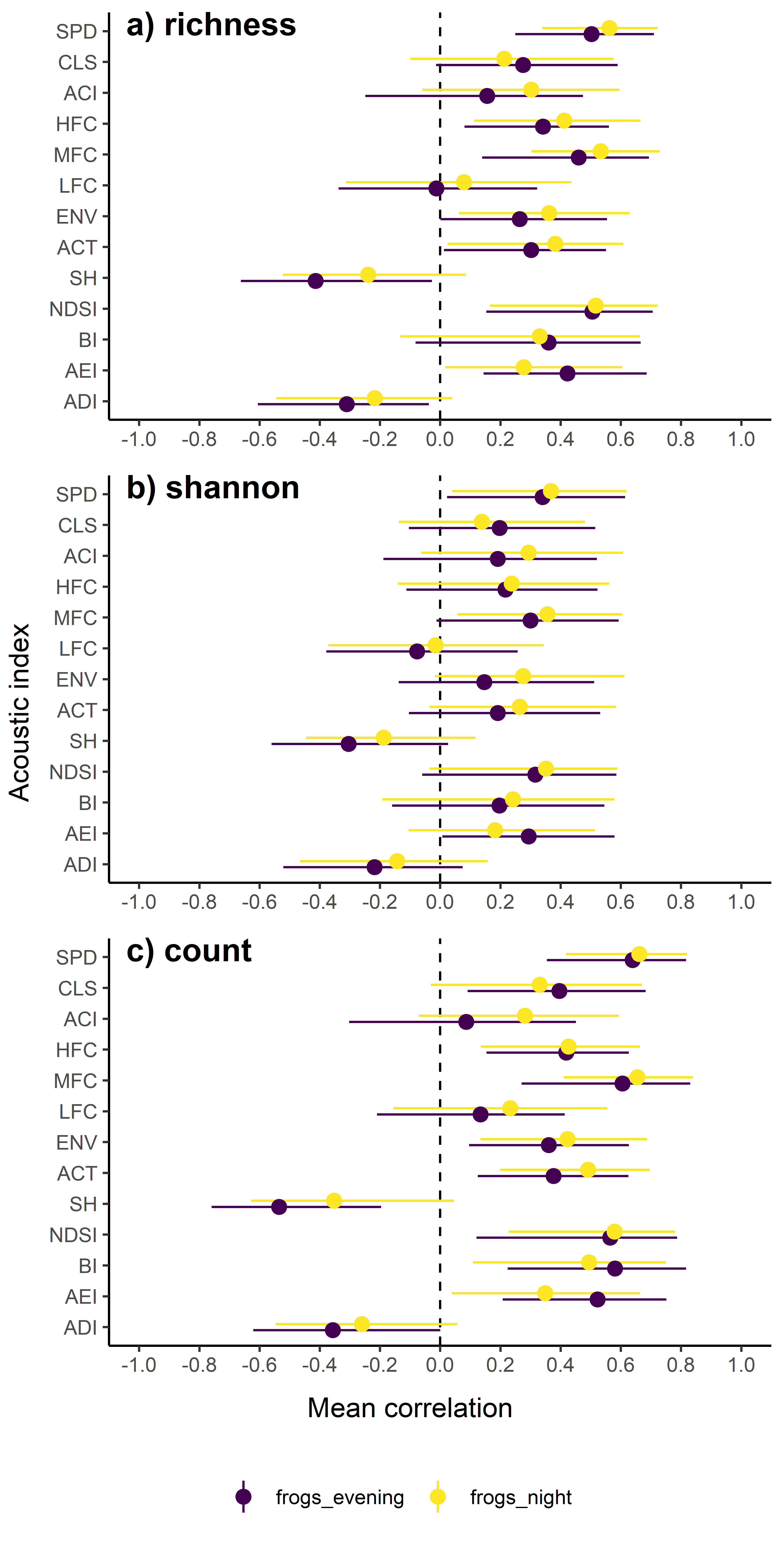


Figure S . Bootstrap Spearman’s rank correlation values (±95% CI) of thirteen acoustic indices and a) species richness, b) Shannon’s diversity and c) total count of frogs using acoustic indices calculated from evening recordings (6pm-9pm; purple) and night recordings (6pm-6am; yellow).

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