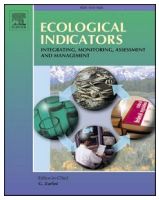
Ecological Indicators 182 (2026) 114533

Contents lists available at ScienceDirect

Ecological Indicators

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



Passive acoustic monitoring predicts higher avian diversity metrics than traditional bird surveys across multiple Australian bioregions

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ARTICLE INFO

Keywords:
Automated species identification
BirdNET
Bird communities
Nocturnal
Soundscape
Threatened species
Woodland birds

ABSTRACT

Technological advances over the last two decades have seen a large uptake in passive acoustic monitoring (PAM) to supplement traditional biodiversity surveys. To address the growing backlog of acoustic recordings these projects create, multispecies acoustic classifiers are now widely used in favour of manually processing data. Despite the uptake of these technologies, the efficacy of these recognisers needs to be evaluated to ensure they are detecting levels of diversity and community structure similar to traditional surveys. This study compared metrics of avian diversity across eastern Australia, between traditional bird surveys (both dawn, and dawn + nocturnal), and PAM processed using BirdNET, a widely used multi-species classifier. On average, PAM and multi-species classifiers returned higher values for all assessed diversity metrics (Species Richness, Chao2 estimators, Petchey's Functional Diversity, Rao's Q and Phylogenetic Distance), however traditional surveys supplemented with nocturnal surveys returned intermediate values. The efficacy of classifiers varied considerably across the study locations, with the number of incorrect identifications in the tropics substantially higher than those in temperate areas. Both methodologies failed to detect certain taxonomic groups, some threatened species, and detected significantly different avian communities. While these results provide a promising outlook for the future of PAM, it underscores the importance of maintaining traditional surveys as part of biodiversity monitoring, and relying on skilled ornithologists to ensure recorded acoustic data is appropriately interrogated. Furthermore, this study cautions against relying solely on automated classifiers in regions where training data for models is depauperate, such as Australia's tropical and subtropical woodlands.

1. Introduction

Ecosystems across the globe are under increased threat as the impacts of human landscape modification (e.g., fragmentation and clearing), and a rapidly changing climate, culminate in successive natural disasters (Hogue & Kathryn, 2022). Effective landscape-scale biodiversity monitoring is therefore crucial for the timely detection and management of population declines (Scheele et al., 2018; Lindenmayer et al., 2022). Traditional biodiversity monitoring requires ecologists to physically travel to sites regularly to undertake surveys, however this approach is time consuming, limits the spatial extent that can be regularly monitored, relies on highly skilled professionals and is prohibitively expensive (Darras et al., 2019). Large-scale monitoring programs may effectively be outsourced to citizen science (Callaghan and Gawlik, 2015); however, this runs the risk of inconsistent data collection regimes and structures, or lack of appropriate long term observer commitment (Bayraktarov et al., 2019; Johnston et al., 2023). It is therefore unsurprising that in a rapidly advancing world, stakeholders are reaching for technologies to supplement or enhance ecological monitoring programs.

One such technology, which has shown considerable interest in the last two decades, is passive acoustic monitoring (PAM). PAM has numerous advantages over traditional surveys; it is less invasive as observers aren't in the field, it can be used in areas which are difficult or costly to access, and recordings are permanent and can be reanalysed in the future as methodologies and analytical techniques advance (Gibb et al., 2019). Devices can be deployed in terrestrial, or aquatic environments, and can be highly customizable to meet the aims of the project (Sugai et al., 2019; Desjonquères et al., 2024). PAM has been highly effective at monitoring a range of taxonomic groups (birds,

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https://doi.org/10.1016/j.ecolind.2025.114533
Received 16 July 2025; Received in revised form 26 November 2025; Accepted 7 December 2025
Available online 19 December 2025

mammals, anurans, insects, etc) across all conceivable biomes, and is increasingly become the prominent way to monitor vocal, cryptic species (Leseberg et al., 2022; Van Klink et al., 2022; Bota et al., 2023; Hoefer et al., 2023). The cost of recording equipment is declining, making it feasible to monitor at a large scale (Hill et al., 2018). Devices now exist which can record 24 h a day, year-round, reducing the frequency of site visits, and acoustic observatories and large-scale recording regimes are present in all major regions of the world (Roe et al., 2021; Darras et al., 2024). Thus, the technology is among the most promising and flexible monitoring tools available, and many researchers advocate for its use in conservation projects (Farina et al., 2024; Teixeira et al., 2024; Wood et al., 2024).

Despite the many advantages, PAM now faces a big data problem, and it is not uncommon for even small-scale projects to be dealing with terabytes of data. While projects until now have relied heavily on experts identifying species from audio (Sugai et al., 2019), projects now regularly collect more data than one person can listen to in a lifetime. To overcome this big data problem, species specific detection methods are increasingly being applied to acoustic datasets. Species specific recognisers offer the potential to trawl through terabytes of recording data searching for vocalisations (or other acoustic signals) of a target species. Using image recognition approaches, algorithms can classify segments of recordings as belonging to the target species and provide some degree of confidence to the identification (Kahl et al., 2021; Zhong et al., 2021). From these outputs, information about the species biology, behaviour and distribution can then be applied, ad-hoc. Advances of programming, and the use of convolutional neural networks have resulted in capacity to create multi-species classifiers (Stowell et al., 2019a, b; Eichinski et al., 2022). BirdNET (Kahl et al., 2021) is one such program, which at time of publishing had the capacity to detect and classify over 6000 bird species around the globe. These multi-species classifiers allow researchers to rapidly process data, extract information like species lists, relative acoustic activity, and species context at a community level, and therefore have the potential to supplement, or augment, traditional surveys.

While these technological developments are of great interest to stakeholders, the efficacy of multi-species classifiers can be highly variable. Firstly, classification models are built on training data, which typically come from existing wildlife recordings or libraries (e.g. Macauly Library and Xeno Canto; Kahl et al., 2021). While these annotated datasets are critically important to classifier construction, they can inherently be biased due to the spatial extent of sampling, leading to variable detection rates for species across their distributions (Metcalf et al., 2022). This is very likely to occur for birds, where vocalisations can vary greatly within species as a response to environmental cues and sexual selection (Podos and Warren, 2007). Furthermore, research on multi-species classifiers is predominately undertaken in the Northern Hemisphere where wildlife recording is widespread, audio collections are typically representative of the regional variation in bird song, and avian diversity is lower (Thomas et al., 2008; Pérez-Granados, 2023). Thus, inferring their reliability of multi-species classifiers in other regions (such as Africa, Southeast Asia, and Australasia), requires thorough examination, particularly if the goal of the project is to monitor diversity over large geographic regions (de Araújo, 2024).

Despite the enthusiastic uptake of PAM to monitor biodiversity, there is a paucity of projects which attempt to compare the efficacy of multi-species classifiers with traditional methods (though see Schuster et al., 2024), particularly in the southern hemisphere. This is concerning as more practitioners consider opting for PAM processed with classifiers in lieu of traditional surveys due to the scalability and lower associated costs. Methodologies may detect completely different patterns in diversity metrics, or community composition, and thus greatly influence project outcomes. It is therefore critical to examine these methods across a large spatial scale to be aware of the potential limitations if stakeholders rely solely on PAM to monitor biodiversity. Our study aims to address this gap by comparing avian species lists generated with PAM processed with BirdNET with those from traditional surveys, across eastern Australian woodlands. The study asked:

I. Do species counts generated by PAM reach similar values to traditional surveys?
II. Do diversity metrics (species richness, SR; species richness estimators, Chao2; Petchey's functional diversity (FD); Rao's quadratic diversity index (Q); and phylogenetic distance) differ between the method of data collection?
III. Do the two methods detect similar community composition?

2. Methods

2.1. Study locations

Field data was collected between the 18th of April 2021 and 28th of November 2022. Six locations in eastern Australia were selected to survey from the Australian Acoustic Observatory (A2O) network (Duval Nature Reserve, Mourachan conservation property, Rinyirru National Park, Tarcutta Hills Reserve, Undara National Park, Wambiana Station; Fig. 1). The study locations were selected to maximise the geographic spread of data so that inferences about the A2O network's capability to monitor biodiversity could be assessed (Allen-Ankins et al., 2023). All locations were similar in habitat structure (open eucalypt woodlands, with sparse tree cover and grassy understories) so that biases in surveys methods were less impacted by variations in vegetation structure and composition. Rinyirru, Undara, and Wambiana, are found in tropical

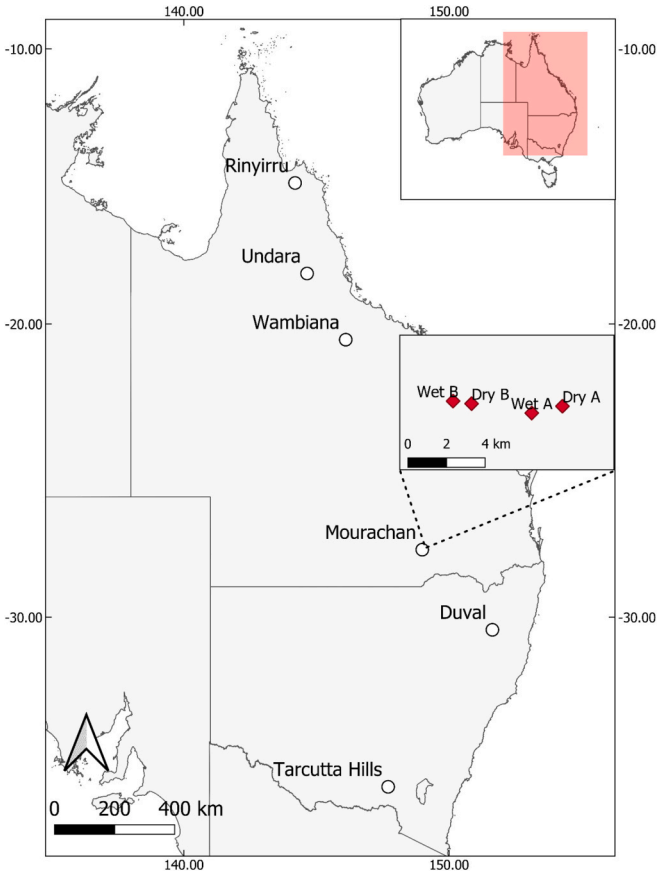

Fig. 1. The six study locations where traditional and acoustic monitoring was conducted. All sites were within open eucalypt woodland vegetation. All study locations had four sample sites (red diamonds above) separated by ~500 m as per the A2O study design, making the total number of sample sites 24. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

bioregions, Mourachan is located in a subtropical bioregion, and Duval and Tarcutta are found in temperate bioregions Department of Climate Change, Energy, the Environment and Water, 2021). Under the Köppen-Geiger climate classification, the former four have distinct wet and dry seasons, while the latter two are temperate bioregions (Kottek et al., 2006) with average yearly rainfall varying between locations (lowest average of 483.8 ml at Mourachan, to the highest average of 1176.3 ml at Rinyirru). Tropical and subtropical locations have large differences in their summer and winter climates, with October to April being dominated by extensive periods of rainfall, and high humidity (colloquially known as the wet season), while the remaining months are mild and dry (i.e. dry season). The study locations also had a range of altitudes (lowest: Rinyirru 18 m above sea level; highest: Duval, 1308 m asl; appendix A1). At each of these locations, the A2O project has four survey plots (hereafter 'sites'), which were used as individual sample sites (for total of 24 unique sample sites in the study). Each site has a permanent passive acoustic monitor (Solar-BAR, Frontier Labs Australia 2020) which records 24 h a day, 365 days a year. Two sites for each location were designated "wet sites" (i.e., within 50 m of water bodies, or permanent or ephemeral water courses), and two were designated "dry sites" (areas at least 100 m away from any permanent water; see Roe et al., 2021 for experimental design). Paired sites (e.g Wet A and Dry A) were typically 500 m apart to avoid sampling the same acoustic community.

2.2. Traditional bird surveys

On-ground surveys (hereafter: traditional surveys) were undertaken to capture avian diversity in two dry, and two wet seasons for each location. Each survey was conducted over a seven-day period, where each of the sites were visited twice daily. Surveys were undertaken during the both the dawn chorus (within two hours post dawn) and during the evening (from 30 min post-dusk to 23:00). The start time of each survey was randomised to ensure the temporal variability of bird behaviour at each survey point was captured during the survey period. Where possible, subsequent visits to undertake the second year of surveys were aligned to the previous year survey dates, however in some cases these surveys' start and end dates varied by up to a month (mean 18.7 days). The surveys consisted of two observers undertaking an active area search of the 100 m × 100 m (1 ha) sensor plots for 15 min. All species seen or heard within and up to 500 m outside of the plot were recorded, and estimates of abundance were given where appropriate. Individuals which could not be identified to species level were identified to a broad taxonomic group (for example, Australasian robins that could not be identified were classed as "robin"). These data were collated into two datasets to represent typical biodiversity monitoring approaches (dawn survey only, and dawn survey and nocturnal survey, hereafter 'traditional' survey and 'traditional + nocturnal' survey respectively).

2.3. Data processing and BirdNET validation

Audio that covered the survey periods was downloaded from the A2O data portal in flac format (https://data.acousticobservatory.org/: Roe et al., 2021). Where possible, 24 h of recordings for each day were downloaded to maximise the number of species detected, and to also reflect a typical recording schedule for solar powered acoustic monitors. These recordings were analysed using BirdNET (model version 2.4) via the command line interface under default settings. To minimize the inclusion of unlikely species, BirdNET was constrained to only return identifications of geographically likely species by using the central GPS coordinates for the survey location. The algorithm provides species identifications with a confidence score as a relative indicator of model performance, and thus IDs were filtered by this metric. Due to the large geographic distribution of the survey locations, and bird species' tendencies to have geographically variable calls, precision of multi-species classifiers may be variable. As such the BirdNET output was filtered by location resulting in location specific species lists. To minimize the number of false positives, the BirdNET output was filtered so that only recordings with a confidence score greater than 0.5 remained. Preliminary analysis on four common species (Magpie-lark, *Grallina cyanoleuca*, Australian Boobook, *Ninox boobook*, Peaceful Dove, *Geopelia placida* and Laughing Kookaburra, *Dacelo novaguineae*) suggested that IDs started to become less reliable at confidence score 0.5, however it is possible a small number of true positives may have been removed during this step. Location specific validation datasets were generated for all species detected at each location. Where possible, ten three-second audio samples from a range between confidence score 0.5–1 were randomly selected for validation. The validation set was then checked by an experienced ornithologist (BD) to remove species where all detections were false positives. Results of the manual audit were compiled into a table (appendix A2).

2.4. Data analysis

All analysis was undertaken in R statistical software (version 4.2.2, R Core Team, 2022). To inform practitioners about the difference in the species diversity detected by each method, PAM data was subsampled down to the same survey window as the on ground traditional surveys. This arbitrary limit was selected as it permitted the creation of three hypothetical situations; a) dawn surveys only, b) both dawn and night surveys, and c) PAM processed with BirdNET. This allowed for comparisons between metrics as if one method was chosen in lieu of another. Due to equipment errors, and access limitations, the number of sample days between the two methods were not always equal. To ensure sample effort was comparable among methods, dates were filtered to include only those where data from both on-ground and acoustic surveys were available. As PAM is increasingly used to supplement traditional surveys, metrics which capture various elements of biodiversity (richness, functional diversity and phylogenetic diversity) were calculated so biases or limitations from the different methods could be interrogated. To compare diversity metrics between the two methods, the on-ground datasets were converted into site-specific daily presence-absence datasets. To determine if the rate of species detection differed between the two methods, species accumulation curves with 100 permutations were generated for all sites using the specaccum() function from the package vegan (Dixon, 2003). From these, site species richness, and site Chao2 species richness estimators were calculated. Chao2 was calculated using the Chao2 function in the fossil package (Vavrek, 2011). The data frame was then split by trip, and species diversity metrics were recalculated.

To determine whether methods were sampling similar functional groups, two functional diversity metrics were calculated (Petchey's FD (Petchey and Gaston, 2002) and Rao's Quadratic entropy (Q; Rao, 1982) in the package FD (Laliberté et al., 2014). Species lists were sorted to return a full list of species detected in both methodologies, before being arranged in a presence-absence matrix for each combination of site, plot, and trip. The functional traits of foraging strata, diet (primary food source), body mass (gram, $\log_{10}$), and daily activity patterns (nocturnal or diurnal) were obtained from Elton Traits 1.0 (Wilman et al., 2014; Table 1). These traits were chosen as the represent a bird's ecological niche and therefore represent likely drivers in differences in detectability. 'Typical foraging strata' was the location where a species spent

Table 1
Functional traits selected from Elton Traits 1.0 to calculate functional diversity.

Trait	Categories
Foraging height	Water – below surface, water – around surface, ground, understory, mid high, canopy, aerial
Diet	Primary diet as determined in Wilman et al., 2014
Daily activity pattern	Diurnal, nocturnal
Body mass	Log10 – mean of the average values provided for both sexes.

>40 % of their time foraging. Where a species had no strata at 40 % or greater (23 species), the values of multiple strata were combined to meet the threshold. The tallest stratum was then selected as it is unlikely the species would be present without this stratum. The dominant foraging category as nominated by Wilman et al. (2014) was used for diet. Bird mass (g) was $\log_{10}$ transformed so data was normally distributed as untransformed data was highly left skewed.

To explore the difference in phylogenetic distance among methods, pruned phylogenetic trees were created in the package U.PhyloMaker using the bird megatree from Jin and Qian (2023). This tree backbone is based on Jetz et al. (2012), and includes nearly 10,000 species, including nearly all species in the current study. Trees were made of all combinations of site, plot and trip, and mean distances between tips was calculated using the cophenetic.phylo function in the package ape (Paradis et al., 2004). Two species (Pacific Emerald doves, *Chalcophaps longirostris* and Purple-back Fairywrens *Malurus assimilis*) detected in the study have been elevated to full species since the publication of Elton-Traits and the Jetz et al. (2012) phylogeny, and thus functional data and genetic data was not available for these species. In these cases, sister species (*Chalcophaps indica* and *Malurus lamberti*) were used to infer functional data and genetic distance.

As sample days were not always consistent between locations and trips, the rarefaction function in the vegan package was used to estimate rarefied functional and phylogenetic diversity metrics. Prior to statistical analyses, data were checked for normality using a Shapiro Wilk test. To test the differences between survey methods in terms of species richness metrics, functional diversity metrics, and phylogenetic distance, generalized mixed effects models were created in the lme4 package (Bates et al., 2015). Due to the paired nature of the data (traditional surveys and PAM were undertaken concurrently), sites were paired using by a grouping term (Plot + Trip). Models were constructed with both site and (Plot + Trip) as random factors and diagnostic plots were generated with the package DHARMa (Hartig; 2017) to ensure that the models did not violate modelling assumptions. A Poisson distribution with offset for uneven sample days was used to model the Species Richness (count) data., while the Chao2 results were modelled with a Gaussian distribution. Models for all rarified metrics violated a Levene's test for homogeneity of variance, so was remodelled in the package glmmTMB (; Magnusson et al., 2017) so that variance structure could be considered in the model. The rarefied PD model also violated the outlier test, so data was log transformed prior to modelling and were modelled using the nlme package (Pinheiro et al., 2017). Mean differences among methods were calculated from the model outputs using the emmeans package (Russell et al., 2017).

To examine the difference between community composition, non-metric multi-dimensional scaling was performed using the R package vegan (Dixon, 2003). First a Jaccard distance matrix was created using the vegdist() function, before an NMDS was generated using the metaMNDS() function. The NMDS was run for 100 permutations. Outputs were examined to ensure stress was within meaningful bounds, and Shepard's plots were used to assess the fit of the NMDS ordination. To test the difference between survey methods, a PERMANOVA was then run in adonis2() using the following grouping terms: survey method, site and trip, and the interactions between each term. Beta diversity (nestedness and turnover) within and between methods was then calculated independently for all sites using the package betapart (Baselga and Orme, 2012). These values were then averaged across all locations to examine study wide patterns in species replacement and loss by the different survey methods. All plots were visualized using ggplot2 (Wickham, 2011).

3. Results

A total of 244 species were detected over the duration of the study (appendix A3). Of these, 166 species were detected by both methods, 27 were detected only by PAM, and 42 were detected only in field observations. A further five species were detected by both nocturnal surveys and PAM, and four were detected only in nocturnal surveys. Field observers could identify most species during both diurnal and nocturnal surveys, with birds not identified to species level representing between 7 and 16 % of the site's species list (Fig. 2, appendix A4). PAM with BirdNET had a higher proportion of incorrect species predictions (i.e., where none of the extracted audio samples were correct for that species) and ranged between 37.5 % and 60.1 %. In both methods, the lowest proportion of uncertain or incorrect predictions were recorded at Tarcutta, while the highest were at Undara National Park. Overall, BirdNET detections were generally correct at higher confidence scores, although the overall performance varied across the study sites. A total of 51 species weren't detected by BirdNET at some of the study sites, despite being found in the same locations by traditional surveys (mean per site = 10.17; appendix A5). Temperate sites had fewer undetected species (Tarcutta and Duval, both 6 species), compared to subtropical and tropical sites (range 9 to 16, average 12.25), and undetected species were present in more subtropical and tropical surveys (temperate mean = 1.823 tropical and subtropical mean = 4.41). A further 31 species (mean six species per site) were detected by both traditional surveys and PAM, but these were later removed from the PAM dataset after the validation process confirmed the audio files attributed to these species consisted solely of incorrect predictions. Furthermore, BirdNET consistently confused wader species with woodland bird species (particularly honeyeaters). Traditional surveys detected more waterbird species (particularly members of Threskiornithidae and Ardeidae), while nightjars, Tyto owls, and rails were almost exclusively detected by PAM unless dawn surveys were complemented with nocturnal surveys. Ten threatened bird species were detected in the study, however only three were detected with both methods. Traditional surveys detected five (Squatter pigeon, *Geophaps scripta*, White-throated Needletail, *Hirundapus caudacutus*, Glossy Black-Cockatoo, *Calyptorhynchus lathami*, Painted Honeyeater, *Grantiella picta*, and Diamond Firetail, *Stagonopleura guttata*), while two were detected exclusively with PAM (Common Greenshank, *Tringa nebularia* and Pink Cockatoo, *Cacatua leadbeateri*).

Species accumulation curves generated with data from all survey trips combined revealed a universal pattern of PAM detecting more species, and sooner, than traditional surveys (Fig. 3). Additionally, including nocturnal surveys in traditional surveys resulted in marginal increases in species accumulations curves (average of 3.46 species difference at asymptotes). For most sites, there was a clear difference between the likely asymptotes of PAM and both forms of traditional surveys, with PAM estimates after the final survey date averaging 20.66 more species than dawn surveys, and 17.21 species more than dawn and nocturnal surveys. The biggest differences between traditional surveys and BirdNET curves was observed at Mourachan and Wambiana (mean difference = 25.5 and 26.75 respectively).

Differences in diversity metrics.

Passive acoustic monitoring and BirdNET returned species richness values that were on average 21.04 species higher (trip mean 50.53) compared to dawn surveys (mean 32.49 respectively) and 19.15 species higher than the mixed dawn and evening surveys (mean 34.38), however the difference depended on the site, and the trip (Fig. 4). Species counts among methods were the most similar at Undara (mean difference 13.07). The sites with the most different species richness counts were Mourachan and Wambiana, where species lists were on average 24.66 species higher with BirdNET assisted PAM. Wambiana recorded the largest difference between the two methods in a single trip (39 species difference at Wet A, on trip three). The mixed model showed a substantial difference between the data collection methods, with methods alone explaining 21 % of the variation in the data. Survey method was a statistically significant predictor of the differences between the species richness counts (Table 2), with PAM detecting 1.6 times as many species than standard traditional surveys after accounting for survey effort. Mean effort adjusted species richness counts from BirdNET-assisted PAM and traditional surveys were significantly

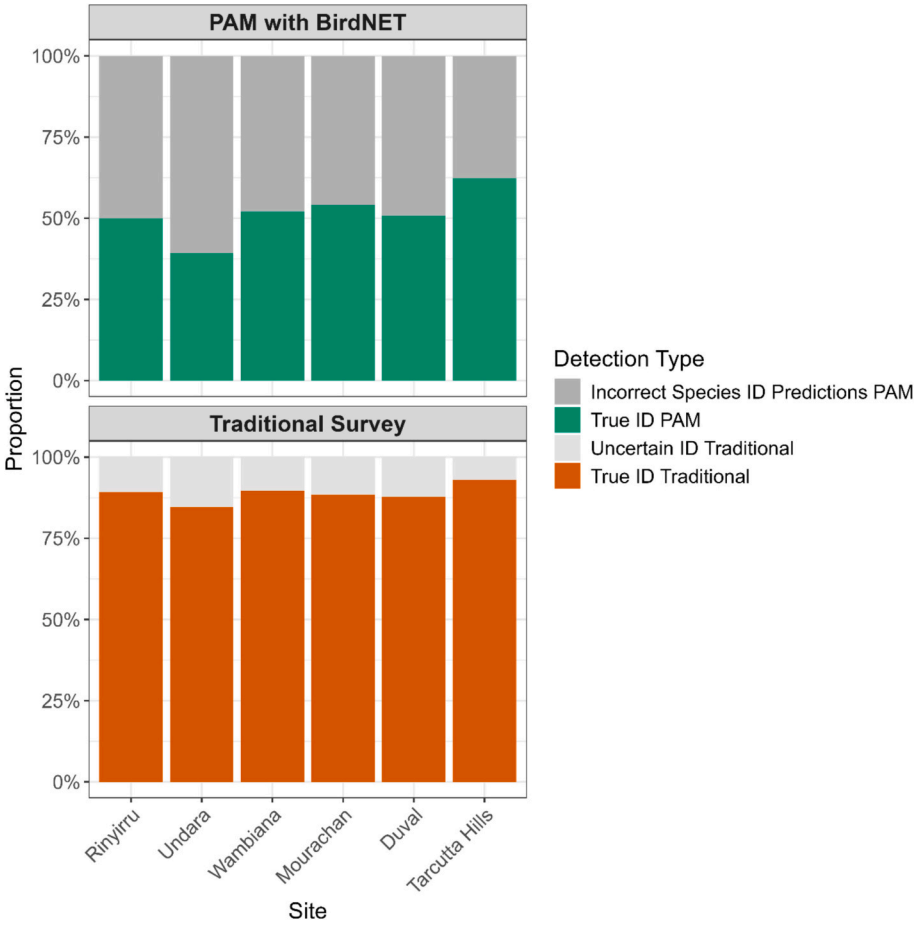

Fig. 2. Proportion of study site bird lists which consisted of either incorrect predictions or species which could not be identified to species level. Colours indicate the method of data collection: i.e., PAM with BirdNET, or traditional bird surveys. Dark grey indicates proportion of incorrect PAM species ID predictions, while light grey indicates uncertain IDs from traditional surveys. Nocturnal results provided in appendix A4.

different (ratio = 1.647, SE = 0.0415, z ratio 19.962, p value ≤0.001).

Species richness estimators (Chao2) were less consistent, however had a similar pattern of PAM returning higher values (mean 67.44) than traditional dawn surveys (mean 46.53 respectively), and mixed dawn and night surveys (mean 50.28; Fig. 4). The lowest Chao2 estimates for both methods were at Undara (PAM mean 47.11, traditional survey mean 34.06), while the estimates for PAM were highest for Wambiana (mean 78.08), and estimates for traditional surveys were highest at Mourachan (mean 53.77). The lowest average difference between the two methods was recorded for Undara (mean 13.05), while the highest was recorded for Wambiana (28.28). Chao2 estimators were higher in traditional surveys five (range − 1.94 to −24.47, mean − 11.01), and 12 times when compared with traditional surveys with additional nocturnal surveys (range − 0.167 to −27.5, mean − 8.157). However, no on-ground surveys consistently outperformed PAM at any one site. Survey method explained a substantial amount of variation in the data with methods describing 23 % of the variation alone (Table 2). There was a significant difference between the PAM and traditional dawn surveys (Means tests estimate = 20.92, SE = 2.14, T ratio = 9.784, p value <0.001) with linear models estimating traditional and traditional with nocturnal detect between ~17 and 21 fewer species at their asymptote than PAM assisted with BirdNET.

Functional diversity metrics largely agreed with the species richness metrics when comparing between PAM and traditional surveys (Fig. 4). Despite this there were substantial differences in functional diversity metrics between dawn surveys and dawn surveys supplemented with nocturnal surveys. Rarefied Petchey's FD was consistently higher with PAM (mean 7.59) than traditional surveys (5.02), as were nocturnal and diurnal surveys combined (mean 5.63). Traditional surveys had a significant, negative effect on the Petchey's FD (p value ≤0.001) and there was a statistically significant difference in mean rarefied Petchey's FD among all three survey methods (PAM vs Traditional: estimate = 2.576, SE = 0.1010, t ratio = 25.393, p value <0.001; PAM vs Traditional + Nocturnal: estimate 1.970, SE = 0.1150, t ratio = 17.138, p value <0.001; Traditional vs Traditional + Nocturnal: estimate −0.606, 0.0985, −6.154, p value <0.001).

Like Petchey's FD, rarefied Rao's Q varied between the survey methods (Fig. 4). The average differences between PAM and BirdNET, across all sites were less than 0.05, suggesting that similar functional diversity was detected. Nevertheless, rarefied Rao's Q was lowest using traditional survey, highest with PAM processed with BirdNET and intermediate with traditional surveys augmented with nocturnal surveys. The model explained a large amount of the variation in Q values (63 %), however much of this was due to random effects (site and plot factors). The model variation explained by method alone was 20 %. Nevertheless, method remained a significant predictor in the model (Table 2). There was also a statistically significant difference between the average of Rao's Q between PAM and Traditional surveys (estimate = 1.075, SE 0.007, z ratio = 11.15, p value <0.001), and Traditional surveys, PAM and traditional with nocturnal surveys (1.039, SE 0.007, z ratio = 5.842, p value ≤0.001), and Traditional surveys with nocturnal surveys (estimate = 0.966, SE 0.006, z ratio = −5.310, p value <0.001).

Phylogenetic distance also varied among survey methods (Fig. 4). The average rarefied PD from species lists detected with PAM was typically higher than both traditional surveys and traditional surveys with nocturnal surveys (mean difference = 4.23 and 4.04 respectively).

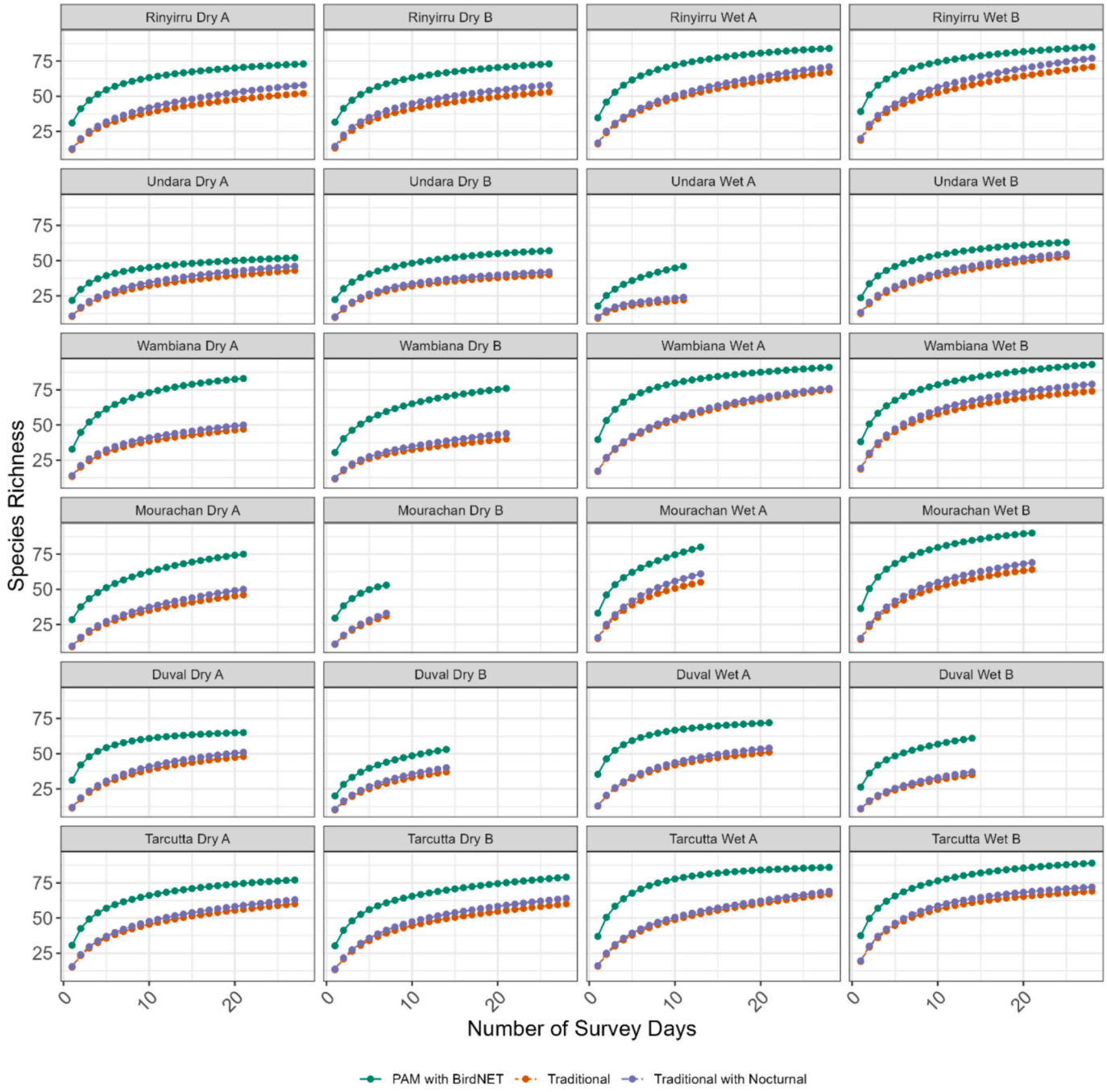

Fig. 3. Species accumulation curves of species detected at each site over the entire study period. Species accumulation curves were generated with 100 permutations. Colours represent the survey method. Data has been split into "plots" to show general trends across the study sites. Sites are ordered from North to South.

Undara had the lowest average phylogenetic distance in PAM (mean 151.51), while Duval has the lowest average phylogenetic distance in both traditional surveys, and traditional surveys with nocturnal surveys (146.94 and 146.84 respectively). Despite this, method remained a significant predictor in the model (Table 2) and the mean difference of PD among methods remained significantly different among all three survey methods (PAM vs Traditional estimate = 5.035, SE = 0.003, t value = 1408.0229, p value ≤0.001; PAM vs Traditional with nocturnal estimate = −0.029, SE = 0.006, t value = −4.191, p value ≤0.001; Traditional vs Traditional with nocturnal estimate = −0.027, SE = 0.006, t ratio = −4.311, p value = 0.001).

3.1. Communitiy composition

While all survey methods shared a large number of species within locations, the communities detected by PAM and traditional surveys remained distinct in ordinal space (Fig. 5). Minor overlaps in ellipses were apparent for four sites (Duval, Mourachan, Tarcutta and Wambiana), however Rinyirru, and to a lesser extent Undara, were largely disjunct suggesting the detection of distinct avian assemblages. The results of the Permanova showed there was a strong site effect (~ 46 % of the variation, Table 3), and this was reflected in the clustering of temperate sites (Duval and Tarcutta), and their separation from tropical savannah sites (Rinyirru, Undara, and Wambiana; appendix A6). Nevertheless, survey method was still a significant predictor of the

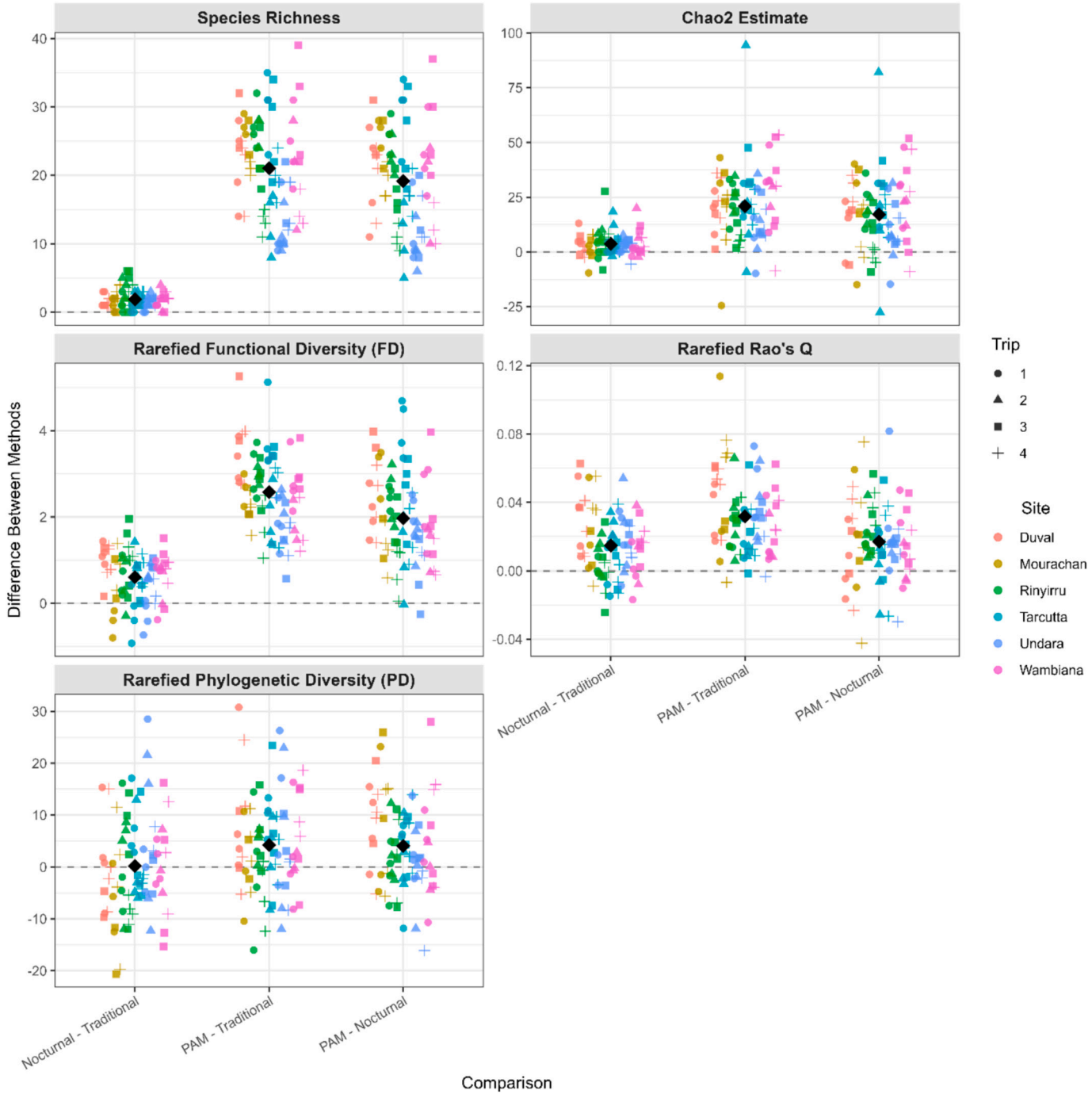

Fig. 4. Mean difference in diversity metrics between survey methods. Colours indicate the site, while symbols represent the trip. Black diamonds show the mean difference between the methodologies.

variation (df = 2, sum of squares = 4.022, F 7.0955, R2 = 0.05718, *P* value = 0.001). Additionally the trip number (proxy for season) also played a minor, but significant role in shaping communitiy composition (Table 3).

Beta diversity metrics (Table 4) revealed that acoustic data processed with BirdNET had the lowest average nestedness (0.07) and average turnover (0.36). Traditional and traditional with nocturnal surveys had similar values for both nestedness and turnover both within, and between, the two methods. Nestedness was highest when comparing between PAM processed with BirdNET, and the two traditional surveying methods (0.19 and 0.21). All methods had moderate turnover (between 0.36 and 0.47).

4. Discussion

This study revealed the advantage of using passive acoustic monitoring to undertake bird surveys across eastern Australia. Species accumulation curves constructed using results from PAM included more species than traditional bird surveys over the same survey period. After accounting for survey effort (number of survey days), all metrics of diversity, (species richness metrics, functional diversity metrics, and phylogenetic distance) were significantly higher when using PAM and BirdNET compared to traditional dawn surveys, and survey method was a significant predictor in all metrics across the study. Furthermore, while incorporating nocturnal surveys to traditional bird protocols increased

Table 2
GLMM results for all diversity metrics. Incidence rates ratios (IRR), estimates (Est.), Confidence intervals (CI), and *P* values provided.

Model		Species Richness			Chao2 Estimate			Rarefied Petchey's FD			Rarefied Rao's Q			Rarefied Phylogenetic Distance (PD)		
	Predictors	*IRR*	*CI*	*p*	*Est.*	*CI*	*p*	*Est.*	*CI*	*P*	*Est.*	*CI*	*p*	*Est.*	*CI*	*p*
Conditional	Method [PAM]	7.73	6.93 – 8.62	**<0.001**	67.67	59.69 – 75.66	**<0.001**	7.57	7.22 – 7.93	**<0.001**	0.45	0.43 – 0.47	**<0.001**	5.04	5.03 – 5.04	**<0.001**
	Method [Traditional]	0.61	0.58 – 0.64	**<0.001**	−20.92	−25.13 – -16.70	**<0.001**	−2.58	−2.78 – −2.38	**<0.001**	0.93	0.82 – 0.94	**<0.001**	−0.03	−0.04 – −0.02	**<0.001**
	Method [Traditional + nocturnal]	0.64	0.61–0.67	**<0.001**	−17.16	−21.37 to −12.95	**<0.001**	−1.97	−2.20 to −1.75	**<0.001**	0.96	0.95–0.97	**<0.001**	−0.03	−0.04 to −0.01	**<0.001**
Dispersion	Method [PAM]	NA	NA	NA	NA	NA	NA	−0.30	−0.48 – −0.13	**<0.001**	NA	NA	NA	NA	NA	NA
	Method [Traditional]	NA	NA	NA	NA	NA	NA	−0.36	−0.48 – −0.13	0.010	NA	NA	NA	NA	NA	NA
	Method [Traditional + nocturnal]	NA	NA	NA	NA	NA	NA	−0.21	−0.30–0.21	0.728	NA	NA	NA	NA	NA	NA
	Random Effects															
	σ^2	0.16			180.52			NA			0.00			0.00		
	$\tau_{00\ Plot+Trip}$	0.01			30.54			0.08			0.00			0.00		
	$\tau_{00\ Site}$	0.01			72.88			0.29			0.00			NA		
	ICC	0.14			0.36						0.53			NA		
	N	16 Plot+Trip			16 Plot+Trip			16 Plot+Trip			16 Plot+Trip			16 Plot+Trip		
		6 Site			6 Site			6 Site			6 Site			6 Site		
	Observations	237			237			237			237			237		
	Marginal R^2 / Conditional R^2	0.215 / 0.325			0.237 / 0.508			NA/NA			0.198 / 0.626			0.147 / NA		

all diversity metrics, PAM still consistently detected higher diversity. Despite these improved diversity outcomes, community composition detected by the methods were dissimilar, and there were clear differences in results between temperate and tropical geographic regions. Furthermore, raw PAM data required thorough interrogation by highly trained ornithologists to remove large numbers of incorrectly predicted species prior to analysis. Nevertheless, the results provide an indication that incorporating PAM into traditional surveying regimes will result in more robust and stable estimates of avian diversity at study sites.

4.1. *Incorrect species IDs and taxonomic biases in surveying methods*

The high number of incorrectly classified birds from acoustic recordings is not an unusual occurrence, as many multi-species classifiers have variable performances when applied to large datasets (Metcalf et al., 2022). While it is common practice to filter BirdNET results by confidence scores, to reduce the number of incorrectly classified species (Pérez-Granados, 2023), recent works have cautioned against relying solely on these values (Wood and Kahl, 2024). These confidence scores vary among species models depending on the amount of training data, do not represent a probability of correct identification, and are not comparable among species (Wood and Kahl, 2024). Additionally, many of these incorrect species' predictions occurred during times of acoustic disturbance (high signal to noise ratio, geophony, and masking by other species). These issues are recurrent in acoustic monitoring programs and thus will likely impact the utility of this approach in "noisy" environments (Thomas et al., 2020; Priyadarshani et al., 2018). Despite the classifier performance issues, BirdNET outputs can still be examined to get a measure of reliability (false positives, recall and precision). These metrics are difficult to calculate with traditional surveys, in which species may not be detected due to observer inexperience, or species' inherent detectability.

The failure of both automated and traditional methodologies to detect certain taxonomic groups is likely to due to the vocal behaviour and ecologies of these families, with these detection biases noted in other studies (Darras et al., 2018). PAM failed to regularly detect members of Threskiornithidae (ibis and spoonbills), and Ardeidae (herons), as they are typically silent outside of their breeding season, and when away from other conspecifics (BirdLife Australia, 2023a, b). However these species are very easy to detect in traditional surveys as they are often very large, and visually conspicuous. The species detected exclusively with PAM consisted of bird groups notoriously difficult to see in person due to their cryptic behaviours (Rallidae), or nocturnal behaviour (Tyto owls and nightjar species). PAM has long been implemented as an effective tool for monitoring similar species, suggesting this methodology is favourable to traditional surveys (Knight et al., 2017; Bobay et al., 2018; Freitas et al., 2023). While incorporating nocturnal surveys with traditional surveys increased the number of nocturnal species detected by on-ground surveys, uncommon nocturnal species were largely missed during these limited search windows. Furthermore, four nocturnal species were not detected by BirdNET (Powerful Owl, *Ninox strenua*, Papuan Frogmouth (*Podargus papuensis*), Red-chested Buttonquail, *Turnix pyrrhothorax*, Black Bittern, *Ixobrychus flavicollis*), likely due to their low frequency calls and scarcity at the study sites.

While the study was not established to monitor threatened species, numerous threatened species were detected over the study's duration. Nevertheless, the two methods managed to detect different threatened species in unexpected ways. Both Common Greenshank (*Tringa nebularia*) and Pink Cockatoo (*Cacatua leadbeateri*) are conspicuous and easily surveyed using traditional surveys (Rowley and Chapman, 1991; Choi et al., 2021), however both were only detected via PAM. These species are highly mobile (migratory or nomadic/dispersive) and thus may have been absent from the plot during the time of the on ground traditional surveys. Threatened species missed via PAM require more scrutiny. While the absence of Squatter Pigeon (*Geophaps scripta*) and

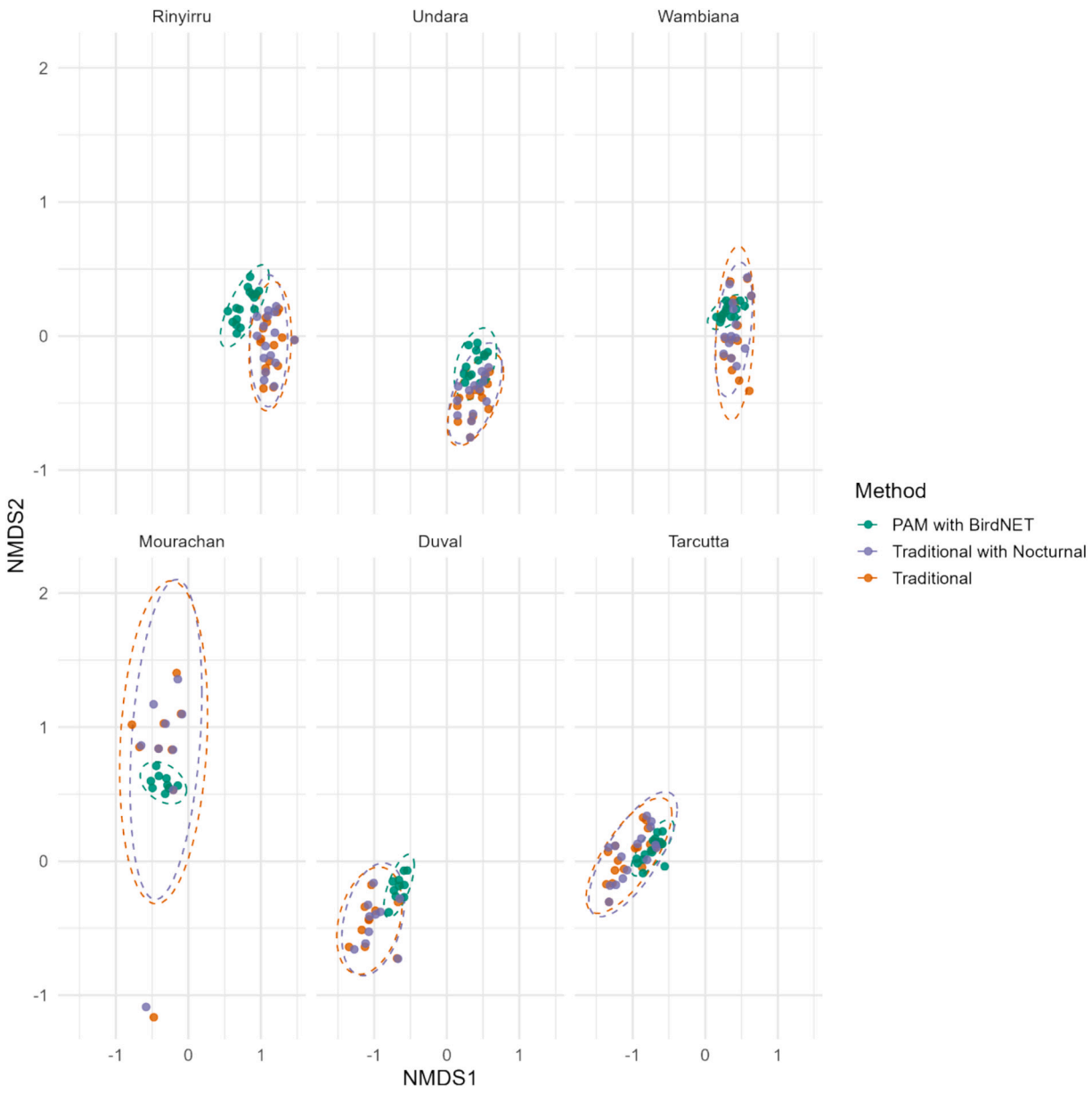

Fig. 5. Species composition among sites indicating methods. Colours represent the method, while points indicate plots. Polygons are drawn around to show the difference in shape. NDMS stress = 0.15.

Table 3
Results of PERMANOVA. Bold text represent significant values.

	Degrees of freedom	Sum Of Squares	R2	F	Pr (>F)
Site	5	31.168	0.44308	56.1186	0.001
Method	2	4.022	0.05718	18.1047	0.001
Trip	3	2.562	0.03642	7.6887	0.001
Site:Method	10	4.178	0.05939	3.7610	0.001
Site:Trip	13	6.384	0.09076	4.4212	0.001
Method:Trip	6	0.646	0.00918	0.9693	0.493
Site:Method: Trip	26	2.389	0.03396	0.8272	0.990
Residual	117	18.995	0.27002		
Total	236	70.344	1		

Table 4
Average beta diversity metrics (nestedness and turnover) for the methodologies.

Method Pairing	Nestedness	Turnover	Total
PAM with BirdNET within	0.07	0.36	0.43
PAM with BirdNET vs Traditional	0.21	0.42	0.63
PAM with BirdNET vs Traditional with Nocturnal	0.19	0.42	0.61
Traditional with Nocturnal within	0.10	0.47	0.58
Traditional within	0.11	0.46	0.57
Traditional_vs_Traditional with Nocturnal	0.10	0.44	0.54

White-throated Needletail (*Hirundapus caudacutus*) in the PAM dataset are understandable (*G. scripta* has a low frequency call which is easily masked, and *H. caudacutus* calls are poorly known; BirdLife Australia, 2023a, b), the failure of PAM to detect Glossy Black-Cockatoo (*Calyptorhynchus lathami*), Painted Honeyeater (*Grantiella picta*), and Diamond Firetail (*Stagonopleura guttata*) in the acoustic dataset is curious. These three species have loud and/or diagnostic vocalisations (Whitmore and Eller, 1983; Teixeira et al., 2020; pers. obvs.), and thus should have been detected via PAM. It is possible the classifiers simply underperformed for these species, suggesting that classifiers should be retrained for

threatened species prior to analysis (Allen-Ankins et al.; in review). Alternatively, the threatened species detected in the point count surveys may have been dispersing through the site, as three of the species (*C. lathami*, *G. picta* and *S. guttata*) were observed only once each in the 595 point count surveys. Finally, these species may be present in the unanalysed recordings from outside of our comparison window (i.e. the same days as on ground surveys), and thus may have been detected if all available acoustic data was processed.

4.2. Diversity metrics and the value of PAM

While there are many studies showing PAM has the potential to detect higher species richness than traditional surveys, many of these studies have relied on manual acoustic identification in favour of multi-species classifiers (Wimmer et al., 2013; Leach et al., 2016; Shaw et al., 2022). Additionally, the few studies that have explored the estimates of species richness quantified using PAM processed by multi-species classifiers have not compared the results to on-ground surveys, or have been conducted at very small spatial scales (Cole et al., 2022; Seibold et al., 2024). The findings from this current study affirm that PAM processed with species classifiers can return higher species richness values than traditional surveys over large latitudinal and spatial scales. While incorporating nocturnal surveys, such as in the study, may modestly improve species richness estimates, the additional efforts and costs associated may not be feasible for large-scale projects, particularly when PAM is effective at detecting these more cryptic species. Furthermore, as we constrained this study to days which had paired traditional bird surveys, the observer effects introduced by surveyors may have reduced the detectability of some species. Thus, the number of species detected by PAM in this study may be conservative.

Functional and phylogenetic diversity metrics calculated from PAM results were typically higher than those for paired on-ground surveys. While initially advocated for use in acoustic studies (Gasc et al., 2013), these metrics are seldom examined in the era of multi-species classifiers. Previously, studies have revealed the capacity for PAM to be effective at detecting changes in these metrics, in response to changes in vegetation structure, altitude and landscape connectivity (Doohan et al., 2019; Seibold et al., 2024; Borrow et al., 2025), however these studies did not compare PAM to traditional surveys. Furthermore, these studies were carried out on relatively discrete geographic scales, and did not cover multiple bioregions. The current study has shown that PAM can detect higher levels of functional and phylogenetic diversity than traditional surveys on a continental scale. This is encouraging given the growing interest and desire to incorporate more informative metrics into biodiversity monitoring and management (Cadotte et al., 2011; Owen et al., 2019; Biggs et al., 2020). However, both FD and PD are positively correlated with species counts in large-scale studies (Montaño-Centellas et al., 2020), and thus the values calculated at some sites may be inflated due to species richness. Despite this, the explanatory power of these metrics in the GLMMs differed from that of species richness, suggesting they provide different insights to diversity. Furthermore, patterns in the two functional diversity metrics (Petchey's FD and Rao's Q) were largely consistent, despite Rao's Q decreasing when species richness is higher (Botta-Dukát, 2005).

The use of PAM to explore differences in species composition are common (Zhang et al., 2024), however few studies compare between on-ground counts and those produced by multi-species classifiers. In studies that have explored this relationship, PAM consistently detects different species compositions to traditional surveys, even when non-soniferous species are removed from the point-count surveys (Thompson et al., 2024). This is also the case in the current study, where the species assemblages detected between the two methods were distinct. While this is somewhat unsurprising given the inclusion of non-soniferous species in the in-person survey data, it reveals that PAM may not always capture the full diversity at a given location. Furthermore, this study was conservative, using presence-absence data instead of number of detections per species to calculate community dissimilarity, as abundance estimates would have greatly influenced distance matrices. Despite this, beta diversity metrics revealed lower turnover and nestedness within the assemblages that PAM detected, suggesting more stable and representative monitoring. Nevertheless, we recommend that if a goal of a survey is to maximise the number of species detected, while also detecting similar species compositions, point-count or active surveys should be undertaken when establishing and servicing acoustic devices.

4.3. Geographic variability in PAM results

BirdNET performance varied considerably at different sites and occasionally failed to detect common species at all sites where they occurred. This was particularly the case at tropical and subtropical sites, which had twice as many undetected species as temperate sites. (appendix A5). While the majority of species that BirdNET failed to detect were uncommon in the dataset (observed in traditional surveys only once or twice), eight species were missed regularly (observed in >10 surveys). The effectiveness of classifiers is largely impacted by the volume and quality of training data, and species that show substantial variability in their vocalisations can become difficult to detect if insufficient training data exists (Stowell et al., 2019a, b). The locations of this study are remote and sparsely populated, and thus training data which reflect the acoustic diversity of these regions is currently depauperate. Furthermore, the failure to detect these species may have been due to the initial filtering of the BirdNET outputs. As we set the confidence score to 0.5, any true positives detected at lower confidence scores were not interrogated by experts. Two potential solutions to overcome this are to either reduce the confidence score of the initial filtering (increasing the number of false positives in the dataset), or to provide more training data to the algorithm to improve performance.

4.4. Limitations and future directions

While the study has provided insights into the value of PAM in monitoring avian biodiversity, there are some limitations. Firstly, due to equipment failure and access issues, some sites lacked sufficient acoustic and survey data to be analysed for all four time periods. While reciprocal dates were removed from the data, the diversity metrics for Mourachan Dry B and Undara Wet A sites are likely to be underestimates. Despite this, effort was statistically corrected, and the difference between the methods in these two sites is consistent across all metrics, so it is likely to be representative of a longer survey. Secondly, the data presented here consist of daily presence-absence for each species. Thus, the BirdNET results come from a 24-h period, while bird survey data comes from traditional 15-min field surveys conducted at dawn, and after dusk. While it could be argued that the discrepancy between these time frames will always produce a higher species richness for PAM, this ignores the fact that both methodologies present daily presence-absence given a monitoring method, and that dates of monitoring were consistent between the two methods. Furthermore, other studies have undertaken similar comparisons between traditional surveys and PAM processed with BirdNET using limited-duration bird surveys and long duration recordings (Schuster et al., 2024). Additionally, species missed by PAM may have been detected in the recordings collected outside of the on-ground survey dates. These long-term recordings exist (access via A2O; https://acousticobservatory.org/), and could be processed to target these undetected species. Finally, this study only examined woodland environments at 24 sites in six locations. Beyond incorporating the broad seasons (wet and dry season), we did not explore the influence of environmental variation on bird diversity estimates. Bird vocal activity, breeding behaviour, and presence varies between seasons, and may in turn impact detectability by different monitoring methods and influence the diversity estimates. Additional environmental data (temperature, rainfall, wind etc.) should be gathered during surveys to account for errors in detectability (Morelli et al., 2022).

Furthermore, these patterns observed in this study may not be reflected in other ecosystem types, particularly sites with persistent geophony which can mask calls and inhibit acoustic recordings. Future studies should examine if PAM consistently outperforms traditional surveys at locations with different environmental conditions (e.g., rainforest, arid shrublands, desert, etc) and increase the number of sample locations and spatial replication to ensure patterns remain consistent.

5. Conclusions

Passive acoustic monitoring is increasingly becoming an effective and versatile tool for monitoring biodiversity, particularly as multi-species classifiers can now provide stakeholders with detailed species information. This study revealed that PAM consistently outperformed traditional bird surveys in all measured diversity metrics. Additionally, statistical models revealed a strong influence of site, suggesting that PAM may become an effective tool for monitoring diversity in tropical woodlands. Despite this, community composition differed considerably between the methods, indicating that traditional surveys should still complement PAM to ensure accurate and maximum diversity is captured. Furthermore, BirdNET identifications were not always reliable and trained ornithologists are required to validate outputs from multi-species classifiers. Future work should explore these relationships in other types of bioregions and habitats.

CRediT authorship contribution statement

Brendan Doohan: Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Sebastian Hoefer:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Slade Allen-Ankins:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Vesla Nilsen:** Writing – review & editing, Formal analysis. **Lin Schwarzkopf:** Writing – review & editing, Supervision, Project administration, Conceptualization.

Ethics

All fieldwork was conducted in accordance with the protocols approved by the James Cook University Animal Ethics Committee (A2727), QPWS (Queensland Research Permit P-PTUKI-100066861 and WA0033038), and NSW Government (New South Wales Scientific Licence SL102511).

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 would like to express our gratitude to the following individuals for their invaluable assistance in conducting field surveys: Lucca Amorim, Ryan Barnaby, Jacopo Bartholomew, Mallory Bissett, Malan Bothma, Martin Cachard, Tomas Cooney, Julian Correia, Gio Fitzpatrick, Mikayla Green, Thomas Heffron, Ryunosuke Kawaguchi, Catherine Kelly, Rosie Kidman, EvlynKok-McCosker, Naomi Laven, Hayden Marriott, Michelle Martinez, Alessandra Metzler, Michael McMaster, Daniel Panizo, Kelly Price, Corryn Porteus, Rory Read, Pia Riddell, David Smith, Daniel Stephens, Kate Stewart, Tessa Stewart, Lucas Tindale, Hayden de Villers, David Watson, Lucy Wright. We also extend our thanks to the Australian Acoustic Observatory (A2O), as well as all partners of Queensland National Parks and Wildlife Services, New South Wales National Parks and Wildlife Services, Wambiana Station, Australia Zoo, and Bush Heritage Australia for their support. We acknowledge the Traditional Custodians of the lands where we conducted this research, the Wulgurukaba, Bindal, Gudjal, Lama Lama, Kuku Thaypan, Ewamian, Kamilaroi, Anaiwanand Wiradjuri people, and pay our respects to Elders past and present. We recognise their continued connection to land, water, and culture.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.114533.

Data availability

Data is available on FigShare: 10.6084/m9.figshare.29578952

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