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# Sounding out Ecoacoustic Metrics: Avian species richness is predicted by acoustic indices in temperate but not tropical habitats

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#### 1 Abstract

2 Affordable, autonomous recording devices facilitate large scale acoustic monitoring and Rapid 3 Acoustic Survey is emerging as a cost-effective approach to ecological monitoring; the success of 4 the approach rests on the development of computational methods by which biodiversity metrics can 5 be automatically derived from remotely collected audio data. Dozens of indices have been proposed 6 to date, but systematic validation against classical, in situ diversity measures are lacking. This study 7 conducted the most comprehensive comparative evaluation to date of the relationship between avian 8 species diversity and a suite of acoustic indices. Acoustic surveys were carried out across habitat 9 gradients in temperate and tropical biomes. Baseline avian species richness and subjective multi-taxa 10 biophonic density estimates were established through aural counting by expert ornithologists. 26 11 acoustic indices were calculated and compared to observed variations in species diversity. Five 12 acoustic diversity indices (Bioacoustic Index, Acoustic Diversity Index, Acoustic Evenness Index, 13 Acoustic Entropy, and the Normalised Difference Sound Index) were assessed as well as three 14 simple acoustic descriptors (Root-mean-square, Spectral centroid and Zero-crossing rate). Highly 15 significant correlations, of up to 65%, between acoustic indices and avian species richness were 16 observed across temperate habitats, supporting the use of automated acoustic indices in biodiversity 17 monitoring where a single vocal taxon dominates. Significant, weaker correlations were observed in 18 neotropical habitats which host multiple non-avian vocalizing species. Multivariate classification 19 analyses demonstrated that each habitat has a very distinct soundscape and that AIs track observed 20 differences in habitat-dependent community composition. Multivariate analyses of the relative 21 predictive power of AIs show that compound indices are more powerful predictors of avian species 22 richness than any single index and simple descriptors are significant contributors to avian diversity 23 prediction in multi-taxa tropical environments. Our results support the use of community level 24 acoustic indices as a proxy for species richness and point to the potential for tracking subtler habitat-25 dependent changes in community composition. Recommendations for the design of compound 26 indices for multi-taxa community composition appraisal are put forward, with consideration for the 27 requirements of next generation, low power remote monitoring networks. 28

*Keywords*: Biodiversity Monitoring, Remote Sensing, Ecoacoustics, Acoustic Indices, Species
 Richness

#### 31 **1. Introduction**

32 Numerous global initiatives aim to conserve biodiversity (e.g. United Nations Sustainable

33 Development Goals, Convention on Biological Diversity AICHI biodiversity targets, REDD++), but

action can only be effectively taken if biodiversity can be measured and its rate of change quantified
(Buckland, Magurran, Green, & Fewster, 2005). Coupled with rapid changes in landscape use (Betts
et al., 2017; Newbold et al., 2015) the impact of climate change (Stocker et al., 2013) and growing
fragmentation of natural landscapes globally (Crooks et al., 2017), the development of cost effective
methods for biodiversity monitoring at scale is an urgent global imperative (Newbold et al., 2015).

#### 39 1.1 Ecoacoustics and Rapid Acoustic Survey

40 Operating within the conceptual and methodological framework of ecoacoustics (Sueur & Farina, 2015) Rapid Acoustic Survey (RAS) (Sueur, Pavoine, Hamerlynck, & Duvail, 2008) has been 41 42 proposed as a non-invasive, cost-effective approach to Rapid Biodiversity Assessment (Mittermeier & Forsyth, 1993) and is gaining interest from researchers, decision-makers and conservation 43 44 managers alike. Whereas bioacoustics infers behavioural information from intra- and interspecific 45 signals, ecoacoustics investigates the ecological role of sound at higher organisational units - from 46 population and community up to landscape scales. Sound is understood as a core ecological component (resource) and therefore indicator of ecological status (source of information). Rather 47 48 than attempting to identify specific species calls, RAS aims to infer biodiversity at these higher 49 levels of organization, through the collection and computational analysis of large scale acoustic 50 recordings. RAS is a highly attractive solution for large scale monitoring, because it is noninvasive, obviates the need for expert aural identification of individual recordings, scales cost-51 52 effectively and is potentially sensitive to multiple taxa. This approach has potential to dramatically 53 improve remote biodiversity monitoring, enabling data collection and analysis over previously 54 inaccessible spatio-temporal scales, including in remote, hostile, delicate regions in both terrestrial 55 and marine environments. The success of the approach rests on the development and validation of 56 computational metrics, or acoustic indices, which demonstrably predict some facet of biodiversity.

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- 58

#### 59 1.2 Acoustic Indices for Biodiversity Monitoring



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Fig. 1 The acoustic environment, or soundscape, is comprised of sounds made by noisy biotic and abiotic processes, including biological organisms (biophony), geological forces (geophony) and humans and machines (anthrophony/ technophony). Acoustic indices provide terse numerical descriptions of the overall soundscape. The use of acoustic indices as a proxy for biodiversity is predicated on the assumption firstly that the acoustic community of vocalising creatures is representative of the wider ecological community and secondly that the facets of soundscape dynamics captured by acoustic indices are ecologically-meaningful. The current working hypothesis is that higher species richness will generate greater acoustic diversity; a suite of indices aimed at capturing spread and evenness of acoustic energy have been proposed but have yet to be conclusively validated against traditional, in situ biodiversity metrics.

61

62 Whereas classical biodiversity indices are designed to enumerate some facet of biotic community 63 diversity at a particular time and place - richness, evenness, regularity, divergence or rarity in species abundance, traits or phylogeny (Magurran, 2013; Magurran & McGill, 2011; Pavoine & Bonsall, 64 2011) - acoustic indices are designed to capture the distribution of *acoustic energy* across time and/or 65 frequency in a digital audio file of fixed length. As illustrated in Fig. 1, the use of acoustic indices 66 (AIs) as ecological indicators is predicated firstly on the assumption that the *acoustic community* 67 (Gasc et al., 2013) is representative of the wider ecological community at the place and time of 68 69 interest; and secondly that computationally measurable changes in the acoustic environment are 70 ecologically relevant. An effective index will reflect ecologically meaningful changes in the acoustic 71 community, whilst being *insensitive* to potentially confounding variations in the wider acoustic 72 environment - or soundscape (Pijanowski et al., 2011). Whilst there is an established tradition of 73 aural survey of individual species (as in point counts), ecoacoustics aims to develop the study and

theory of population, community or landscape level bioacoustics. The prevailing predicate of RAS is
that higher species richness in a given community will produce a greater 'range' of signals, resulting
in a greater *acoustic diversity* (Gasc et al., 2013; Sueur, Farina, Gasc, Pieretti, & Pavoine, 2014a;
Sueur et al., 2008).

78 Based on this premise, indices to measure within-group (alpha) and between-group (beta) indices 79 have been proposed (Sueur et al., 2014b). The current concern is validation against traditional metrics derived from species counts, therefore we focus on alpha indices. These are designed to 80 81 estimate amplitude (intensity), evenness (relative abundance), richness (number of entities) and 82 heterogeneity of the acoustic community. A suite of indices was made available via R packages 83 seewave [1] (Sueur et al., 2008) [1] and soundecology [2] (Villanueva-Rivera, Pijanowski, Doucette, 84 & Pekin, 2011) and has been rapidly taken up in ecological research – the libraries exceeding 61,000 85 downloads since 2012. However, experimental investigation of the relationship between these, and 86 other acoustics metrics, with traditional, in situ biodiversity measures reveals mixed, and at times 87 contradictory results (Boelman, Asner, Hart, & Martin, 2007; Fuller, Axel, Tucker, & Gage, 2015; 88 Mammides, Goodale, Dayananda, Kang, & Chen, 2017). Furthermore, simulation studies (Gasc et 89 al., 2013) demonstrate that acoustic diversity can be influenced by sources of acoustic heterogeneity 90 other than species richness, including variation in distance of animals to the sensors, and inter- and 91 intra-specific differences in calling patterns and characteristics (e.g. duration, intensity, complexity 92 of song, mimicry). The premise that biodiversity can be inferred from acoustic diversity is percipient 93 but not fully substantiated: before these proposed indices can be confidently adopted for monitoring 94 purposes, it is critical to understand i) how well AIs capture ecologically meaningful changes in 95 community composition and ii) how robust they are to diverse ecological, environmental, and 96 acoustic conditions. To this end, this study carried out the largest systematic, comparative study of 97 the relationship between acoustic indices and observed avian diversity to date.

98

#### 99 **1.3 Acoustic Indices**

#### 100 1.3.1 Ecologically inspired diversity indices

101 Early research led to the development of indices derived from landscape metrics (Turner, 1989) to 102 measure changes at the level of soundscape (Gage, Napoletano, & Cooper, 2001; Napoletano, 2004). 103 The Normalised Difference Sound Index (NDSI) (Kasten, Gage, Fox, & Joo, 2012) seeks to describe 104 the level of anthropogenic disturbance by calculating the ratio of mid-frequency biophony to lower 105 frequency technophony in field recordings, the values for each being computed from an estimate of 106 power density spectrum (Welch, 1967). In long term studies, the NDSI has been shown to reflect 107 assumed seasonal and diurnal variation across landscapes (Kasten et al., 2012). It has subsequently 108 been shown to be sensitive to biophony and anthrophony levels in urban areas (Fairbrass, Rennett, 109 Williams, Titheridge, & Jones, 2017) and to be an indicator of anthropogenic presence in the 110 Brazilian Cerrado (Alquezar & Machado, 2015). NDSI has also been evaluated as a proxy for 111 species diversity with mixed results: significant relationships with bird species richness have 112 reported across mixed habitats in China (Mammides et al., 2017); in Brazilian savanna habitats no 113 relationships were observed (Alquezar & Machado, 2015).

114 Based on the foundational premise that biodiversity can be inferred from acoustic diversity. 115 several indices draw an analogy between species distribution and distribution of energy in a 116 spectrum, where each frequency band is seen to represent a specific 'species'. The entropy indices 117 Hf and Ht (Sueur et al., 2008) are calculated as the Shannon entropy of a probability mass function 118 (PMF) and designed to increase with species diversity. For Hf the PMF is derived from the mean 119 spectrum, for Ht from the amplitude envelope. Their product is H. Early studies reported higher 120 values for intact over degraded tropical forests (Sueur et al., 2008), but subsequent testing in a 121 temperate woodland reported contradictory results, attributed to background technophonies 122 (Depraetere et al., 2012). H has since been reported to show positive, moderate correlations with 123 avian species richness across multiple habitats in China (Mammides et al., 2017) and a variant of Ht 124 (Acoustic Richness) was shown to be positively associated with observed species richness

(Depraetere et al., 2012). These entropy and evenness measures encapsulate the foundational
assumption of RAS, but are not intuitive to interpret.

127 The Acoustic Evenness and Acoustic Diversity Indices (AEI, ADI) are motivated by a similar 128 analogy between species distribution and distribution of sound energy. Both are calculated by first 129 dividing the spectrogram into N bins across a given range (typically 0 - 10 kHz) and taking the 130 proportion of signal in each bin above a set threshold. ADI is the result of the Shannon Entropy (Jost, 131 2006) applied to the resultant vector; AEI is the Gini coefficient (Gini, 1971), providing a measure of 132 evenness. These were originally developed to assess habitats along a gradient of degradation under 133 the assumption that ADI and AEI would be respectively positively and negatively associated with 134 habitat status as the distribution of sounds became more even with increasing diversity (Villanueva-135 Rivera et al., 2011): ADI was shown to increase from agricultural to forested sites; AEI was shown 136 to decrease over the same gradient, as expected. Negative, if weak, associations between AEI and 137 biocondition (Eyre et al., 2015) have subsequently been corroborated (Fuller et al., 2015) and a 138 significant positive association between ADI and avian species richness has been reported in the 139 savannas of central Brazil (Alquezar & Machado, 2015).

140 Rather than applying extant ecological metrics to acoustic data, other ecoacoustic indices 141 have been designed more intuitively; the Bioacoustic Index (BI) was designed to capture overall 142 sound pressure levels across the range of frequencies produced by avifauna (Boelman et al., 2007). 143 BI was originally reported to correlate strongly with changes in avian abundance in Hawaiian forests 144 (Boelman et al., 2007), but subsequent assessments have been mixed, showing significant 145 association with avian species richness (Fuller et al., 2015) and both positive and negative weaker 146 correlations (Mammides et al., 2017) in areas with multiple vocalizing taxa. Despite an initially 147 strong demonstration of efficacy, and conceptual and computational simplicity, this index has been 148 excluded from many recent analyses (Harris, Shears, & Radford, 2016). In response to observations 149 that many of these indices are over-sensitive to 'background' noise, the Acoustic Complexity Index 150 (ACI) was developed (Pieretti, Farina, & Morri, 2011). ACI reports short-time averaged changes in

151 energy across frequency bins, with the aim of capturing transient biophonic sounds, whilst being 152 insensitive to more continuous technophonies such as airplanes and other engines. ACI has been 153 reported to correlate significantly with the number of avian vocalisations in an Italian national park 154 (Pieretti et al., 2011), with observed species evenness and diversity in temperate reefs (Harris et al., 2016) and to be positively related to observed changes in migratory avian species numbers in a 155 156 multi-year Alaskan study (Buxton, Brown, Sharman, Gabriele, & McKenna, 2016). A recent urban study reports correlations between ACI and biotic activity and diversity, as well as anthrophonic 157 158 signals (Fairbrass et al., 2017), as expected, given the full range analyses carried out. 159 1.3.2 Machine learning derived indices 160 In contrast to these relatively simple indices, more sophisticated supervised and unsupervised 161 machine learning methods have also been proposed (Phillips, Towsey, & Roe, 2018; Towsey, 162 Wimmer, Williamson, & Roe, 2014). In a single site comparative study (Towsey et al., 2014) 163 describe a spectral clustering algorithm which is shown to be the strongest indicator of species 164 number, outperforming many of the indices described above. In previous work (Eldridge, Casey, 165 Moscoso, & Peck, 2016; Guyot et al., 2016) we have suggested that more complex analyses that 166 operate in time-frequency (rather than time or frequency) domain are necessary in order to rigorously investigate the dynamic composition of acoustic environments. However, in applied 167 168 monitoring tasks, we are primarily concerned with cost-effectiveness, validity and reliability across

169 ecological conditions. Looking toward future application of *in situ* analyses, efficiency in

170 computational and logistical terms become important factors; with this in mind it becomes pertinent

171 to consider how new ecological acoustic metrics might take inspiration from machine listening

172 applications in other domains.

173 *1.3.3 Simple acoustic descriptors* 

As micro-processors become smaller, cheaper and more powerful and techniques for data transfer in low-power networks of embedded systems advance, the possibility for *in situ* computation becomes very real. This could be very useful for long-term applications where collection and storage of raw

177 audio data is unreasonable, such as phenology monitoring. Under this emerging protocol, 178 computational efficiency of AIs becomes more important as lower computational cost equates to 179 lower energetic cost, or energy complexity (Zotos, Litke, Chatzigeorgiou, Nikolaidis, & Stephanides, 180 2005); reducing energetic cost could afford the development of networks of solar-powered devices, 181 further increasing feasibility of long term monitoring in remote locations. Machine learning methods 182 are too computationally intensive for these situations and we look instead to parsimonious solutions 183 which are computationally and energetically cheap. A large body of research in machine listening in 184 music, speech and non-ecological environmental sound analyses demonstrates the power of simple 185 acoustic descriptors in automated classification tasks. Here we select three to test alongside the suite 186 of existing ecoacoustic diversity indices. These provide information about amplitude, spectral, and 187 temporal characteristics: Root-mean-square (RMS) of the raw audio signal, spectral centroid (SC)

188 and zero-crossing rate (ZCR), described below.

189 The root-mean-square (RMS) of the raw audio signal gives a simple description of signal 190 amplitude; RMS has been demonstrated to track ecologically-relevant temporal and spatial dynamics 191 in forest canopy (Rodriguez et al., 2014), and shown to be strongly positively correlated with 192 percentage of living coral cover in tropical reefs (Bertucci, Parmentier, Lecellier, Hawkins, & 193 Lecchini, 2016), but has not been investigated in recent terrestrial correlation studies. Mean values 194 are expected to increase with acoustic activity, variance may more accurately track avian 195 vocalisations under the same logic as ACI. Spectral centroid provides a measure of the spectral 196 centre of mass; it is widely used in machine listening tasks where is it recognized to have a robust 197 connection with subjective measures of brightness. This and related spectral indices have been 198 shown to be effective in automated recognition of environmental sounds in urban environments 199 (Devos, 2016). Zero-crossing rate (ZCR) is one of the simplest time-domain features, which in 200 essence reflects the rate at which sound waves impact on the microphone. ZCR provides a measure 201 of noisiness (being high for noisy, low for tonal sounds) and is widely used in speech recognition 202 and music information retrieval, for example as a key feature in the classification of percussive

sounds (Gouyon, Pachet, & Delerue, 2002). SC and ZCR have been demonstrated to be useful
descriptors in classification of habitat type (Bormpoudakis, Sueur, & Pantis, 2013), but have yet to
be evaluated as proxies for species diversity. We expect a negative association with avian activity for
both: relative to the quiet broad-band noise of inactivity, avian vocalisations are predicted to be of
lower frequency and more harmonic, resulting in a lower spectral centroid and zero-crossing rate.
We might also expect the variance of each to positively track activity as the onsets of avian calls will
cause rapid changes in values.

210

#### 211 **1.4 Validation Requirements**

To assess the potential for these indices as ecological indices, explicit comparison with established biodiversity metrics is a critical first step (Gasc, Francomano, Dunning, & Pijanowski, 2017). In order to validate the near-term application of existing AIs in monitoring tasks and to inform the development of more effective indices for the future, we suggest at least three experimental conditions are necessary: i) *variation in ecological conditions* ii) *spatial and or temporal replication* iii) *comparisons between individual indices as well as compound metrics*.

218 Any ecological indicator must be demonstrably robust to variation in ecological conditions. For 219 acoustic indices, this includes variations in habitat structure, which affects signal propagation, as 220 well as heterogeneity of acoustic environment due to non-biotic sound sources (anthrophony and 221 geophony) and crucially, the diversity and density of vocalising taxa. The impact of environmental 222 dissimilarity on correlations between the diversity indices and avian species richness was recently 223 shown to be non-significant (Mammides et al., 2017). Responding to recognition that existing 224 indices are known to be sensitive to 'background' noise (Depraetere et al., 2012), Fairbrass et al., 225 (2017) compared the response of four AIs (ACI, BI, ADI, and NDSI) in urban environments and 226 demonstrated that all were sensitive to anthrophony, questioning their application in urban areas 227 (Fairbrass et al., 2017). Although understanding the performance of AIs in environments with 228 varying diversity and density of vocalising taxa is fundamental, few studies have explicitly addressed

229	this. Recent correlation studies have focused on avian species richness alone, without tracking other
230	taxa, despite being carried out in tropical environments characterised by high insect and amphibian
231	activity (Alquezar & Machado, 2015; Fuller et al., 2015; Mammides et al., 2017). This makes
232	interpretation of results difficult. Where other multiple taxa have been considered, the focus has
233	generally been on identifying and removing specific categories of sound, such as cicada choruses
234	(Towsey et al., 2014). Correlation studies to date have also been predominantly carried out at the
235	peak activity of dawn chorus (Boelman et al., 2007; Mammides et al., 2017), which is a
236	demonstrably efficient sampling strategy (Wimmer, Towsey, Roe, & Williamson, 2013), but
237	precludes investigation of the response of AIs to variation in vocalization density.
238	Carrying out spatially and/or temporally replicated surveys is important because existing
239	indices are known to be sensitive to local differences in vocalisation patterns (Gasc et al., 2013;
240	Sueur et al., 2014b). If there are strong community level differences in acoustic communities we
241	might expect that as survey size increases, the effect of local variation in individuals, species,
242	vegetation structure or other acoustic events will decrease, cancelling out as noise.
243	Finally, <i>comparative</i> studies are vital because no single index is likely to give complete and
244	reliable information about the diversity and state of any given ecosystem - just as no single
245	biodiversity index will reliably estimate all levels of local or regional biodiversity (Sueur et al.,
246	2014b). Towsey et al. (2014) provided a thorough investigation of multiple indices relative to a
247	comprehensive avifauna census dataset and showed that a linear combination can be more powerful
248	than any single index, however they also note that their results are over-fitted, and do not generalise
249	to other habitats, further stressing the importance of multi-habitat studies. Similarly, more recent
250	research evaluating indices directly against observed species diversity in terrestrial (Alquezar &
251	Machado, 2015; Mammides et al., 2017), aquatic (Harris et al., 2016) and urban (Fairbrass et al.,
252	2017) contexts conclude that whilst the approach holds promise, no single index can yet be reliably
253	adopted as a proxy for biodiversity. These studies have tended to focus on small sets of indices and
254	been carried out in a constrained set of biomes: the requisite comparative correlation study across

habitats which support diverse acoustic communities and acoustic density gradients has yet to beperformed.

257	Here we carry out a systematic, comparative analysis of AIs across a wide range of	
258	ecological conditions in both temperate and neotropical ecozones. The principle aim was to evaluate	
259	the response of a range of acoustic indices to observed changes in avian diversity, across a range of	
260	ecological conditions, in order to both evaluate current indices as ecological indicators and to inform	
261	the design of future indices suitable for low power devices. To this end, the suite of diversity indices	
262	proposed in Sueur et al. (2014b) were compared with parsimonious acoustic descriptors commonly	
263	used in other machine listening tasks.	
264	Two principle questions were addressed:	
265	i) Do existing AIs track observed differences in avian diversity?	
266	ii) Are compound indices more powerful predictors of avian species diversity than any single	
267	index?	
268	Two meta questions applied to both:	
269	- How does the presence of other vocalising species impact these relationships?	
270	- How do simple acoustic descriptors compare to bespoke ecoacoustic diversity indices?	
271		
777	2 Methods	
212	2. Memous	
273	2.1. Study Sites	
274	Acoustic surveys were carried out along a gradient of habitat degradation (1 forested, 2 regenerating	
275	forest and 3 agricultural land) in South East (SE) England and North Western (NW) Ecuador. The	
276	six sites (UK1, UK2, UK3, EC1, EC2, EC3) were sampled consecutively from May 6th - Aug 25th	
277	2015.	
278	All UK sites were in the county of Sussex, in SE England, an area of weald clays (Fig. 2, left) and	

279 included ancient woodland (UK1), regenerating farmland with patches of woodland (UK2) and a

- downland barley farm (UK3). Ecuadorian sites (Fig. 2, right) were situated in the NW of the country
- and included primary forest (EC1), secondary forest (EC2) and palm oil plantation (EC3). See
- supplementary material A for details.

283

Fig. 2. Locations of sampling sites in the UK (left) and Ecuador (right): Forest Site, UK1 (N 50° 55' 16.763'' E 0°5' 23.071''); Secondary Forest,
UK2 (N 50° 58' 8.548'' W 0° 22' 40.646''); Agricultural site, UK3 (N 50° 58' 8.548'' W 0° 22' 40.646''. Primary Forest, EC1, (N 0° 32' 17.628''
W 79° 8' 34.728''); Secondary Forest, EC2 (N 0° 7' 12.320'' W 9° 16' 37.103'') Agricultural, EC3 (N 0° 7' 48.864'' W 79° 12' 59.543''

#### 287 2.2. Acoustic Survey Methods

288 Ten day acoustic surveys were carried out consecutively at each study site using 15 Wildlife 289 Acoustics Song Meter audio field recorders. Sampling points were arranged in a grid at a minimum distance of 200 m to minimise pseudo replication (the sound of most species being attenuated over 290 291 this distance in all biomes). Altitudinal range of sample points across sites was minimised in order to 292 prevent introduction of extraneous, confounding gradients. UK sites were within an elevational range 293 of 10 m - 50 m and Ecuador 130 m - 390 m. Recording schedules captured 1 min every 15 min 294 around the clock for 10 days at each site, resulting in 960 stereo recordings at each of 15 sample 295 points for 3 habitat types in 2 different climates (86,400 1 minute stereo recordings in total). Data 296 across the 15 sample points was pooled; inter-site variation was not explored in the current analyses. 297 In the UK 3<sup>1</sup>/<sub>2</sub> hours of each dawn chorus was sampled starting at 1 hour before sunrise. This range 298 was determined to capture the onset, progression and peak of the dawn chorus, creating a temporal

299	gradient. The equatorial dawn chorus is more compact and was sampled for 2 <sup>1</sup> / <sub>4</sub> hours starting 15
300	mins before sunrise, capturing a comparable chorus onset and peak.

The Song Meter is a schedulable, off-line, weatherproof recorder, with two channels of omnidirectional microphone (flat frequency response between 20 Hz and 20 kHz). Seven SM2<sup>+</sup> and eight SM3 devices were deployed. Gains were matched between models (analogue gains at +36 dB on SM2<sup>+</sup> and +12 dB on SM3 which has inbuilt +12 dB gain) and recordings made at resolution of 16 bits with a sampling rate of 48 kHz.

Local weather was recorded for each site using Met Office data from the nearest station in the UK (max 20 km distance) and a portable weather station located within 1 km of each study site in Ecuador. These data were used to select a subset of 3 consecutive days based on lowest wind speeds and rainfall for each habitat.

#### 310 **2.3.** Avian species identification and soundscape descriptors

In both ecozones all 15 survey points for each habitat were analysed over the 3 day subset for each of the 3 habitat types in both ecozones, giving a total of 2025 UK files (15 samples for each dawn over 3 days for 15 points for 3 sites) and 1350 Ecuadorian files (10 samples at dawn over 3 days for 15 sample points across 3 habitats). Stereo files were split and the channel with least distortion (due to wind, rain or faults) for each habitat type was preserved.

316 These data subsets (2025 mono files for the UK and 1350 for Ecuador) were labelled with 317 avian species and soundscape descriptors by ornithologists. Files were anonymised, randomised and 318 presented to ornithologists expert to each ecozone (Joseph Cooper in the UK and Manuel Sanchez in 319 Ecuador) who established vocalising species richness (N0) values by identifying each avian species 320 heard in each minute file; an abundance proxy (NN) was achieved by recording the maximum 321 number of simultaneous vocalisations heard for each species. Their labels were verified by a second 322 expert for each ecozone (Penny Green in the UK and Jorge Noe Morales in Ecuador) who each 323 listened to a randomized 10% of the labelled files for their respective ecozone. Pearson's correlation

coefficient on species richness between these verified subsets showed acceptable agreement (R = 0.85 for UK and 0.77 for Ecuador). Species ID from recording has recently been shown to be more powerful than traditional *in situ* point count, despite the loss in visual registers, and adopted here to ensure compatibility with acoustic computational methods (Darras et al., 2017).

In order to establish the presence of other vocalizing species and enable comparison of 328 329 indices with overall activity of the acoustic community, a subjective measure of *biophonic density* 330 (BD) was recorded in the range 0-3, describing the percentage of time vocalisations of specific taxa occurred across each 1 min sample (0-25%, 25-50%, 50-75% and 75-100%). In the UK biophonic 331 332 density included only avian calls; in Ecuador avian, amphibian and insect vocalisations were logged 333 separately and combined (averaged) to provide an indication of the contribution of non-avian taxa to 334 the acoustic community. Ordinal descriptors of rain, wind, motor noise, human and 'other' sounds 335 were also recorded and assigned a value in the range 0-4 to describe the level of other soundscape 336 components. See supplementary material B for instructions given to ornithologists.

#### 337 **2.4. Filtering and screening**

338 All recordings were pre-processed with a high pass filter (HPF) with a cut off of 300 Hz (12 dB). 339 Pre-processing recordings with a high pass filter (HPF) at 1 kHz is common as low frequency energy 340 is often considered difficult to interpret, being affected by atmospheric noise (Napoletano, 2004); we 341 reduced the threshold in order to minimise loss of relevant low frequency biophony of Ecuadorian 342 species. The HPF also rectified a variable DC offset inherent in the SM3 machines. The main 343 analyses focused on the files which had been listened to by the ornithologists. Of these, files labelled as distorted by wind, rain or electrical fault (assigned values of 4) were dropped from the main 344 345 analyses, leaving 1976 and 1201 samples for UK and Ecuador respectively. This data set, henceforth 346 the labelled data set, was used for the main analyses.

#### 347 **2.5. Acoustic Indices**

Seven of the core indices included in R libraries *Seewave* and *Soundecology* were investigated from five categories (ACI, ADI & AEI, BI, Hf & Ht, NDSI) along with three simple low level acoustic descriptors (RMS, SC, ZCR). Acoustic Richness was not used as it is a ranked index, obviating inclusion in correlation analyses where each record is treated as a statistical individual. Indices were calculated across 0-24 kHz for each 1 minute file otherwise stated.

Acoustic Complexity Index (ACI) (Pieretti et al., 2011) is calculated as the average absolute
 fractional change in spectral amplitude (across 0.3-24 kHz) for each frequency bin in consecutive
 spectrums. The main ACI value is the average value over 1 minute using default parameters (J = 5
 bins per second).

Acoustic Diversity Index (ADI) and Acoustic Evenness Index (AEI) (Villanueva-Rivera et
al., 2011) are calculated by first dividing a spectrogram into 10 bins (min-max 0-10 kHz),
normalizing by the maximum, and taking the proportion of the signals in each bin above a
threshold (-50 dBFS). AD is the result of the Shannon Entropy of the resultant vector; AE is the
Gini coefficient, providing a measure of evenness.

Bio-acoustic Index (BI) (Boelman et al., 2007) is calculated as the area under the mean
 spectrum (in dB) minus the minimum dB value of this mean spectrum across the range 2-8 kHz.
 Spectral and Temporal Entropy (Hf and Ht) (Sueur et al., 2008) are calculated as the
 Shannon entropy of a probability mass function (PMF). For Hf the PMF is derived from the mean
 spectrum, for Ht from the amplitude envelope.

367 5. Normalised Difference Sound Index (NDSI) (Kasten et al., 2012) is the ratio (biophony anthrophony) / (biophony + anthrophony). The values for each are computed from an estimated
power spectral density using Welch's method (win = 1024) where anthrophony is the sum of energy
in the range 1-2 kHz and biophony across 2-11 kHz.

371 6. **Root-Mean-Square** (RMS) is calculated by taking the root of the mean of the square of 372 samples in each frame (N = 512).

3737.Spectral Centroid (SC) (Peeters, 2004) is calculated as the weighted mean of the

frequencies present in the signal, per frame, determined from an SSFT where the weights are themagnitudes for each bin.

376 8. Zero-Crossing Rate (ZCR) (Peeters, 2004) is the number of times the time domain signal
377 value crosses the zero axis, divided by the frame size.

378

379 Calculations were carried out using a bespoke python library to facilitate rapid computation [3].

380 Indices in categories 1-5 were based on implementations in the *seewave* library (Sueur et al., 2008)

381 [1] and soundecology [2] R packages; results from the python library were validated experimentally

382 to ensure absolute equivalence with the R packages. For indices in categories 2-5 a single value was

383 calculated for each 1 minute file. Indices based on frequency analyses (1-5, 7) were calculated from

a spectrogram computed as the square magnitude of an FFT using window and hop size of 512 and

385 256 frames respectively. Indices based on short sections (frames) of audio (1, 6, 7, 8) were

calculated for 512 samples. Mean, variance, median, minimum or maximum are recognized to track
different facets of the acoustic environment; each of these 5 statistical variants were calculated for

388 frame-based indices (ACI, SC, RMS and ZCR) giving a total of 26 indices.

389

#### 390 **2.6 Baseline Avian Diversity**

Baseline community measures of diversity and abundance (Santini et al. 2016) were calculated for
the subset of labelled data. Avian, amphibian and insect densities were compared per habitat type
and registers of other vocalizing species recorded.

394

395 2.7 Statistical Analyses

396 2.7.1 Do AIs track changes in avian diversity?

Three aspects of avian diversity were evaluated i) changes in species richness and abundance across
sample points; ii) diurnal variation in vocalization density; iii) habitat dependent variation in
community composition.

400 Correlation Analyses (Q1 a): To test the relationship between each of the AIs, and avian species
401 diversity and biophonic diversity across all sample points, two-tailed Spearman's rank correlations
402 were carried out between each of the 26 AIs, species richness, species abundance and biophonic
403 density (BD). In line with previous research (Mammides et al., 2017) species richness (N0) was seen
404 to correlate strongly with abundance (NN) in both ecozones, presumably due to short survey times,
405 so further analyses were carried out using N0 only.

406

407 Time series plots (Q1 b): In order to observe how AIs relate to a gradient of vocal community 408 density, time series plots of the full data set were made; AI values (1 min every 15) for each channel 409 over each of the 10 sampling days were calculated and plotted relative to dawn for each of the 15 410 sample sites at each habitat (28,800 values per habitat per ecozone).

411 **Multivariate Classification (Q1 c)**: To evaluate whether AIs reflect observed differences in 412 community composition *between* habitats, clustering analyses were performed on species abundance 413 data and AIs for the labelled data (UK = 1976, EC = 1201). A multivariate random forest classifier 414 (MRF) (Breiman, 2001) was built for each ecozone, with habitat type as response and either species 415 relative abundance (EC = 90, UK = 65) or AI (n=26) as predictors. The out of bag (OOB) error rate 416 gives the MRF predictive power and OOB confusion matrices obtained from the MRF predictor. 417 Error rates are taken as a measure of how distinct each habitat is, in terms of either avian community

419

418

#### 420 **2.7.2** Are compound indices more powerful than any single metric?

#### 421 Multivariate Regression Analyses (Q2)

composition or acoustic environment.

422 To test whether compound indices are more powerful predictors of avian species richness than any 423 single AI, and to investigate the *relative* contributions of each, a multivariate random forest 424 regression model was built for each ecozone using all 26 AIs as predictors and species richness as 425 the response. Nine AIs were used at each split with a minimum terminal node size of 10. AIs and species richness values were first standardised ( $\mu$ = 0,  $\sigma$ = 1). Random forests (Breiman, 2001) are 426 427 not parsimonious, but use all available variables in the construction of a response variable. For each 428 variable we examined two metrics: the minimum depth of each variable in the tree, as a proxy for 429 relative predictive importance (Ishwaran, Kogalur, Gorodeski, Minn, & Lauer, 2010) and the partial 430 effect of each variable to understand its relationship to the response variable (i.e. removing the 431 effects of interactions) (Friedman, 2001), this provided a means to assess relative contributions of 432 AIs in predicting species diversity. Although error rates plateaued around 250 trees, a full 1000 433 strong forest was generated in order to allow predictors to stabilize. Models were constructed using 434 the randomForestSRC package in R 3.3.3 (minimum terminal node size 10, 9 variables tried at each 435 split). Results were plotted using ggplot2 (Wickham, 2009).

#### 436 **3. Results**

437 3.1 Measures of acoustic diversity: Avian species richness and multi-taxa biophonic density 438 A total of 65 avian species were registered in the UK (52 in UK1, 61 in UK2 and 49 in UK3) and 83 439 in Ecuador (53 in EC1, 69 in EC2 and 58 in EC3). Per sample site avian species richness (Fig. 3) 440 followed the same pattern, with medians being highest in the secondary habitats of both ecozones 441 and lowest in the agricultural site for UK and the primary forest for Ecuador (Fig. 3). Subjective 442 ratings of biophonic density per species (Fig. 4) show the same pattern for UK species richness, with 443 highest overall avian vocalization density in UK2 and lowest in UK3. In Ecuador avian activity was 444 consistently high in EC2 and EC3, with greater variation in EC1; Amphibian activity was higher in 445 EC1 than EC2 and EC3 where calls are much sparser and insect activity was lowest in EC3 relative 446 to EC1 and EC2 during the dawn chorus.



448Fig. 3 Tukey's box plots of avian species richness per sample site for each habitat in UK (left) and Ecuador (right). The highest median avian449species richness per sample site was observed in secondary habitats in both ecozones. Horizontal lines represent medians; the box represents the450interquartile range; whiskers represent min and max values within 1.5 IQR. Shapiro-wilk normality test showed neither data set to be normal (UK W =4510.966, p < 0.0001; EC W = 0.968, p < 0.001). Non-parametric two sample tests confirmed observed differences in species richness between each452habitat in the UK to be significant (p < 0.001); in Ecuador richness in both secondary forest and agricultural plantation was significantly greater than in</th>453the primary (p < 0.001), but differences between secondary and agricultural habitats were non-significant (p = 0.175). See supplementary material C for</td>454full details.





462

#### 3.2.1 Correlation Analyses

Each one of the 26 AIs showed a significant correlation between both UK species richness and
biophonic density (Fig. 5). In Ecuador significant correlations between richness and biophonic
density were observed in 19 and 24 of the 26 indices respectively. Correlations were strong between
many AIs and both measures of biodiversity in the UK, but weak between AIs and richness in
Ecuador (Fig. 5 and supplementary material D for scatter plots).



469 Fig. 5. Spearman's rank coefficients for correlations between each acoustic index and species richness (top) and biophonic density (bottom) for UK 470 (left, N = 1976) and Ecuador (right, N = 1201). Stars denote p-values (\*\*\* < 0.001, \*\* < 0.01, \* < 0.05, . < 0.01), colours group class of index.

471

472	In the UK the highest correlation coefficients were for ADI, AEI and BI; they all had coefficients
473	greater than 0.6 with both biophonic density and species richness. All indices show positive
474	relationships, save the entropy indices (Ht, Hf and ADI) which are negatively associated with both
475	(Fig. 5). However, the simple descriptors (RMS, SC and ZCR) all also indicated moderate
476	correlations (> $0.5$ ) with both biophonic diversity and species richness; RMS metrics all showed
477	positive relationships, ZCR and SC were negatively associated with both measures of acoustic

478 community diversity, except for the variances, which showed smaller, positive associations.
479 Correlations between AIs and species richness in Ecuador were generally low; in contrast, moderate
480 significant relationships are observed between AIs and biophonic density, with relative strengths
481 following a very similar pattern to those observed in the UK. Overall there were no strong consistent
482 differences between the variants of each index, although the variances had a tendency toward lower
483 correlations. In the UK, variance of ZCR and SC shows a positive relationship, as expected.

#### 484 **3.2.2 Time Series Plots**

Examination of the response of AIs to diurnal changes in acoustic activity seen in the full data set 485 helps to interpret the results of the correlation analyses of the labelled subset, including the negative 486 487 correlations observed for the entropy indices. Diurnal soundscape patterns in all habitats are clearly 488 observable in the temporal variation of AI values over 24 hour periods (Fig. 6). UK nights (Fig. 6 489 top) are quiet relative to day time avian activity: this is seen in low nocturnal values of ACI, AEI, BI 490 and RMS. Entropy indices (ADI, Hf and Ht), SC and ZCR show the reverse pattern, as per 491 correlation results. In contrast, Ecuadorian nights (Fig. 6 bottom) show an increase in acoustic 492 activity. Peak activity at dawn and dusk anuran choruses are clearly visible as strong peaks in the 493 AEI, inverted in Ht.





495



496

497 Fig. 6 Main AI values for each 1 min file for all 15 sample sites averaged over 10 days in each UK (top) and EC (bottom) habitat type and plotted

498 relative to dawn (vertical dashed line). Central band shows mean and standard deviation; IQR is denoted by dashed lines. N = 28,800 per habitat.

#### 499 **3.2.3 Classification Analyses**

- 500 Overall, errors were lower for multivariate classification by AIs than by species in both the UK and
- 501 Ecuador (Fig. 7 right versus left, top and bottom) but follow the same pattern or relative magnitudes.
- 502 This suggests that differences in acoustic environments between sites are greater than inter-site
- 503 differences in community composition but track changes in community composition: Errors for UK
- 504 by species are lowest for UK3 (5%) compared to the two forested habitats UK1 (15%) and UK2
- 505 (22%); classification errors by AIs, are lowest of UK3 (3%), suggesting that UK3 has the most
- 506 distinct soundscape as well as the most distinct avian community.

50	38	633
51	504	3
562	103	32

0.75

507

508	
	Fig. 7. Confusion matrices for multivariate classification of habitat by species (left) and acoustic
	indices (right); actual habitats are shown in columns and predictions as rows for EC (N = 1201: 424,
500	420, 357) and UK (N = 1976: 663, 645, 668). Overall OOB classification errors are shown in each
509	subplot title, and error rates per habitat type on the x-axes.

510 For Ecuador, errors for classification by species were lowest in EC1 (1%) with higher errors in EC2



- the primary forest of EC1. Similarly, errors for acoustic indices are negligible for each habitat in
- 513 Ecuador (1%, 3% and 1% respectively), suggesting soundscapes at each site are highly distinct.
- 514 **3.3. Multivariate Random Forest Regression Analyses**

515 MRF regression analyses confirm that compound indices are stronger predictors of species richness than any single index: BI is the strongest single predictor of N0 in both UK (34% variance 516 517 explained) and Ecuador (13% variance explained) (Fig. 8). For the UK, AEI also makes a significant 518 contribution (18%), followed by ACI.med, ACI, ADI, ACI.min, ACI.max and ZCR.mean, NDSI and 519 ACI.var. In Ecuador, the simple acoustic descriptors make significant contributions: ZCR.mean 520 accounts for an additional 13% variance, followed by SC.max, NDSI, ZCR.med, ACI.var and 521 RMS.var. All other indices exceed the analytic threshold (Ishwaran et al., 2010), suggesting that 522 they all make a contribution to predictive power, however small. These results clearly demonstrate 523 that a compound index has more predictive power than any single AI alone. Partial dependence plots 524 which elucidate the nature of these relationships are given in supplementary material E.



AI - ordered by decreasing impact on prediction





530

AI - ordered by decreasing impact on prediction



#### 531 Discussion

The observed correlations between species richness and AIs in temperate habitats approach the strengths expected for AIs to be adopted as indicators of biodiversity and are stronger than those reported in recent smaller scale terrestrial correlation studies. Thus although it has been suggested that there are many other sources of acoustic heterogeneity that could *undermine* the value of AIs as proxies for biodiversity (Gasc et al., 2013), the present results suggest that with sufficient spatial and temporal replication these local individual differences may be ameliorated by community level effects.

We report five key findings which contribute to the interpretation, development and application of acoustic indices for biodiversity monitoring in the future: i) Vocalising species richness does not necessarily increase with ecological status ii) AIs track changes in acoustic community composition and reveal strong differences in acoustic environments between habitats iii) AIs correlate strongly with vocalising avian species richness in temperate (mono-taxa) environments and with subjective

measures of biophonic density in both tropical and temperate ecozones; iv) Performance of simple acoustic descriptors approaches that of bespoke diversity indices across ecological conditions and contributes more to predictive power than most diversity indices in multi-taxa environments; v) compound indices are more effective than any single index in predicting species richness.

548 4.1 Vocalising avian species richness does not increase with habitat status. Registered avian 549 species richness was significantly higher in the secondary habitats than the ancient temperate and 550 primary tropical forests. The relationship between habitat status and species diversity was not a 551 central question of the current study, but a positive relationship between habitat status and acoustic 552 diversity is a foundational assumption of RAS (Sueur et al., 2008) and ecoacoustics (Villanueva-553 Rivera et al., 2011). Our results challenge this assumption and are in line with previous studies: a 554 similar pattern was observed in a study in the Ecuadorian Cloud Forest (Eldridge et al., 2016); 555 greater diversity has also been reported in young, evolving forests compared to mature forests 556 (Depraetere et al., 2012); and recent studies evaluating the relationship between soundscape and 557 landscape in Australian Gum forests similarly find no clear, positive relationship between 558 biocondition and species richness (Fuller et al., 2015). That the secondary forest sites show greater 559 avian species richness is not unexpected: all exhibited over a decade of regrowth, providing a range 560 of niche space for a wide diversity of avian species (Reid, Harris, & Zahawi, 2012). More generally, 561 it is recognized that high diversity does not ensure that a site has a high ecological value (Dunn, 562 1994), and that species richness alone may not be sufficient to fully understand ecosystem resilience 563 and functioning (Chillo, Anand, & Ojeda, 2011). Therefore, the assumption that acoustic 564 diversity is a proxy for habitat health may be questioned.

565

4.2 AIs track changes in community composition across habitat types and reveal strong
differences in acoustic environments between habitats. Multivariate classification analyses
showed that AIs follow the same pattern of change across habitats as species composition; errors for
classification by AIs were even smaller than errors by species lists, suggesting that between habitats

570 differences in acoustic environment are even greater than differences in acoustic community 571 composition. The ecological relevance of these differences is unclear but warrants further 572 investigation. Explanations include: i) differences in vocalization characteristics of registered 573 species. For example, the agricultural land in the UK differed from the forest sites in the presence of 574 skylarks and absence of pheasants, both species having very distinct calls which strongly impact 575 many of the indices values; ii) Prevalence of non-avian taxa. As seen in Fig. 4 there were marked differences in anuran and invertebrate activity across sites; iii) site-specific differences in 576 577 anthrophonies such as airplanes, generators or human voice; iv) site-specific differences in 578 geophonies (wind, rain), potentially augmented by the impact of habitat structural variation on 579 propagation of acoustic signals. These results tentatively point to the possibility that **acoustic** 580 assessments could potentially provide a more complete measure of biodiversity than traditional 581 avian surveys; further research should investigate the potential for acoustic assessment of 582 community composition and ecologically relevant differences in acoustic environments.

583

#### 584 **4.3** AIs correlate with vocalising avian species richness in temperate (mono-taxa)

environments. Strong correlations were also observed between AIs and subjective measures of
biophonic density in both tropical and temperate ecozones. Overall, we observe stronger
relationships between AIs and species richness in temperate habitats than have been reported in
recent correlation studies, possibly because these previous studies were carried out in tropical
environments where results may have been confounded by other vocalizing taxa. This interpretation
is supported by the fact that AIs correlate significantly with the subjective multi-taxa measure of
biophonic density in both ecozones in the current study.

592 These results suggest firstly that AIs successfully track acoustic communities, (even in the presence 593 of considerable anthrophony and geophony), and secondly reiterate the **need to develop and test** 594 **acoustic methods to assess multi-taxa communities**.

595 Observed relationships between avian species richness and BI, ACI and NDSI are largely in line 596 with previous findings. In contrast, entropy and evenness indices (AEI, ADI, Hf, Ht) show an *inverse* 597 relationship to many previous findings. Results for each class of index are discussed below:

598 The Bioacoustic Index showed the best overall performance, being the strongest 599 predictor of avian species richness in both ecozones and showing strong positive correlations 600 with species richness in the UK and biophonic density in Ecuador and the UK. This result 601 corroborates previous studies which report strong correlations between BI and avian species 602 abundance (Boelman et al., 2007), number of bird vocalizations (Pieretti et al., 2011) and 603 biotic diversity (Fairbrass et al., 2017). The superior performance of BI over other indices 604 could be attributed to the fact that it is calculated across a narrower frequency range, 605 potentially strengthening the relationship with biophony by reducing sensitivity to low 606 frequency engine and wind noise and high frequency components of insect calls. This is a 607 simple but important considering in the design of future indices. Future indices could be 608 band limited and tuned to the range of calls of interest.

609 Correlations between ACI and species richness in the UK are in line with many previous findings which report positive relationships between ACI and number of avian 610 611 vocalisations (Pieretti et al., 2011) and reef fish abundance in temperate (Harris et al., 2016) 612 and tropical (Bertucci et al., 2016) marine environments. The weaker relationship between 613 ACI and observed species richness and negative relationship to biophonic diversity in Ecuador 614 is understandable given the other biophonies present: ACI acts as an event detector, so it will 615 likely track insect and amphibian calls with rapid onsets; similar negative trends have recently 616 been reported in other areas of high species diversity (Mammides et al., 2017). It is of note but 617 not surprising that median values performed a little better than the standard mean value, being 618 less susceptible to extreme changes which may be due to wind, electronic error or other biasing outliers. Median, rather than mean values may be more robust metrics in general. 619

620 Although NDSI was developed to capture anthropogenic disturbance, rather than acoustic community diversity, significant relationships with bird species richness have been 621 622 reported elsewhere (Fuller et al., 2015), however weak and non-significant correlations have 623 also been observed (Mammides et al., 2017). The moderate, positive correlations observed here between species richness and biophonic density likely reflect an overall increase in 624 625 biophonies relative to background technophonies - which were present in all habitats here -626 supporting the use of NDSI as a high-level measure of anthropogenic disturbance. As has 627 been highlighted elsewhere, assumptions over frequency range of anthrophony and biophony 628 may be over simplistic: frequency components of anthropogenic and biotically generated 629 sounds are not necessarily strictly band-limited, but could potentially be tuned to meet local characteristics. For example, calls of the Ecuadorian Toucan barbet (*Semnornis ramphastinus*) 630 631 contain spectra as low as 300 Hz, well below the default 2 kHz lower limit of biophony in NDSI. Ranges for frequency-dependent indices could be tuned to particular 632 633 characteristics of local communities of interest.

634 The Acoustic Evenness Index (AEI) showed the highest correlation with species richness in the UK and contributed strongly to prediction in the multivariate regression model. 635 The observed strong *positive* correlations between species richness and Acoustic Evenness 636 637 Index and *negative* correlations between species richness and the entropy indices show that 638 evenness of the spectra *decrease* with increasing richness for ADI, Ht and Hf. These finding 639 are at odds with some previous short term correlation studies, but show the same patterns 640 observed in longer term soundscape investigations (Gage & Farina, 2017) and shed light on 641 inconsistencies previously reported for entropy indices (Depraetere et al., 2012; Sueur et al., 642 2014b). Given that the measurement of acoustic diversity is foundational to RAS, reconciling 643 these inconsistencies is important, as conflicting accounts exist both empirically and 644 hypothetically.

646 4.3.1. Interpretation of Entropy Indices. AEI, ADI and Hf are derived by calculating Gini and 647 Shannon indices on the relative distribution of acoustic energy across frequency bands in a given 648 recording. The motivational logic is that an increasing number of species will generate signals across 649 a wider range of frequencies due to partitioning (Sinsch, Lümkemann, Rosar, Schwarz, & Dehling, 650 2012; Sueur, 2002), resulting in increased evenness (AEI tends to zero and ADI and H to 1). 651 However, this is only true over the bandlimited range of bird song (often cited as 2 - 8 kHz). Over a 652 wider frequency range, the inverse prediction also stands: as the mid- and high-frequency range of 653 songbird vocalisations increase relative to acoustic energy at the top and bottom of the spectrum, 654 evenness would decrease (AEI tends to 1). Therefore, both the strength and direction of relationship 655 between biophonic diversity and entropy indices is related to the frequency range analysed. 656 The bimodal response of entropy indices also makes interpretation difficult. Entropy metrics in both 657 time and frequency domains report high values for signals with diametrically opposed acoustic and 658 ecological characteristics: As noted in the seewave documentation, the temporal entropy of signals of 659 high acoustic activity (with many amplitude modulations) and a quiet signal will both tend towards 660 0, but a sustained sound with an almost flat envelope will also show a very high temporal entropy. 661 Similarly, for any given frequency range, the spectral entropy of a signal of high acoustic activity 662 and diversity (lots of species calls across different frequencies) will produce a high value, whereas 663 the call of a single species will produce an isolated spike and a low value. However, recordings with very low acoustic activity and low signal:noise ratio will also result in a high diversity value due to 664 665 the low magnitude, flat spectra. Entropy indices have a bimodal, rather than unimodal response. 666 Thus, whether ADI and AEI decrease or increase with increasing species richness depends on whether you compare high activity either to silence or low activity, i.e. the length of acoustic density 667 668 gradient. Inconsistencies in results for H indices have previously been attributed to the presence of 669 technophony (plane, car, farm machinery or train) (Depraetere et al., 2012) which produce a flat 670 spectrum similar to the broadband white noise of silence. The sampling regime deployed here 671 highlights that low signals (silence) gives similar results. Thus, when a long gradient of vocalization

density is included in the sampling protocol, inequality and entropy *decrease* with species richness,

673 in direct contrast to standard ecological interpretations of Gini-Simpson and Shannon-Wiener indices

674 when applied to species counts. Entropy indices are non-intuitive and must be interpreted

- 675 carefully.
- 676

677 4.4 Performance of simple acoustic descriptors. The performance of simple acoustic descriptors RMS, ZCR and SC suggest alternatives to single temporal or spectral diversity metrics and inspire 678 679 further research in the development and testing of acoustic indices. Correlation strengths of RMS, 680 ZCR and SC approached that of the diversity indices and, in Ecuadorian habitats, ZCR and SC made 681 significant contributions to species richness predictions. As expected, RMS shows a positive 682 association with increasing vocal activity and ZCR and SC are negatively associated. Rather than 683 measuring acoustic diversity, these simple descriptors track changes in amplitude (RMS), spectral (SC) and temporal characteristics of signals (ZCR). RMS and SC are intuitive to interpret; the 684 685 contribution of ZCR to predicting avian richness in complex multi-taxa environments can be 686 understood in light of its recognized power in percussion classification tasks. The ZCR of the decay 687 portion of percussive sounds is reported to out-perform more complex computations in separating the high pitch sharp attacks of snare drum hits from lower frequency, slower onset, bass drum strikes 688 689 (Gouyon et al., 2002). The possibility that such a simple descriptor may track distinct characteristics 690 of the vocalisations of different taxa - such as the rapid onset of harmonic bird vocalisations versus 691 the continuous noise of some invertebrates - warrants further investigation. Computational simplicity 692 translates to low energy requirements, making these simple descriptors ideal candidates for 693 implementation of *in situ* analysis for the emerging generation of monitoring networks built from the 694 emerging generation of embedded devices.

4.5 Compound indices are more effective than any single index in predicting species richness.
Multivariate regression results demonstrating the superior performance of compound over single
indices are in line with results of previous studies (Wimmer et al., 2013) and follow intuition.

698 Besides increasing predictive power, another advantage of compound indices is that they are likely to 699 be less biased by dominant species vocalisations. Some indices are particularly sensitive to certain 700 call characteristics, compromising their reliability as a biodiversity proxy. For example, we have 701 noticed in previous work that the high frequency short, rapid shrill of the Dusky Bush Tanager 702 (Chlorospingus semifuscus) generates high ACI values. The first generation of ecoacoustic indices 703 aimed to provide single values of acoustic diversity; future research should focus on development and testing of a suite of complementary features for use in a compound index, 704 705 capturing timbral as well as temporal and spectral characteristics. Site-specific compound 706 indices could then be developed, for example by tuning relative weights by carrying out a PCA on a 707 sample recording.

708

#### 709 **4.6 Future Directions in Acoustic Indices**

710 The development of indices for RAS in multi-taxa environments can be approached under one of two 711 principles: either focus on a single identified indicator taxon (birds or amphibians) and removing 712 unwanted sounds (insect choruses, wind rain); or attempting to capture the global interplay of multi-713 species multi-taxa choruses. Exciting advances are being made in both areas using machine learning: 714 source separation algorithms can be used to tackle the former (Xie et al., 2016), and unsupervised 715 clustering algorithms have been productively applied to analyse the variety of sounds sources in long 716 term monitoring projects (Phillips et al., 2018). Whilst powerful these approaches are too 717 computationally intensive to run on microcomputers in situ. The use of simple acoustic descriptors 718 which track changes across spectral, temporal and timbral dimensions of vocalisations offer an 719 alternative, parsimonious approach to monitoring the integrated chorus and point to new directions 720 for the development of tuneable, compound ecoacoustic indices capable of tracking the dynamics of 721 multi-taxa acoustic communities.

#### 722 **5. Conclusion**

723 Results from acoustic surveys across a wide range of ecological conditions, in temperate and tropical 724 ecozones support the use of acoustic indices to appraise avian species richness in temperate but not 725 in the multi-taxa acoustic communities of tropical habitats. Compound indices appear to be sensitive 726 to habitat-dependent changes in acoustic community composition, which could provide a potentially 727 more cost-effective and nuanced assessment than current standard avian surveys against which we 728 are validating. These results both highlight the need for, and inspire the development of, new indices 729 for monitoring more complex multi-taxa communities. Our results clearly demonstrated that 730 compound indices are to be recommended, and that development and testing of new simple timbral, 731 spectral and temporal indices to complement existing diversity indices deserves further investigation. 732 Future research should confirm these results and further integrate extant knowledge from machine 733 listening and bioacoustics research to create more powerful computational methods for the analysis 734 of acoustic community dynamics at extended spatio-temporal scales. By doing so we can maximize 735 the potential for ecoacoustics methods to provide robust, cost-effective tools for ecological 736 monitoring and prediction.

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