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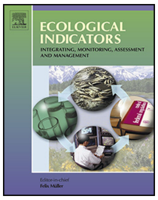

Connecting soundscape to landscape: Which acoustic index best describes landscape configuration?

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ABSTRACT

Soundscape assessment has been proposed as a remote ecological monitoring tool for measuring biodiversity, but few studies have examined how soundscape patterns vary with landscape configuration and condition. The goal of our study was to examine a suite of published acoustic indices to determine whether they provide comparable results relative to varying levels of landscape fragmentation and ecological condition in nineteen forest sites in eastern Australia. Our comparison of six acoustic indices according to time of day revealed that two indices, the acoustic complexity and the bioacoustic index, presented a similar pattern that was linked to avian song intensity, but was not related to landscape and biodiversity attributes. The diversity indices, acoustic entropy and acoustic diversity, and the normalized difference soundscape index revealed high nighttime sound, as well as a dawn and dusk chorus. These indices appear to be sensitive to nocturnal biodiversity which is abundant at night in warm, subtropical environments. We argue that there is need to better understand temporal partitioning of the soundscape by specific taxonomic groups, and this should involve integrated research on amphibians, insects and birds during a 24 h cycle. The three indices that best connected the soundscape with landscape characteristics, ecological condition and bird species richness were acoustic entropy, acoustic evenness and the normalized difference soundscape index. This study has demonstrated that remote soundscape assessment can be implemented as an ecological monitoring tool in fragmented Australian forest landscapes. However, further investigation should be dedicated to refining and/or combining existing acoustic indices and also to determine if these indices are appropriate in other landscapes and for other survey purposes.

1. Introduction

Soundscape ecology is the study of sounds in the landscape ('soundscape') and is based on how sounds from biological, geophysical and anthropogenic sources can be used to understand natural and human systems at multiple temporal and spatial scales (Pijanowski et al., 2011a). Biophony, geophony and anthrophony are terms used to characterize sounds that occur in the landscape (Pijanowski et al., 2011a). Biophony refers to the sounds produced by living organisms, usually sounds that are used by animals as a means of communication. This may include birds, amphibians, insects, mammals, fish, amphipods, and crustaceans in both terrestrial and aquatic systems. Geophony is the collection of sounds caused by physical processes such as wind, water flow, thunder, rainfall, and earth movement. The sound created when humans use mechanical devices is referred to as anthrophony (or technophony). This includes the sounds that come from stationary machines such as fans and air conditioners, and mobile machines used for transportation and construction such as aircraft, cars, trucks, boats, building cranes, bulldozers etc.

There has been considerable interest and research to develop and compute acoustic indices that represent the characteristics of the soundscape. Early research in this field led to the application of landscape metrics (reviewed in Turner, 1989) to the soundscape using acoustic diversity indices (Gage et al., 2001; Napoletano, 2004). These indices were based on the quantification of spectrogram images, calculated by dividing the spectrum into frequency bins and using automated processing of multiple spectrograms (Gage and Napoletano, 2004). A computation approach using the power density spectrum (Welch, 1967) was then developed and used to characterize temporal changes in the soundscape in Sequoia National Park (Krause et al., 2011). The computation of

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acoustic metrics from multiple recordings was further developed to compute soundscape power (Matlab code can be obtained from the authors). Subsequently, the normalized difference soundscape index (Joo, 2009; Kasten et al., 2012) was created to estimate the relative amount of biophony and anthrophony in the soundscape by computing the ratio of anthrophony to biophony found in field-collected acoustic recordings.

Farina et al. (2005) examined landscape ecology from a cognitive perspective and described new thinking about how organisms perceive landscapes according to signals and signs in the context of energy flows within the landscape. The acoustic complexity index was developed based on the observation that many biotic sounds, such as bird songs, are characterized by an intrinsic variability of intensities, while human-generated noise is often constant in intensity (Pieretti et al., 2011). Pieretti et al. (2011) found that this index correlates with the number of bird vocalizations, while efficiently filtering airplane noise. The acoustic complexity index has been used to describe avian soundscapes (Farina et al., 2011), relate avian soundscapes to vegetation complexity (Farina and Pieretti, 2014) and describe the influence of traffic noise (Pieretti and Farina, 2013). It is calculated as the average absolute fractional change in spectral amplitude, averaged over all frequency bins for the entire recording. Similarly, Boelman et al. (2007) developed a bioacoustic index which was a function of both the spectral amplitude and the number of frequency bands in a sound recording. This index was shown to be strongly correlated with avian abundance in Hawaiin forests experiencing weed invasion.

Acoustic diversity indices have also been developed to facilitate automated surveying of ecosystems for rapid biodiversity appraisal (Sueur et al., 2008b, 2012). The acoustic entropy index is one such index and is computed as the product of both the temporal (acoustic energy dispersal within a recording) and spectral entropies (acoustic energy dispersal through the spectrum) following application of the Shannon index (Sueur et al., 2008b). Simulations revealed a correlation between the acoustic entropy index and species diversity and in field studies this index was found to be sensitive to disturbance in Tanzanian forests (Sueur et al., 2008b). The acoustic diversity index (Villanueva-Rivera et al., 2011) is a modification of spectral entropy and is also calculated using the Shannon index, while the acoustic evenness index uses the Gini coefficient as a measure of evenness (Villanueva-Rivera et al., 2011).

The theoretical underpinning of the application of acoustic indices is that communities with more audible species have a greater acoustic diversity and that biodiversity will correlate positively with acoustic diversity (Gage et al., 2001; Qi et al., 2008). Despite the existence of a suite of acoustic indices, few comparative studies have been undertaken. Towsey et al. (2014) provided a thorough investigation of multiple indices relative to a comprehensive avifauna census dataset. However, the focus of their study was to develop a computer assisted sampling methodology to obtain a more efficient estimate of species richness than random sampling alone, rather than to evaluate acoustic indices relative to landscape condition or configuration.

While it has been proposed that there is an intrinsic relationship between the soundscape and the landscape (Pijanowski et al., 2011b), there have been few studies that have tested this explicitly (see Bormpoudakis et al., 2013; Tucker et al., 2014). Furthermore, recent studies in urban environments have highlighted the importance of land use planning regarding the evaluation of the soundscape using a landscape perspective (Kuehne et al., 2013; Votsi et al., 2012). However, while a range of studies have recorded and analyzed acoustic signals produced by birds, insects and other audible organisms to assess the effects of disturbance on biodiversity (Blumstein et al., 2011; Depraetere et al., 2012; Laiolo, 2010; Proppe et al., 2013; Sueur et al., 2008b), a lack of standardized methods to evaluate landscape characteristics has probably inhibited research on linking soundscape with landscape configuration. Recently, an ecological condition framework that assesses landscape characteristics has been developed to meet biodiversity offset policy demands (Eyre et al., 2011). Tucker et al. (2014) conducted an evaluation of fragmented spotted gum forests in eastern Queensland, Australia using this framework and found that there was a significant relationship between the soundscape and the size and connectedness of forest patches, but other landscape features such as road fragmentation and land use were not studied. Consequently, our study aims to investigate the patterns of six acoustic indices and relate these patterns to an array of landscape features and ecological condition in nineteen fragmented forest sites in south-eastern Australia.

2. Methods

2.1. Study sites

The study area was situated in South-east Queensland, Australia; a region characterized by a subtropical climate, fast growing population and increasing urban and peri-urban pressures including reduced native forest cover and habitat fragmentation. Nineteen sites were selected in forest patches ranging in size from 3 ha to 44,110 ha (see Supplementary Material 1 for site location details). Ten sites were located in patches of remnant spotted gum (*Corymbia citriodora* ssp. *variegata*) open forest and nine sites were in scribbly gum (*Eucalyptus racemosa*) woodland.

2.2. Ecological condition survey

In a terrestrial context, ecological condition relates to the viability or health of an ecosystem (Gibbons and Freudenberger, 2006) and is commonly measured by the structural and compositional integrity of native vegetation (Yapp et al., 2010). Ecological condition surveys were conducted according to biocondition V2.1 guidelines outlined by Eyre et al. (2011). A reference or benchmark site for each forest type was selected based on the knowledge of a professional botanist with extensive local experience. A range of site-based vegetation attributes, including number of large trees, recruitment of canopy species, tree canopy height, native grass, forb, shrub and tree species richness, native grass, shrub and tree canopy cover, non-native plant cover, leaf litter and course woody debris, were measured. Each vegetation attribute was scored as a comparison to those values associated with the reference site. Total vegetation attributes were scored out of 80. Patch size, patch connectivity and patch context variables were derived using a GIS based tool developed by the Queensland Herbarium (Kelley and Kelly, 2012) and scored as a comparison to those values associated with the reference site. A total landscape score (with a maximum possible value of 20) was calculated. An ecological condition score between 0 and 1 was computed for each site based on the addition of vegetation and landscape scores divided by one hundred. A score of 1 indicates very high ecological condition.

2.3. Soundscape recordings

Song Meter SM2 (Wildlife Acoustics 2013) recording devices were deployed at each site for approximately one month during September 2012 (spotted gum sites, 28 days) and September 2013 (scribbly gum sites, 36 days). Recording devices were placed in vegetation away from the patch edge and any walking tracks or disturbance and attached to trees at eye height. Song Meters were configured to record for 1 min every 30 min and monaural 16 bit recordings were made at a frequency of 22,050 Hz and stored in WAV file format.

2.4. Acoustic indices

Using the R statistical computing environment (R Core Team, 2014), we computed six acoustic indices for each of the half-hourly sound recordings (a total of 27,902) using the "multiple_sounds" function in the soundecology package (Villanueva Rivera and Pijanowski, 2013) and seewave-R (Sueur et al., 2008a). The acoustic complexity index (ACI) (Pieretti et al., 2011) was calculated across the frequency range of 0–11,025 Hz using default parameters and J set to 5. The bioacoustic index (BIO) (Boelman et al., 2007) was calculated from 2000 to 8000 Hz using default parameters. Seewave-R was used to compute acoustic entropy (*H*; Sueur et al., 2008b) across the frequency range of 0–11,050 Hz using default parameters. Both the acoustic diversity (ADI) and acoustic evenness (AEI) indices (Villanueva-Rivera et al., 2011) were calculated across the frequency range of 0–10,000 Hz using 1000 steps and a decibel threshold of −50. The normalized difference soundscape index (NDSI) (Kasten et al., 2012) was calculated as the ratio ([biophony − anthrophony]/[biophony + anthrophony]) of the normalized power spectral density values (W/kHz) for the frequency intervals corresponding to anthrophony (1000–2000 Hz) and biophony (2000–11,050 Hz). A separate file for each index was created in csv format and the acoustic data were joined with landscape data using Microsoft Access (Microsoft 2013). For time series plots, acoustic data were collated and an hour-of-day average for each index was calculated for each site.

2.5. Bird species identification

Bird species were identified from recordings by an expert 'birder' using aural and visual examination of spectrograms. A species list was compiled for each site from twenty randomly selected minutes from the dawn chorus (between 0430 h and 0600 h) over twenty separate days. Recent studies in South-east Queensland forest systems have shown that targeted sampling of recorded bird call data from the dawn chorus detected the highest number of species (Wimmer et al., 2013).

2.6. Data analysis

Landscape metrics were quantified using GIS for each of the nineteen sites. These variables included patch size, patch connectivity, patch context, extent of highway, main and local roads surrounding a patch and the proximity to conservation and residential areas (within a 500 m radius of the patch). Tests of normality of metrics by forest type were performed and parametric statistical tests were found to be appropriate. Two-tailed Pearson's correlations implemented in the R Statistical Program (R Core Team, 2014) were used to examine relationships among landscape variables and between landscape variables, bird species richness and biocondition.

Given that acoustic sampling occurred within a relatively small time frame within one season, acoustic metric values were averaged by hour across all days of the month resulting in 24 hourly acoustic metric values per day per site (for a total of 456). Acoustic metrics were modeled using a random intercepts model in a mixed model analysis (Pinheiro and Bates, 2000). Hourly acoustic metrics were not independent data points, but rather repeated samples (by hour of day) within sites (Gutzwiller and Riffell, 2007; Schielzeth and Forstmeier, 2009). We used a mixed model as it is seen as an improvement over traditional repeated-measures analysis of variance (Gutzwiller and Riffell, 2007) because 'time' can be explicitly incorporated using a covariance structure.

Initially, a linear mixed-effects model ($Y = X\beta + Z\gamma + \varepsilon$) was fit using restricted maximum likelihood estimation (REML) without a temporal covariance structure (i.e., as an independent errors model) with the nlme package in R Statistical Program (Bates et al., 2014; R Core Team, 2014). Fixed main effects included acoustic metric (Y) and biocondition or bird richness (X). Sites were modeled as a random effect (Z). While the fixed intercept effect (β) is common to all sites, random intercepts (γ) were incorporated to allow site specific variation in the model coefficients (Mikkonen et al., 2008). In the case of ACI, it was necessary to use a mixed model with nested random effects (site nested within forest type).

Additional models were fit using one of three candidate residual covariance structures (ε) to account for potential temporal autocorrelation. An advantage of using this approach is the ability to compare models of different covariance structure using Akaike's Information Criterion (AIC). While an autoregressive covariance structure (corAR1) was deemed the most biologically reasonable covariance structure (Gutzwiller and Riffell, 2007), we also tested an autoregressive moving average (corARMA) which models the dependence of hourly acoustic metrics on past acoustic data (Gałecki and Burzykowski, 2013). In some cases an autoregressive covariance structure with heterogeneous variances (corARH) was a better fit than autoregressive alone. Final model selection for each metric was made by selecting the model with the smallest AIC. ΔAIC was calculated as the difference in AIC for a model with an autoregressive correlation structure and without (i.e., independent errors model).

3. Results

3.1. Time-of-day acoustic indices

The pattern of each acoustic index is plotted over hour of day during the soundscape recording period averaged over the ten spotted gum sites (Fig. 1A) and nine scribbly gum sites (Fig. 1B). The overall patterns for the same acoustic index are similar across the two forest types. The ACI and the BIO have similar patterns; they rise rapidly at the dawn chorus, decline until the evening chorus, increase slightly then decline until the dawn chorus is reached in the morning (about 0600 h). *H* and ADI also reveal a common pattern of high values at nighttime, declining during the daytime, rising slightly at evening chorus, declining and then rising again as nighttime approaches. Conversely, the AEI is low at night, rises steadily during the day and falls as evening approaches. The NDSI is high during nighttime, falls at the dawn chorus, declines steadily during the day, drops further at the evening chorus and then rises at nighttime until it peaks at 0200 h.

3.2. Comparison of acoustic indices across sites and forest types

Our analyses revealed considerable variation in all acoustic indices, except ACI, across sites and little congruence across the six indices (Fig. 2). Sites with low mean NDSI generally exhibited high mean values for BIO and AEI, but intermediate values for ADI and *H*. In most cases, mean ADI and *H* values were similar across sites. Mean AEI values presented a mostly inverse pattern relative to mean ADI and *H*. Mean NDSI provided a very different pattern in comparison with all other indices.

With the exception of ACI, there was no difference in acoustic metric means across forest types. Consequently, forest type was not included as a random effect except in the mixed model analysis of ACI data.

3.3. Correlation analyses

There was high correlation between landscape metrics and between each landscape metric and biocondition (Fig. 3). Based on this, biocondition was considered a useful proxy for the suite of landscape metrics. Bird species richness was correlated with patch

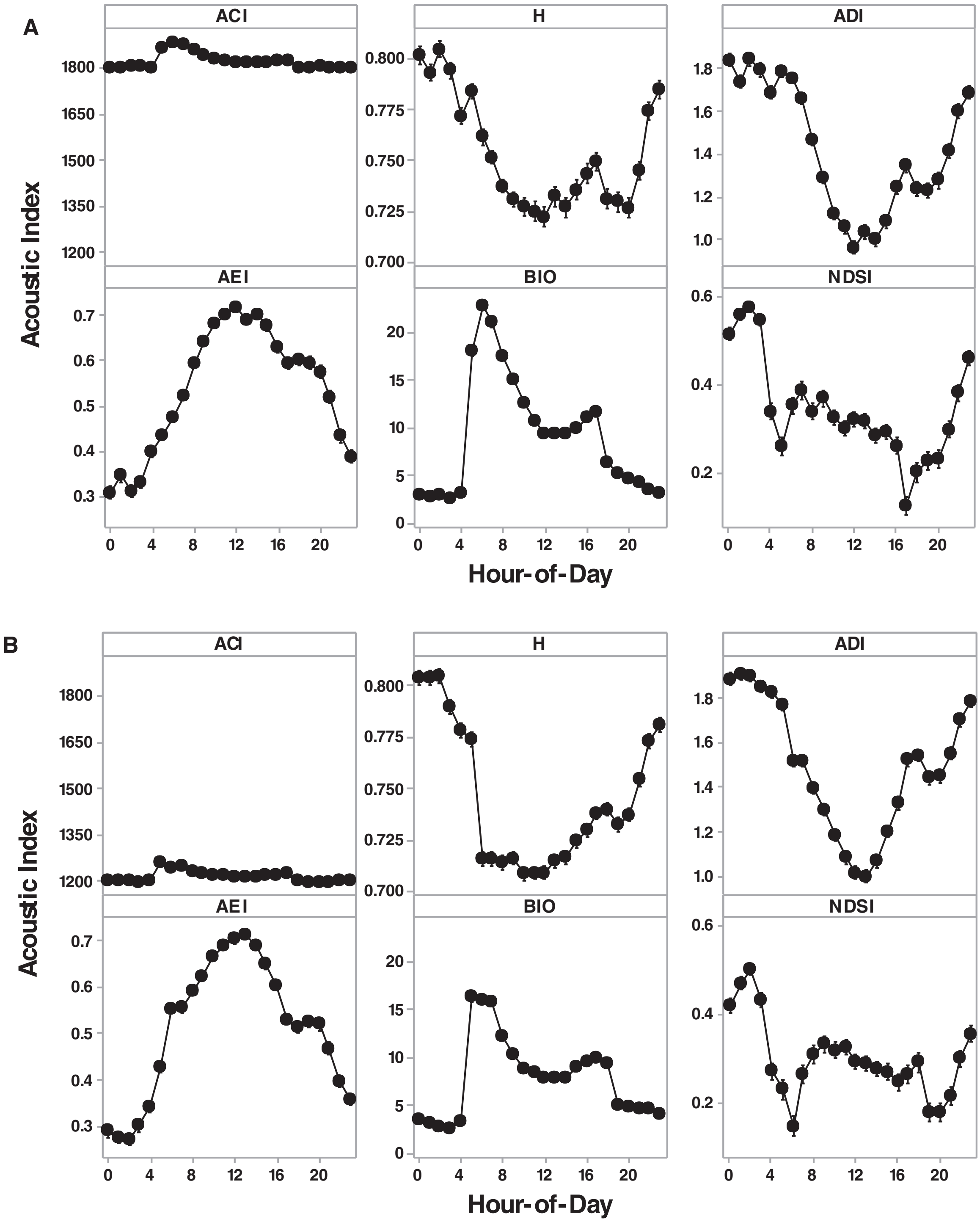

Fig. 1. Acoustic indices averaged according to time of day for one month and across combined spotted gum (10 sites) (A) and scribbly gum sites (9 sites) (B). The *x* axis = time of day (24 h); *y* axis = value for each acoustic index. Confidence intervals are standard errors.

size and extent of nearby local roads, but was not correlated with any other landscape metric or biocondition.

3.4. Mixed model analyses

A summary of the landscape attribute and biodiversity data for each site is given in Supplementary Material 1. Models to test the relationship between each acoustic index and biocondition or bird species richness were best fit with a linear mixed model with autoregressive correlation structure as indicated by lowest AIC values. Estimates of the fixed effects for best models for biocondition are displayed in Table 1. Of the six acoustic metrics modeled, three (NDSI, AEI, and *H*) showed significant relationships with biocondition. The estimated autocorrelation, phi, was high in all cases confirming the appropriateness of models with autoregressive correlation structure. Variability of acoustic indices due to the random effects of site was large in all cases, except ACI. In this case, variability due to forest type was much larger than that of site.

The estimate of the model for AEI and biocondition was 0.956 (Table 1) with mean AEI declining as biocondition increased (see

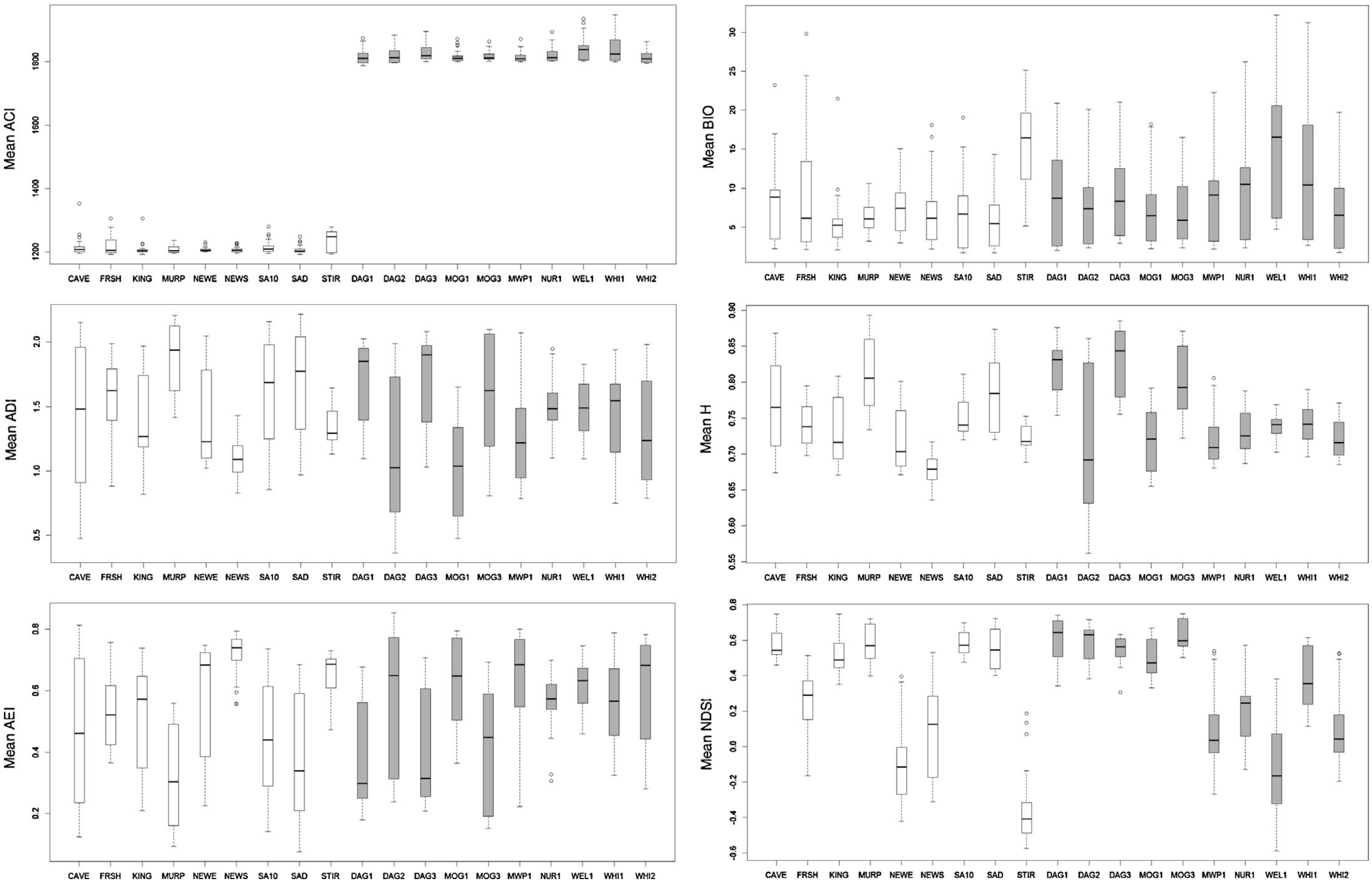

Fig. 2. Boxplots of mean acoustic metrics (y axis) by site (x axis) and forest type (white = scribbly gum, gray = spotted gum).

scatter plots in Supplementary Material 2A). The majority of sites exhibited large variation in AEI across the 24 hourly values, but those with the least variation (STIR, WEL1, NEWS, and NUR1) shared in common small patch size, well below-average biocondition score, and an above average extent of roads.

The estimate of the model for H and biocondition was 0.59 (Table 1). This value was approximately mid-point between a noisy signal ($H = 1$) and a pure tone signal ($H = 0$); as biocondition increased, so did H, but not steeply (see scatter plots in Supplementary Material 2B). The greatest variation in H is observed at very high biocondition sites with no surrounding residential area and a small extent of roads (DAG2, CAVES, MURP, and SAD).

The estimate of the model for NDSI and biocondition was −0.960 (Table 1) and NDSI has the steepest slope (1.699) of the three

Table 1
Linear mixed models between acoustic indices and biocondition. Estimates of fixed effects and their significance; model covariance structure; and model selection ΔAIC are indicated.

Effect	Estimate	Standard error	d.f.	*t*-Value	*p*-Value	Covariance structure	Phi Φ	ΔAIC
NDSI						AR(1) *H*	0.854	−498.08
Intercept	−0.960	0.337	437	−2.845	0.005			
Biocondition	1.699	0.410	17	4.139	0.001			
H						AR(1)	0.926	−667.41
Intercept	0.590	0.066	437	8.943	<0.0001			
Biocondition	0.228	0.082	17	2.788	0.013			
AEI						AR(1)	0.937	−810.39
Intercept	0.956	0.228	437	4.192	<0.0001			
Biocondition	−0.671	0.283	17	−2.372	0.030			
ADI						AR(1)	0.913	−713.76
Intercept	0.983	0.452	437	2.174	0.030			
Biocondition	0.796	0.561	17	1.419	0.174			
BIO						AR(1)	0.796	−407.40
Intercept	12.558	5.014	437	2.504	0.013			
Biocondition	−6.573	6.222	17	−1.056	0.306			
ACI						AR(1)	0.754	−314.46
Intercept	1814.147	495.197	437	3.663	0.000			
Biocondition	−354.704	614.465	17	−0.577	0.571			

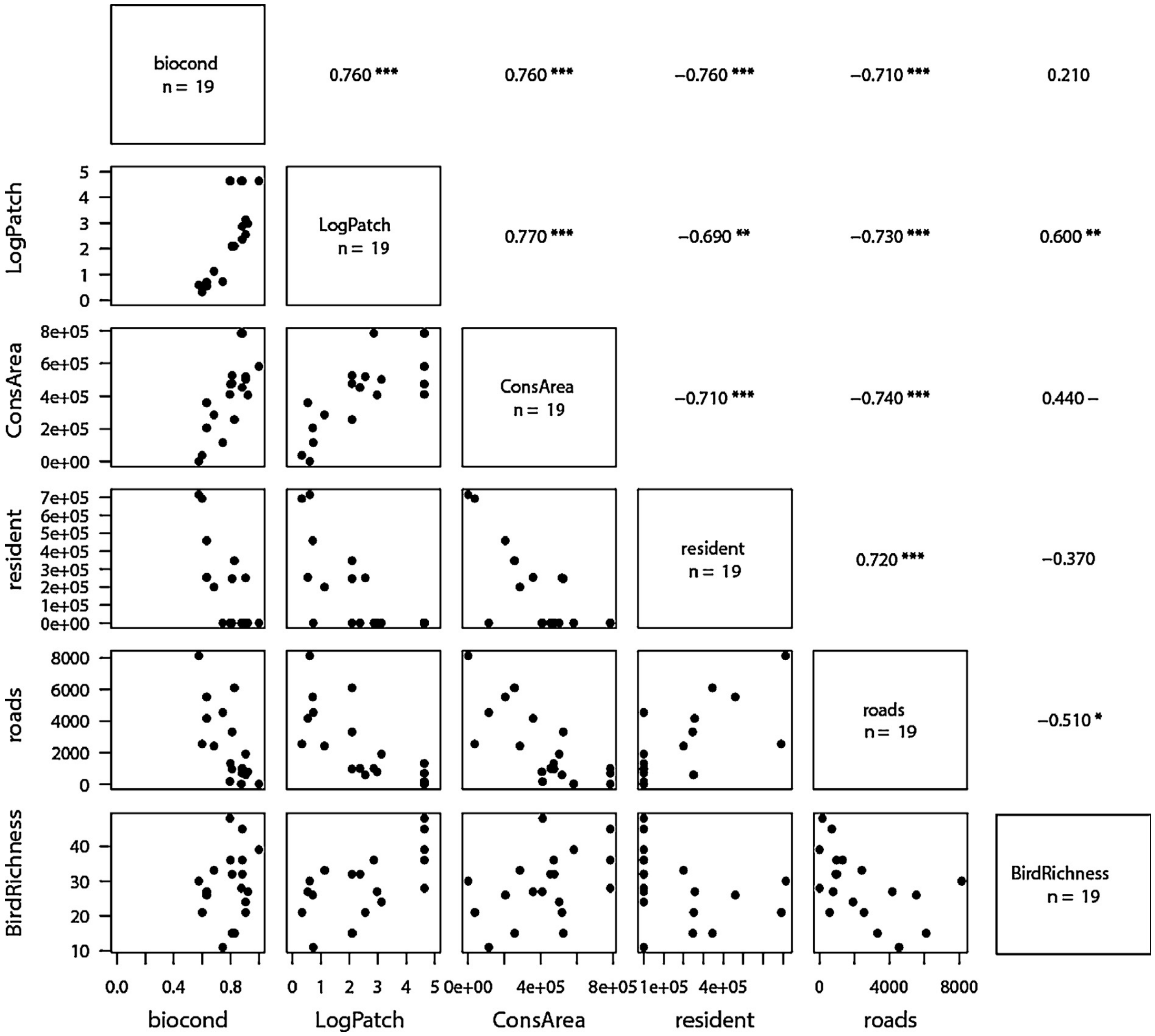

Fig. 3. Scatter plots of landscape metrics, biocondition, and bird species richness. Pearson's correlation coefficient values are shown for each relationship in the upper half of the matrix (significance: ***$p < 0.0001$, **$p < 0.001$, *$p < 0.01$). The diagonal shows the variables and the sample size. Labels: biocond = biocondition score, LogPatch = patch size ($\log_{10}$ ha), ConsArea = conservation area (m^2), resident = residential area (m^2), roads = extent of local roads (m).

significant models (Table 1). There was a strong positive trend between NDSI and biocondition. In addition, there was a clear trend in the variation of NDSI values across the 24 hourly values with low biocondition sites generally exhibiting more variability than high biocondition sites (see scatter plots in Supplementary Material 2C). Some high condition sites (DAG3, MOG1, CAVES, and SA10) exhibited very little variation and these were characterized as having no residential area, and lower than average extend of roads.

Estimates of the fixed effects for best models for bird species richness are displayed in Table 2. Of the six acoustic metrics modeled, two (NDSI and *H*) showed significant relationships with bird species richness. Again, the estimated autocorrelation, phi, was high in all cases confirming the appropriateness of models with autoregressive correlation structure.

The estimate of the model for NDSI and bird species richness was −0.091 (Table 2). Sites with the lowest bird species richness generally exhibited far more variation in NDSI over the 24 h than sites with higher bird species richness (see scatter plots in Supplementary Material 3A). However, four sites with near average bird richness still exhibited high variation in mean NDSI over the 24 h sampling period (WEL1, MWP1, NUR1, and NEWE). These sites were smaller patches than sites with similar or greater bird species richness, and all had a higher than average extent of roads surrounding them.

The estimate of the model for *H* and bird species richness was 0.698; as bird species richness increased, so did *H* (see scatter plots in Supplementary Material 3B). As with biocondition, values of *H* in sites with low bird species richness were more closely clustered than those in sites with higher bird species richness, but mean *H* values were observed across a larger range of bird species richness than biocondition.

4. Discussion

Automated soundscape recording and analysis technologies have the potential to serve as a powerful conservation planning tool for measuring the influence of disturbance, fragmentation and declining ecological condition on biodiversity. While studies have shown that anthropogenic sound has a negative impact on biodiversity (e.g. Bayne et al., 2008; Proppe et al., 2013; Reed and Merenlender, 2008) and that the integration of soundscape and landscape studies can result in improved landscape planning and biodiversity outcomes (Votsi et al., 2012), few studies have explicitly examined the influence of landscape configuration on

Table 2
Linear mixed models between acoustic metrics and bird species richness. Estimates of fixed effects and their significance; model covariance structure; and model selection ΔAIC are indicated.

Effect	Estimate	Standard error	d.f.	*t*-Value	*p*-Value	Covariance structure	Phi Φ	ΔAIC
NDSI						AR(1) *H*	0.85	−498.03
Intercept	−0.091	0.175	437	−0.521	0.603			
Bird richness	0.017	0.006	17	2.960	0.009			
H						AR(1)	0.93	−667.25
Intercept	0.698	0.032	437	22.124	<0.0001			
Bird richness	0.003	0.001	17	2.498	0.023			
AEI						AR(1)	0.94	−812.84
Intercept	0.596	0.112	437	5.327	<0.0001			
Bird richness	−0.006	0.004	17	−1.682	0.111			
ADI						AR(1)	0.92	−713.79
Intercept	1.463	0.216	437	6.780	<0.0001			
Bird richness	0.005	0.007	17	0.768	0.453			
BIO						AR(1)	0.80	−407.40
Intercept	12.558	5.014	437	2.504	0.013			
Bird richness	−6.573	6.222	17	−1.056	0.306			
ACI						AR(1) *H*	0.77	−440.74
Intercept	1320.161	227.051	437	5.814	<0.0001			
Bird richness	7.341	7.496	17	0.979	0.341			

soundscapes. In this study we compared six acoustic indices and found that three indices (NDSI, *H* and AEI) were related to landscape configuration. These indices were also representative of ecological condition and bird species richness.

4.1. Comparison of acoustic indices

Our comparison of the six acoustic indices according to time of day revealed that ACI and BIO presented similar patterns that highlighted a distinct dawn and dusk avian chorus. The ACI and BIO metrics are both calculated based on the change in spectral amplitude (or signal intensity), although the BIO index does not take into consideration sounds in the anthrophony range (0–2 kHz), while ACI does. These indices reflect the intensity of sound in the landscape and have been shown to be correlated with the number of bird vocalizations (Pieretti et al., 2011) and native avian species abundance (Boelman et al., 2007). ACI and BIO both presented very low values during the night; a pattern previously noted by Towsey et al. (2014).

The pattern shown by BIO and ACI was very different to that shown by the diversity indices (*H* and ADI). The high nighttime pattern presented by *H* and ADI may indicate that these indices are sensitive to nocturnal biophony; for example insects, which are abundant at night in warm, subtropical environments. Gasc et al. (2013) reported highest acoustic activity at night in the tropical forests of New Caledonia corresponding to a dominance of Orthoptera. They suggest that indices like ACI would not be sensitive to the constant, sustained acoustic signals produced by Orthoptera (Boulard, 2006) and our results provide support for this hypothesis. The acoustic evenness index (AEI) presented an inverse pattern to *H* and ADI. This was expected given that the Gini coefficient scales as a mirror opposite to the Simpson's index of diversity (Peet, 1974), which is similar to the Shannon index on which *H* and ADI are based.

The NDSI provided a pattern that was broadly a combination of both ACI/BIO and *H*/ADI. High nighttime values of this index reflect high biophony relative to anthrophony, suggesting that like *H* and ADI, there is a high level of nocturnal biophony (insects, amphibians) that is detected during the quiet of night, when there is low anthrophony and other background sounds. According to Krause's acoustic niche partitioning hypothesis, amphibians and insects tend to signal at night to avoid bird predators as the soundscape is a finite resource in which animals compete for spectral space (Krause, 2012). The drop in NDSI just before dawn may likely represent a transition from night signaling species to day signaling species. Clear temporal windows occupied by specific groups (insects at night, distinct dawn and dusk bird choruses) have also been observed in New Caledonian forests (Gasc et al., 2013). The relatively low NDSI values observed throughout the day may also indicate a shift in the ratio of anthrophony to biophony with higher levels of anthropogenic sound increasing throughout the day relative to biological sounds.

With the exception of ACI, there was no significant difference in mean acoustic index values according to forest type and little congruence was found among the six indices across sites. Sites with low mean values for one index did not have low mean values for all the other indices. This was particularly evident at sites that experienced high traffic noise, such as STIR which was located next to a highway and WEL1 which was surrounded by an urban network of local roads. In these instances, NDSI appears to reflect the high level of anthrophony generated by traffic, while the other indices appear to incorporate anthrophony resulting in elevated index values.

4.2. Acoustic index variation relative to landscape configuration and bird species richness

Increasing urbanization is leading to increased habitat fragmentation as remnant vegetation is lost to expanding residential development and forests are dissected by roads and highways. Habitat loss and fragmentation produce a suite of measurable, broad scale changes including increased isolation and edge to area ratios among an increased number of small patches of habitat (Fahrig, 2003; Watson et al., 2005) and changes in the spatial configuration of fragments (Alados et al., 2009). Fragmentation can also impede the dispersal and reproduction of organisms (Addicott et al., 1987), increase the susceptibility of populations to stochastic events (Driscoll et al., 2012) and long term climate change (Opdam and Wascher, 2004) and have acute effects on species diversity, abundance and distribution (Fischer and Lindenmayer, 2006; Ockinger et al., 2012).

Fragmentation and a coincident increase in human activity will have consequences on the soundscape as increased anthrophony coincides with decreased biophony (Pijanowski et al., 2011b). Our mixed model analyses indicated that only three of the tested indices (NDSI, *H* and AEI) provided a good representation of the landscape configuration. There was strong correlation between each landscape metric and biocondition and based on this, biocondition was used as a proxy for the suite of landscape metrics in the mixed models analyses. These analyses revealed a significant positive relationship between NDSI and biocondition, with sites having high levels of anthropogenic sound disturbance and low biophony experiencing low biocondition and increased landscape fragmentation. Similarly, a significant positive relationship was found between H and biocondition. From these results, we conclude that NDSI and H are effective indicators of sites with small patch size, situated near residential areas, and surrounded by a large extent of roads. Likewise, NDSI and H indicate sites with high ecological condition that are not surrounded by residential development and have minimal extent of roads, yet vary widely in patch size. This suggests that the response of these acoustic metrics is not limited strictly to patch size, but rather they differentiate between similar sized sites with different levels of acoustical noise associated with urbanization. Based on our findings, we conclude that the NDSI and H are suitable indices for identifying high condition habitat within human-dominated environments.

AEI was negatively associated with biocondition; high condition habitat was characterized by low acoustic evenness. During times of chorus activity in high condition habitat, one would expect less evenness across frequency bands as signals in the biophony range, especially mid- and high-frequency songbird vocalizations, would exceed signals in the low frequency range of anthrophony. Most sites exhibited high variation in AEI across the 24 h sampling period. However, those sites with low variation were small patches surrounded by a high extent of local roads and therefore, low variation may signify depleted bird fauna at low condition sites affected by urbanization.

Our mixed model analyses also revealed that only two indices, NDSI and H, were significantly associated with bird species richness. While strong, positive relationships for both NDSI and H with bird species richness and biocondition were identified, it is interesting to note that site level differences reveal patterns that would not be seen without plotting site specific effects of the mixed model. For instance, sites that have high NDSI and H values tend to also have high biocondition scores, but this trend does not generally hold for bird species richness. Differences in response of the acoustic metrics between bird species richness and biocondition are not surprising given that biocondition and bird species richness are not correlated, but it suggests that birds are responding more strongly to specific aspects of landscapes that do not necessarily represent the overall condition of the ecosystem. In other words, birds may not be the best taxon to use as a proxy for ecological condition in the landscapes studied in this investigation, as they appear to be responding more strongly to patch size than to a combination of factors that best describe overall ecological condition.

Furthermore, it should be noted that without hourly sampling, it would be impossible to illustrate the variation in acoustic metrics exhibited throughout the day. And yet, this variation appears to be an effective means of discriminating between sites of different ecological condition. Therefore, we strongly recommend that acoustic sampling take place throughout the day and night and that data be collected for at least several days. Acoustic metrics calculated using snapshot data of a day or two may not be representative of ecological condition.

4.3. Conclusions

Our results confirm that the acoustic complexity (ACI) and bioacoustic (BIO) indices are good metrics for the study of avian vocalizations (and reputedly avian abundance; Boelman et al., 2007), but these indices were not related to landscape parameters or any of the biodiversity attributes examined in this study. The three indices that best connected the soundscape with landscape characteristics, ecological condition and bird species richness were acoustic entropy (H), acoustic evenness (AEI) and the normalized difference soundscape index (NDSI). However, caution should be used when interpreting the AEI as it provides an inverse relationship. Although the acoustic diversity index (ADI) is similar in derivation to acoustic entropy (H), it was not significantly associated with any of the attributes that we examined.

This study involved utilizing a landscape condition assessment framework developed in Australia to investigate acoustic metrics. These acoustic indices now need to be tested in temperate, tropical, coastal and arid ecosystems worldwide, using standardized landscape assessment measurements to confirm the importance of landscape factors in driving soundscape patterns. We suggest that investigations need to provide a better understanding of how the acoustic indices are influenced by traffic noise and geophony (e.g. wind and waves) as this will have practical implications for sensor placement. Furthermore, we need to know more about the effect on the metrics of loud versus soft calling species, constant insect humming versus sporadic loud chirps, as well as detection differences and sample radius in different vegetation structures (see Farina and Pieretti (2014) for preliminary work in this area). We also argue that there is need to better understand nocturnal biodiversity. Too often amphibian, insect and avian research is not well integrated, but to understand the soundscape, we need data recorded at all times during the day and night. Clearly, there is much research required before remote soundscape assessment becomes a routine ecological condition monitoring tool. However our results indicate that some of the metrics that are currently publicly available provide a good indication of landscape and biodiversity attributes, but further investigation should be dedicated to refining and/or combining existing acoustic indices and also to determine if these indices are appropriate in other landscapes and for other survey purposes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2015.05.057

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