Original Article

Changes in the acoustic structure of Australian bird communities along a habitat complexity gradient

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Avian vocalizations have evolved in response to a variety of abiotic and biotic selective pressures. While there is some support for signal convergence in similar habitats that are attributed to adaptation to the acoustic properties of the environment (the "acoustic adaptation hypothesis," AAH), there is also evidence for character displacement as a result of competition for signal space among coexisting species (the "acoustic niche partitioning hypothesis"). We explored the acoustic space of avian assemblages distributed along six different habitat types (from herbaceous habitats to warm rainforests) in southeastern Queensland, Australia. We employed three acoustic diversity indices (acoustic richness, evenness, and divergence) to characterize the signal space. In addition, we quantified the phylogenetic and morphological structure (in terms of both body mass and beak size) of each community. Acoustic parameters showed a moderately low phylogenetic signal, indicating labile evolution. Although we did not find meaningful differences in acoustic diversity indices among habitat categories, there was a significant relationship between the regularity component (evenness) and vegetation height, indicating that acoustic signals are more evenly distributed in dense habitats. After accounting for differences in species richness, the volume of acoustic space (i.e., acoustic richness) decreased as the level of phylogenetic and morphological resemblance among species in a given community increased. Additionally, we found a significantly negative relationship between acoustic divergence and divergence in body mass indicating that the less different species are in their body mass, the more different their songs are likely to be. This implies the existence of acoustic niche partitioning at a community level. Overall, while we found mixed support for the AAH, our results suggest that community-level effects may play a role in structuring acoustic signals within avian communities in this region. This study shows that signal diversity estimated by diversity metrics of community ecology based on basic acoustic parameters can provide additional insight into the structure of animal vocalizations.

Key words: **acoustic niche, Australia, bioacoustics, bird assemblages, competition, signal space**.

INTRODUCTION

Sound is the preferred mode of communication for many animals. A wide array of organisms, including birds, mammals, frogs, and insects, use acoustic signals to attract mates or defend their territory (reviewed in Marler and Slabbekoorn 2004). According to one of the main principles of animal communication, signals should be detectable and convey a clear and unequivocal message against a noisy background (Bradbury and Vehrencamp 2011).

This background often involves the direct overlap of acoustic signals produced by a variety of other species. Consequently, to avoid interference among sounds, animals should adapt their signaling behavior to reduce acoustic competition as the acoustic niche hypothesis (ANH) posits, and this should be enhanced in complex communities where the likelihood of masking signals is greater (Luther 2009). We, therefore, expect that species will evolve signaling strategies that minimize the risk of misidentification (e.g., signaling at a frequency not used by others). A key prediction of the ANH is that there will be an evenly spaced signal structure at the community level, with a larger distance between co-occurring signals than

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predicted by chance. In support of this, Chek et al. (2003) found that in some South-American frog communities, the vocalizations of the different species are more widely and regularly distributed in acoustic space than expected at random (see also Allen-Ankins and Schwarzkopf 2022). However, few studies so far have provided evidence for acoustic niche partitioning (divergence) in birds (Luther 2009; Cardoso and Price 2010; Tobias et al. 2014; but see Planqué and Slabbekoorn 2008).

In addition to the ambient noise generated by heterospecific acoustic signals, a variety of abiotic attributes (wind, topography) can also impose major constraints on vocal communication behavior and hence drive signal evolution. Specifically, habitat structure has been considered as an ecological driver of birdsong evolution (reviewed in Boncoraglio and Saino 2007; Ey and Fischer 2009). The habitats in which birds live and communicate are very complex auditoriums whose acoustic properties influence sound propagation. In order to maximize (or optimize) transmission distance, the "acoustic adaptation hypothesis" (AAH) predicts that vocalizations are adapted to the physical structure of their habitat (Morton 1975). For instance, the use of long-drawn tonal notes at one frequency is favored in densely vegetated habitats due to the accumulation of reverberations (Slabbekoorn et al. 2002; Nemeth et al. 2006; Hao et al. 2021). Thus, according to the AAH, songs with low frequencies, narrow bandwidths, and low-frequency modulations (whistles) should be prevalent in closed forests, whereas high maximum frequencies, high-frequency modulations (trills), and wide bandwidths are expected in herbaceous habitats like grasslands and steppes (Tubaro and Lijtmaer 2006; Badyaev and Leaf 2007). Despite a strong theoretical underpinning, empirical evidence for the predicted relationship between habitat type (open vs. closed) and sound frequency is equivocal (Wiley 1991; Blumstein and Turner 2005; Derryberry et al. 2018; Crouch and Mason-Gamer 2019; Mikula et al. 2021; Friis et al. 2021).

In addition to environmental constraints (landscape structure) and the background noise generated by other members of the local community (biophony), sounds are shaped by species anatomy. Animals with a relatively large body have correspondingly large vocal organs (larynges in mammals and syrinxes in birds) and tend to produce lower-pitched vocalizations (Ryan and Brenowitz 1985; Bertelli and Tubaro 2002; García-Navas and Blumstein 2016). In songbirds, it has been shown that beak size and shape are also related to vocal performance (Podos 2001; Mejías et al. 2020; Friis et al. 2021, 2022). For instance, in a study on honeyeaters (Meliphagidae), Friedman et al. (2019) reported that species with elongate-shaped beaks sing at higher frequencies, while species with large beaks sing at a slower pace. Consequently, divergent vocal frequencies may be a predictable consequence of divergent morphologies (Krishnan and Tamma 2016). Hence, closely related species (which frequently share phylogenetically conserved morphological traits) may exhibit similar vocal attributes and, as a result, acoustic interference might occur more often among members of the same clade.

Examining the distribution of sound-producing species in signal space while accounting for phylogenetic and trait structure can help us to better understand the role of community-level processes such as competition or environmental filtering in driving sensory signal evolution. For instance, while competition between vocalizing species should favor partitioning of signal space (signal overdispersion), bird species living in one particular habitat may show convergence (clustering) in acoustic features due to shared selection pressures.

Thus, the integration of the principles of community phylogenetics (Webb 2000; Cavender-Bares et al. 2004) into the theoretical framework of animal communication opens up important avenues in community bioacoustics (Chhaya et al. 2021; Sugai et al. 2021).

Recent studies have employed an analogous approach to that employed in functional diversity research (Mason et al. 2005; Villeger et al. 2008) to characterize the multidimensional acoustic parameter space of biological communities from three general components; richness, regularity, and divergence (Zsebök et al. 2021). Although some authors have adopted the methodological toolbox from community ecology to study the acoustic fingerprint of species assemblages, most studies are based on a small number of communities and/or are limited to comparing two habitat types (Krishnan 2019; Kleyn et al. 2021; Lahiri et al. 2021). We are aware of no previous studies that have examined how acoustic community structure varies across an environmental gradient in birds.

Here, we study the acoustic space of avian assemblages distributed along six different habitat types (from herbaceous habitats to warm rainforests) in south eastern Queensland, Australia. First, we examined the species compositions in these communities. Second, we quantified the signal space occupied by bird species in each habitat, and assessed whether they exhibit similar distributions in signal space after accounting for phylogenetic and morphological similarities between species.

MATERIALS AND METHODS
Bird communities and study plots

Bird community compositions during the breeding season were extracted from the Australian Atlas which is the result of surveys based on a standardized protocol conducted by a volunteer network coordinated by BirdLife Australia (https://birdata.birdlife.org.au). The census method involves searching for birds in a two-hectare area for 20 min. During this period, the volunteer records the geographical reference at the center of their site and all birds seen or heard in their survey area, including those flying overhead. The data are then validated by experts, ensuring that the geographical references are sensible and that the species are within their known range. Our dataset comprised a total of 116 localities across the South Eastern Queensland region (Figure 1A). Almost all sampling localities (94%) were located in one of these three adjacent bioregions: Moreton Basin, Scenic Rim, and Sunshine Coast - Gold Coast Lowlands. This region is biologically very diverse and hosts a great variety of environments. The sampling localities were distributed along six different habitat types representing a continuum from structurally complex to simple habitats (Figure 1B): 1) warm temperate rainforests ($n = 26$), 2) *Melaleuca* open forests ($n = 15$), 3) *Eucalyptus* woodlands with a tussock grass understory ($n = 19$), 4) mangroves ($n = 11$), 5) heathlands ($n = 6$), and 6) cleared areas (including croplands) ($n = 39$). Thus, we compared close (rainforests), semi-close (open forests), semi-open (woodlands and shrublands), and open (grasslands) habitats. Localities were also characterized using a continuous variable, vegetation height, which ranged from 1 to 36.7 m (Figure 1B). Vegetation (canopy) height constitutes a reasonable surrogate for vegetation structure as it has been shown that this variable correlates with other indices of vegetation complexity such as the number of vegetation strata and the summed vegetation cover of vegetation strata (i.e., herbaceous, shrub, subcanopy, and canopy; see Remeš and Harmáčková
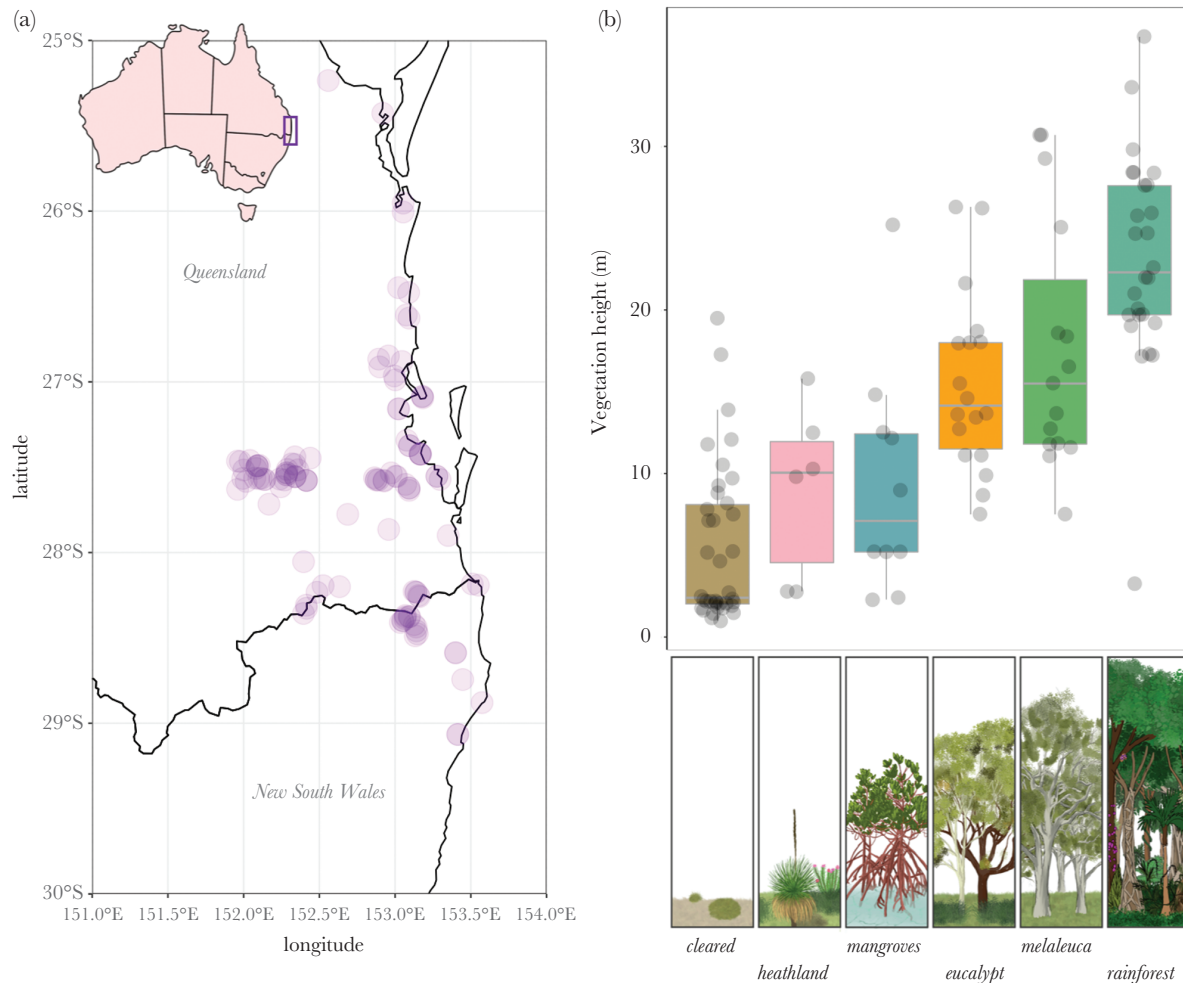
Figure 1
(A) Map of the study area in eastern Australia with the location of the sampled communities (purple dots). (B) Differences in vegetation height among habitat categories (cleared areas (including croplands), heathlands, mangroves, *Eucalyptus* woodlands with a tussock grass understory, *Melaleuca* open forests, and warm temperate rainforests) in the study region. The six habitat types are schematically represented below (illustration: Paula Martín). Means ± SD are shown.

2018; Remeš et al. 2021). Consequently, canopy height reliably expresses overall vegetation volume and is frequently used as an index of habitat complexity (Loke and Chisholm 2022) and vertical vegetation richness and productivity (e.g., Coops et al. 2018; Feng et al. 2020) in ecological studies. Vertical plant profiles were derived from Landsat data products (https://portal.tern.org.au/vegetation-height-structure-australia-coverage/21777).

Phylogenetic data and phylogenetic structure

We computed a Maximum Clade Credibility (MCC) tree from a sample of 500 phylogenetic trees retrieved from the open-source Bird Tree of Life Project (www.birdtree.org) (Jetz et al. 2012). From this MCC tree, we obtained a matrix of phylogenetic distances using the *cophenetic* function of the "ape" package (Paradis and Schliep 2019).

We examined the phylogenetic structure of bird communities using the mean pairwise phylogenetic distance (MPD). We then calculated the standardized effect size (SES) of MPD (MPD$_{SES}$) by randomly reshuffling the tips of the phylogeny 999 times. MPD$_{SES}$ represents the deviation of the observations from the null

expectation; that is, if species recorded in the same plot are more (or less) closely related than expected by chance (phylogenetic clustering or phylogenetic overdispersion, respectively) (Webb et al. 2002).

Trait data and morphological dissimilarity

For each species, we collected average body mass values (log-transformed) from Garnett et al. (2015) as a proxy for body size. To characterize species beak morphology, we employed four traits included in a global dataset (Tobias et al. 2022): 1) bill length of the culmen; 2) bill length measured from the nares; 3) bill depth; and 4) bill width. From these measurements, we carried out a phylogenetic Principal Component Analysis (*phylo*-PCA; Revell 2009) that reduced the original dataset into a single axis (*PCb*) accounting for 95% of the total variance in beak morphology. Body size (mass) and beak size are considered "magic traits" because under divergent ecological selection, they give rise "as if by magic" to signal divergence, and ultimately nonrandom mating (Derryberry et al. 2018).

We calculated mean pairwise functional (morphological) distances (MFD) for each of the two morphological traits, body

size, and *PCb*. Observed values were compared with mean values obtained from 999 randomly generated communities using null models (independent-swap algorithm) as previously indicated. In this way, we assessed whether coexisting species in communities were more or less similar than expected by chance in terms of body size and beak shape.

Birdsong recordings and acoustic measurements

We obtained birdsong recordings from Xeno-canto (http://xeno-canto.org) and AVoCET (https://avocet.integrativebiology.natsci.msu.edu/). We selected the sound files categorized as songs with a preference for those with a high-quality rating. When possible, we excluded recordings that were deemed of poor quality, particularly those in which background noise or the overlap with other bird vocalizations prevented the accurate measurement or identification of the target species. We also tried to choose sound files recorded in Queensland or adjacent areas. Since Queensland is one the most populated regions of the continent (accounting for >1300 recordings), it was possible in most cases. After excluding 13 species for not meeting these requirements (most of them belonging to two families: Columbidae and Psittaculidae), our final data set comprised 113 species of Australian birds from 45 families (Supplementary Table S1). For each species, we attempted to compile three to five recordings; however, for some species, the number of recordings was smaller (mean: 4.5, range: 1–5). Overall, a total of 307 audio recordings (6191 elements) were analyzed. All recordings were standardized and checked for distortion to ensure the quality and format before analysis and avoid potential artifacts resulting from gathering field recordings made in a wide range of habitats and collected from different sources. We converted MP3 to WAV (Waveform Audio File) files and used a sample rate of 44.1 kHz with a bit depth of 16.

For measuring spectral and temporal features of acoustic signals, we used Raven Pro v.1.6 (Cornell Laboratory of Ornithology, Ithaca, NY, USA) sound analysis software (Charif et al. 2010). Before extracting acoustic metrics, spectrogram parameters were manually standardized for all recordings using a Hanning window size of 512 points with a 90% window overlap for a time resolution of 1.161 ms and a frequency resolution of 86.1 Hz. All songs were analyzed by a single observer (N.F.) trained until measurements were consistent. Temporal and frequency measurements were extracted from the amplitude curve (waveform) and from the spectrogram with the use of the power spectrum (Figure 2).

We extracted one to three songs for each recording, and made annotations for all elements in every song. We defined an element as the smallest unit of sound, delimited as a discrete, continuous trace on a spectrogram and separated from other elements by silence or abrupt changes in the acoustic properties (without the presence of a gap) (i.e., note) (see Kershenbaum et al. 2016). Decomposing the acoustic signals into elements is recommended for broad comparative studies of acoustic structure, as it leads to the least subjectivity when not having much knowledge of hierarchical patterning of the song syntax (Odom et al. 2021), and therefore we gathered data from the element level to the song level. We used decibel thresholds
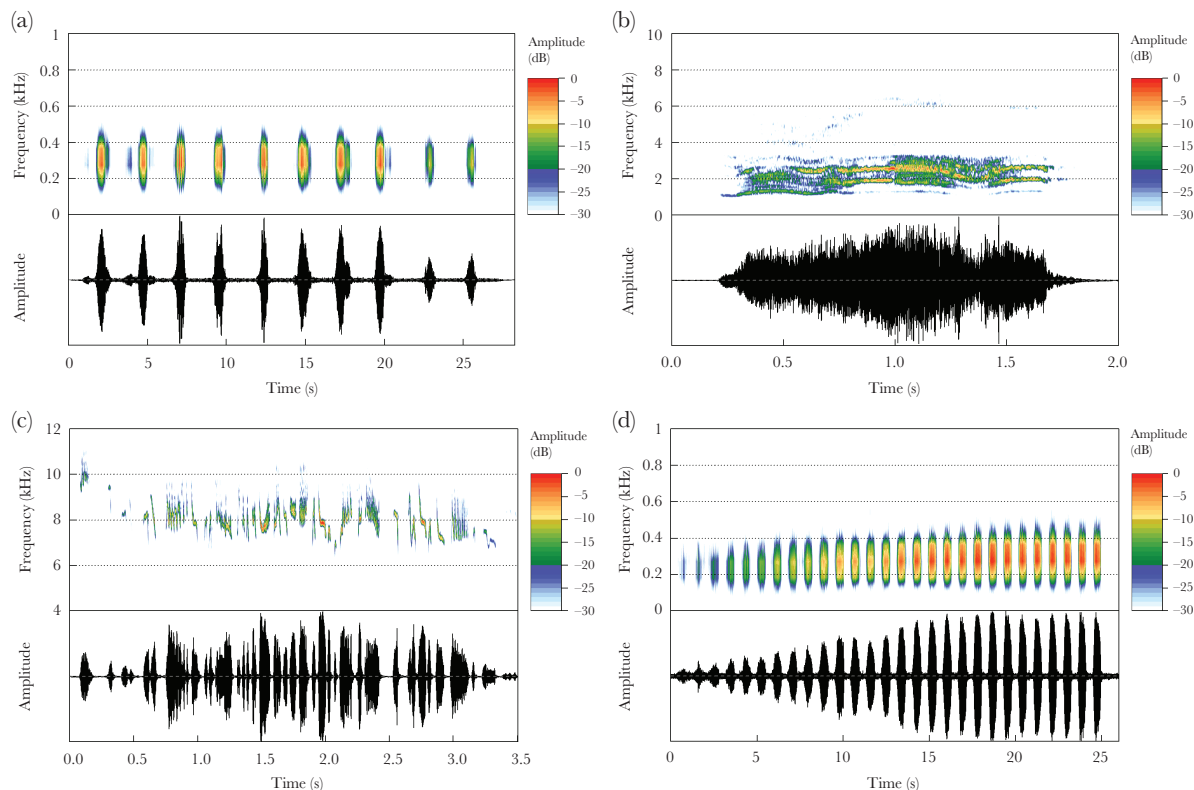

Figure 2
Song spectrograms and oscillograms showing the frequency profile and the relative amplitude over time for four species that occupy extreme positions of the acoustic space: (A) the common bronzewing (*Phaps chalcoptera*), (B) the green catbird (*Ailuroedus crassirostris*), (C) the southern emu-wren (*Stipiturus malachurus*), and (D) the painted buttonquail (*Turnix varius*). Catalogue numbers of recordings: (A) XC434564, (B) XC351500, (C) XC40691, (D) XC336304.

(i.e., the frequency range within a power or amplitude spectrum where the power or amplitude remains above a threshold that is a specified number of decibels below the peak power or amplitude) and energy-based measurements, as these are based only on the higher-intensity parts of the sound and are more consistent and recommended for taking measurements (Zollinger et al. 2012; Odom et al. 2021). Specifically, we generated and extracted 18 acoustic variables quantifying how the acoustic energy was spread across the frequency spectrum and duration of the signal (Supplementary Table S2). In order to calculate the mean value of every acoustic variable for each species, all selections were exported to R using the "Rraven" package (Araya-Salas 2020). Additionally, we obtained from the elements composing each song the following parameters using "warbleR" (Araya-Salas and Smith-Vidaurre 2017): song duration, element number (total number of elements per song), element duration, and song rate (element number divided by song duration) (Supplementary Table S2). We tested for phylogenetic signal of each acoustic parameter by means of Blomberg's K using the "phytools" package (Revell 2012).

Community bioacoustics analyses

First, we explored the interdependencies among the 22 acoustic variables by calculating Pearson's correlations. Since several of them were strongly correlated ($r > 0.70$), we decided to use only a subset of uncorrelated variables that included the low (F_{min}) and high (F_{max}) frequency, bandwidth90 (BW; the difference between the 5% and 95% frequencies), peak time relative (the first time in the selection at which a sample with amplitude equal to peak amplitude occurs), average entropy (average disorder in a sound quantified in terms of energy distribution), song duration, element duration, and number of elements. To standardize the eight acoustic variables (so that they would have the same weight), we transformed them between 0 and 1. Next, from this set of variables, we computed a pairwise dissimilarity matrix representing the acoustic (Euclidean) distance for each pair of species. On this matrix, we performed a principal coordinate analysis (PCoA), and the resulting axes were employed to compute different acoustic spaces. We assessed the quality of PCoA-based acoustic spaces with up to seven dimensions using the function *quality.fspaces* of the R package "mFD" (Magneville et al. 2022). We chose an acoustic space defined by three dimensions (mean squared deviation, mSD index = 0.0061; see Maire et al. 2015). In this acoustic space, the common bronzewing *Phaps chalcoptera*, the green catbird *Ailuroedus crassirostris*, the southern emu-wren *Stipiturus malachurus*, and the painted buttonquail *Turnix varius* occupied extreme positions (Supplementary Figure S1). From this three-axes acoustic space, we then computed three different indices of acoustic diversity: acoustic richness (ARic), acoustic divergence (ADiv), and acoustic evenness (AEve). These indices are analogous to those employed to characterize functional diversity; they represent the richness, divergence and regularity components of diversity (Villeger et al. 2008; Schleuter et al. 2010; Mason et al. 2013). By definition, AEve was unaffected by species richness, whereas ARic increased with the number of species (the more species there are, the larger the functional space occupied), and ADiv tended to exhibit an asymptotic relationship (ADiv decreased after reaching a threshold). ADiv quantifies the proportion of biomass on the periphery of the space (based on the average distance from the centroid), representing species with extreme (singular) acoustic traits. This index is commonly used as a proxy for the level of resource competition (niche differentiation). AEve measures whether mean species acoustic traits are regularly distributed within the signal space, so it indicates the existence of under- or over-utilization of acoustic frequencies. Acoustic indices were computed using a modified version of the *multidimFD* function written by S. Villeger (Magneville et al. 2022).

Statistical analysis

We built mixed-effects models including either AEve, $ARic_{SES}$, or $ADiv_{SES}$ as response variables, and habitat type, phylogenetic similarity (MPD_{SES}), and morphological similarity in terms of body mass as predictor variables. The sampling site (region) was also added as a random factor. The significance of our focal variable (i.e., habitat type) was assessed using Type III analysis of variance and the Satterthwaite's method to estimate degrees of freedom for fixed effects (R package "lmerTest"; Kuznetsova et al. 2017). Since $ARic_{SES}$ did not show a normal distribution (even after log-transforming), it was fitted using a Poisson distribution (*glmer* function). The *lmer* function does not provide *P*-values for coefficients, whereas the *glmer* function provides *P*-values for coefficients (but not for factors/effects) using the Wald Z-test, which is not a very accurate method (e.g., Dickey 2020). So, we used the function *anova* ("lmerTest" package) to obtain *P*-values. In addition, we determined the weight of evidence for the effect of habitat type by computing a likelihood ratio test, in which we compared the fit of two models: a full model as above detailed, and a restricted one (excluding habitat type as fixed effect). In a preliminary step, since both ARic and FDiv were correlated with species richness, we used a null model approach to eliminate the effect of taxonomic richness on the acoustic richness. To calculate the standardized effect sizes (SES) of ARic and ADiv, the following formula was used: SES = (Mean$_{obs}$ - Mean$_{null}$)/SD$_{null}$, where Mean$_{obs}$ is the mean of observed measurements in a certain species assemblage; Mean$_{null}$ is the mean of 1000 iterations generated under the null model ("independentswap" algorithm); and SD$_{null}$ is the standard deviations of iterations on measures. Lastly, we calculated Spearman's correlations to address the relationship between the three acoustic indices and the following variables: vegetation height (our continuous habitat descriptor), phylogenetic community structure (MPD_{SES}), and functional community structure (in terms of both body mass and beak morphology). All analyses were conducted using R version 4.1.3. (R Core Team 2022),

RESULTS
Habitat differences in richness, phylogenetic structure, and morphological similarity

Average species richness (per habitat) ranged from 8 (in *Melaleuca* open forests and heathlands) to 12 species (in cleared habitats). The minimum and maximum number of species detected in a given plot was 3 and 26, respectively (average richness per plot: 10.8 ± 5.2).

Rainforests and *Melaleuca* open forests were the habitat types that showed a higher degree of phylogenetic clustering (Table 1), whereas in the other extreme, assemblages located in heathlands were phylogenetically over-dispersed (Table 1). In terms of morphology (body mass and beak shape), assemblages from eucalypt woodlands and mangroves were the ones that exhibited a higher level of divergence (i.e., overdispersion) (Table 1). Rainforest assemblages showed the highest level of clustering in body mass (but not in beak morphology), whereas the highest level of resemblance in beak morphology was detected in communities from *Melaleuca*

Table 1

Habitat differences in terms of taxonomic richness, environmental features (vegetation height; annual rainfall), and phylogenetic and morphological similarity for 116 bird communities (2-ha plots) in South Eastern Queensland, Australia

	Species richness	Vegetation height (m)	Rainfall (mm)	Mean pairwise phylogenetic distance (MPD_{SES})	Mean pairwise morphological distance (body mass)	Mean pairwise morphological distance (beak shape)
Cleared habitat	12.2 [3; 26]	5.4	913	−0.089 [−1.57; 1.40]	−0.412 [−2.30; 1.55]	−0.234 [−2.18; 1.51]
Heathland	8.3 [6; 12]	9.0	1580	0.712 [−0.16; 1.47]	−0.070 [−0.76; 0.19]	−0.423 [−1.67; 0.77]
Mangroves	11.4 [4; 26]	9.4	1396	0.032 [−2.20; 1.42]	0.221 [−1.51; 1.40]	0.032 [−0.58; 1.99]
Eucalypt woodland	9.0 [6; 18]	15.5	1086	0.108 [−1.10; 1.32]	0.237 [−1.37; 1.47]	0.982 [−0.72; 1.94]
Melaleuca forest	8.1 [5; 16]	17.7	1416	−0.107 [−1.43; 1.28]	−0.133 [−2.91; 1.50]	−0.634 [−1.55; 1.37]
Warm rainforest	11.5 [5; 24]	23.1	1689	−0.165 [−1.89; 1.59]	−0.867 [−1.88; 2.17]	0.033 [−2.12; 1.32]

Mean values are shown (ranges are given in square brackets).

forests (Table 1). Thus, the observed values of phylogenetic and morphological structure do not fit a simple habitat complexity gradient.

Acoustic diversity

None of the eight acoustic parameters that were employed to obtain the three acoustic diversity indices (ARic, ADiv, AEve) had a significant phylogenetic signal (Table 2).

When testing for differences in acoustic diversity indices among habitat categories, we did not find significant effects of habitat type on $ADiv_{SES}$ or AEve (Table 3). None of the models that included habitat type as predictor significantly improved the reduced model (both ΔAIC values < 1.5). There was a significant effect of habitat type on $ARic_{SES}$ (Table 3), which was largely due to the high values observed in the heathland communities as post-hoc comparisons revealed (analyses not shown). Overall, we found no differences between open and closed habitats (Figure 3).

Acoustic evenness (AEve) increased with vegetation height (r = 0.26, P = 0.004; Figure 4A); plots where the structure of the vegetation was less complex (herbaceous layer) had reduced evenness. This means that acoustic traits are more regularly distributed within the acoustic space in avian communities located in sites with dense vegetation. There was no significant relationship between vegetation height and the remaining acoustic indices (P-values >0.05).

Acoustic richness ($ARic_{SES}$) was positively related to MPD_{SES}, indicating that after accounting for differences in taxonomic richness, assemblages made up of closely related species tended to have lower acoustic richness than those composed by phylogenetically less similar species (r = 0.40, P < 0.001; Figure 4B). There was no significant relationship between MPD_{SES} and either AEve or $ADiv_{SES}$ (P-values >0.05).

We also found a significantly positive relationship between $ARic_{SES}$ and divergence in body mass (r = 0.27, P = 0.003), and a negative relationship between $ADiv_{SES}$ and divergence in body mass (r = −0.21, P = 0.02); assemblages more similar in terms of their body size tend to exhibit lower acoustic richness and greater acoustic divergence (differentiation) than those composed by morphologically disparate species (Figure 4C,D). There was no significant relationship between divergence in body mass and AEve (P =

Table 2

Values of Blomberg's K for all acoustic parameters and results of randomization test assessing whether traits were more similar in related species than would be expected by chance (i.e., if traits were distributed randomly on the tree)

Acoustic parameter	K	P-value
Max frequency	0.205	0.054
Min frequency	0.193	0.117
Bandwidth 90	0.161	0.242
Peak time relative	0.196	0.119
Average entropy	0.144	0.357
Song duration	0.069	0.905
Number of elements	0.095	0.781
Element duration	0.179	0.273

Values of K < 1 indicate that traits are less similar than would be expected under a Brownian motion model of evolution.

0.75), nor was there a significant relationship between divergence in beak shape (PCb) and the three acoustic indices (P-values >0.05).

DISCUSSION

Environmental gradients (i.e., gradual changes in elevation, abiotic factors, or habitat characteristics) influence the distribution and composition of animal species and reflect ecological and evolutionary processes that have unfolded over millennia. Although during the last decade several authors have addressed how the phylogenetic and functional structure of bird communities varies along ecological gradients (e.g., García-Navas et al. 2020; Montaño-Centellas et al. 2020), there is still a lack of information about the relationship between the acoustic structure of communities and the variation in the physical environment. Here, we adopted an integrative approach in which we addressed the acoustic, phylogenetic, and ecological characteristics of bird communities along an ecological gradient in eastern Australia. Specifically, we examined whether communities belonging to different habitat types exhibited a similar acoustic signature, and how species traits and their phylogenetic relatedness influenced the distribution of frequency categories of sounds emitted by the

Table 3

Results of mixed models used to assess effects of habitat type (main effect; categorical variable) and phylogenetic and functional community dissimilarity on the regularity, divergence, and richness components of acoustic diversity

Class	Model	Statistics			
		NumDF	DenDF	*F*	*P*-value
	Evenness (AEve)				
	Habitat type	5	4.49	1.49	0.34
	MFD (body mass)	1	107.48	0.38	0.54
	MPD$_{SES}$	1	107.48	0.42	0.52
Linear mixed models (lmer)	*Divergence (ADiv$_{SES}$)*				
(family: Gaussian)	Habitat type	5	2.00	0.23	0.91
	MFD (body mass)	1	106.84	3.55	0.06
	MPD$_{SES}$	1	105.48	0.10	0.75
Generalized linear mixed model (glmer) (family: Poisson)		estimate	SE	*t*	*P*-value
	Richness (ARic$_{SES}$)				
	Habitat type				0.045
	MFD (body mass)	0.007	0.004	1.63	0.10
	MPD$_{SES}$	0.016	0.004	3.42	<0.001

SES indicates standardized effect sizes.
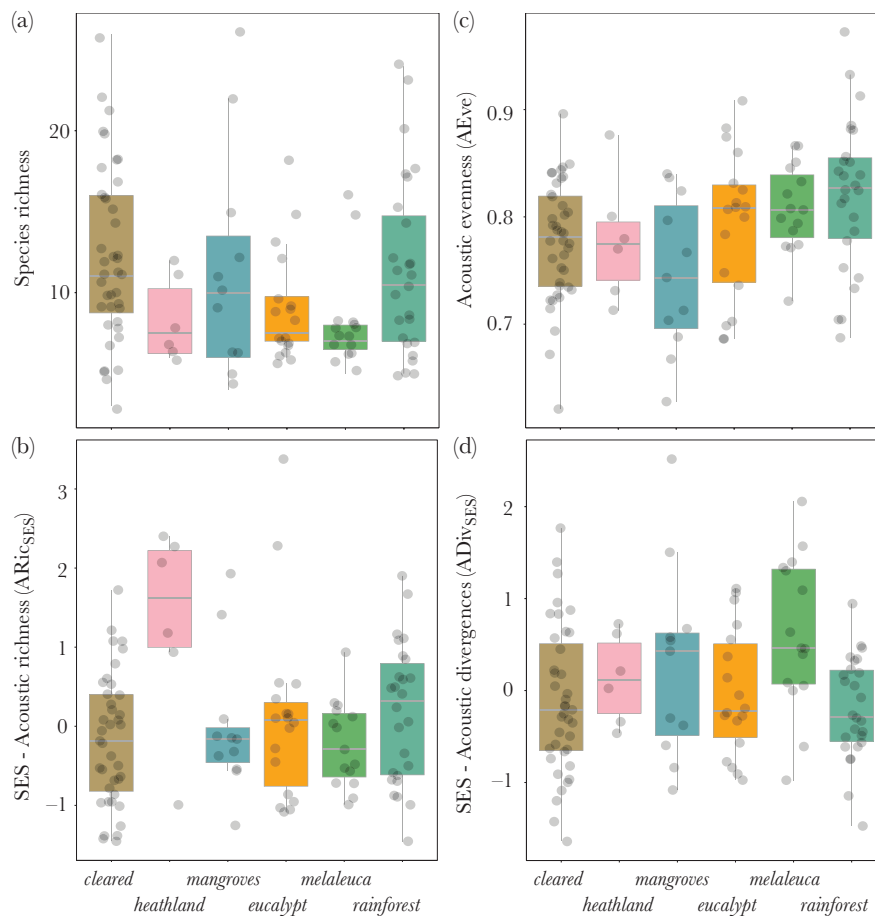
Figure 3

Habitat differences in (A) species richness and (B–D) acoustic diversity indices (acoustic richness, acoustic divergence, and acoustic evenness). Since acoustic richness and acoustic divergence depend on the number of species, we computed the standardized effect sizes (SES) of these two indices using null models. Means ± SD are shown. Each dot corresponds to a different community (2 ha-plots).

species comprising a community over the signal space. Overall, our results partly support the acoustic adaptation hypothesis (AAH). While we found that the regularity in the distribution of

species across the acoustic space tended to correlate with vegetation structure, habitat categories had little predictive power at our broad taxonomic level.
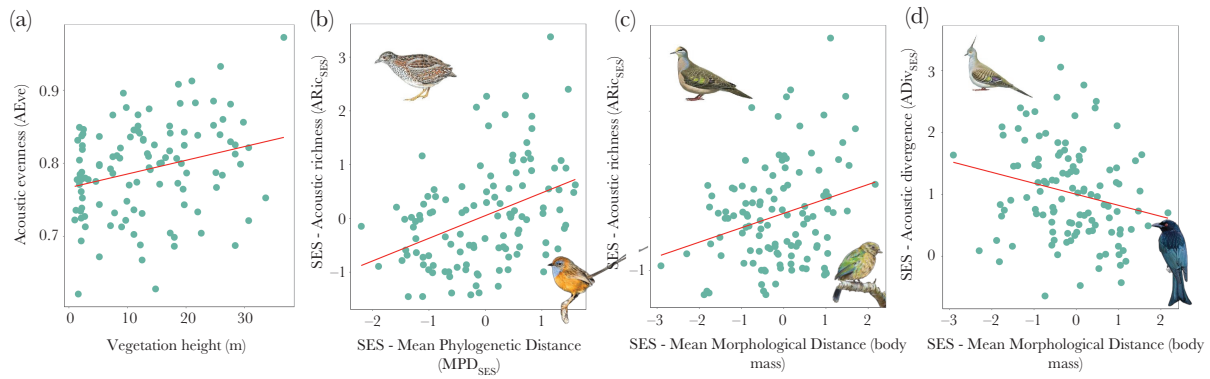
Figure 4

Scatterplots showing the relationship between (A) acoustic evenness (AEve) and vegetation height, (B) standardized acoustic richness (ARic$_{SES}$) and mean pairwise phylogenetic distance (MPD$_{SES}$), (C) standardized acoustic richness (ARic$_{SES}$) and mean pairwise morphological distance based on body mass dissimilarity, and (D) standardized acoustic divergence (ADiv$_{SES}$) and mean pairwise morphological distance based on body mass. Bird species that occupy extreme positions in the acoustic space (*Turnix varius*, *Phaps chalcoptera*, *Ocyphaps lophotes*, *Stipiturus malachurus*, *Ailuroedus crassirostris*, and *Dicrurus bracteatus*) are represented for illustrative purposes. Each dot corresponds to a different community (2 ha-plots).

The lack of meaningful differences among habitat categories in terms of acoustic diversity indices indicates that habitat type has a limited influence in explaining variation of acoustic indices. We only found a significant effect of habitat type on the standardized acoustic richness, and this effect was largely due to the exceptionally high values observed in heathland communities. Protea heathlands are major repositories of Australia's unique and iconic flora and also support a specialized fauna (Keith et al. 2014), which may explain this pattern. However, we cannot rule out that this result might be attributed to the low sample size (only six communities) we obtained for this habitat type compared to the other categories. Examining Figure 3B–D, one can conclude that there are no large differences in acoustic characteristics at the community level between open and closed habitats. We did not find evidence for convergent community structure due to acoustic adaptation to environmental features; avian communities from structurally similar habitat types (e.g., cleared habitats and heathlands; and *Eucalyptus* woodlands and *Melaleuca* open forests) did not show convergent distributions in acoustic signal space. Our results contrast with those recently reported by Lahiri et al. (2021), yet they compared assemblages from two almost identical habitat types (dry and wet grasslands) and used a different methodology. While, Cardoso and Price (2010) compared the songs of European and North American Mediterranean climate passerine communities in open and closed habitats and they found that only a single parameter—peak frequency—varied across different habitats but not continents. They did not apply a null model approach and used average measurements per species (maximum number of species = 23) instead of acoustic community indices (Cardoso and Price 2010). For these reasons, our findings are not strictly comparable with the existing literature because no studies have addressed the effect of habitat features on bird vocalizations across such a broad spectrum of vegetation structure (from steppe-like habitats to rainforests) and using a community-based approach.

Despite the absence of large differences in acoustic signal characteristics among the six categories, when characterizing habitat types using a continuous variable, we found a significant relationship between community acoustic evenness (AEve) (which describes how regularly the acoustic elements fill out the signal space) and

vegetation height. Thus, acoustic signals are more evenly distributed in dense habitats, which means that the vocalizations of different bird species are increasingly evenly distributed across the space as vegetation structure increases, regardless of the number of species inhabiting that plot. This result is consistent with previously reported in soundscape studies, where the acoustic evenness index (AEI) (band evenness using the Gini index; Villanueva-Rivera et al. 2011) was related to plot-scale vegetation structure. For instance, Dröge et al. (2021) recently found that in Madagascar, the AEI values were lowest (i.e., sound intensity restricted to few frequencies) in rice paddies and fallow land, and highest in old-growth forests. Similarly, Do Nascimento et al. (2020) reported that the best index linking soundscapes to vegetation structure was acoustic evenness, which was strongly associated with changes in canopy cover in the Amazon. Thus, the way in which the acoustic energy is distributed across the space provides habitat-specific information and could be employed as monitoring tool for biodiversity assessments (for instance, to discriminate land-use types).

The acoustic index that best characterized the phylogenetic and morphological structure of the communities was (standardized) acoustic richness, ARic$_{SES}$. Acoustic richness represents the volume of acoustic space encompassed by the outermost vertices of the assemblage. After accounting for the effect of taxonomic richness (the more species there are, the larger the acoustic space occupied), we observed a statistically significant relationship between acoustic richness and phylogenetic dispersion indicating that phylogenetically clustered communities had a lower range of acoustic attributes regardless of the number of species. That is, there is greater acoustic redundancy between species in these communities composed of phylogenetically similar taxa. In turn, we found that this acoustic index was significantly related to morphological dispersion for one of the two analyzed traits (body mass). It means that communities whose members were more similar in size to each other were poorer in terms of acoustic traits. These findings could be explained considering the existence of phylogenetic and allometric constraints on bird vocalizations as seen in some avian clades of vocal learners (e.g., Päckert et al. 2003; Price and Lanyon 2004; Mejías et al. 2020) and vocal non-learners (Medina-García et al. 2015; see also Arato and Tecumseh 2021). However, regarding the

effect of shared ancestry, it seems that song evolution is more labile at a broad taxonomic level (Friis et al. 2022). Here, we found relatively a weak phylogenetic signal for most of the analyzed song traits. Only the maximum frequency exhibited a marginally significant phylogenetic signal, which suggest that acoustic parameters in the Australian avifauna are not highly conserved across evolution. It may due to an effect of sexual selection (which presents some of its more prominent examples in some Australian bird families (e.g., Irestedt et al. 2009; Greig et al. 2013; Ligon et al. 2018) which may bring about evolutionary contingency, lowering the evolutionary conservatism of acoustic signals. Whereas, the lack of a relationship between beak morphology and acoustic richness suggests that body size has a more important role than beak shape in explaining differences in acoustic features. In agreement with this, Friis et al. (2022) recently reported shared effects of body and bill sizes on the sound frequency of songs, but they found that species differences in frequency bandwidth were solely predicted by body size. Our findings support the view that body size is one of the strongest correlates of sound frequency across avian species (Cardoso 2010; Mikula et al. 2021).

This study is the first to report a relationship between divergence in body mass and divergence of acoustic signals at the community scale (Figure 4D). The existence of greater acoustic divergence in assemblages with smaller variation in size amongst species suggests that community-level effects play a role in structuring acoustic signals within avian communities in this region. Assemblages made up of morphologically similar species may exhibit a wider range of frequencies (divergence higher than expected by random chance) to avoid masking. Evidence for acoustic niche partitioning in birds or anurans is scarce, although few studies have tested it properly (Chek et al. 2003; Tobias et al. 2014; Sugai et al. 2021; Allen-Ankins and Schwarzkopf 2022). To test hypotheses about community ecological processes, the average response of many assemblages must be compared with a null model. Here, we have revealed the existence of signal character displacement among coexisting species (i.e., species present in a local community) after considering their level of phenotypic resemblance. This result is striking since some previous authors have suggested that convergence in signal space may arise as a by-product of phylogenetic/morphological similarity (e.g., Tobias et al. 2014). To our knowledge, this is the first study to examine acoustic niche partitioning in birds using random distributions and providing support for the partitioning hypothesis.

A shortcoming of this study is that acoustic measurements were not obtained from birdsongs recorded in the field. Rather, we used recordings from digital repositories, which do not provide habitat information. Consequently, we did not use habitat-specific recordings, yet the high within-species repeatability of song traits (average repeatability: 76%; see Supplementary Table S3) allow us to conjecture that the variability between species (among-species variation) will always be much greater than the variability within species, which is assumed to be negligible in comparative studies (e.g., Garamszegi 2014; Freckleton and Rees 2019).

Although there is limited room for birds to shifts their frequencies in response to heterospecific' sounds and it is expected that within-species variability in acoustic attributes being almost negligible in comparison with among-species variation, this approach would benefit from recent advances in hardware (automated digital recorders) (Gasc et al. 2017). Indeed, ecoacoustic research is an important new methodology to monitor wild ecosystems (e.g., shifts in songbird phenology). Technical improvements in passive acoustic recorders and soundscape analysis tools make now possible to assess the acoustic diversity of multiple communities at the same time and over long time periods (Müller et al. 2022). This information is extremely valuable to detect processes of homogenization and assess the conservation status of biological communities (e.g., Tucker et al. 2014; Burivalova et al. 2019). The use of passive acoustic recorders also allows accounting for the influence of ambient biotic noise. Regarding this, it must also be noted that the acoustic space used by birds could be constrained by the acoustic space occupied by insects like cicadas and katydids (Hart et al. 2015; Aide et al. 2017). Insect vocalizations tend to dominate the mid and high-frequency ranges in tropical forests, which bounds the vocalizations' upper limit of most birds in these habitats (Morton 1975). It must be taken into account when interpreting our results.

CONCLUSIONS

Although habitat, when measured continuously, was strongly associated with one of the analyzed indices of acoustic diversity (the regular spacing of song features), our categorical descriptions of habitat did not explain much variation in any metric. Thus, our results only provide partial support for the AHH. This hypothesis has been tested with unequal support in many comparative studies in which the song attributes of species inhabiting open habitats (e.g., grasslands) are compared with those from congenerics that occupy closed habitats (e.g., forests) (Boncoraglio and Saino 2007). Nevertheless, the present study is the first one to examine the AHH using an approach based on multi-species assemblages. Our findings support the view that the effect of habitat type on avian vocalizations is generally small and variable across taxonomic groups (Friis et al. 2022), so that the influence of the AAH may not be as widespread as suggested by some authors (Morton 1975). In turn, our study provides evidence that acoustic diversity indices reflect both the phylogenetic and functional diversity in bird communities, a finding similar to that which Gasc et al. (2013) discovered in France using different acoustic metrics. We also reported a negative relationship between acoustic divergence and divergence in body mass (i.e., the more similarity in species' sizes, the more different their vocalizations are likely to be). This finding suggests that interspecific acoustic competition plays a role in structuring song phenotypes within these communities. Overall, we have shown that by decomposing the acoustic diversity into different components (in an analogous way to that used to describe functional diversity in community ecology), it is possible to obtain additional biologically meaningful insights into the structure of birdsong.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco. oxfordjournals.org/.

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CONFLICT OF 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.

AUTHOR CONTRIBUTIONS

Vicente García-Navas (Conceptualization [Lead], Data curation [Lead], Formal analysis [Equal], Funding acquisition [Equal], Investigation [Lead], Methodology [Equal], Project administration [Equal], Writing – original draft [Lead], Writing – review & editing [Lead]), Daniel Blumstein (Conceptualization [Equal], Methodology [Equal], Writing – original draft [Equal], Writing – review & editing [Equal]), and Naliny Feliu (Data curation [Equal], Formal analysis [Equal], Validation [Equal], Visualization [Equal])

DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by García-Navas et al. (2023).

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