

Original Articles

Evaluating acoustic indices in the Valdivian rainforest, a biodiversity hotspot in South America

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ARTICLE INFO

Keywords:

Acoustic diversity indices
Biodiversity assessment
Passive acoustic monitoring

ABSTRACT

Passive acoustic monitoring is becoming an extensively used tool to evaluate the status and variation of populations of sound producing animals. The analyses of extensive acoustic recordings for identification and detection of acoustic signals of different species is highly time-consuming, either by traditional audiovisual procedures or by developing effective automated recognizers. These drawbacks in data analysis have promoted research efforts aimed to develop acoustic diversity indices, which are relatively easily obtained by means of different algorithms considering spectral and/or temporal properties of the sounds contained in the recordings. Nevertheless, studies performed in different environments and geographical areas reveal inconsistencies in the association between acoustic diversity indices and biodiversity, suggesting the need of new studies to evaluate commonly used acoustic diversity indices as proxies of the richness of sound producing animal species. The Valdivian rainforest from Chile, South America, is recognized as a biodiversity hotspot because of the high proportion of endemic species and their threatened status associated to anthropogenic activity. As it is imperative to evaluate cost-effective strategies for biodiversity monitoring, in this study we evaluated seven acoustic indices to assess their reliability as proxies of the variation in bird and anuran species richness, two important components of the biodiversity of this threatened environment. Our results indicate that most of the acoustic indices tested fail to describe satisfactorily the variation in species richness. Nevertheless, two indices, namely the Temporal Entropy and the Acoustic Evenness Index, may potentially serve as an indicator of bird richness, but future studies should fine-tune these indices to obtain a robust validation of its use within this environment. We expect that this work will contribute to the understanding of the significance and potential use of acoustic indices within this biodiversity hotspot as well as in other regions of interest for conservation.

1. Introduction

Monitoring biodiversity is a main issue in the current scenario of global change, and passive acoustic monitoring is becoming an extensively used tool to evaluate the status and variation of populations of sound producing animal species (Sueur et al., 2008a, 2014; Llusia et al., 2013; Gasc et al., 2015; Bertucci et al., 2016; Krause and Farina, 2016; Linke et al., 2018). Automated acoustic recording systems allow

sampling at large spatiotemporal scales, reducing research efforts and expenses in fieldwork, and also decreasing potential impacts of observers on the normal activity of animals. These are relevant factors due to their potential negative effects on biodiversity assessments (Acevedo and Villanueva-Rivera, 2006; Obrist et al., 2010; Blumstein et al., 2011; Sueur et al., 2012). In spite of these advantages, the analyses of extensive acoustic recordings for detection and identification of acoustic signals of different species is highly time-consuming, either by

Abbreviations: Hf, Spectral Entropy; Ht, Temporal Entropy; H, Total Entropy; ACI, Acoustic Complexity Index; ADI, Acoustic Diversity Index; AEI, Acoustic Evenness Index; BI, Bioacoustic Index

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<https://doi.org/10.1016/j.ecolind.2019.03.024>

Received 17 June 2018; Received in revised form 12 March 2019; Accepted 18 March 2019

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traditional audiovisual procedures or by developing effective automated recognizers (Blumstein et al., 2011; Wimmer et al., 2013). These drawbacks in data analysis have promoted research aimed to develop acoustic diversity indices, which are relatively easily obtained based on different algorithms considering spectral and/or temporal properties of the sounds contained in the recordings (Sueur et al., 2008a; Pieretti et al., 2011; Sueur et al., 2014).

In general, the sounds of animals coexisting in sympatric and syntopic conditions are species-specific. A potential explanation for such differentiation is provided by the Acoustic niche hypothesis, which proposes that masking among signals of different species promotes their segregation across different dimensions of the acoustic space (Krause, 1993; Farina et al., 2011). As such, communities having high diversity levels are expected to generate richer acoustic environments, and therefore, indices unveiling such acoustic variety are expected to provide proxies of conventional biodiversity measurements (Sueur et al., 2014). However, competition and niche partitioning are apparently not the only agents driving the composition of acoustic communities, as recent studies have shown that the signals of coexisting species may also show convergence trends (Tobias et al., 2014). As such, the level of acoustic differentiation among coexisting species may affect the success of acoustic indices for biodiversity assessments (Gasc et al., 2013a,b). In addition, when performing acoustic recordings aimed at biodiversity monitoring, natural abiotic (e.g. wind and water) and anthropogenic (e.g. road traffic and machine noises) sounds are likely to be concomitant components included in the recordings. A relatively high contribution of these two components can decrease the signal-to-noise ratio, impairing the performance of acoustic indices (Depraetere et al., 2012; Sueur et al., 2014; Fairbrass et al., 2017). Other sources that may impact negatively the estimates of acoustic indices include the relative abundance of highly vocal species and the differences in vocal repertoires of species composing the community sampled (Gasc et al., 2015).

As the calculation of different indices rely on different combinations of acoustic properties, their effectiveness may vary in different environments. For instance, a pioneering study developing and testing an acoustic diversity index, i.e. the Acoustic Entropy Index, has been found to be effective in Tanzanian forests (Sueur et al., 2008a), but when applied in a Temperate woodland in France, this index was sensitive to background noise, prompting the design of a new index (Depraetere et al., 2012). Recent studies have tested several indices simultaneously. A study conducted in central Brazil reported that one out of six indices employed was associated to bird species richness (Machado et al., 2017). In southern China three out of seven tested indices were correlated with bird diversity (Mammides et al., 2017), and similar results were obtained in forests of eastern Australia (Fuller et al., 2015). In addition, in London, England, an urban area dominated by anthropogenic noise, none of four indices tested reflected satisfactorily the extant biodiversity patterns (Fairbrass et al., 2017). These studies performed in different environments and geographical areas reveal a lack of a general clear association between acoustic diversity indices and biodiversity. This suggests the need of new studies to evaluate commonly used acoustic diversity indices as proxies of the richness of sound producing animal species.

The Valdivian rainforest from Chile, South America, is recognized as a biodiversity hotspot because of the high endemic level of inhabiting species and by their threatened status associated to anthropogenic influence (Myers et al., 2000). Extensive areas of native forest have been replaced by agriculture and pasture lands and by exotic pine and eucalyptus plantations. Furthermore, the Valdivian rainforest is also being affected by logging for commercial purposes, and by the occurrence of large-scale fires and climate change (Echeverría et al., 2012; Miranda et al., 2017). Two vertebrate taxa that are important components of the biodiversity of this threatened environment and which are susceptible of acoustic monitoring are birds and anurans (Bartheld et al., 2011). About 44 bird species are found here, from which 13 are endemic, and

at least 10 species occur commonly (Díaz, 2005; Bartheld et al., 2011). Regarding anurans, a high level of endemism close to 75% of species has been reported, and although the taxonomic status has been modified during recent years, the endemism level remains high (Armesto et al., 1996; Vidal and Díaz-Páez, 2012; Correa et al., 2016). Anuran choruses are composed of few species, ranging from two to four species (Penna and Veloso, 1990). This relative low diversity of sound producing animal species generates acoustic environments that are relatively simple as compared to those found in tropical forest. In addition, this acoustic environment is also characterized by a relatively high proportion of abiotic background noise mainly generated by heavy rain and strong winds (Penna and Veloso, 1990; Bartheld et al., 2011; Moreno-Gómez et al., 2013). Considering that it is highly important to evaluate cost-effective strategies for biodiversity monitoring, in this study we aim to evaluate a suit of commonly used acoustic diversity indices as proxies of bird and anuran species richness. We expect that this work will contribute to the understanding of the significance and potential use of acoustic indices within this biodiversity hotspot as well as in other regions of interest for conservation.

2. Methods

2.1. Study site and acoustic sampling

The study was carried out in Parque Oncol, a private reserve within the Valdivian rainforest. Recordings were conducted in the summer between January and March 2017 in three different sampling stations (S1: 39°41'58.16"S, 73°17'41.51"W; S2: 39°42'17.67"S, 73°18'33.85"W; S3: 39°42'0.26"S, 73°18'25.46"W), where the minimum distance among stations was 600 m approximately. Each site had relatively similar conditions, for instance, the nearness of small streams of water was avoided in order to reduce the masking of biotic sounds. We used three automated acoustic recorders (SM1, SM3 and SM4, Wildlife Acoustics), where each equipment was placed only in one sampling station, i.e. SM1 in S1, SM3 in S2 and SM4 in S3. Each equipment was attached directly to a tree at an elevation of 5 m and was set to record (sampling rate: 44100 Hz, sample size: 16 bit, WAV format and recording only with the left channel) during one minute per hour, 24 h per day, a sampling design that allowed us to record the sounds produced by birds and anurans during hours that are relevant to both taxa. Because birds and anurans show specific daily activity patterns, this sampling design allowed us to determine if the presence of calls within recordings (once confirmed) is associated to the variation in acoustic indices. As a caution note, we will refer to bird and anuran richness as the presence of species-specific calls in acoustic recordings, e.g. if a recording contained calls from eight different species, a richness value equal to eight was assigned to that recording. Recordings at the three different stations were conducted between January 9th or 10th and 20th or 21st. Recordings conducted in February and March started on 1st and ended on the 12th. The equipment placed in S2 experienced a technical problem, and thus recordings at this site were performed from February 1st through February 5th and no recordings were obtained during March. We made the acoustic recordings between January and March as these months are within the austral summer. Within this season the probability of obtaining recordings with abiotic noises such as heavy rain or strong wind is lower than in other seasons.

2.2. Acoustic analyses

Using Raven Pro 1.4 (Bioacoustics Research Program, 2011), all recordings were audio-visually inspected by experienced researchers (JB and AASB) in order to classify and identify bird and anuran calls. Visual inspections did not indicate issues associated to call identification among different recorders, although some differences between recorders in detectability cannot be dismissed. Because abiotic sounds can mask the sounds of the target species, recordings including high

Table 1
Summary of the effects included in linear mixed effects models to evaluate the variation on acoustic indices.

Model	Fixed effects	Random Intercepts	Random Slopes for Station
M1	Intercept + Birds + Anurans	Station + Month + Hour	Birds + Anurans
M2	Intercept + Birds + Anurans	Station	Birds + Anurans
M3	Intercept + Birds	Station	Birds
M4	Intercept + Anurans	Station	Anurans
M5	Intercept	Station + Month + Hour	
M6	Intercept	Station	

levels of heavy rain or strong wind background noise were excluded from the analysis. The exclusion of these recordings and also the technical problem mentioned in the previous section yielded 1827 audio files for further analysis: 798 from S1, 258 from S2 and 771 from S3.

For each audio file, we obtained seven acoustic indices with an automated custom procedure implemented in R (R Core Team 2017, version 3.4.1) using the packages “tuneR” (Ligges et al, 2016), “seewave” (Sueur et al., 2008b) and “soundecology” (Villanueva-Rivera and Pijanowski, 2016). From the “seewave” package, Spectral Entropy (Hf), Temporal Entropy (Ht), Total Entropy (H) and Acoustic Complexity Index (ACI) were obtained. From the “soundecology” package, Acoustic Diversity Index (ADI), Acoustic Evenness Index (AEI) and Bioacoustics Index (BI) were obtained. Briefly, the Hf is computed following the Shannon evenness index applied to the mean spectrum, where frequency bins are considered as categories and their corresponding amplitudes indicate the importance of each frequency bin. The Ht is calculated similarly but from the amplitude envelope of the time series, and where the envelope points correspond to the categories. The H index considers Hf and Ht and is computed as the product of both indices. The ACI index considers a matrix of frequency bins and their corresponding amplitude values (i.e. spectrogram). For each frequency bin, this index obtains the summation of the differences between contiguous amplitude values, and this value is then weighted by the total sum of amplitude values. This procedure is applied to each frequency bin and subsequently all the values obtained are added. If more than one temporal window is specified, the values obtained for each window are added. The ADI index is obtained from a matrix of frequency bins within a specified frequency interval and their respective amplitude values. Then, the proportion of amplitude values above a threshold is obtained and the Shannon entropy index is applied to these values. The AEI index follows the same initial procedures to calculate the ADI index, but the Gini index is applied to the values obtained. Finally, the BI is calculated as the area under the curve of the mean dB spectrum values within two frequency limits (Sueur et al., 2014; Sueur, 2018).

Previous to acoustic indices calculation, each file was down-sampled to a sample rate of 22050 Hz in order to enhance computation time and spectral resolution. We also applied a high-pass filter of 100 Hz in order to remove abiotic low-frequency background noise and a 10000 Hz low-pass filter was also applied to remove frequencies above the calls of birds and anurans found in these environments (Bartheld et al., 2011). As the maximum frequency that can be measured equals half of the sampling rate used, applying a low pass filter also helps to eliminate artificial frequencies produced by the sampling process (e.g. Sueur 2018). Down-sampling and filtering were performed using the R (R Core Team 2017, version 3.4.1) package “seewave” (Sueur et al., 2008b). For indices that compute the spectrum, a window length of 512 points was used, yielding a frequency resolution of 43 Hz. When indices required specifying frequency limits, these values corresponded to the high- and low-pass filters used, i.e. 100 and 10000 Hz. All other parameters were set to default values, except for the nbwindows parameter of ACI, which was set to a value of 10, as a preliminary exploration showed almost no variation using the default parameter value (value = 1).

2.3. Statistical analysis

As a first approach to evaluate the association between bird and anuran richness and acoustic diversity indices, we performed Spearman correlations between these variables separately for each station using a bootstrapped routine with 1000 iterations. We performed this analysis because it is relatively simple and easy to interpret. For each iteration, we obtained random observations with replacement and performed the correlation analysis, and the number of samples obtained for each iteration was the same as the number of samples obtained for each station. We performed this analysis routine in order to minimize issues that may arise as result of our sampling design which involve spatial and temporal data dependence. For this analysis, we used as an indicator of a good index performance that in the three stations the confidence intervals of bootstrapped correlations contained no zero-correlation values, significant p-values and also the consistency observed for the correlations signs. All the analyses were performed within the R environment.

In addition, in order to evaluate the relevance of bird and/or anuran richness for variation in acoustic indices and also the potential effect of hour and month sampled (as these factors may also account for variation in acoustic properties of sound recordings), we fitted linear mixed effects models (LMMs) using the R package “lme4” (Bates et al., 2015). This type of analysis allows to control for spatial and temporal data dependence resulting from obtaining data from the same experimental units (Pinheiro and Bates, 2000). For each acoustic index, six models (M1, M2, M3, M4, M5 and M6) were fitted using different combinations of the following effects: bird richness, anuran richness, recording hour, month sampled and station (Table 1). Specifically, M1 included the intercept, bird richness and anuran richness as fixed effects, random intercepts were included for station, hour and month, and random slopes were included for bird and anuran richness by station; M2 included the intercept, bird richness and anuran richness as fixed effects, random intercepts for station and random slopes for bird and anuran richness by station; M3 included the intercept and bird richness as fixed effects, random intercepts for station and random slopes for bird richness by station; M4 included the intercept and anuran richness as fixed effects, random intercepts for station and random slopes for anuran richness by station; M5 included the intercept as fixed effect, and random intercepts for station, month and hour; and M6 included the intercept as fixed effect and random intercepts for station. Random effects were included to account for spatial (station) and temporal (hour and month) data dependence, where the inclusion of station also account for potential differences resulting from using different equipment models at each station. Prior to model fitting, acoustic indices were normalized using the “bestNormalize” (Peterson, 2017) R package, which automatically evaluates, chooses and applies the best procedure to normalize data. In addition, collinearity among covariates was evaluated using the R code and the recommendations provided by Zuur et al. (2010). Following these procedures, the variance inflation factors were below 1.3 for all the factors included in the full model and therefore were not dropped. Model fitting was evaluated by visual inspection of the residuals versus fitted values. For each acoustic index, models fitted with different combinations of fixed and random effects were evaluated using Akaike’s Information Criteria corrected for small

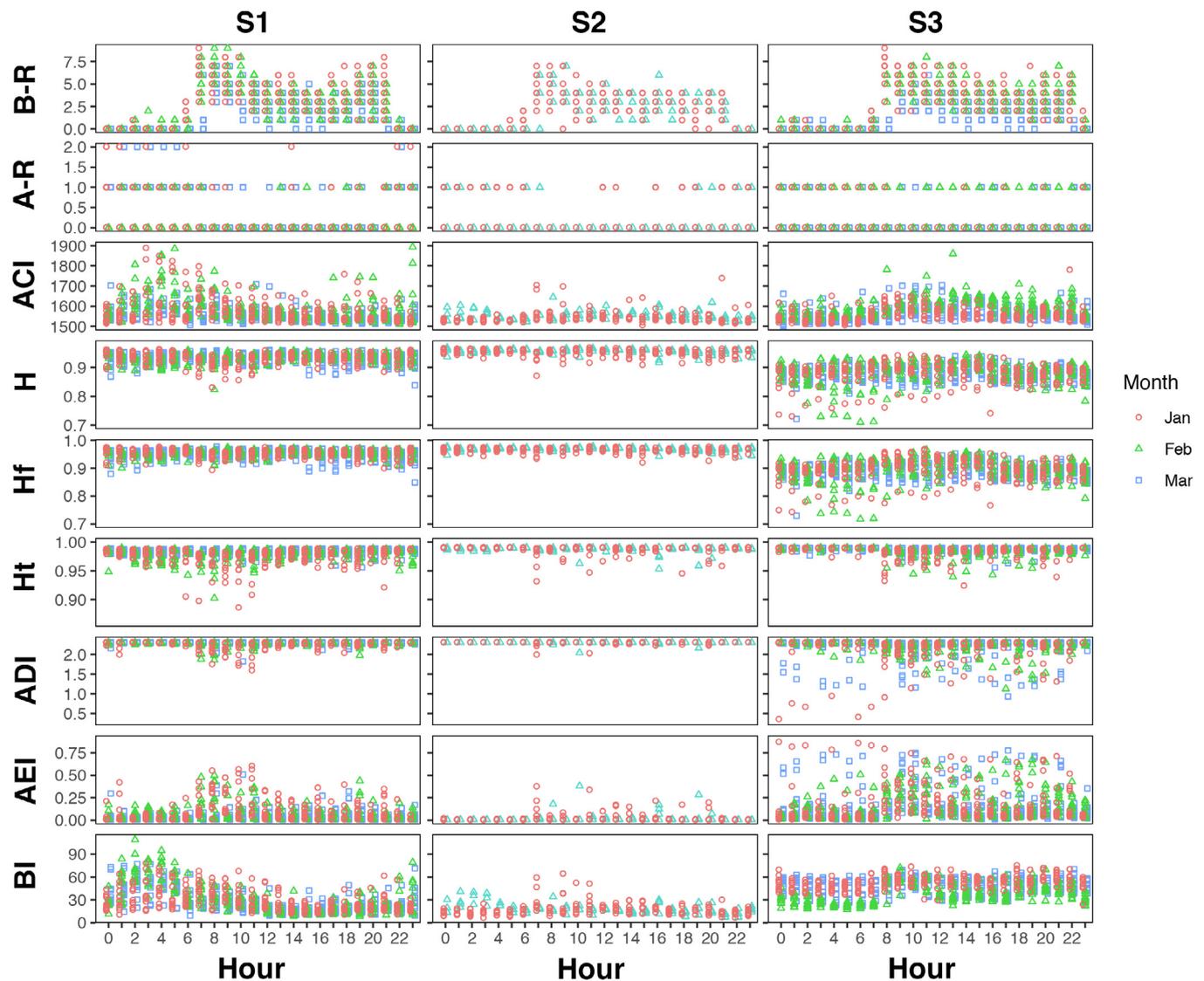


Fig. 1. Variation of Bird richness (B-R), Anuran richness (A-R), Acoustic complexity index (ACI), Total entropy (H), Spectral entropy (Hf), Temporal entropy (Ht), Acoustic diversity index (ADI), Acoustic evenness index (AEI) and Bioacoustic index (BI) throughout hours and months in the three stations sampled. It is expected that an index with good performance follow a similar pattern as shown by bird and/or anuran richness.

sample sizes using the R package “AICcmodavg” (Mazerolle, 2017). We followed the recommendations of Anderson (2008) to evaluate the models.

We applied these two analyses aiming to obtain a clearer idea of the factors that may account for the variation in acoustic diversity indices and also to facilitate its interpretation. The combined result of these two analyses allowed a better evaluation of the performance of the acoustic indices.

3. Results

Variation in bird richness, anuran richness and acoustic diversity indices are shown in Fig. 1. Bird richness was higher at day-time, showing the highest values at dawn and dusk. Anuran richness seems to follow a site-specific pattern, as in S1 and S2 higher values were concentrated at night and in S3 was higher during both day and night. The maximum richness of birds and anurans was around 8 and 2 species, respectively. These richness values are in agreement with the common number of bird species observed and also with the range of the number of frog species participating in choruses in this area (Díaz, 2005; Bartheld et al., 2011; Penna and Veloso, 1990). The lowest richness

found in recordings was equal to zero, as there were recordings that did not contain calls of any species. Among the seven acoustic indices obtained, three apparently follow patterns related to bird richness: at times when bird richness attained higher values, Ht and ADI showed lower values, and AEI had higher values. On the other hand, Fig. 1 also shows that apparently no indices were related to anuran richness.

Our first statistical analyses suggest different levels of association between richness and acoustic indices. For Ht, ADI and AEI, bootstrapped Spearman correlations with bird richness had consistent confidence intervals lacking zero-correlation values in the three stations sampled, nevertheless the ADI index included non-significant p-values in the upper limit of the confidence interval in S3. Bird richness was negatively correlated with Ht and positively correlated with AEI, with absolute correlation values between 0.2 and 0.4. For anuran richness, AEI was the only index having consistent confidence intervals lacking zero-correlation values. This index was negatively correlated with anuran richness but in the stations S2 and S3 the upper confidence interval limits were close to zero-correlation values and p-values included non-significant values within the confidence interval (Fig. 2, Table 2).

Results from LMMs analyses reveal differential effects of bird and anuran richness, recording hour and month sampled on the variation of

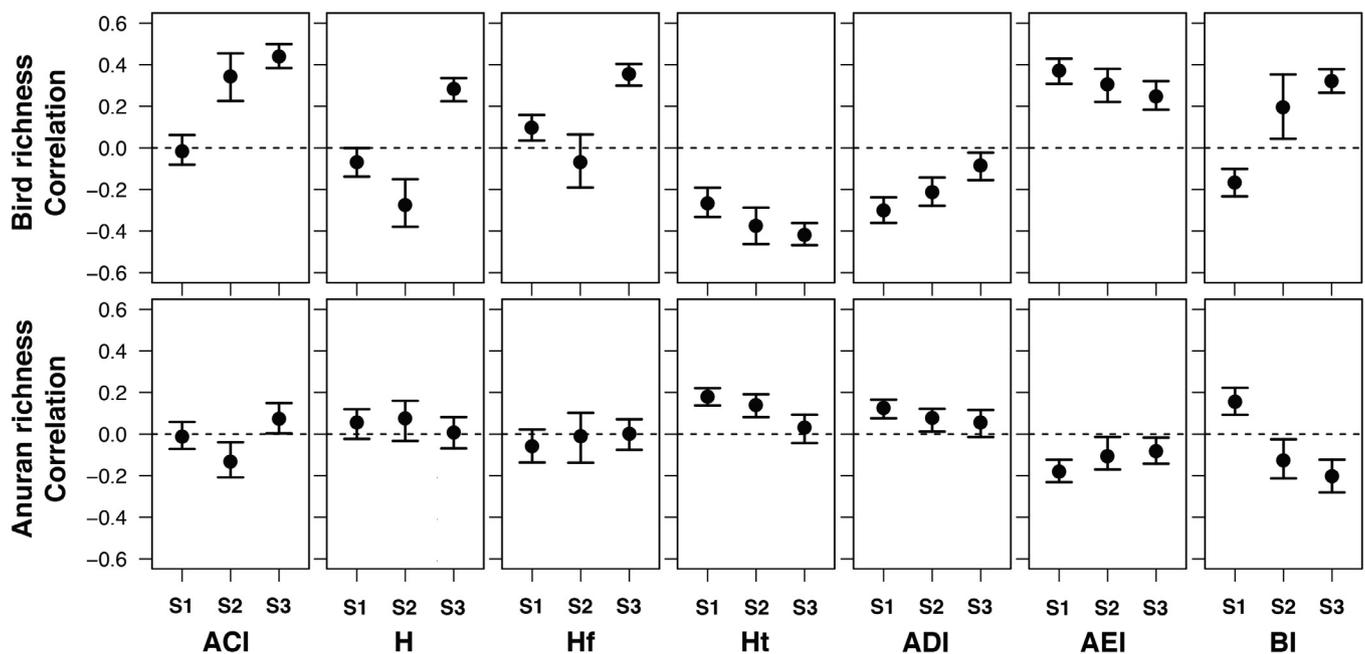


Fig. 2. Results from bootstrapped correlations computed by Spearman tests between bird and anuran richness and acoustic diversity indices in the three stations sampled. Median and confidence interval at 0.95 for correlation values are provided. Abbreviations of acoustic indices as in Fig. 1.

acoustic indices (Table 3). For ACI, H, Hf, Ht, and BI the full model, i.e. M1 which contained the intercept, bird richness and anuran richness as fixed effects, random intercepts for station, hour and month, and random slopes for birds and anurans by station was the top ranked model. This model had AICc weights (i.e. probabilities) > 0.95 and Delta-AICc relative to the second ranked model with values > 7, showing that M1 has strong support relative to the other models fitted, implying therefore that all the factors included in this model help to explain the variation shown by these five acoustic indices. Among these indices, the highest effect sizes for species richness were found in ACI, BI and Ht, this last index having the highest effect size for bird richness. For ADI and AEI, the top ranked models corresponded to M1 and M2, respectively. However, for both models AICc weights were < 0.5 and Delta-AICc relative to the second ranked model had values < 1, implying that other models cannot be dismissed. In this case, other models that must be considered are included in the model-set that had a cumulative probability > 0.95. Specifically, while in the case of ADI this model-set included M1, M3 and M2, in the case of AEI it included M2, M1 and M3. These other models did not include hour and month as random effects and they differ in that while M3 includes bird richness, M2 includes bird and anuran richness. These results imply that

although month and hour should be considered, species richness are of higher importance to explain the variation in the two indices. Among these two indices, the highest effect sizes for richness were found in AEI.

4. Discussion

We evaluated seven acoustic indices to assess their relationship with variation in bird and anuran species richness, as measured by the occurrence of species-specific calls in acoustic recordings. Our first analysis indicates that most indices are not correlated with bird and/or anuran richness, the exceptions being Ht and AEI, which showed significant correlations with bird richness in the three stations sampled, although their correlation values were low to moderate. Our second analysis indicates that for the set of acoustic indices evaluated, Ht and AEI were among the indices showing highest effect sizes for bird richness, nevertheless, all factors considered (i.e., bird richness, anuran richness, hour and month) are of potential importance. Previous studies performed in other environments showed differential performances of acoustic diversity indices, including the lack of reliable associations with biodiversity (Fuller et al., 2015; Mammides et al., 2017; Machado

Table 2

P-values from bootstrapped correlations computed by Spearman tests between bird and anuran richness and acoustic diversity indices in the three stations sampled. Median and confidence interval at 0.95 (in parenthesis) are provided. Abbreviations of acoustic indices as in Fig. 1.

Richness	Acoustic index	S1	S2	S3
Bird	ACI	0.456 (0.020–0.960)	< 0.001 (< 0.001–< 0.001)	< 0.001 (< 0.001–< 0.001)
Bird	H	0.054 (< 0.001–0.876)	< 0.001 (< 0.001–0.016)	< 0.001 (< 0.001–< 0.001)
Bird	Hf	0.005 (< 0.001–0.315)	0.273 (0.002–0.935)	< 0.001 (< 0.001–< 0.001)
Bird	Ht	< 0.001 (< 0.001–< 0.001)	< 0.001 (< 0.001–< 0.001)	< 0.001 (< 0.001–< 0.001)
Bird	ADI	< 0.001 (< 0.001–< 0.001)	0.001 (< 0.001–0.022)	0.020 (< 0.001–0.492)
Bird	AEI	< 0.001 (< 0.001–< 0.001)	< 0.001 (< 0.001–< 0.001)	< 0.001 (< 0.001–< 0.001)
Bird	BI	< 0.001 (< 0.001–0.004)	0.002 (< 0.001–0.482)	< 0.001 (< 0.001–< 0.001)
Anuran	ACI	0.498 (0.038–0.972)	0.034 (0.001–0.525)	0.041 (< 0.001–0.771)
Anuran	H	0.116 (0.001–0.894)	0.217 (0.010–0.930)	0.433 (0.014–0.968)
Anuran	Hf	0.105 (< 0.001–0.901)	0.515 (0.026–0.977)	0.462 (0.020–0.973)
Anuran	Ht	< 0.001 (< 0.001–< 0.001)	0.024 (0.002–0.194)	0.328 (0.010–0.961)
Anuran	ADI	< 0.001 (< 0.001–0.032)	0.208 (0.052–0.815)	0.117 (0.001–0.882)
Anuran	AEI	< 0.001 (< 0.001–< 0.001)	0.092 (0.006–0.787)	0.024 (< 0.001–0.613)
Anuran	BI	< 0.001 (< 0.001–0.009)	0.044 (0.001–0.655)	< 0.001 (< 0.001–0.001)

Table 3

Model selection to evaluate the effects of bird richness, anuran richness, month and hour on the variation of acoustic diversity indices. Estimates of fixed effects and standard errors (in parenthesis) are provided for the intercept, bird richness and anuran richness. Abbreviations of acoustic indices as in Fig. 1. K: number of estimated parameters, AICc: Akaike's Information Criteria corrected for small sample sizes. Delta AICc: difference between the best model and the other models, LL: log likelihood of the model, AICc Wt: weight of the evidence of the model (probability of the model), Cum. Wt: cumulative weight of the ranked models (cumulative probability).

Acoustic Index	Model	K	AICc	Delta AICc	LL	AICcWt	Cum.Wt	Intercept	Bird	Anuran
ACI	M1	9	4793.0	0	-2387.5	1	1	-0.45 (0.24)	0.15 (0.05)	0.15 (0.05)
	M2	7	4943.0	150.0	-2464.5	0	1	-0.42 (0.18)	0.13 (0.05)	0.15 (0.09)
	M3	5	4952.5	159.4	-2471.2	0	1	-0.37 (0.18)	0.12 (0.05)	
	M5	5	4953.0	160.0	-2471.5	0	1	-0.12 (0.25)		
	M6	3	5133.1	340.1	-2563.6	0	1	-0.10 (0.15)		
	M4	5	5134.9	342.0	-2562.5	0	1	-0.10 (0.14)		0.01 (0.10)
H	M1	9	3347.6	0	-1664.7	0.997	0.997	0.29 (0.60)	-0.01 (0.04)	0.05 (0.03)
	M3	5	3359.8	12.2	-1674.9	0.002	0.999	0.31 (0.61)	-0.01 (0.05)	
	M2	7	3362.7	15.1	-1674.3	0.001	1	0.29 (0.60)	-0.01 (0.04)	0.036 (0.03)
	M5	5	3425.5	77.9	-1707.7	0	1	0.28 (0.51)		
	M6	3	3446.6	99.1	-1720.3	0	1	0.29 (0.51)		
	M4	5	3447.6	100.1	-1718.8	0	1	0.28 (0.51)		0.06 (0.03)
Hf	M1	9	3336.4	0	-1659.2	1	1	0.18 (0.56)	0.03 (0.03)	0.03 (0.03)
	M3	5	3362.7	26.3	-1676.3	0	1	0.20 (0.56)	0.03 (0.03)	
	M2	7	3366.4	30.0	-1676.2	0	1	0.19 (0.56)		0.02 (0.033)
	M5	5	3401.2	64.8	-1695.6	0	1	0.24 (0.49)		
	M6	3	3460.5	124.1	-1727.3	0	1	0.26 (0.49)		
	M4	5	3464.3	127.9	-1727.2	0	1	0.27 (0.49)		-0.01 (0.03)
Ht	M1	9	4106.1	0	-2044.0	0.978	0.978	0.60 (0.44)	-0.18 (0.04)	-0.01 (0.04)
	M3	5	4114.1	8.0	-2052.0	0.018	0.996	0.60 (0.42)	-0.19 (0.04)	
	M2	7	4117.0	10.9	-2051.5	0.004	1	0.61 (0.43)	-0.19 (0.04)	-0.02 (0.06)
	M5	5	4338.8	232.7	-2164.4	0	1	0.25 (0.40)		
	M4	5	4522.6	416.5	-2256.3	0	1	0.16 (0.36)		0.19 (0.06)
	M6	3	4539.8	433.7	-2266.9	0	1	0.21 (0.35)		
ADI	M1	9	4321.6	0	-2151.8	0.370	0.370	0.44 (0.38)	-0.11 (0.01)	0.08 (0.04)
	M3	5	4321.7	0.1	-2155.8	0.361	0.731	0.48 (0.37)	-0.12 (0.01)	
	M2	7	4322.3	0.6	-2154.1	0.269	1	0.45 (0.37)	-0.11 (0.01)	0.08 (0.04)
	M5	5	4406.1	84.5	-2198.1	0	1	0.240 (0.39)		
	M4	5	4467.6	145.9	-2228.8	0	1	0.16 (0.38)		0.25 (0.04)
	M6	3	4499.5	177.9	-2246.7	0	1	0.22 (0.38)		
AEI	M2	7	4056.0	0	-2021.0	0.437	0.437	-0.57 (0.47)	0.15 (0.03)	-0.10 (0.04)
	M1	9	4056.2	0.2	-2019.1	0.405	0.843	-0.56 (0.47)	0.15 (0.03)	-0.10 (0.04)
	M3	5	4058.1	2.1	-2024.0	0.157	1	-0.61 (0.47)	0.16 (0.03)	
	M5	5	4172.6	116.5	-2081.3	0	1	-0.28 (0.44)		
	M4	5	4288.0	231.9	-2139.0	0	1	-0.19 (0.43)		-0.30 (0.04)
	M6	3	4341.5	285.4	-2167.7	0	1	-0.27 (0.43)		
BI	M1	9	4149.1	0	-2065.5	1	1	-0.41 (0.40)	0.10 (0.05)	-0.10 (0.06)
	M5	5	4291.4	142.3	-2140.7	0	1	-0.24 (0.41)		
	M2	7	4322.4	173.3	-2154.2	0	1	-0.32 (0.40)	0.04 (0.04)	-0.02 (0.12)
	M3	5	4336.6	187.5	-2163.3	0	1	-0.31 (0.40)	0.04 (0.05)	
	M4	5	4370.9	221.8	-2180.4	0	1	-0.23 (0.40)		-0.06 (0.16)
	M6	3	4409.9	260.8	-2201.9	0	1	-0.23 (0.40)		

et al., 2017). The fact that most of the acoustic indices tested in our study fail to describe satisfactorily the variation in species richness is in general agreement with these previous studies.

It is important to note that we applied virtually no signal processing to the recordings and that the indices were not fine-tuned. Further studies should evaluate the effectiveness of acoustic indices using simulated choruses, different recording durations, different background noise levels and explore different combinations of adjustable parameters available for each index, as these procedures are likely to affect the performance of acoustic indices (Gasc et al., 2015). The relative better performance shown by Ht and AEI suggest that these indices may be good candidates to perform these future studies.

The Ht is computed following the Shannon evenness index applied to the amplitude envelope of the time series, and where the envelope points correspond to the categories (Sueur, 2018). It is expected that acoustic recordings with several amplitude modulations yield higher values for the index, nevertheless, an envelope with almost no variation may also return higher values (Sueur et al., 2008a,b). As such, the relative low diversity of birds within this environment and the acquisition of acoustic recordings containing mostly abiotic background noise may explain the negative relation of this index with bird richness. On the other hand, the AEI is computed from the spectrogram, and

takes into account the proportion of signals within each bin that are above certain amplitude threshold and uses these values to calculate the Gini index (Villanueva-Rivera and Pijanowski, 2016). As environments having larger biodiversity are expected to yield acoustic recordings having sounds spread over larger number of frequency bands, it is expected that AEI correlates inversely with diversity (Villanueva et al., 2011; Mammides et al., 2017). Nevertheless, recent studies have shown that signals of coexisting species may also show convergence trends (Tobias et al., 2014), which may affect the expected trend of the index. Our study shows that the AEI was positively associated with bird richness. The relative low bird richness observed in recordings and the fact that most species show dominant frequency values within a relative narrow frequency range (i.e., between 2 and 5 kHz, Bartheld et al., 2011) is consistent with the observed trend. The behavior of acoustic indices that measure inequality (e.g. Gini index) should be further studied in animal communities where the sounds produced by different species are not evenly spaced in the acoustic space.

Regarding anurans, the poor performance shown by the indices is likely to be explained by the low species richness of this group within recordings. Future studies may evaluate the use of acoustic indices using different approaches. For instance, it may be possible to associate indices to the acoustic properties of monospecific and heterospecific

anuran choruses or to species producing calls with different levels of acoustic complexity (Lozano et al., 2014), and to compare variation in vocal activity over time taking into account only nightly recordings, time at which anuran choruses are the main biotic sounds sources below 10 kHz in the Valdivian rainforest (Moreno-Gómez et al., 2013).

To date, several indices have been proposed, and studies have shown that combinations of them may also be used (Sueur et al., 2014; Towsey et al., 2014). It is important to consider that acoustic indices may also serve as indicators of other hierarchical levels of diversity, such as functional and phylogenetical diversity (Gasc et al., 2013a). In addition, these indices may also be used to determine phenology patterns (Buxton et al., 2016), the effects of anthropogenic noise (Pieretti and Farina, 2013; Raynor et al., 2017) and the effects of disturbances such as wildfires (Gasc et al., 2018). However, as with species richness, more studies are needed to obtain a general validation of these additional applications of acoustic indices.

The acoustic indices evaluated in our study correspond to α -indices, which aim to quantify diversity within a sample unit. However, there are also β -indices designed to measure the similarity or difference among sample units (Sueur et al., 2014), and when performing studies at large spatial scales the use of these indices can facilitate the recognition of acoustic features of particular significance for conservation issues (Gasc et al., 2013b). β -indices may also serve to evaluate temporal changes in communities (Lellouch et al., 2014). Therefore, the use of combinations of acoustic α -indices and β -indices could set up effective tools to monitor biodiversity at large spatiotemporal scales, and in the future, they may enhance results obtained using more traditional methodologies (e.g. Jarzyna and Jetz, 2018). Furthermore, ecological acoustic researchers have put forward the term soundscape to refer to the combination of biotic (biophonies), abiotic (geophonies) and anthropogenic (anthropophonies) sound sources in a spatial context (Farina, 2006; Pijanowsky et al., 2011). Associations between acoustic indices, landscape configuration and ecological condition have also been reported (Tucker et al., 2014; Fuller et al., 2015) and currently, acoustic monitoring and the use of acoustic indices are also being employed to analyze the diversity and variation of aquatic environments (Parks et al., 2014; Bertucci et al., 2016; Pieretti et al., 2017; Linke et al., 2018).

Chilean laws state that evaluations of diversity levels are needed before the implementation of projects that could alter natural environments, including the Valdivian rainforest. As such, the implementation of low-cost acoustic monitoring procedures is likely to promote appropriate evaluations of biodiversity, including the use of more proper spatiotemporal sampling scales and the reduction of biases dependent on the observers' experience. Furthermore, implementations of long-term acoustic monitoring plans in different areas may serve to evaluate ongoing effects of climate change. However, the use of acoustic tools for biodiversity monitoring needs of further validations of the accuracy of the different methodologies involved. We expect that this first evaluation of the use of acoustic diversity indices in the Valdivian rainforest encourages further studies within this biodiversity hotspot as well as in other regions of similar relevance for conservation issues.

5. Conclusions

Cost-effective strategies for biodiversity monitoring employing acoustic diversity indices are highly promising tools to describe and quantify changes in biodiversity. However, recent studies conducted in different environments and geographical areas have reported unreliable associations between acoustic diversity indices and biodiversity, prompting for further evaluations of commonly used acoustic diversity indices as proxies of the richness of sound producing animal species. Our results indicate that most of the acoustic indices tested fail to describe satisfactorily the variation in species richness, nevertheless, Ht and AEI may potentially serve as indicators of bird richness but future

studies should fine-tune these indices aiming to obtain a robust validation of its use within the Valdivian rainforest. This implies to determine the best procedures to calculate their values to improve the association of these indices with bird richness. Because currently it is not completely clear how well acoustic indices serve for biodiversity assessments and monitoring, its use should be cautiously. This initial evaluation of the use of acoustic diversity indices in this biodiversity hotspot in South America should also encourage further studies to assess their value as proxies of different measures of diversity in this as well as in other regions of similar relevance for conservation issues.

Acknowledgements

FNMG was supported by FONDECYT 11160778 and by Plan de Mejoramiento Institucional UCM1310, MINEDUC, Chile. MP was partially supported by grant ENL032/2017, Vicerrectoría de Investigación y Desarrollo, Universidad de Chile. The authors appreciate the very constructive comments and suggestions made by three anonymous reviewers. The authors declare no conflict of interests.

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