1

2 <u>Acoustic indices perform better when applied at ecologically meaningful time and frequency scales</u>

3 Oliver C. Metcalf[1], Jos Barlow[2,3,4], Christian Devenish[1], Stuart Marsden[1], Erika Berenguer,[3,5],

4 Alexander C. Lees[1,6]

5   1. Division of Biology and Conservation Ecology, Department of Natural Sciences, Manchester

6   Metropolitan University, Manchester, UK

7   2. Departamento de Biologia, Universidade Federal de Lavras, Lavras, Minas Gerais, Brazil

8   3. Lancaster Environment Centre, Lancaster University, Lancaster, Lancashire, UK

9   4. MCTIC/Museu Paraense Emílio Goeldi, Belém, Pará, Brazil

10   5. Environmental Change Institute, School of Geography and the Environment, University of

11   Oxford, OX1 3QY, Oxford, UK

12   6. Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14850, USA

13 Contact author:

14 Oliver C. Metcalf[1]

15 o.metcalf@mmu.ac.uk

16 Division of Biology and Conservation Ecology, Department of Natural Sciences, Manchester

17 Metropolitan University, Manchester, UK

18

19

20 Running headline: Acoustic indices impacted by signal masking

21 Word count: 6736

22

23 Abstract:

24   1.   Acoustic indices are increasingly employed in the analysis of soundscapes to ascertain

25   biodiversity value. However, conflicting results and lack of consensus on best practices for

26   their usage has hindered their application in conservation and land-use management

27   contexts. Here we propose that the sensitivity of acoustic indices to ecological change and

28   fidelity of acoustic indices to ecological communities are negatively impacted by signal

29   masking. Signal masking can occur when acoustic responses of taxa sensitive to the effect of

30   interest are masked by less sensitive acoustic groups, or target taxa sonification is masked by

31   non-target noise. We argue that by calculating acoustic indices at ecologically appropriate

32   time and frequency bins, masking effects can be reduced and the efficacy of indices

33   increased.

34   2.   We test this on a large acoustic dataset collected in Eastern Amazonia spanning a

35   disturbance gradient of undisturbed, logged, burned, logged-and-burned, and secondary

36   forests. We calculated values for two acoustic indices: the Acoustic Complexity Index and the

37   Bioacoustic Index, across the entire frequency spectrum (0-22.1 kHz), and four narrower

38   subsets of the frequency spectrum; at dawn, day, dusk and night.

39   3.   We show that signal masking has a large impact on the sensitivity of acoustic indices to

40   forest disturbance classes. Calculating acoustic indices at a range of narrower time-

41   frequency bins substantially increases the classification accuracy of forest classes by random

42   forest models. Furthermore, signal masking led to misleading correlations, including

43   spurious inverse correlations, between biodiversity indicator metrics and acoustic index

44   values compared to correlations derived from manual sampling of the audio data.

45   4.   Consequently, we recommend that acoustic indices are calculated either at a range of time

46   and frequency bins, or at a single narrow bin, predetermined by *a priori* ecological

47   understanding of the soundscape.

48

49   1 – Índices acústicos são cada vez mais utilizados em análises de paisagens sonoras para entender

50   padrões de biodiversidade. Entretanto, sua aplicação em biologia da conservação e em contextos de

51   manejo do uso do solo têm sido atrasada devido a resultados conflitantes e a uma falta de consenso

52   sobre as melhores práticas a serem empregadas. Aqui nós propomos que a sensibilidade de índices

53   acústicos em capturar mudanças ecológicas, assim como a fidelidade com que índices acústicos

54   capturam comunidades ecológicas, são severamente impactados por mascaramento do sinal. O

55   mascaramento do sinal pode ocorrer quando respostas acústicas sensíveis aos efeitos que estão

56   sendo monitorados são mascaradas por outros grupos menos sensíveis ou quando a vocalização do

57   taxa alvo dos estudos é mascarado por barulho de outros taxa. Nós argumentamos que ao calcular

58   índices acústicos em intervalos apropriados de tempo e frequência, efeitos mascaradores podem ser

59   reduzidos e a eficácia dos índices acústicos aumentada.

60

61   2 – Nós testamos isso em um vasto grupo de dados acústicos coletados na Amazônia oriental,

62   abrangendo um gradiente de distúrbios antrópicos, incluindo florestas primárias não perturbadas e

63   aquelas afetadas por extração madeireira, incêndios florestais, extração madeireira e incêndios,

64   assim como florestas secundárias. Nós calculamos os valores de dois índices acústicos, o Índice de

65   Complexidade Acústica e o Índice Bioacústico. Para isso, empregamos todo o espectro de

66   frequências (0-22.1kHz) e quatro subgrupos menores do espectro de frequências: o amanhecer, o

67   dia, o anoitecer e a noite.

68

69   3 – Nós mostramos que o mascaramento do sinal tem um grande impacto na sensibilidade dos

70   índices acústicos a distúrbios florestais. Calculando índices acústicos em um intervalo menor de

71   tempo-frequência aumentou substancialmente a acurácia da classificação das classes florestais por

72   modelos do tipo Random Forest. Além disso, o mascaramento do sinal levou a correlações errôneas,

73   incluindo correlações negativas espúrias entre métricas de biodiversidade e valores de índices

74   acústicos, quando comparados com correlações geradas a partir de amostragem manual dos dados

75   de áudio.

76

77   4 – Consequentemente, nós recomendamos que índices acústicos sejam calculados em intervalos de

78   tempo e frequência menores, pré-determinados por conhecimento ecológico a priori da paisagem

79   sonora.

80

81   Key words:

82   Acoustic indices, ecoacoustics, remote sensing, bioacoustics, biodiversity, Amazonia, soundscape,

83   tropical ecology

84

85   **Introduction**

86   Acoustic monitoring is rapidly becoming a key tool to measure biodiversity, with strident calls for

87   broader uptake (Burivalova et al., 2019; Deichmann et al., 2018; Wagner Ribeiro Jr et al., 2017).

88   Despite increasing ease of data collection, there remain significant obstacles to the analysis of

89   acoustic data, with species-level classification limited by the expertise and effort required to train

90   machine-learning models, and the limited availability of both open source software and large audio

91   libraries (Gibb et al., 2019; Priyadarshani et al., 2018). Consequentially, the use of acoustic indices

92   has grown in popularity, often used as proxies for more traditional biodiversity metrics like species

93   richness and composition, and presented as alternative effective tools for rapid biodiversity

94   assessments (Sueur et al., 2008). There are a wide range of acoustic indices, but most involve

95   calculating and comparing acoustic power within temporal and frequency bins (Farina, 2014; Sueur,

96   Farina, Gasc, Pieretti, & Pavoine, 2014; Buxton et al., 2018; Gibb et al., 2019). These are, in turn,

97   used to assess soundscape qualities such as evenness, entropy and complexity. Acoustic indices infer

98 community level information from entire soundscapes, in contrast to species-level classification

99 approaches that require time-consuming complex model-training techniques necessitating large

100 training libraries, indices are relatively simple and readily available on a range of open-source

101 platforms.

102

103 Despite their increasing popularity, acoustic indices are not always effective at answering key

104 questions related to conservation or natural resource management. The first issue relates to their

105 *sensitivity* to changes in environmental conditions. Acoustic indices have been shown to effectively

106 distinguish between disparate land uses (Bradfer-Lawrence et al., 2019; Carruthers-Jones et al.,

107 2019; Depraetere et al., 2012). However, they are less successful in distinguishing differences

108 between similar land uses; for example between different types of forest (Bormpoudakis et al.,

109 2013, Eldridge et al., 2018, Do Nascimento et al., 2020), or require a very large number of spatial

110 replications to do so (Mitchell et al., 2020). The second issue relates to their *fidelity* as indicators of

111 biodiversity, as they can be inconsistent predictors of traditionally-used biodiversity metrics such as

112 species richness (Eldridge et al., 2018; Fuller et al., 2015; Jorge et al., 2018; Mammides et al., 2017).

113 The problems of low sensitivity and inconsistent fidelity are potentially caused by signal

114 masking – whilst certain vocalising taxa or taxonomic groups may respond strongly to

115 changes in environmental condition, others may not. By measuring acoustic indices at

116 intervals that measure across multiple taxonomic groups, sensitivity to these varied

117 responses is lost, which may not be the case if indices were measured with multiple

118 intervals. Similarly, fidelity to a single taxonomic group is lost by the use of broad time and

119 frequency intervals, which may be improved by the use of narrower, tailored intervals.

120 There are two key ways in which signal masking can occur in acoustic indices. The first,

121 temporal masking, can occur when acoustic indices are measured over time periods that

122 are too long, so that sounds from sensitive time periods may be confounded by a lack of

123   change or contrasting responses in other time periods. For example, the vocal community

124   at dawn may respond to a disturbance event very differently from the dusk community

125   (Deichmann et al., 2017), so that measuring both together masks overall community

126   responses. To avoid this, the analysis of acoustic indices often involves temporally limiting

127   or splitting the data analysed into discrete periods, such as dawn and dusk (Bradfer-

128   Lawrence et al. 2020, Deichmann et al., 2017; Fuller et al., 2015, Eldridge et al., 2018;

129   Machado et al., 2017), selecting time periods that coincide with the peak communication

130   time for certain groups.

131 The second form of signal masking, frequency masking, can occur when acoustic indices are

132 measured at frequency bins that are too broad, so that sounds at sensitive frequencies are swamped

133 by contrasting or null responses at other frequencies. Although the importance of frequency

134 masking has not been explicitly considered in relation to acoustic index functioning, there is strong *a*

135 *priori* reason to believe it may be important, and has been postulated by others (Eldridge et al.,

136 2018). There is a broad negative relationship between body size and the frequency at which animals

137 vocalize (Gillooly and Ophir, 2010; Ryan and Brenowitz, 1985; Seddon, 2005; Wilkins et al., 2013),

138 meaning that the largest species, predominantly mammals, vocalize at the lowest frequencies, whilst

139 orders composed of smaller species such as orthopterans predominate at higher frequencies. In

140 addition, neotropical bird vocalisations exhibit both temporal and frequency partitioning to avoid

141 signal masking from cicadas and other loud insects (Aide et al., 2017, Hart et al., 2015). At its

142 simplest, this should result in different frequency bins being dominated by sounds from different

143 broad taxonomic groupings.

144

145 Here, we use a data set from one of the world's most speciose ecosystems - the Brazilian Amazon –

146 to explore how the use of time and frequency bins (henceforth TFBs) can improve the sensitivity and

147 fidelity of acoustic indices. By calculating acoustic index values within restricted frequency bands,

148 the potential masking effect could be reduced, and correlations with specific taxonomic groups

149 increased. Initially, we establish whether measuring indices at broad time and frequency scales, as is

150 standard practice, masks variation in acoustic responses across narrower TFBs. Next, we look at the

151 impact of signal masking on the efficacy of acoustic indices as a proxy for biodiversity and test the

152 suitability of using TFBs as a solution by asking two questions of high relevance to practitioners and

153 policy makers. First, do TFBs improve the sensitivity of acoustic indices to changes in forest condition

154 (e.g. disturbance)? This is key to monitoring forest recovery following disturbances such as selective

155 logging or wildfire, analyses which underpin many applied ecology questions. Second, do TFBs

156 improve the fidelity of acoustic indices as proxies for traditional field surveys aimed at establishing

157 species richness and composition? These field surveys can be expensive and inefficient for a range of

158 taxonomic groups (Gardner et al., 2008), and if acoustic indices can be shown to be a reliable

159 replacement for traditional survey methods, such as point count bird surveys, then they may offer a

160 significant cost-saving.

161

162 Methods

163 Study area and data collection:

164 We collected acoustic data in the eastern Brazilian Amazon in the municipalities of Santarém-

165 Belterra-Mojuí dos Campos (latitude -3.046, longitude -54.947, hereafter Santarém) in Pará state,

166 between 12 June 2018 and 16 August 2018. We used the permanent transects of the Sustainable

167 Amazon Network (Gardner et al. 2013) distributed in *terra firme* forest habitats. We sampled 28 300-

168 m transects distributed into five forest classes: undisturbed primary forests (n = 4), logged primary

169 forests (n = 4), burned primary forests (n= 5), logged-and-burned primary forests (n = 12), and

170 secondary forests (n = 3); forests recovering after being completely felled). We installed Frontier

171 Labs Bioacoustic Recording Units with a 16 bit 44.1 kHz sampling rate at points halfway along each

172 transect. Recorders were placed in trees at a height of 7-10 m, with the microphone placed in a

173   downward facing position, at a distance of 10-20 m from the transect to reduce the chance of

174   recorder theft. Recording units were placed away from immediately overhanging dense vegetation

175   to avoid sound being blocked and to limit geophony from leaves and branches. The microphones

176   used have 80 dB signal to noise ratio and 14dBA self-noise, a fixed gain pre-amp of 20dB, a flat

177   frequency response (±2dB) from 80Hz to 20kHz and an 80Hz high-pass filter to filter out low-

178   frequency wind noise (Frontier Labs, 2015). All files were recorded in wav format. Recordings were

179   made continuously (Frontier Labs software writes a new file every ~6 hrs) over multiple discrete time

180   periods of differing length at each point with discrete time periods ranged in duration between 3

181   and 20 days. Total recording duration and first and last recording dates are included in SOM 1

182   Appendix 1. The inaccessibility of some transects used in previous studies meant that a balanced

183   survey design was impossible across the disturbance categories (Table 1).

184   *Table 1: Audio sampling by forest class after automated removal of recordings containing heavy*

185   *rainfall*

Forest Class	Sampled points (n)	Total sampling time (minutes)
Primary	4	90,600
Logged primary	4	89,540
Burned primary	5	139,720
Logged-and-burned primary	12	238,130
Secondary	3	60,970

186

187   Data Analysis:

188   We selected two acoustic indices, the Acoustic Complexity Index and the Biodiversity Index as they

189   are two of the commonest indices used in ecoacoustic studies. However the Acoustic Complexity

190   Index is commonly applied across broad frequency ranges, and the Bioacoustic Index is typically

191   applied at restricted frequency ranges, making an ideal comparison for this study as in combination,

192   they are likely to be representative of how many acoustic indices will be affected by the use of

193   narrower time and frequency bins. The Acoustic Complexity Index is intended to quantify biotic

194   sound whilst being robust to non-target noise (Duarte et al., 2015; Fairbrass et al., 2017; Pieretti et

195   al., 2011), and is commonly applied across broad frequency bins. Acoustic Complexity Index

196   measures the irregularity in amplitude across time samples by frequency bin, relative to the total

197   amplitude of the frequency bin. The Acoustic Complexity Index has been found to significantly

198   correlate with species richness for some taxa (Bertucci et al., 2016, Bradfer-Lawrence et al. 2020,

199   Eldridge et al., 2018, Mitchell et al., 2020), whilst in others it showed little or no correlation (Fuller et

200   al., 2015; Mammides et al., 2017; Moreno-Gomez et al., 2019) although this may be due to

201   limitations in methodology and small sample sizes. In contrast, the Bioacoustic Index (BI) is generally

202   applied to narrower frequency bins, and is intended to provide relative abundance of avian

203   community within a frequency range that contains most bird sound (Boelman et al., 2007). It

204   measures the disparity between the quietest and loudest 1 kHz frequency bins. Again, the

205   Bioacoustic Index has been found to be a good predictor of diversity in some studies (Eldridge et al.,

206   2018, Hilje et al., 2017, Gasc et al., 2017, Mitchell et al., 2020) whilst others have found it to be poor

207   (Fuller et al.,2015, Moreno-Gomez et al., 2019), although concerns about the limitations of the

208   methodologies used in these studies apply here too. We expect both indices to increase with

209   increasing species richness and species abundance, and for correlations between both abundance

210   and richness with the indices to be strongest in the frequency and time bins that are most

211   dominated by the target taxa (Table 2), particularly diurnal bird species at dawn between 0.3-12 kHz

212   and nocturnal taxa at night between 0.3-4 kHz.

213

214   We calculated the indices using the soundecology package (Villanueva-Rivera et al., 2011, v1.3.3) in

215   R (R Core Team, 2019) which includes minimum and maximum frequency limits for both the Acoustic

216   Complexity Index and Bioacoustic Index, allowing easy and consistent index calculation at a range of

217   frequency bins. To limit microphone self-noise the lowest frequency included in analysis was 300 Hz.

218   We then calculated the mean index value per 10 minute interval of data collected for each acoustic

219   index and each of the 20 TFBs (Fig.1a), having first screened out recording periods containing heavy

220   rainfall (n = 527) using the hardRain package in R Studio (Metcalf et al., 2020, v0.1.1).

221   We selected TFBs with the objective of capturing periods of time and frequency bands that

222   are most taxonomically homogenous. TFBs were not quantitatively optimised, but rather

223   subjective approximations that aimed to effectively capture broad taxonomic groupings in

224   tropical forest landscapes. Temporal limits were determined by patterns in animal

225   communication in the diel cycle, to encapsulate dawn, dusk, daytime and night-time

226   periods (Pieretti et al., 2015; Rodriguez et al., 2014); commonly used sampling periods in

227   acoustic recording (Sugai et al., 2019). 'Dawn' was assigned to the period from 30 minutes

228   prior to sunrise and for the following 2 hours, whilst 'Dusk' was the 2 hour period ending

229   at 30 minutes after sunset. 'Day' and 'Night' are the respective intervening periods.

230   Frequency limits were determined by a review of the literature and our own experience of

231   manually analysing 100s of hours of acoustic data from the region. The taxonomic

232   groupings we hypothesize dominate each TFB are illustrated in Figure 1a. Table 2 contains

233   some of the TFBs likely to contain particularly high activity from particularly homogenous

234   groupings. 0.3-22.1 kHz frequency bin (hereafter 'baseline') was used as baseline data,

235   representative of how most terrestrial acoustic indices are currently calculated across the

236   spectrum of human hearing or the common sampling rate of 44.1 kHz. However, it is

237   worth noting that the Bioacoustic Index is commonly calculated with a narrower frequency

238   bin than the baseline, typically from 2 to 8 or 11 Khz (Boelman et al., 2007, Bradfer-

239   Lawrence et al., 2019, Villanueva-Rivera et al., 2011). We have used the same baseline as

240   the Acoustic Complexity Index for ease of comparison, and because the mechanisms

241   causing masking between ecologically relevant and non-relevant frequency bins is the

242   same regardless of absolute frequency. Of course, macro frequency bands will never solely

243   encompass single taxonomic groups, and boundaries will always be somewhat arbitrary

244   due to variations in acoustic communication at species, temporal and even individual

245   levels.

246   *Table 2: Selected time-frequency bins and the taxonomic groups expected to dominate each sample.*

Frequency Band (kHz)	Time Period	Taxonomic group	References
0.3-4	Night	Terrestrial/arboreal mammals, anuran and birds	Chek, Bogart, & Lougheed, 2003; Lima, Pederassi, Pineschi, & Barbosa, 2019
4-12	Day	Hemiptera/Orthoptera	Hart et al., 2015, Schmidt et al., 2013
4-12	Night	Hemiptera/Orthoptera	Hart et al., Schmidt et al., 2013
0.3-12	Dawn	Diurnal/crepuscular birds	Tobias, Planqué, Cram, & Seddon, 2014
12-22.1	Dusk	Insects, bats and frogs	Lima, Pederassi, Pineschi, & Barbosa, 2019, Schmidt et al., 2013
12-22.1	Night	Insects	Schmidt et al., 2013

247

248 <u>Signal Masking</u>

249 To investigate whether the soundscape responds differently to human-driven disturbance across

250 time and frequency, we looked at the variation in response of each disturbance class for each TFB.

251 Having removed periods with extreme outlying index values, we took a random sample of acoustic

252 index values for each acoustic index and TFB from each forest class (n=500), giving a total sample

253 size of n=2500 per TFB/index. For each TFB and acoustic index we conducted a Kruskal-Wallis

254 (Kruskal and Wallis, 1952) test between the five forest classes, and calculated the effect size (ε^2).

255 When significant differences between the classes were found, we used a Dunn's test (Dunn, 1964) to

256 establish how many of the ten forest class pairs were significantly different from each other.

257

258 <u>The sensitivity of acoustic indices to habitat</u>

259 To assess whether the use of TFBs increased acoustic index sensitivity to forest classes, we built

260 distributed random forest models from the 'h2o' R package (LeDell et al., 2020 v3.30.0.1), varying

261 the number of TFBs used as predictors. Firstly, we tested if the use of TFBs improved classification

262 accuracy between the two most ecologically distinct sampled habitats; undisturbed primary forest

263 and secondary forest (Moura et al., 2013). To do so, we built two binomial random forest models,

264 the first using training data only from the baseline frequency bin across all time periods, the second

265 using training data from all frequency bins and time periods. Next, models were trained and tested

266 on data from all five forest classes, which previous studies (e.g. Moura et al. 2013) suggest would

267 provide a more challenging classification problem.

268 We used each combination of index and TFB as a separate predictor. The training datasets required

269 subsampling to obtain predictors of equal length, as not all time periods were of the same duration,

270 and forest classes had unequal survey effort. We used the same subsample as above (see Signal

271 Masking), so that each TFB predictor had n=2,500 samples, with 500 samples from each forest class.

272   This resulted in a greatly reduced dataset for training the models with 100,000 acoustic indices

273   values compared to 1,277,560 in the original dataset. Prior to model training, the dataset was split

274   with 75% of observations used for training and 25% as a test dataset. Model parameters were kept

275   constant across all models (SOM 1 Appendix 2). We used balanced accuracy (Fielding and Bell, 1997),

276   F1 scores (Chinchor, 1993) and Matthew's Correlation Coefficient (Guilford., 1954) as accuracy

277   metrics (Table 3), which were calculated per forest class based on predictions of the test dataset and

278   are presented here as an unweighted mean across all forest classes included in the respective

279   model.

280

281   <u>Fidelity of acoustic indices to taxonomic measures of biodiversity</u>

282   We assessed correlations between acoustic index scores and biodiversity indicator metrics, to see

283   how representative the indices were of commonly used indicators of diversity. Data on the

284   presence/absence of three sets of species were generated from two subsets of the audio data. Each

285   audio subset consisted of 28 hrs of sound recordings, in the form of 240 15 s recordings from each

286   point. The first data set was restricted to the dawn period (hereafter dawn birds), in which all

287   identifiable avian vocalisations were assigned to species by an ornithologist (Nárgila Gomes De

288   Moura) with extensive field experience of point counts in the same sites (e.g. Moura et al. 2013).

289   This method of species detection is likely to produce comparable results to traditional point count

290   surveys as several papers have shown that experienced observers reviewing recordings and

291   spectrograms can be more or equally effective at detecting species than field-based surveys (Darras

292   et al., 2019; Shonfield et al., 2018). The second set of data was restricted to the nocturnal period

293   (hereafter nocturnal birds), and again all identifiable avian vocalisations were assigned to species by

294   an experienced ornithologist (OCM). The third set was generated from the nocturnal data subset

295   again (hereafter nocturnal taxa), but comprises all biophony below 4kHz, identified (by OCM) where

296   possible or sonotyped if not. It is worth noting that all of the bird species identified at night vocalized

297   below 4 kHz, so that the nocturnal bird set is wholly a subset of the nocturnal taxa set.

298

299   For each of these matrices (i.e. dawn birds, nocturnal birds and nocturnal taxa), five metrics were

300   calculated; total number of encounters (the sum of the number of 15 s recordings each species was

301   present in), species richness, Shannon diversity, Pielou's evenness, and the first axis from a

302   nonmetric multidimensional scaling ordination (hereafter MDS1) using the Jaccard method from the

303   vegan package (Oksanen et al., 2019). Total encounters was included as a proxy for the abundance

304   of sounds, to test if indices responded more strongly to more sources of noise, regardless of

305   composition. Estimated species richness from the dawn matrix was calculated for each point at

306   98.5% coverage based on rarefaction/extrapolation using the iNEXT package (Hsieh et al., 2020,

307   v2.0.20), as some of the survey files were removed as they contained periods of heavy rain which

308   affected the number of vocalizing species. Observed species richness was used for metrics from the

309   nocturnal matrix, as the data were pre-screened for rain. Shannon diversity, Pielou's evenness and

310   species richness were included as standard measures of ecological diversity (Oksanen et al., 2019).

311   MDS1 was included to reflect turnover mediated by disturbance, as high values correspond with less

312   disturbed habitats, whilst lower values have communities associated with more disturbed habitats.

313   Correlations between these metrics are available in SOM 1 Appendix 3. Median values of each

314   acoustic index were calculated for each point and TFB, and Spearman's rank order correlations (α =

315   0.05) were calculated between these and the biodiversity metrics. Significant differences between

316   each correlation and the respective baseline correlation were calculated using Zou's confidence

317   interval test (Zou, 2007) in the 'cocor' package (Diedenhofen and Musch, 2015 v.1.1-3).

318

319   Results

320   Sensitivity: forest disturbance

321   The Kruskal-Wallis and Dunn's test revealed strong evidence that acoustic masking affects the

322   sensitivity of acoustic indices, both temporally and by frequency. All of the Kruskal-Wallis tests were

323   significant ($p < 0.05$), showing that acoustic indices are sensitive to at least some disturbance events

324   regardless of frequency band or time period. There were significant differences between all ten

325   forest class pairs in every time period and with both indices when considering all frequency-

326   restricted TFBs together. In contrast, there were no time periods with significant differences

327   between all forest class pairs when using only the baseline TFBs, but Acoustic Complexity did have

328   significant differences between nine forest class pairs in three time periods, and Bioacoustic Index

329   once. Twelve TFBs showed significant difference ($p < 0.05$) between more forest classes than the

330   corresponding baseline, and 21 TFBs had higher effect sizes than the corresponding baseline,

331   suggesting that in many cases stronger responses to disturbance events at narrower frequency bins

332   are masked by the use of broad frequency bins (Fig. 2). No baseline TFB achieved perfect separation

333   between all ten forest-class pairs but this was achieved by three of the non-baseline TFBs.

334   Furthermore, Acoustic Complexity Index at dusk and the baseline frequency bin produced the lowest

335   number of significantly different forest class pairs, just two, suggesting that using only the broadest

336   frequency bin can result in relatively poor differentiation between forest disturbance classes. No

337   one frequency bin or time period had a consistently larger effect size, or consistently differentiated

338   between more forest classes. There were several occasions in which effect size increased in

339   comparison to the baseline, whilst the number of different forest classes decreased (e.g. Acoustic

340   Complexity Index at dawn, 0.3-4 kHz, Bioacoustic Index at night, 0.3-4 kHz). This suggests that the

341   soundscape at this frequency bin is showing a particularly strong response to disturbance in one or

342   more of the forest classes (in SOM 1 Appendix 4)."

343

344   Sensitivity: Forest class differentiation

345   The random forest models generated using all of the TFBs as predictors were able to classify forest

346   classes with a high degree of accuracy, with 99.6% balanced accuracy between secondary and

347   undisturbed forest and 88.2% between the five forest classes (Fig. 3). The models using all TFBs as

348   predictors outperformed the corresponding baseline models in both tests, but as expected the

349   baseline models performed particularly poorly when classifying between all five forest classes,

350   achieving just 62.1%. The confusion matrix for the random forest model using all TFBs across all five

351   classes suggest that acoustic indices do respond to soundscapes in ecologically meaningful ways, as

352   both burned forest classes had comparatively high error between them, as did the two most

353   disturbed classes, logged and burned vs secondary forest (SOM 1 Appendix 5).

354

355   Fidelity: Biodiversity Correlations

356   Correlations with traditional biodiversity metrics revealed complex patterns, underpinned by strong

357   variation across index, frequency bins and time periods. For simplicity, we have focussed on time

358   periods in which acoustic index values most directly reflect variation in manually reviewed datasets -

359   dawn and day time for the dawn bird dataset, and night for the nocturnal datasets (Fig. 4),

360   Correlations at other time periods are presented in SOM 2 Appendix 6. The two strongest

361   correlations, were at night between Bioacoustic Index and diurnal avian MDS1 at 4-12 kHz (r_s =0.74)

362   and dusk at 0.3-12 kHz (r_s = 0.72).

363   The correlation scores provide strong evidence that the use of TFBs increase the fidelity of

364   correlations. We found that correlation directions of the frequency/ bins differed from the

365   corresponding baseline frequency bin for at least one of the metrics in every time period in both

366   indices. The strongest examples of this were between Bioacoustic Index at dawn with dawn birds,

367   which saw predominantly significant positive correlations at frequency bands at which dawn birds

368   vocalize, but negative correlations in the baseline and 12-22.1 kHz frequency bins. We also found 28

369   instances in which correlations were significantly different to the corresponding baseline frequency

370   bin.

371   Overall, the Acoustic Complexity Index was inconsistently correlated with biodiversity indicator

372   metrics with predominantly negative and significant correlations with diversity metrics at dawn, but

373   mostly positive correlations during the day and at night for most frequency bands, with far fewer

374   significant correlations. In contrast, the Bioacoustic Index showed predominantly positive

375   correlations with most diversity metrics except MDS1 across all three time periods and all three

376   frequency bins only including sound below 12 kHz. For the community metrics most likely to be

377   useful to ecologists, species richness and Shannon diversity, there were 19 significant correlations.

378   However, where we found significant correlations with these metrics, there were still strong reasons

379   for doubting the fidelity of acoustic indices as proxies. At dawn, correlations for both indices were

380   weaker than the respective correlations with total encounters or MDS1, suggesting the indices were

381   more sensitive to the number of individual sounds or the overall community. At night, nocturnal

382   birds and taxa correlations with the Bioacoustic Index showed conflicting patterns with correlations

383   at frequency bins more likely to be relevant to the relevant taxonomic group, suggesting a strong

384   masking effect by vocalisations of non-target taxa. The exception to this is the correlation between

385   dawn birds and BI during the day at 0.3-4 kHz, which shows strong correlations with species richness

386   and Shannon diversity (r_s = 0.44 and 0.40), a similar correlation with total encounters (r_s = 0.40) and

387   no significant correlation with MDS1.

388

389   <u>Discussion</u>

390   We found that calculating acoustic indices at narrower TFBs results in large increases in the

391   sensitivity of acoustic indices to the soundscape response of different forest classes. Calculating

392   acoustic indices across a single broad frequency bin, as is commonplace in the ecoacoustic literature

393   (Sueur et al., 2014; Buxton et al., 2018; Gibb et al., 2019) can mask varied responses across time

394 periods and frequency bins, reducing the sensitivity of acoustic indices. Furthermore, when acoustic

395 indices are used as proxies for biodiversity indicator metrics, masking can have a serious impact on

396 the fidelity of the correlations. Correlating broad frequency bins with biodiversity metrics generated

397 from taxa whose vocalisations do not occur across the entire frequency range is likely to be highly

398 misleading. It not only misrepresents the magnitude of correlations, but potentially results in

399 spurious inverse correlations caused by the responses of acoustically dominant species or patterns

400 from acoustic space that are not biologically relevant.

401

402 The sensitivity gains of this new methodology are particularly apparent when using acoustic indices

403 to differentiate between environments with classification accuracy greatly increased. Accuracy

404 scores are as good or better than many in the literature (Bormpoudakis et al., 2013; Bradfer-

405 Lawrence et al., 2019; Eldridge et al., 2018, Do Nascimento et al., 2020), especially considering that

406 model hyperparameters are not optimised, fewer acoustic indices were used, and that the forest

407 classes considered here are all of the same land cover (tropical forest) and within the same

408 landscape. In addition, these results have been achieved whilst using only approximately one sixth of

409 the training data compared to the models using only a single baseline frequency band, suggesting

410 that by using TFBs, large efficiency savings can be made in terms of data collection. We therefore

411 recommend that acoustic indices are calculated across a range of frequency bins and temporal

412 periods in any study using acoustic index values to characterise and identify land use.

413 The impact of signal masking, and the benefits of using narrower time-frequency bins to avoid it, are

414 equally apparent when correlating acoustic indices with biodiversity metrics. However, despite the

415 increased fidelity of the correlations, the use of single acoustic indices as direct proxies for

416 biodiversity indicator metrics is still problematic. Whilst we found the predicted positive correlations

417 between diversity, richness and the Bioacoustic Index at the most relevant TFBs, we found a

418 negative correlation between the Acoustic Complexity Index at dawn with bird species richness and

419   abundance. This contrasts with other similar studies in comparable habitats that found positive

420   relationships (Bradfer-Lawrence et al., 2020, Eldridge et al., 2018, Mitchell et al., 2020). However,

421   Mitchell et al., (2020) found high Acoustic Complexity values in oil-palm plantations where diversity

422   was low, and noted that the significant relationships they found were within habitat types, but not

423   across different habitats. Furthermore, the complex mechanisms determining abundance and

424   species richness in tropical forests remain poorly understood, particularly in relation to the impacts

425   of disturbance (Barlow et al., 2016, Terborgh et al., 1990). It is possible that idiosyncratic responses

426   of single or a few taxa to disturbance could create such a negative correlation (Moura et al., 2016),

427   especially if the taxa are acoustically dominant. In general, the strongest correlations we found were

428   with total encounters and MDS1 – metrics that would only be of ecological interest if the

429   underpinning species were well understood, requiring extensive manual surveys and undermining

430   the purpose of acoustic indices. Despite this, the strong positive correlation between Bioacoustic

431   Index and dawn bird species richness and diversity in the day at 0.3-4 kHz is interesting. It is plausible

432   that this time-frequency bin contains the least vocalization from non-target taxa, insects sonify

433   predominantly around >4 kHz and after the dawn chorusing of acoustically dominant vertebrates,

434   particularly red-handed howler monkey *Alouatta belzebul* (Sekulic, 1982). Furthermore, it is after the

435   end of the bird dawn chorus, during which it is possible that intense vocal activity of a few species

436   may mask underlying richness and diversity.

437   We have deliberately chosen to use subjective frequency bins determined by *a priori* knowledge of

438   acoustic space use in our study system, to demonstrate both the wide applicability of this method,

439   and that frequency bin selection need not be onerous to generate substantial benefits. However,

440   choosing narrower or different frequency bins and time periods based on prior quantification of

441   acoustic space use could provide substantial further benefits in understanding the effects of signal

442   masking on correlations. Several existing methods exist to do so, either comprehensively through

443   the multiscalar fractal approach (Monacchi and Farina, 2019), or more broadly using measures of

444   acoustic space use or biophonic density (Aide et al., 2017,Eldridge et al., 2018) Quantifying TFB

445   dominance by even broad acoustic clades could be highly informative and could provide quantifiable

446   data on the relative effect size of the impact of disturbance types on those clades. Additionally,

447   variation in the granularity of TFBs may well reveal further unknown ecological patterns. Whilst we

448   have focused primarily on masking in the frequency domain, and across the diel cycle in the

449   temporal domain, it is entirely plausible that analysis of acoustic indices at both greater and finer

450   temporal scales, and broad frequency ranges, could reveal other patterns. For instance, within dawn

451   choruses where we already know bird species can hold very specific temporal niches in the tropics

452   (Fjeldså et al, 2020), or across seasonal scales such as the winter midday chorus in temperate forests

453   (Farina and Gage, 2017)."

454   We found that acoustic indices are sensitive to soundscapes modified by habitat disturbance and can

455   therefore be highly cost-effective tools for assessing forest condition and monitoring changes in

456   conservation value in response to management interventions or other environmental changes.

457   Acoustic indices are however highly susceptible to signal masking, where divergent responses across

458   temporal and frequency spectrums are masked by calculating indices at inappropriate scales. We

459   therefore recommend that acoustic indices are calculated either at a range of time and frequency

460   bins when used to characterise a landscape, or a narrow bin predetermined by *a priori* ecological

461   understanding of the soundscape when used as a proxy for the biodiversity of a specific taxonomic

462   group.

463

475   Author's contributions:

476   OCM designed the study, undertook data collection, analysed the data and drafted the article. ACL,

477   JB and SM made significant contributions to the study conception and design, aided in data analysis

478   and made substantial revisions to manuscript drafts. CD contributed significantly to the data analysis

479   and made substantial revisions to manuscript drafts. EB contributed greatly to the study design,

480   collection of the data, and made substantial revisions to manuscript drafts.

481   Data Availability:

482   The following datasets are available on the Dryad respository:

483   1. All of the indices values used in this research

484   2. The subset of indices values used for the sensitivity analysis

485   3. The full set of results from the sensitivity analysis

486   4. All of the diversity metrics used in the correlation analysis

487   Available at DOI:10.5061/dryad.dr7sqv9wt.

490   References:

491   Berenguer, E., Ferreira, J., Gardner, T.A., Aragão, L.E.O.C., De Camargo, P.B., Cerri, C.E.,…Barlow, J.,

492   2014. A large-scale field assessment of carbon stocks in human-modified tropical forests. Glob.

493   Chang. Biol. 20, 3713–3726. https://doi.org/10.1111/gcb.12627

494   Boelman, N.T., Asner, G.P., Hart, P.J., Martin, R.E., 2007. Multi-trophic invasion resistance in Hawaii:

495   Bioacoustics, field surveys, and airborne remote sensing. Ecol. Appl. 17, 2137–2144.

496   https://doi.org/10.1890/07-0004.1

497   Bormpoudakis, D., Sueur, J., Pantis, J.D., 2013. Spatial heterogeneity of ambient sound at the habitat

498   type level: Ecological implications and applications. Landsc. Ecol. 28, 495–506.

499   https://doi.org/10.1007/s10980-013-9849-1

500   Bradfer-Lawrence, T., Bunnefeld, N., Gardner, N., Willis, S.G., Dent, D.H., 2020. Rapid assessment of

501   avian species richness and abundance using acoustic indices. Ecol. Indic. 115, 106400.

502   https://doi.org/10.1016/j.ecolind.2020.106400

503   Bradfer-Lawrence, T., Gardner, N., Bunnefeld, L., Bunnefeld, N., Willis, S.G., Dent, D.H., 2019.

504   Guidelines for the use of acoustic indices in environmental research. Methods Ecol. Evol.

505   https://doi.org/10.1111/2041-210x.13254

506   Burivalova, Z., Game, E.T., Butler, R.A., 2019. The sound of a tropical forest. Science (80). 363, 28–29.

507   https://doi.org/10.1126/science.aav1902

508   Burivalova, Z., Towsey, M., Boucher, T., Truskinger, A., Apelis, C., Roe, P., Game, E.T., 2018. Using

509   soundscapes to detect variable degrees of human influence on tropical forests in Papua New Guinea.

510   Conserv. Biol. 32, 205–215. https://doi.org/10.1111/cobi.12968

511   Buxton, R., McKenna, M.F., Clapp, M., Meyer, E., Stabenau, E., Angeloni, L.M.,..., Wittemyer, G.,

512   2018. Efficacy of extracting indices from large-scale acoustic recordings to monitor biodiversity.

513   Conserv. Biol. https://doi.org/10.1111/cobi.13119

514   Carruthers-Jones, J., Eldridge, A., Guyot, P., Hassall, C., Holmes, G., 2019. The call of the wild:

515   Investigating the potential for ecoacoustic methods in mapping wilderness areas. Sci. Total Environ.

516   695. https://doi.org/10.1016/j.scitotenv.2019.133797

517   Chek, A.A., Bogart, J.P., Lougheed, S.C., 2003. Mating signal partitioning in multi-species

518   assemblages: a null model test using frogs. Ecol. Lett. 6, 235–247. https://doi.org/10.1046/j.1461-

519   0248.2003.00420.x

520   Chinchor N., 1992. MUC-4 evaluation metrics. In: Proceedings of MUC-4 – the 4th Conference on

521   Message Understanding. McLean: Association for Computational Linguistics: p. 22–9.

522   Deichmann, J.L., Acevedo-Charry, O., Barclay, L., Burivalova, Z., Campos-Cerqueira, M., d'Horta, F.E.,

523   Mitchell Aide, T., 2018. It's time to listen: there is much to be learned from the sounds of tropical

524   ecosystems. Biotropica 50, 713–718. https://doi.org/10.1111/btp.12593

525   Deichmann, J.L., Hernández-Serna, A., Delgado C., J.A., Campos-Cerqueira, M., Aide, T.M., 2017.

526   Soundscape analysis and acoustic monitoring document impacts of natural gas exploration on

527   biodiversity in a tropical forest. Ecol. Indic. 74, 39–48. https://doi.org/10.1016/j.ecolind.2016.11.002

528   Depraetere, M., Pavoine, S., Jiguet, F., Gasc, A., Duvail, S., Sueur, J., 2012. Monitoring animal

529   diversity using acoustic indices: Implementation in a temperate woodland. Ecol. Indic. 13, 46–54.

530   https://doi.org/10.1016/j.ecolind.2011.05.006

531   Diedenhofen, B., Musch, J., 2015. cocor: A Comprehensive Solution for the Statistical Comparison of

532   Correlations. PLoS One 10, e0121945. https://doi.org/10.1371/journal.pone.0121945

533   Do Nascimento, L.A., Campos-Cerqueira, M., Beard, K.H., 2020. Acoustic metrics predict habitat type

534   and vegetation structure in the Amazon. Ecol. Indic. 117, 106679.

535   https://doi.org/10.1016/j.ecolind.2020.106679

536   Dunn, O.J., 1964. Multiple Comparisons Using Rank Sums. Technometrics 6, 241–252.

537   https://doi.org/10.1080/00401706.1964.10490181

538   Eldridge, A., Guyot, P., Moscoso, P., Johnston, A., Eyre-Walker, Y., Peck, M., 2018. Sounding out

539   ecoacoustic metrics: Avian species richness is predicted by acoustic indices in temperate but not

540   tropical habitats. Ecol. Indic. 95, 939–952. https://doi.org/10.1016/j.ecolind.2018.06.012

541   Farina, A., 2014. Soundscape ecology: Principles, patterns, methods and applications, Soundscape

542   Ecology: Principles, Patterns, Methods and Applications. https://doi.org/10.1007/978-94-007-7374-5

543   Farina, A., Ceraulo, M. 2017. The Acoustic Chorus and its Ecological Significance. In Ecoacoustics: The

544   ecological role of sounds (Farina, A., Gage, S. Editors). Wiley, DOI:10.1002/9781119230724

545   Fjeldså, J., Marks, J. S., and Sharpe, C.J. (2020). Cryptic Forest-Falcon (*Micrastur mintoni*), version 1.0.

546   In Birds of the World (del Hoyo, J. , Elliott, A., Sargatal, J., Christie, D. A., and de Juana, E., Editors).

547   Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.cryfof1.01

548   Frontier Labs, 2015. Bioacoustic Audio Recorder User Guide.

549   Fuller, S., Axel, A.C., Tucker, D., Gage, S.H., 2015. Connecting soundscape to landscape: Which

550   acoustic index best describes landscape configuration? Ecol. Indic. 58.

551   https://doi.org/10.1016/j.ecolind.2015.05.057

552   Gardner, T.A., Barlow, J., Araujo, I.S., Cristina Vila-Pires, T., Bonaldo, A.B., Costa, J.E.,…Peres, C.A.,

553   2008. The cost-effectiveness of biodiversity surveys in tropical forests. Ecol. Lett. 11, 139–150.

554   https://doi.org/10.1111/j.1461-0248.2007.01133.x

555   Gardner, T.A., Ferreira, J., Barlow, J., Lees, A.C., Parry, L., Vieira, I.C.,…Zuanon, J., 2013. A social and

556   ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network.

557   Philos. Trans. R. Soc. Lond. B. Biol. Sci. 368, 20120166. https://doi.org/10.1098/rstb.2012.0166

558   Gibb, R., Browning, E., Glover-Kapfer, P., Jones, K.E., 2019. Emerging opportunities and challenges

559   for passive acoustics in ecological assessment and monitoring. Methods Ecol. Evol.

560   https://doi.org/10.1111/2041-210X.13101

561   Gillooly, J.F., Ophir, A.G., 2010. The energetic basis of acoustic communication. Proc. R. Soc. B Biol.

562   Sci. 277, 1325–1331. https://doi.org/10.1098/rspb.2009.2134

563   Guilford JP. Psychometric Methods. New York City: McGraw-Hill; 1954.

564   Hsieh, T. C., Ma K. H., Chao.A., 2020 iNEXT: iNterpolation and EXTrapolation for species diversity. R

565   package version 2.0.20 URL: http://chao.stat.nthu.edu.tw/wordpress/software-download/.

566   Jorge, F.C., Machado, C.G., da Cunha Nogueira, S.S., Nogueira-Filho, S.L.G., 2018. The effectiveness

567   of acoustic indices for forest monitoring in Atlantic rainforest fragments. Ecol. Indic.

568   https://doi.org/10.1016/j.ecolind.2018.04.001

569   Kruskal, W.H., Wallis, W.A., 1952. Use of Ranks in One-Criterion Variance Analysis. J. Am. Stat. Assoc.

570   47, 583–621. https://doi.org/10.1080/01621459.1952.10483441

571   LeDell, E., Gill, N., Aiello, S., Fu, A., Candel, A., Click, C., Kraljevic, T.,…M., Malohlava, M., (2020). h2o:

572   R Interface for the 'H2O' Scalable Machine Learning Platform. R package version 3.28.0.4.

573   https://CRAN.R-project.org/package=h2o

574   Lima, M.S.C.S., Pederassi, J., Pineschi, R.B., Barbosa, D.B.S., 2019. Acoustic niche partitioning in an

575   anuran community from the municipality of Floriano, Piauí, Brazil. Brazilian J. Biol. 79, 566–576.

576   https://doi.org/10.1590/1519-6984.180399

577   Mammides, C., Goodale, E., Dayananda, S.K., Kang, L., Chen, J., 2017. Do acoustic indices correlate

578   with bird diversity? Insights from two biodiverse regions in Yunnan Province, south China. Ecol. Indic.

579   82, 470–477. https://doi.org/10.1016/j.ecolind.2017.07.017

580   Metcalf, O.C., Lees, A.C., Barlow, J., Marsden, S.J., Devenish, C., 2020. hardRain: An R package for

581   quick, automated rainfall detection in ecoacoustic datasets using a threshold-based approach. Ecol.

582   Indic. 109, 105793. https://doi.org/10.1016/j.ecolind.2019.105793

583   Metcalf, Oliver et al. (2020), Acoustic indices perform better when applied at ecologically meaningful

584   time and frequency scales, Dryad, Dataset, https://doi.org/10.5061/dryad.dr7sqv9wt

585   Mitchell, S.L., Edwards, D.P., Bernard, H., Coomes, D., Jucker, T., Davies, Z.G., Struebig, M.J., 2018.

586   Riparian reserves help protect forest bird communities in oil palm dominated landscapes. J. Appl.

587   Ecol. 55, 2744–2755. https://doi.org/10.1111/1365-2664.13233

588   Monacchi, D., Farina, A. A Multiscale Approach to Investigate the Biosemiotic Complexity of Two

589   Acoustic Communities in Primary Forests with High Ecosystem Integrity Recorded with 3D Sound

590   Technologies. Biosemiotics 12, 329–347 (2019). https://doi.org/10.1007/s12304-019-09361-z

591   Moreno-Gómez, F.N., Bartheld, J., Silva-Escobar, A.A., Briones, R., Márquez, R., Penna, M., 2019.

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

593   Indic. 103. https://doi.org/10.1016/j.ecolind.2019.03.024

594   Moura, N.G., Lees, A.C., Andretti, C.B., Davis, B.J.W., Solar, R.R.C., Aleixo, A.,…Gardner, T.A., 2013.

595   Avian biodiversity in multiple-use landscapes of the Brazilian Amazon. Biol. Conserv. 167, 339–348.

596   https://doi.org/10.1016/j.biocon.2013.08.023

597   Moura, N.G., Lees, A.C., Aleixo, A., Barlow, J., Berenguer, E., Ferreira, J., Mac Nally, R., Thomson, J.R.,

598   Gardner, T.A., 2016. Idiosyncratic responses of Amazonian birds to primary forest disturbance.

599   Oecologia 180, 903–916. https://doi.org/10.1007/s00442-015-3495-z

600   Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, Dan., Minchin,

601   P.R., …Wagner, H., (2019). vegan: Community Ecology Package. R package version 2.5-6.

602   https://CRAN.R-project.org/package=vegan

603   Pieretti, N., Duarte, M.H.L., Sousa-Lima, R.S., Rodrigues, M., Young, R.J., Farina, A., 2015.

604   Determining temporal sampling schemes for passive acoustic studies in different tropical

605   ecosystems. Trop. Conserv. Sci. 8. https://doi.org/10.1177/194008291500800117

606   Pieretti, N., Farina, A., Morri, D., 2011. A new methodology to infer the singing activity of an avian

607   community: The Acoustic Complexity Index (ACI). Ecol. Indic. 11, 868–873.

608   https://doi.org/10.1016/j.ecolind.2010.11.005

609   Priyadarshani, N., Marsland, S., Castro, I., 2018. Automated birdsong recognition in complex acoustic

610   environments: a review. J. Avian Biol. https://doi.org/10.1111/jav.01447

611   R Core Team (2017). R: A language and environment for statistical computing. R Foundation for

612   Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

613

614   Rodriguez, A., Gasc, A., Pavoine, S., Grandcolas, P., Gaucher, P., Sueur, J., 2014. Temporal and spatial

615   variability of animal sound within a neotropical forest. Ecol. Inform. 21, 133–143.

616   https://doi.org/10.1016/j.ecoinf.2013.12.006

617   Ryan, M.J., Brenowitz, E.A., 1985. The role of body size, phylogeny, and ambient noise in the

618   evolution of bird song. Am. Nat. 126, 87–100. https://doi.org/10.1086/284398

619   Schmidt, A.K.D., Römer, H., Riede, K., 2013. Spectral niche segregation and community organization

620   in a tropical cricket assemblage. Behav. Ecol. 24, 470–480. https://doi.org/10.1093/beheco/ars187

621   Seddon, N., 2005. Ecological adaptation and species recognition drives vocal evolution in Neotropical

622   suboscine birds. Evolution (N. Y). 59, 200–215. https://doi.org/10.1111/j.0014-3820.2005.tb00906.x

623   Sedláček, O., Vokurková, J., Ferenc, M., Djomo, E.N., Albrecht, T., Hořák, D., 2015. A comparison of

624   point counts with a new acoustic sampling method: a case study of a bird community from the

625   montane forests of Mount Cameroon. Ostrich 6525.

626   https://doi.org/10.2989/00306525.2015.1049669

627   Sekulic', R., 1982. The Function of Howling in Red Howler Monkeys (Alouatta seniculus).

628   Behaviour,81(1), 38-54.

629   Sueur, J., Farina, A., Gasc, A., Pieretti, N., Pavoine, S., 2014. Acoustic indices for biodiversity

630   assessment and landscape investigation. Acta Acust. united with Acust. 100.

631   https://doi.org/10.3813/AAA.918757

632   Sueur, J., Pavoine, S., Hamerlynck, O., Duvail, S., 2008. Rapid acoustic survey for biodiversity

633   appraisal. PLoS One 3. https://doi.org/10.1371/journal.pone.0004065

634   Sugai, L.S.M., Silva, T.S.F., Ribeiro, J.W., Llusia, D., 2019. Terrestrial Passive Acoustic Monitoring:

635   Review and Perspectives. Bioscience. https://doi.org/10.1093/biosci/biy147

636   Tobias, J.A., Planqué, R., Cram, D.L., Seddon, A.N., 2014. Species interactions and the structure of

637   complex communication networks. Proc. Natl. Acad. Sci. U. S. A. 111, 1020–1025.

638   https://doi.org/10.1073/pnas.1314337111

639   Towsey, M., Wimmer, J., Williamson, I., Roe, P., 2014. The use of acoustic indices to determine avian

640   species richness in audio-recordings of the environment. Ecol. Inform. 21, 110–119.

641   https://doi.org/10.1016/j.ecoinf.2013.11.007

642   Villanueva-Rivera, L.J., Pijanowski, B.C., Doucette, J., Pekin, B., 2011. A primer of acoustic analysis for

643   landscape ecologists. Landsc. Ecol. 26, 1233–1246. https://doi.org/10.1007/s10980-011-9636-9

644   Wagner Ribeiro Jr, J., Larissa Sayuri Moreira Sugai, B., Marconi Campos-Cerqueira, B., by Dirk Sven

645   Schmeller, C., 2017. Passive acoustic monitoring as a complementary strategy to assess biodiversity

646   in the Brazilian Amazonia. Biodivers. Conserv. 26, 2999–3002. https://doi.org/10.1007/s10531-017-

647   1390-0

648   Wilkins, M.R., Seddon, N., Safran, R.J., 2013. Evolutionary divergence in acoustic signals: Causes and

649   consequences. Trends Ecol. Evol. https://doi.org/10.1016/j.tree.2012.10.002

650   Zou, G.Y., 2007. Toward Using Confidence Intervals to Compare Correlations. Psychol. Methods 12,

651   399–413. https://doi.org/10.1037/1082-989X.12.4.399

652

653

654