

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA
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**EFEITOS DA INSULARIZAÇÃO SOBRE A COMUNICAÇÃO
ACÚSTICA EM AVES DO RESERVATÓRIO DA UHE DE BALBINA,
AMAZONAS**

THIAGO BICUDO KREMPEL SANTANA

Manaus, Amazonas

Maio, 2015

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Orientadora: Dra. Marina Anciães

Co-orientador: Dr. Pedro Ivo Simões

Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requerimentos para obtenção do título de Mestre em Biologia (Ecologia) em Maio de 2015.

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BANCA EXAMINADORA DA DEFESA ORAL PÚBLICA

Dr. Renato Cintra Soares
(INPA)

Dr. Fabricio Beggiato Baccaro
(UFAM)

Dr. Igor Luis Kaefer
(UFAM)

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Sinopse :

Verificou-se a existência de variação vocal em duas espécies de aves suboscines entre ilhas fluviais de diferentes tamanhos e graus de isolamento, e se esta variação vocal relacionava-se com o tamanho, grau de isolamento e estrutura da vegetação das ilhas.

Palavras-Chave: Character release, Adaptação acústica, Suboscines, Isolamento, Ilhas

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"Te esconde bem-te-vi, Voa
bicudo, Voa sanhaço, Vai juriti,
Bico calado, Muito cuidado,
Que o homem vem aí, O
homem vem aí"

(Chico Buarque)

RESUMO

Alterações ambientais podem impor mudanças importantes aos sistemas de comunicação das espécies. Em aves, tais alterações podem desencadear variações em sinais acústicos utilizados para a comunicação a longa distância. Em florestas tropicais contínuas, há uma alta riqueza de espécies vocalmente ativas, as quais, entre outras estratégias, evitam a sobreposição de seus sinais no espaço acústico emitindo-os em faixas de frequência relativamente estreitas. Em contrapartida, ambientes insulares abrigam menos espécies e um espaço acústico menos saturado, possibilitando que sinais acústicos variem mais em suas propriedades espectrais e temporais. Ao mesmo tempo, tais propriedades são adaptadas de forma a otimizar a distância de propagação no habitat predominante. Apesar das vocalizações serem relativamente bem estudada em sistemas naturais, não sabemos ainda se a insularização de paisagens naturais promovidas pela ação humana em tempo recente é capaz de desencadear mudanças nos sistemas de comunicação em aves suboscines. Neste estudo, investiguei a variabilidade em propriedades espectrais e temporais dos sinais acústicos de duas espécies (*Lipaugus vociferans* e *Tyrannetes virescens*) em ilhas de um lago artificial criado pelo represamento do rio Uatumã, Estado do Amazonas, Brasil. Especificamente, testei se esta variabilidade relacionava-se à variação em área e isolamento, como proxies da comunidade acústica, e em estrutura da vegetação presente nas ilhas. Obtive gravações de 67 indivíduos de *L. vociferans* e 69 indivíduos de *T. virescens* em 12 ilhas do lago, totalizando 322 e 345 cantos de cada espécie, respectivamente. Variações nas médias da largura de banda do canto de *L. vociferans* relacionaram-se com área e isolamento das ilhas enquanto para *T. virescens* não houve relação. As médias da frequência mais baixa e de pico das duas espécies relacionaram-se com variações na estrutura da vegetação, onde frequências mais altas foram encontradas em ilhas com maiores valores de área basal. As propriedades temporais dos cantos das duas espécies não apresentaram relação com variações em área, isolamento e estrutura da vegetação. Nossos resultados demonstram que mesmo em espécies suboscines, onde os cantos são inatos, mudanças sutis no ambiente e em um curto espaço de tempo, podem levar a variações nas propriedades acústicas espectrais dos cantos. Estudos futuros deverão avaliar o potencial evolutivo que estas variações nos sinais acústicos podem ter, analisando a variação genética entre as populações das espécies estudadas.

ABSTRACT

Effects of insularization on acoustic communication in birds on the hydropower reservoir of Balbina, Amazonas.

Environmental change may impose significant shifts to natural communication systems. In birds, such changes may trigger variations in acoustic signals used for communication over long distances. In tropical forests there is a high proportion of species that are vocally active, which, among other strategies, avoid overlap of signals in the acoustic space by calling in narrow frequency bands. On the other hand, islands have fewer species and less saturated acoustic space, allowing for acoustic signals to vary in spectral and temporal properties. At the same time, these properties are adapted in a way that optimizes the propagation distance in the predominant habitat. Despite acoustic signals being relatively well studied in natural systems, it is unclear whether insularization promoted by human activity on natural landscapes in recent time is able to trigger changes in communication systems in suboscines birds. This study investigated the variability in spectral and temporal properties of acoustic signals of two suboscines birds (*Lipaugus vociferans* and *Tyrannetes virescens*) on islands of an artificial lake created by damming the Uatumã River in the state of Amazonas, Brazil. Specifically, I tested whether this variability was related to variation in the islands area and isolation, as proxies of the acoustic community, while considering the vegetation structure present on the islands. I obtained recordings from 67 *L. vociferans* individuals and 69 *T. virescens* on 12 islands across the lake, totaling 322 and 345 songs recordings for each species, respectively. Variations in bandwidth of *L. vociferans* songs were related to the area and isolation of the islands, whereas such relationships were not observed for songs of *T. virescens*. In both species, average lower and peak frequencies of songs were related to variation in vegetation structure, where higher frequencies were found in islands with greater basal area. The temporal properties of the songs of the two species were not associated with variations in area, isolation and structure of vegetation. Our results show that even in suboscines species, where the songs are innate, subtle changes in the environment in a short time, can lead to changes in spectral acoustic properties. Future studies should evaluate the potential evolutionary impacts that these changes in acoustic signals may have, by assessing genetic variation among birds inhabiting islands in this system.

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INTRODUÇÃO GERAL

As alterações no ambiente influenciam a seleção de características importantes para as espécies, como a seleção de fenótipos. Para as aves, os efeitos das modificações ambientais podem ser percebidos através de mudanças nos sinais acústicos (cantos) que elas emitem (Laiolo and Tella 2006). Os sinais acústicos carregam diversas informações sobre o emissor (e.g. tamanho, estado reprodutivo) portanto, a detecção de tais mudanças nos sinais acústicos emitidos pode ser útil para prever de forma mais rápida os efeitos de modificações ambientais sobre a sobrevivência e reprodução das espécies, já que sinais disfuncionais podem afetar o sucesso reprodutivo de indivíduos (Ey and Fischer 2009; Slabbekoorn 2013).

A eficiência dos sinais acústicos em transmitir informação à longa distância depende, entre outros fatores, de sua adaptação à comunidade acústica local e ao ambiente de transmissão. Sinais acústicos emitidos por espécies residentes em ambientes ocupados por um grande número de espécies filogeneticamente próximas tendem a serem menos variáveis, ocupando faixas de frequência estreitas evitando assim a sobreposição com os sinais acústicos das outras espécies (hipótese de *character release* - Kroodsma 1985; Naugler and Ratcliffe 1994). Por outro lado, ilhas representam ecossistemas mais simples e isolados, tendo uma menor riqueza de espécies (MacArthur and Wilson 1967) e menor saturação do espaço acústico, possibilitando maior variabilidade dos sinais acústicos (Morinay et al. 2013). Pressões seletivas adicionais sobre características dos sinais acústicos são determinadas por características do meio de transmissão, onde as características da vegetação (e.g. árvores, folhagens) irão moldar os sinais acústicos de forma a otimizar sua transmissão em sistemas de comunicação a longa distância (hipótese adaptação acústica - Morton 1975), portanto os sinais acústicos de espécies que habitam ambientes florestais mais densamente vegetados estarão sujeitos a pressões seletivas distintas das quais estão sujeitos os sinais de espécies que habitam ambientes abertos, devido à influência de troncos, ramos e folhagem sobre sua reverberação e atenuação (Slabbekoorn et al. 2002).

No presente estudo, investiguei o efeito da insularização ocasionada pelo represamento de um rio para a instalação de uma Usina Hidrelétrica na Amazônia central brasileira sobre características espectrais e temporais dos sinais acústicos de duas espécies de aves suboscines, *Lipaugus vociferans* e *Tyrannetes virescens*. Especificamente avaliei a existência de relações entre a variação em área e isolamento de ilhas deste arquipélago artificial, usados aqui como *proxies* para a complexidade da comunidade acústica, e a variação em propriedades espectrais e temporais dos sinais acústicos das duas espécies, como previsto pela hipótese de *character*

release. Além disto, investigamos se a variação destas propriedades entre ilhas poderiam estar relacionadas a diferenças na estrutura da vegetação presente em cada ilha, como previsto pela hipótese de adaptação acústica.

OBJETIVOS

Objetivo Geral

Avaliar o efeito da insularização causada por um reservatório hidrelétrico na Amazônia central sobre os sinais acústicos de duas espécies de aves suboscines, *Lipaugus vociferans* e *Tyranneutes virescens*.

Objetivos Específicos

- Avaliar se o canto das espécies focais varia em suas características espectrais e temporais em função da área e do grau de isolamento de ilhas distribuídas ao longo do lago artificial criado pela UHE de Balbina, no rio Uatumã, Estado do Amazonas.
- Avaliar como diferenças na estrutura da vegetação presente em cada ilha relacionam-se com a variabilidade das características espectrais e temporais do canto das espécies focais.

Capítulo I.

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Insularization effects on acoustic signals of two suboscine Amazonian birds

Thiago Bicudo^{1,2*}, Marina Anciães², Diego Gil³, Maira Benchimol^{4,5}, Carlos A. Peres⁴,
Pedro Ivo Simões⁶

¹ Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da
Amazônia, Manaus, Amazonas, Brazil.

² Laboratório de Evolução e Comportamento Animal; Coordenação de Biodiversidade
(CBio); Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil.

³ Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC),
José Gutiérrez Abascal 2, 28006 Madrid, Spain

⁴ School of Environmental Sciences, University of East Anglia, Norwich Research Park,
Norwich NR47TJ, UK.

⁵ Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, Rodovia
Ilhéus Itabuna, Km 16, 45650-000, Ilhéus, BA – Brazil

⁶ Laboratório de Sistemática de Vertebrados, Faculdade de Biociências (FABIO),
Pontifícia Universidade Católica do Rio Grande do Sul.

*Corresponding author

E-mail Address: bicudo_se@hotmail.com

Telephone/Fax: (0xx92) 36431823

1 LAY SUMMARY

2 We investigated whether the fragmentation of an originally continuous Amazon
3 rainforest caused by river damming could be associated with differences in acoustic
4 traits of two birds with innate song repertoire. We found that birds of one species
5 emitted songs at bandwidths wider than expected when recorded in small and isolated
6 islands. Also, that in both species characteristics of particular notes of the song varies
7 independently according to the forest structure in the impacted landscape.

8

9 Insularization effects on acoustic signals of two suboscine Amazonian birds

10 ABSTRACT

11 Environmental change may alter the communication systems of birds by imposing shifts
12 in their acoustic signals. In tropical forests, vocally active species usually avoid
13 overlapping signals in the acoustic space by calling in narrow frequency ranges,
14 whereas in islands a less saturated acoustic space allows acoustic signals to vary. Some
15 signals are also adapted to optimize their propagation in the prevailing habitat. Despite
16 the accumulated knowledge about the drivers of acoustic variation, it is unclear if men-
17 induced insularization of natural landscapes is able to unleash alterations in the
18 communication systems of birds. The variability of acoustic signal properties was
19 investigated in two species of suboscine birds (*Lipaugus vociferans* and *Tyrannetes*
20 *virescens*) in islands within an artificial lake created by the damming of Uatumã River,
21 in central Brazilian Amazon. We tested if signal variability was related to variation in
22 acoustic community proxies (island area and isolation), while considering vegetation
23 structure. Bandwidth variation in *L. vociferans* song was related to island's area and
24 isolation, though those relations were not observed in *T. virescens* songs. Mean lowest
25 and peak frequencies of both species songs were also higher in islands with greater tree
26 basal area. None of the temporal properties of either species songs were associated to
27 variations in islands characteristics. Our study suggests that land use changes may lead
28 to alterations in particular traits of acoustic signals for species in which songs are innate.

29 KEYWORDS: Acoustic adaptation, character release, islands, habitat fragmentation,
30 hydropower.

31 INTRODUCTION

32 Environmental changes influence the selection of important characteristics to species
33 (Gienapp et al. 2008). When an environment is altered and new selective pressures are
34 imposed, resident populations may fit the new environment by phenotypic plasticity,
35 when only the phenotype is modified without underlying genetic change, or by
36 adaptation to the new selection system, resulting on the setting of the modified
37 phenotype (Gross et al. 2010). Landscape changes often lead to alterations in the
38 communication systems of birds, and these are detected as directional variations in their
39 acoustic signals (Laiolo and Tella 2006; Slabbekoorn and den Boer-Visser 2006; Luther
40 and Baptista 2010; Salaberria and Gil 2010; Slabbekoorn 2013; Luther and Magnotti
41 2014; Gil et al. 2014). Acoustic signals may carry several cues about their sender (*e.g.*
42 size, reproductive condition, behavioral state), playing an important role in conspecific
43 communication and in sexual selection processes (Brumm 2006; Ey and Fischer 2009).
44 Furthermore, they mediate many ways of inter-individual interactions, such as neighbor
45 recognition, territory defense, mate attraction, and the location and condition of the
46 sender, having a direct influence on the individual's survival and on its reproductive
47 success (Catchpole and Slater 2008).

48 Contiguous tropical forests have a high richness of vocally active species, which
49 amongst other strategies avoid overlapping their signals in acoustic space by emitting
50 sounds in relatively narrow frequency ranges. Competition over the use of acoustic
51 space would thus lead to reduced variability in bird songs in those environments
52 (Brumm and Slabbekoorn 2005; Brumm 2006; Planqué and Slabbekoorn 2008; Luther
53 2009). On the other hand, island environments usually have a more reduced number of
54 habitats, supporting fewer species and, consequently, have a less saturated acoustic

55 space, enabling acoustic signals to vary more in their spectral and temporal properties
56 without impairing its function in conspecific communication systems (MacArthur and
57 Wilson 1967; Kroodsma 1985; Naugler and Ratcliffe 1994; Morinay et al. 2013). The
58 increase in acoustic signal variability resulting from a smaller number of competing
59 species in certain areas of a species distribution is an evolutionary process known as
60 character release, and its occurrence was proposed based on songbird (Oscines) signals
61 in temperate habitats (Kroodsma 1985; Naugler and Ratcliffe 1994).

62 Additional selective pressures over acoustic signal features are determined by
63 characteristics of the transmission path. The integrity of acoustic signals is usually
64 affected by physical obstacles present throughout its propagation route represented, for
65 example, by vegetation (Morton 1975; Slabbekoorn et al. 2002; Slabbekoorn and den
66 Boer-Visser 2006). In general, acoustic signals are adapted to optimize its propagation
67 distance in the prevailing habitat and some common patterns are shared between signals
68 emitted by species that inhabit similar environments (Acoustic Adaptation Hypothesis –
69 Morton 1975). Species that primarily occur in high tree density environments tend to
70 emit acoustic signals at relatively low frequencies, with narrower bandwidths and long
71 intervals between notes (Morton 1975) that those species that inhabit open
72 environments, which in turn tend to generate higher frequency acoustic signals, with
73 broader bandwidths and short intervals between notes (Boncoraglio and Saino 2007).
74 These adaptations supposedly diminish the loss of information contained in the signals
75 due to reverberation effects or excess attenuation during propagation (Slabbekoorn et al.
76 2002).

77 Compared to contiguous environments, islands usually represent simpler and
78 more isolated ecosystems, where there is frequently lower number of species, of

79 available habitats and of conspecific competition, enabling resident species to expand
80 their ecological niche (Blondel et al. 1988). Recent studies suggest that the spectral
81 variation in island environments is related to the number of congeneric species present,
82 with a narrower bandwidth in places occupied by a larger number of phylogenetically
83 close species (see a recent review in Morinay et al. 2013). Thus, insularization, and the
84 associated reduced environmental variability, seems to be important in determining the
85 vocal repertoire, inducing small but significant shifts in the fine features of acoustic
86 signals. However, those studies were restricted to natural oceanic islands, with a high
87 degree of historical and geographical isolation from the nearest continent (Morinay et
88 al. 2013). Relationships between variation in birds' acoustic signals and insularization
89 caused by recent human activity are yet to be investigated. Such information is
90 important since landscape change triggered by anthropogenic actions may induce
91 alterations in avian communication systems just in a few decades (Laiolo 2010; Luther
92 and Baptista 2010). The detection of such alterations may be useful to predict in a faster
93 way the effects of environmental change over the survival and reproduction of species,
94 since dysfunctional signals may affect the individuals' reproductive success.

95 In this study, we investigated possible associations between insularization caused
96 by damming of a river in central Brazilian Amazon, and the variation in spectral and
97 temporal features of acoustic signals in two suboscines bird species, *Lipaugus*
98 *vociferans* and *Tyranneutes virescens*. These species persisted in islands of different
99 sizes and isolation levels after the artificial lake was filled about three decades ago.
100 Variation in island size and isolation, in turn, has a predictable relation with the number
101 of bird species present in each island, where smaller and more isolated islands has a
102 smaller number of species (Silva 2010).

103 Most studies show that suboscines do not learn their songs, although some levels
104 of learning have been shown in some species (Saranathan et al. 2007; Kroodsma et al.
105 2013) Although this implies a lower level of plasticity, previous studies do show that
106 suboscines also show seemingly adaptive song modifications, although to a lesser extent
107 than oscines (Ríos-Chelén et al. 2012).

108 Thus, differences between islands in suboscine species would likely imply the
109 action of natural selection, since drift and vocal plasticity are reduced. Specifically, we
110 assessed the existence of relations between the variation in area and isolation of
111 artificial islands in this archipelago (here used as *proxies* for the complexity of the
112 islands' acoustic community) and the variation in temporal and spectral properties of
113 the acoustic signals of both species, as predicted by the character release hypothesis.
114 Moreover, we investigated if the variation of these properties between islands could be
115 related to the difference in vegetation structure of each island, as predicted by the
116 acoustic adaptation hypothesis (Morton 1975).

117

118 MATERIAL AND METHODS

119 Study Area

120 The study was conducted in Balbina Hydroelectric Dam's (BHP) reservoir, Amazonas
121 State, Brazil, created in 1986 by the damming of Uatumã River. The resulting lake
122 covers an area of approximately 4,000 km², in which about 3,500 forest islands of
123 several sizes (~ 0.1–4,878.0 ha) and shapes are scattered, surrounded by fresh water
124 (Benchimol and Peres 2015a). The vegetation in the region is classified as dense
125 submontane forest, with annual mean temperature of 28 °C and average rainfall of 2,376

126 mm. The islands sampled in this study are within or in adjacent areas of the Uatumã
127 Biological Reserve (0° 50' – 1° 55' S; 58° 50' – 60° 10' W), a federal conservation unit
128 that covers both the island landscape and the contiguous adjacent areas in higher
129 terrains in the east bank of Uatumã River, Amazonas State, Brazil.

130

131 Sampling design and exploratory variables

132 We selected 13 islands from the BHP's reservoir, varying in area from 14 to 700 ha.
133 The islands were chosen based on its accessibility, with a minimum distance of 2 km
134 between each other, and with broad distribution throughout the reservoir (Fig. 1).
135 Moreover, islands were selected based on the existence of environmental and metric
136 spatial data, obtained from previous studies (Benchimol and Peres 2015a). For each
137 island, the total area in hectares ($\log_{10} x$; "AREA") was calculated using Landsat
138 ETM+ scenes (230/061 and 231/061; year 2009) in the software Arc View 10.1 (ESRI
139 2011).

140 The degree of island isolation in relation to the local landscape was estimated
141 through an adaptation of the proximity index (PROX), by McGarigal et al. (2012),
142 based on the sum of areas of all islands within the landscape and divided by the squared
143 distance from the focal island to each island in the landscape, using a buffer of 250 m
144 (see Benchimol and Peres 2015b for details). In each island, specific variables of the
145 vegetation structure that could be related to transmission and acoustic signals distortions
146 were measured. Tree density estimates (TD) and tree basal area (BA) were obtained
147 with a diameter at breast height (DBH) ≥ 10 cm in 34 rectangular plots (250 m X 10 m)
148 distributed amongst the 13 islands, accordingly to its size. Islands with up to 100 ha

149 (n=7) had two plots, islands between 100 and 500 ha (n=4), three plots, and islands with
150 more than 500 ha (n=2), four plots (for details see Benchimol and Peres 2015a). TD
151 estimates consisted on the mean tree value per plot of 0.25 ha. The tree basal area
152 values were first obtained by calculating the BA value by individual within each plot.
153 Then, all the individual values of BA in each plot were summed, generating a total
154 value of BA by plot. To obtain an average BA value per island, an arithmetic mean was
155 calculated out of the total BA values between plots, which were used in the statistical
156 analyses.

157

158 Focal Species

159 *Lipaugus vociferans* (Passeriformes, Cotingidae) and *Tyranneutes virescens*
160 (Passeriformes, Pipridae) are species commonly found within forest remnants of the
161 BHP reservoir's (Silva 2010). Both species are vocally very active in these areas and
162 their songs are easily recognizable.

163 *L. vociferans* vocalizes in frequencies between 2.0–5.0 kHz and its song is
164 composed of one introductory note with low frequency, emitted at a narrow bandwidth
165 and low sound amplitude, followed by two "Pee Haw" notes of high amplitude and
166 extreme frequency modulation (Fig. S1). The first has exclusively ascending
167 modulation frequency and the second has a first portion with steep ascending frequency
168 modulation, followed by a second portion of descending frequency modulation and a
169 final portion with short bandwidth and no modulation (Fitzsimmons et al. 2008). The
170 species inhabits the forest midstory, where males group in *leks* within a 40 to 60 m

171 distance from one another, vocalizing regularly from the same branch throughout the
172 day (Kirwan and Green 2011).

173 *T. virescens* has a relatively simple song, composed by four "chuckle-de-dee"
174 notes. The fourth note is longer than the initial three notes, but all elements are emitted
175 at a relatively narrow frequency bandwidth, around 3.0 kHz (Beeb 1910; Fig. S2). It
176 inhabits the forest midstory where males group in disperse *leks*, distancing 25 to 30 m
177 from each other (Snow 1961).

178

179 Song Recordings

180 The recordings were undertaken between October and November 2013 and in October
181 2014. Continuous focal recordings were taken of at least five complete songs per
182 individual and from at least five individuals of each species per island. All individuals
183 were recorded using a Sennheiser ME 66 directional microphone and a Tascam DR-100
184 digital recorder. The recordings of each species were conducted in a single day in each
185 island. The geographic location of each recorded individual was obtained by a GPS,
186 avoiding duplicated recordings of the same individual. In six islands it was not possible
187 to get the minimum number of five recorded individuals of one of the species in just one
188 day. Thus, we took a second trip to these islands and conducted the remaining
189 recordings on the diametrically opposite side from where we obtained the first set of
190 recordings, to avoid recording twice the same individual. During recordings, focal
191 individuals remained in stable positions within their territories (at least 30 m from
192 neighboring males), enabling us to monitor the position of recorded individuals and
193 allowing individual identification based on spatial location (Fitzsimmons et al. 2008).

194 All recordings were done using a sampling rate of 48 kHz and 24 bits, stored in .WAV
195 format, and later analyzed in Raven Pro 1.4 (Cornell Lab of Ornithology, Ithaca, NY,
196 USA)

197

198 Acoustic parameters

199 For *L. vociferans*, we measured for each note of the song the following parameters
200 (based in Fitzsimmons et al. 2008): highest frequency (HF), lowest frequency (LF),
201 bandwidth (BW), peak frequency (PF), note duration (ND), song duration (SD) and the
202 inter-note silent interval between the introductory note and the first note of the song
203 ($IN_{IntroN1}$) (Table S1; Fig. S1). Some individuals produced more than one introductory
204 note, but, for this study, we considered only the introductory note closest to the song in
205 the analyses.

206 For *T. virescens* we measured the highest frequency (HF), lowest frequency (LF),
207 bandwidth (BW), peak frequency (PF) and duration (ND) of each note that formed the
208 song. We also measured song duration (SD) and the silent intervals between
209 consecutive notes (IN) (Table S1; Fig S2).

210 For both species temporal variables were estimated from oscillograms and
211 spectral variables from power spectra. Highest and lowest frequencies were measured
212 20 dB below the peak frequency, avoiding overlap with background noise. All
213 recordings were filtered to reduce background noise outside the frequency range used
214 by the species. For *T. virescens* we used a 2000 Hz high-pass frequency and a 5000 Hz
215 low-pass frequency. For *L. vociferans*, a 450 Hz high-pass frequency and a 6500 Hz
216 low-pass frequency were used. The selected songs were chosen from the original

217 continuous recordings, based on the highest signal/noise ratio, through visual inspection
218 of the spectrograms (configuration: window type: Hann; FFT: 1024 samples; DFT:
219 2048 samples, overlap: 86.4%; hop size: 2.90 ms; grid spacing: 23.4 Hz).

220 From each individual recording, five songs were analyzed, from which the
221 individual arithmetic mean of each acoustic variable was calculated. Individual means
222 were used to calculate the mean values of the acoustic variables of each sampled island
223 in multiple regression analyses, described as follows.

224

225 Statistical Analyses

226 Pearson's correlation test was applied to verify whether correlations between the
227 environmental variables (AREA, PROX, TD and BA) existed. To test the character
228 release hypothesis we first performed multiple regressions between the bandwidth (BW)
229 of each of the song's note for both species and the variables that represent the size and
230 isolation of the islands (AREA, PROX). To assess the existence of relations between
231 song acoustic properties of both species not explicitly predicted by the *character*
232 *release* hypothesis, we applied multivariate multiple regressions (MMR), considering as
233 dependent variables the first two axes generated by a principal component analysis
234 (PCA) on the island means of all acoustic variables. AREA and PROX were log-
235 transformed to normalize the data, and used as independent variables.

236 To assess if variation in acoustic characters of each species could reflect acoustic
237 adaptation to differences in the vegetation structure between islands, we first applied
238 multiple regressions between the means per island of spectral (BW, PF, HF, LF) and
239 temporal (SD and IN) acoustic variables of each note and the descriptor variables of the

240 vegetation structure (TD and BA). According to assumptions of the acoustic adaptation
241 hypothesis, BW, PF, HF, LF, SD and IN should be particularly affected by changes in
242 the transmission medium due to variations in the vegetation structure and, therefore,
243 were tested individually. On a second approach, we applied MMRs considering as
244 dependent variables the first two axes resulting from a PCA over means, per island, of
245 all acoustic variables. The estimated TD and BA from each island were considered as
246 independent variables.

247 We have also created a more complex model in order to control possible effects of
248 TD over the model. For this, we considered the first two axes of the PCA as dependent
249 variables, of all acoustic variables, and AREA and PROX as independent variables
250 inserting the TD as a co-variable in the MMR. All analyzes were conducted in the
251 software R version 3.1.1 (R Development Core Team 2011).

252

253 RESULTS

254 Of the 13 sampled islands, two had only one of the species (Relógio: *L. vociferans*;
255 Moita: *T. virescens*). Therefore, only 12 islands per species were used in all analyses for
256 each species. We obtained a total of 67 independent recordings of *L. vociferans* and 69
257 recordings of *T. virescens*. Overall, we analyzed 335 and 345 songs of each of these
258 species, respectively (Table 1). Correlations between descriptor variables of the islands
259 environment were generally weak (Pearson's $r = 0.00-0.42$), except between island
260 isolation (PROX) and tree basal area (BA) (Pearson's $r = 0.67$, $p = 0.01$).

261 Character release

262 Variation in bandwidth of acoustic signals of *L. vociferans* among islands was overall
263 related to variation in island area and isolation. However, the direction of the
264 relationships varied among different elements (notes) of the song (Table 2). Average
265 bandwidth of signals was usually wider among recordings proceeding from more
266 isolated islands and with smaller area. However, average bandwidth of the introductory
267 note was generally wider in less isolated islands (Table 2). The average bandwidth of
268 notes that constitute *T. virescens* songs did not change as a function of variation in area
269 or isolation of the islands (Table 2).

270 A principal component analysis (PCA) on the means by island of acoustic
271 variables of *L. vociferans* resulted in two first main axes that represented approximately
272 60% of the total acoustic variation (PC1: 37.67%; PC2: 22.35%). Both axes were more
273 closely associated with the spectral acoustic variables of the song's second note (Table
274 S2), which has a steep ascending frequency modulation. A PCA on the means by island
275 of acoustic variables of *T. virescens* recovered two first main axes which also
276 summarized about 60% of the total acoustic variation (PC1: 38.25%; PC2: 21.97%).
277 The highest and peak frequencies of notes 1, 3 and 4, as well as the bandwidth of note 4,
278 had high loadings on the first component. The second component was more strongly
279 related to lowest frequency variation of the song's second note (Table S2).

280 The multivariate multiple regression analysis (MMR) considering the two first
281 axes generated by the PCA on *L. vociferans* acoustic variables as dependent variables,
282 indicated that variation in properties of *L. vociferans* songs was related to variation in
283 island characteristics, and more strongly associated with differences in the degree of

284 isolation among islands (AREA: $F_{8,9} = 2.30$, $p = 0.16$, $N = 12$; PROX: $F_{8,9} = 4.74$, $p =$
285 0.04 , $N = 12$). In *T. virescens*, MMR using the first and second principal components
286 produced by the PCA indicated that the variation in acoustic features of the songs was
287 not related to variation in area or isolation of the islands (AREA: $F_{8,9} = 0.13$, $p = 0.87$,
288 $N = 12$; PROX: $F_{8,9} = 1.26$, $p = 0.04$, $N = 12$).

289 When we controlled possible effects that TD might had over the analyses (*i.e.*
290 islands of the same size may vary in tree density) by adding it as a covariate, the
291 uncovered relationships between acoustic traits and island isolation are still significant
292 for *L. vociferans* (AREA: $F_{7,8} = 2.04$, $p = 0.19$, $N = 12$; PROX: $F_{7,8} = 5.04$, $p = 0.04$, N
293 $= 12$), and variation in TD was negligible in explaining variation in acoustic traits of
294 this species in this model (TD: $F_{7,8} = 1.42$, $p = 0.30$, $N = 12$). For *T. virescens*, the
295 RMM model considering first and second principal components as dependent variables
296 and including TD as a covariate confirmed that acoustic traits of the song did not vary
297 according to island characteristics, even when accounting for differences in forest
298 structure among islands (TD: $F_{7,8} = 0.08$, $p=0.91$, $N = 12$; AREA: $F_{7,8} = 0.12$, $p = 0.88$,
299 $N = 12$; PROX: $F_{7,8} = 1.11$, $p = 0.37$, $N = 12$).

300

301 Acoustic adaptation to the transmission environment

302 Mean values of acoustic parameters from the different elements that constitute the song
303 of both species related independently to variation in tree density and basal area among
304 islands. In *L. vociferans*, average peak frequency of the introductory note was higher in
305 islands with greater tree density (Fig.2A) and basal area (Fig. 2B) ($r^2 = 0.5$, $p = 0.01$,
306 $GL = 9$, $N = 12$). Average peak frequency of the end portion of the second note did not

307 vary according to changes in forest structure when TD and BA were considered jointly
308 in the same model ($r^2 = 0.25$, $p = 0.1$, $GL = 9$, $N = 12$), but was positively associated
309 with variation in BA when effects of BA and TD considered separately ($p = 0.04$) (Fig.
310 3A). In *T. virescens*, peak frequency of the fourth note showed no association with the
311 joint variation of islands TD and BA ($r^2 = 0.27$, $p = 0.09$, $GL = 9$, $N = 12$), despite
312 having a positive relation to BA when effects of BA and TD considered separately ($p =$
313 0.03) (Fig. 3B).

314 The lowest frequency of the different elements of acoustic signals from both
315 species also varied independently according to variation in vegetation structure among
316 islands. In *L. vociferans*, average lowest frequency of the introductory note was higher
317 in islands with greater tree density (Fig. 4A) and basal area (Fig. 4B) ($r^2 = 0.65$, $p =$
318 0.00 , $GL = 9$, $N = 12$). Average lowest frequency of the end portion of the second note
319 also had higher values in islands with greater tree basal area ($r^2 = 0.41$, $p = 0.03$, $GL =$
320 9 , $N = 12$), despite not being related to variations in tree density ($p = 0.77$). In *T.*
321 *virescens*, average lowest frequency of second and fourth notes had higher values in
322 islands with greater tree basal area (N2: $r^2 = 0.64$, $p = 0.00$, $GL = 9$, $N = 12$; N4: $r^2 =$
323 0.43 , $p = 0.03$, $GL = 9$, $N = 12$), despite not being associated with variation in tree
324 density (N2: $p = 0.37$; N4: $p = 0.59$). No significant associations were found between
325 variation in vegetation structure and variation in temporal properties (song duration,
326 notes duration, silence interval between notes) and in some spectral properties
327 (bandwidth and highest frequency) of songs of both species.

328 MMR analyses considering the main components generated for both species with
329 the means by island as dependent variables, indicated that, overall, variation in songs of
330 both species were related to variations in tree basal area of each island ($F_{8,9}=5.44$,

331 $p=0.03$, $N=12$ in *L. vociferans*; $F_{8,9}=5.88$, $p=0.02$, $N=12$ in *T. virescens*). In contrast,
332 there was no relation between the songs of both species and tree density ($F_{8,9}=1.73$,
333 $p=0.23$, $N=12$ in *L. vociferans*; $F_{8,9}=0.13$, $p=0.87$, $N=12$ in *T. virescens*).

334

335 DISCUSSION

336 Shifts in bird acoustic communication systems due to contemporary environmental
337 change is a recent topic in ecology and behavioral evolution studies, being mainly
338 investigated in urban areas (*e.g.* Salaberria and Gil 2010, Slabbekoorn 2013, Gil et al.
339 2014). The relation between spectral and temporal traits of the acoustic signals and the
340 insular distribution of some species was also studied in rather general contexts, usually
341 through comparisons of signal parameters emitted by continental species and
342 evolutionarily related lineages distributed in oceanic islands (Morinay et al. 2013). A
343 third common paradigm to studies involving acoustic adaptation is that the majority of
344 them had as models oscines birds (whose vocal repertoire is learned) and hence
345 susceptible to accumulate modifications acquired as quickly as along the lifetime of a
346 single individual (Kroodsma 1982; Naugler and Ratcliffe 1994). The cultural evolution
347 of acoustic signals may puzzle variation patterns associated with selective pressures
348 over them, since such patterns may be affected by the learning process (Podos and
349 Warren 2007).

350 In this study we investigated variations in songs of two suboscines bird species
351 related to the alteration of a natural landscape caused by habitat insularization. The vast
352 fragmentation occasioned by the artificial lake created an adequate system to analyse
353 several hypotheses on the adaptation of communication signals. First, species
354 composition of bird assemblages occurring in islands of the new archipelago predictably

355 responds to effects predicted by the theory of island biogeography, with smaller and
356 more isolated islands sustaining a lower number of species (MacArthur and Wilson
357 1967; Silva 2010). Thus, area and degree of isolation may be used as proxies for the
358 number of species potentially competing for acoustic space in each island. Second,
359 islands present substantial variability in the structure of remaining forest vegetation
360 (Benchimol and Peres 2015a).

361 We have shown that, between islands, there is measurable variation in features of
362 bird acoustic signals, and that some components of this variation are related to island
363 characteristics that potentially affect the acoustic community present and the sound
364 propagation environment. For example, the bandwidth occupied by elements of *L.*
365 *vociferans* songs was wider in smaller and more isolated islands. It is proposed that
366 groups of individuals that inhabit environments with a smaller number of species will
367 suffer less selective pressure by interference over their acoustic signals, allowing a
368 higher spectral diversity (Kroodsma 1985, Naugler and Ratcliffe 1994). Interspecific
369 spectral overlap will depend on the acoustic signal bandwidth occupied by the focal
370 species and on its position in relation to the bandwidth of the local acoustic community
371 (Planque and Slabbekoorn 2008). As one of the song's function is to identify the
372 individual who is vocalizing, living in an environment with a reduced number of species
373 makes this recognition easier, since there will be a smaller amount of songs to be
374 discriminated, and thus allowing for greater variation in spectral space (Morinay et al.
375 2013).

376 Few studies on acoustic adaptation in birds assessed alterations in acoustic signals
377 in relation to subtle environmental changes in the same type of tropical forest matrix.
378 Birds that inhabit tropical forests dominated by bamboo, for instance, seem to emit

379 acoustic signals adapted to the peculiar transmission environment, which differentiate in
380 several parameters from those emitted by species which preferably inhabit neighboring
381 forests, where bamboo is absent (Tobias et al. 2010). However, gradual variations in
382 vegetation structure are rarely measured and used in this sort of approach.

383 In forest environments, attenuation of acoustic signals is diminished in the mid-
384 strata of the understory or above the canopy. Signal degradation in function of
385 reverberation is also smaller in frequencies between 2–5 kHz (Ellinger and Hödl 2003).
386 Both focal species of this study utilize the mid-strata of the understory and their signals
387 peak frequencies occupy that frequency range (mean peak frequency for island *L.*
388 *vociferans* between 1.1–4.5 kHz / mean peak frequency for *T. virescens* 2.7–3.3 kHz).
389 However, the directionality of relationships between acoustic signal properties of both
390 species and the variation in vegetation structure was different from that predicted by the
391 acoustic adaptation hypothesis (*sensu* Morton 1975) in most cases where those
392 associations were detected. In both species, elements of the acoustic signals were
393 emitted in higher frequencies in more densely vegetated environments, contrary to
394 general patterns suggested by studies of the hypothesis (Morton 1975; Morinay et al.
395 2013). Similar results were reported for other passerine species, for example, amongst
396 species of the manakin family (Pipridae), for which signals with higher peak
397 frequencies were recorded in more densely forested areas (Deslandes and Pie 2014).
398 The authors attributed this pattern to the existence of sexual selection over acoustic
399 signals, since they are emitted in *leks* as part of exhibitions that integrate acoustic and
400 visual signals, and that the characteristics of the environment may not be as relevant to
401 song evolution in this family. The same association pattern also occurs in species of the
402 Columbidae family, amongst which species typical of densely vegetated environments

403 emit songs with higher frequencies than do species that inhabit open environments, even
404 when morphological and genetic differences amongst species are accounted for (Tubaro
405 and Mahler 1998).

406 An important assumption for the existence of acoustic adaptation is that signals
407 are adapted in order to maximize its propagation distance in the environment. However,
408 acoustic signals may be selected to optimize the transmission of information instead of
409 maximizing its reach (Lemon 1981). Nevertheless, degraded signals (*e.g.* reverberated,
410 attenuated) may be used by the receiver to estimate the distance to the sender (Richards
411 1981; Morton and Derrickson 1996). As *L. vociferans* and *T. virescens* take part in lek
412 behavior, in which songs are emitted in groups of spatially close males in a way that
413 maximizes their location by females, changes in the transmission environment
414 determined by differences in tree density may be less important as a source of selective
415 pressure over acoustic signals than sexual selection or conspecific competition for
416 acoustic space.

417 Another interesting result is that different elements of songs (notes) varied in
418 opposite directions in relation to environmental gradients, showing that more subtle
419 changes within the song were associated to environmental changes. Therefore, future
420 studies should try to focus on existent variations in each of the song's notes instead of
421 taking into consideration only variations in the song as a whole.

422 These results suggest, along with accumulated knowledge available on acoustic
423 adaptation and acoustic character release, that it is possible to relate ecological pressures
424 imposed by the environment (*e.g.* acoustic community, transmission medium) to
425 variation of particular traits of birdsongs. Apparently, such traits can shift quantitatively

426 as a response to environmental change in a rather short space of time (Luther and
427 Baptista 2010). The fact that some of the relations predicted by the current hypotheses
428 were not observed may be because perhaps there is still considerable flow of individuals
429 among islands, or even that the isolation time of the islands is still too recent (~28
430 years) for modifications of acoustic traits to have been fixed in populations of different
431 islands. Future work should assess genetic structure and diversity among birds
432 inhabiting different islands in the BHP reservoir and the potential evolutionary
433 implications of the variation in acoustic signals reported herein.

434

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571 FIGURE LEGENDS

572 Figure 1 - The Balbina Hydroelectric Reservoir, located about 100 km north of the city
573 of Manaus, Amazonas State, Brazil. Islands highlighted in black correspond to islands
574 sampled in this study. Width of island perimeter corresponds to a 250 m buffer zone
575 used to derive island isolation metrics.

576 Figure 2 - Partial relationships between peak frequency of the introductory note of
577 *Lipaugus vociferans* song and (A) tree density and (B) basal area occupied by trees in
578 each of 12 islands sampled throughout the Balbina Hydroelectric Reservoir, as inferred
579 from a multiple regression analysis.

580 Figure 3 - Partial relationships between (A) peak frequency of the end component of the
581 second note of *Lipaugus vociferans* song and tree basal area in each of 12 islands
582 sampled throughout the Balbina Hydroelectric reservoir; and (B) peak frequency of the
583 fourth note of *Tyranneutes virescens* and tree basal area. Both inferred from multiple
584 regression analyses.

585 Figure 4 - Partial relationships between lower frequency of the introductory note of
586 *Lipaugus vociferans* song and (A) tree density and (B) basal area occupied by trees in
587 each of 12 islands sampled throughout the Balbina Hydroelectric reservoir, as inferred
588 from a multiple regression analysis.

589 Figure S1- Spectrogram (upper graph) and waveform (lower graph) of a single song of
590 *Lipaugus vociferans*. Sections delimited by solid lines stand for song components from
591 which acoustic variables were measured.

592 Figure S2- Spectrogram (upper graph) and waveform (lower graph) of a single song of
593 *Tyrannetes virescens*. Sections delimited by solid lines stand for song components
594 from which acoustic variables were measured.

595

596 TABLES

597 **Table 1.** Number of individual birds recorded and characteristics of islands of Balbina
 598 Hydroelectric reservoir sampled in this study. N° Individuals = number of individual
 599 birds recorded in each island; N° Songs = number of songs analyzed proceeding from
 600 each island; AREA = island area (\log_{10} of actual area measured in hectares); PROX =
 601 island isolation index in \log_{10} (see text for detailed variable description); TD =average
 602 tree density (trees/0.25 ha); BA = average tree basal area (m^2/ha) Only trees with
 603 diameter at breast high > 10cm were considered.

Islands	Spatial metrics		Vegetation metrics		Species			
					N° Individuals		N° Songs	
	AREA	PROX	TD	BA	<i>L. vociferans</i>	<i>T. virescens</i>	<i>L. vociferans</i>	<i>T. virescens</i>
Piquiá	1.13	2.21	109.00	7.05	6	4	30	20
Coata	1.24	4.40	123.00	8.59	4	5	20	25
Neto	1.52	2.33	135.00	6.79	5	5	25	25
Bacaba	1.73	2.06	94.00	6.58	7	9	35	45
Relógio	1.86	4.64	100.00	7.39	5	-	25	-
Sapupara	1.89	2.70	144.00	6.86	6	5	30	25
Moitá	1.99	3.23	116.00	6.42	-	5	-	25
Furo Luzia	2.29	4.34	119.00	7.75	5	5	25	25
Cipoal	2.34	3.82	157.00	7.26	6	6	30	30
Martelo	2.67	4.32	121.00	7.23	6	7	30	35
Tristeza	2.69	3.29	176.00	7.03	7	5	35	25
Mascote	2.83	3.68	96.00	7.19	4	7	20	35
Beco	2.80	4.01	129.00	8.43	6	6	30	30
				total	67	69	335	345

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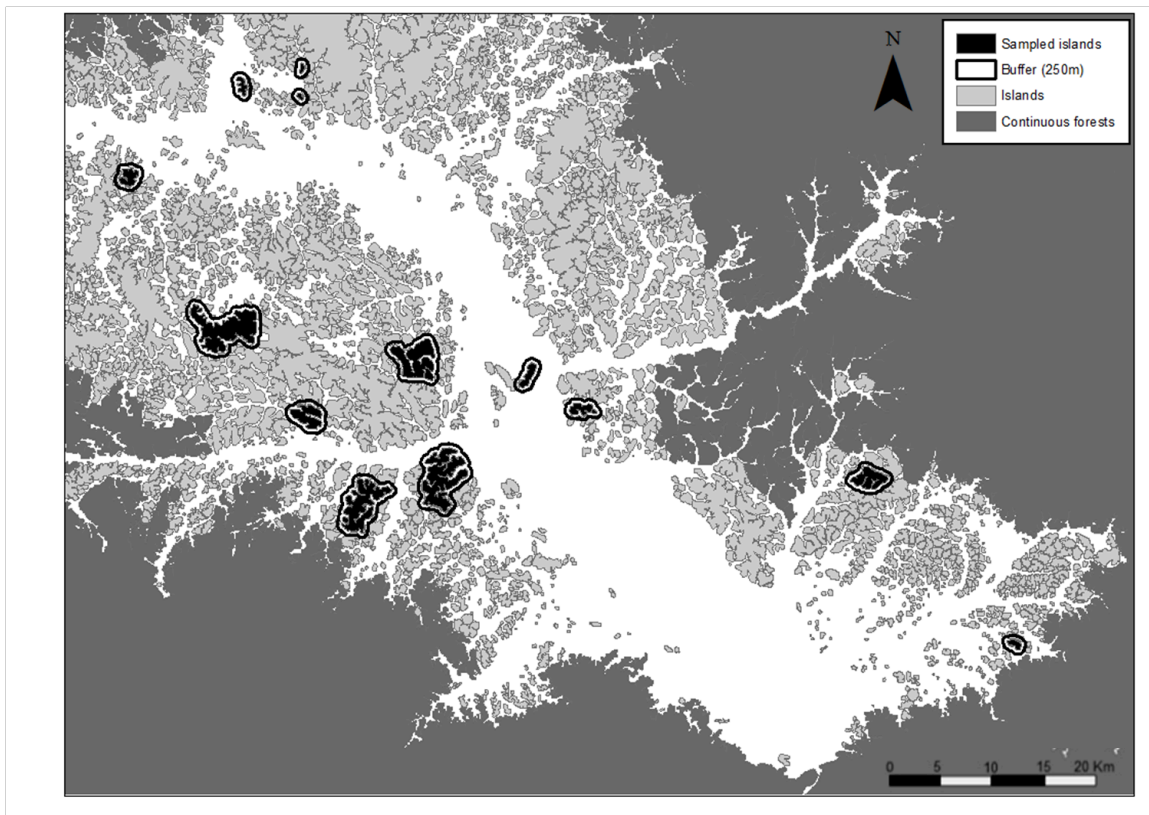
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606 **Table 2.** Relationships between the average bandwidth of the elements that constitute
 607 the songs of *Lipaugus vociferans* and *Tyrannetes virescens* and the island's metrics of
 608 12 islands in Balbina Reservoir, Amazonas State, Brazil, where individuals of the
 609 species were recorded. Relations were estimated from multiple regression analyses on
 610 each variable separately. Values in bold indicate significant relationships and
 611 coefficients. AREA = area of the island; PROX = Island isolation index.

Species	Acoustic parameter	r^2	F	p	Metrics	Coefficient	Standard erro	p
<i>L. vociferans</i>	BWintro	0.63	10.64	0.00	AREA	2.77	16.84	0.87
					PROX	-46.17	10.87	0.00
	BWN1	0.51	6.72	0.01	AREA	-179.65	52.71	0.00
					PROX	91.03	34.05	0.02
	BWN2A	0.64	10.93	0.00	AREA	-172.52	42.27	0.00
					PROX	103.65	27.30	0.00
	BWN2D	0.25	2.91	0.10	AREA	-181.13	75.13	0.03
					PROX	55.09	48.53	0.20
	BWN2H	-0.15	0.27	0.76	AREA	-439.07	722.57	0.55
					PROX	-63.52	466.73	0.89
<i>T. virescens</i>	BWN1	-0.20	0.05	0.94	AREA	-4.58	96.48	0.96
					PROX	-17.12	67.25	0.80
	BWN2	-0.08	0.58	0.57	AREA	70.49	71.66	0.35
					PROX	-44.10	49.95	0.40
	BWN3	-0.19	0.11	0.89	AREA	2.55	62.11	0.96
					PROX	-18.38	43.29	0.68
	BWN4	-0.21	0.04	0.95	AREA	14.07	54.57	0.80
					PROX	-0.90	38.04	0.98

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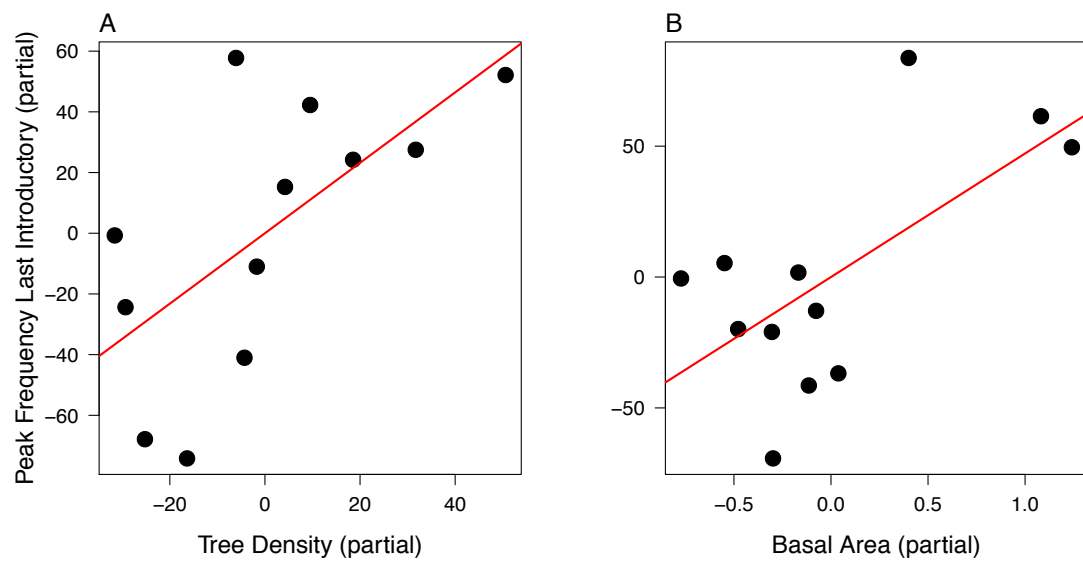
613 FIGURES



614

615 **Figure 1**

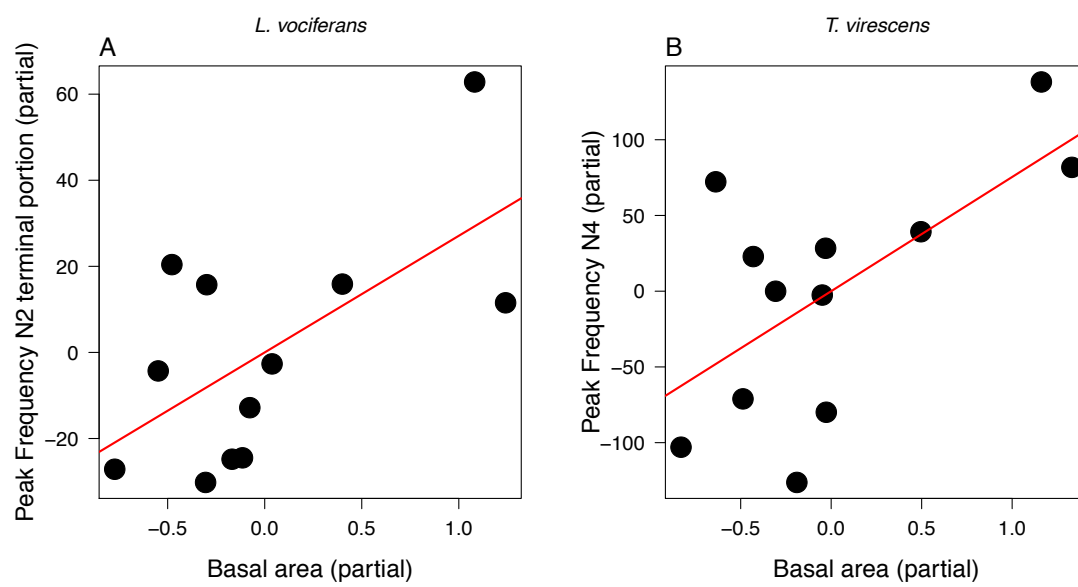
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618 **Figure 2**

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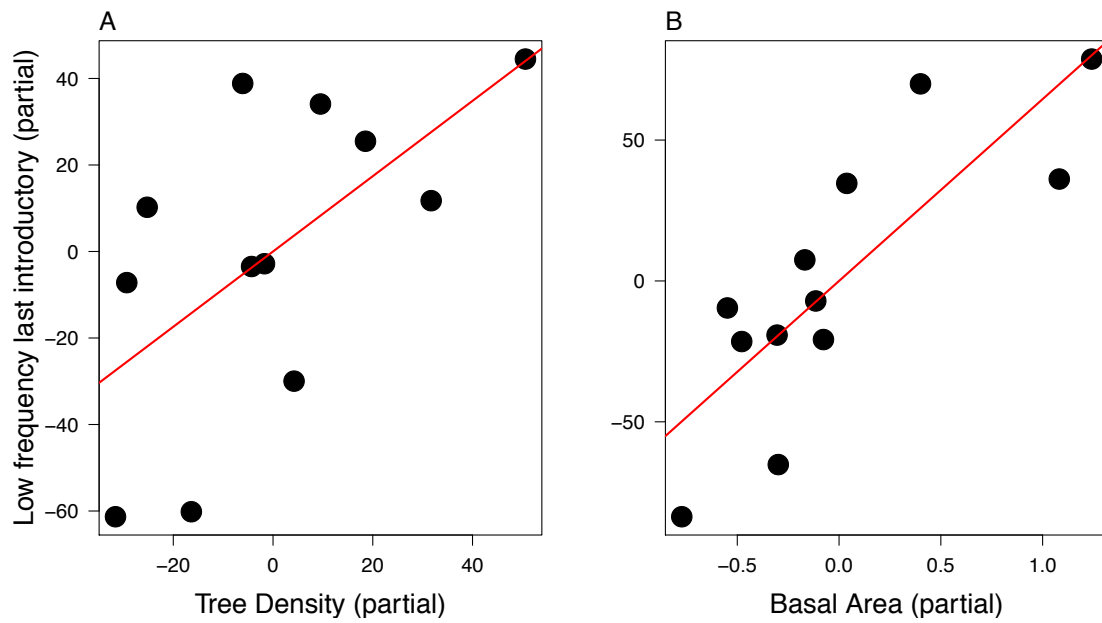


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621 **Figure 3**

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624

625 **Figure 4**

626

627 CONCLUSÃO

628 Diante de todos os fatos abordados na literatura e juntamente com os nossos
629 resultados, podemos concluir que pressões ecológicas impostas pelo ambiente (e.g.
630 comunidade acústica presente, meio de transmissão) podem gerar mudanças em
631 características fenotípicas das espécies, como acontece com os cantos. Estas mudanças
632 geralmente ocorrem em um curto espaço de tempo, sendo proveniente de mudanças
633 rápidas no habitat. Como para uma das espécies, diferentes elementos do canto (notas)
634 apresentarão direção de relação diferente entre as hipóteses, estudos futuros deverão
635 utilizar nas análises acústicas as variações existentes em cada um das notas do canto
636 separadamente ao invés de levar em consideração somente as variações no canto inteiro.
637 Como houve ausência de relação para algumas hipóteses testadas, de forma a avaliar se
638 existe uma movimentação de indivíduos entre as ilhas, ou se o tempo de isolamento
639 ainda é recente para que algumas características acústicas tenham se fixado, estudos
640 futuros deverão avaliar o potencial evolutivo que estas variações nos sinais acústicos
641 podem ter, analisando a variação genética entre as espécies estudadas.

642 APÊNDICES

643 Table S1. Acoustic parameters analyzed by note for both species with the respective
 644 abbreviations.

Specie	Acoustic parameters	Song note	Abbreviations
<i>L. vociferans</i>	Highest frequency	Last introductory	HFIntro
		First note	HFN1
		Ascending portion 2nd note	HFN2A
	Lowest frequency	Descending portion 2nd note	HFN2D
		Terminal portion 2nd note	HFN2T
		Last introductory	LFIntro
	Bandwidth	First note	LFN1
		Ascending portion 2nd note	LFN2A
		Descending portion 2nd note	LFN2D
	Peak frequency	Terminal portion 2nd note	LFN2T
		Last introductory	BWIntro
		First note	BWN1
	Duration	Ascending portion 2nd note	BWN2A
		Descending portion 2nd note	BWN2D
		Terminal portion 2nd note	BWN2T
Duration	Last introductory	PFIntro	
	First note	PFN1	
	Ascending portion 2nd note	PFN2A	
Duration	Descending portion 2nd note	PFN2D	
	Terminal portion 2nd note	PFN2T	
	Last introductory	DIntro	

	First note	DN1
	Ascending portion 2nd note	DN2A
	Descending portion 2nd note	DN2D
	Terminal portion 2nd note	DN2T
	Entire song	SD
Inter-note silent intervals	Introductory and first note	IN _{IntroN1}
	First note	HFN1
Highest frequency	Second note	HFN2
	Third note	HFN3
	Fourth note	HFN4
	First note	LFN1
Lowest frequency	Second note	LFN2
	Third note	LFN3
	Fourth note	LFN4
	First note	BWN1
<i>T. virescens</i> Bandwidth	Second note	BWN2
	Third note	BWN3
	Fourth note	BWN4
	First note	PFN1
Peak frequency	Second note	PFN2
	Third note	PFN3
	Fourth note	PFN4
	First note	DN1
Duration	Second note	DN2
	Third note	DN3

	Fourth note	DN4
Inter-note silent interval	First and second note	IN_{N1N2}
	Second and third note	IN_{N2N3}
	Third and fourth note	IN_{N3N4}

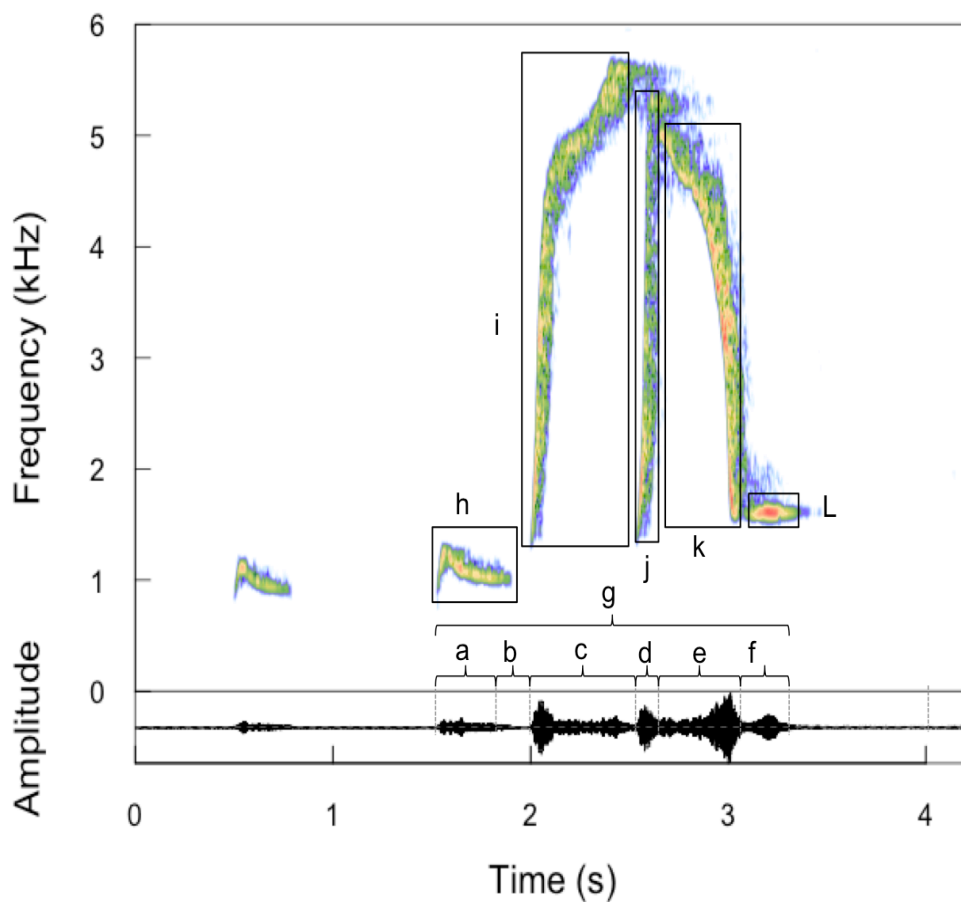
646 Table S2. Loadings, eigenvalues, and percentage of explained variation of the temporal
 647 and spectral acoustic variables from the songs of *L. vociferans* (n = 77) and *T. virescens*
 648 (n = 69) in the first two axes generated by a principal component analysis (PCA) on
 649 individual average values of these variables.

Specie	Acoustic variables	Loadings	
		PC1	PC2
	LFIntro	0.92	-0.07
	PFIntro	0.79	0.36
	LFN2T	0.75	-0.23
	BWN2T	-0.73	-0.64
	DN2T	-0.73	-0.46
	HFN2T	-0.72	-0.65
	HFN2D	0.71	-0.63
	DIntro	-0.69	-0.67
<i>L. vociferans</i>	DN2A	-0.67	-0.66
	HFN2A	0.65	-0.72
	BWN2A	0.65	-0.70
	IN _{IntroN1}	0.64	0.63
	HFN1	0.63	-0.71
	BWN2D	0.63	-0.46
	BWIntro	-0.60	0.10
	DN2D	0.59	0.54
	PFN2D	0.59	-0.46
	BWN1	0.57	-0.71
	PFN2T	0.53	-0.09

HFIntro	0.52	0.02
LFN1	0.52	-0.06
LFN2A	0.48	-0.28
SD	-0.47	-0.43
PFN1	0.45	-0.09
DN1	0.36	-0.01
LFN2D	0.28	-0.25
PFN2A	-0.05	0.15
Eigenvalues	10.17	6.03
% Explained variation	37.67	22.35

<i>T. virescens</i>	LFN1	-0.10	-0.53
	HFN1	0.83	0.42
	BWN1	0.68	0.59
	DN1	0.37	0.72
	PF1	0.87	0.29
	IN _{N1N2}	-0.21	-0.60
	LFN2	0.17	-0.83
	HFN2	0.83	0.05
	BWN2	0.66	0.56
	DN2	0.14	0.55
	PF2	0.79	0.07
	IN _{N2N3}	-0.38	-0.46
	LFN3	0.68	-0.54
	HFN3	0.89	-0.08
	BWN3	0.76	0.24

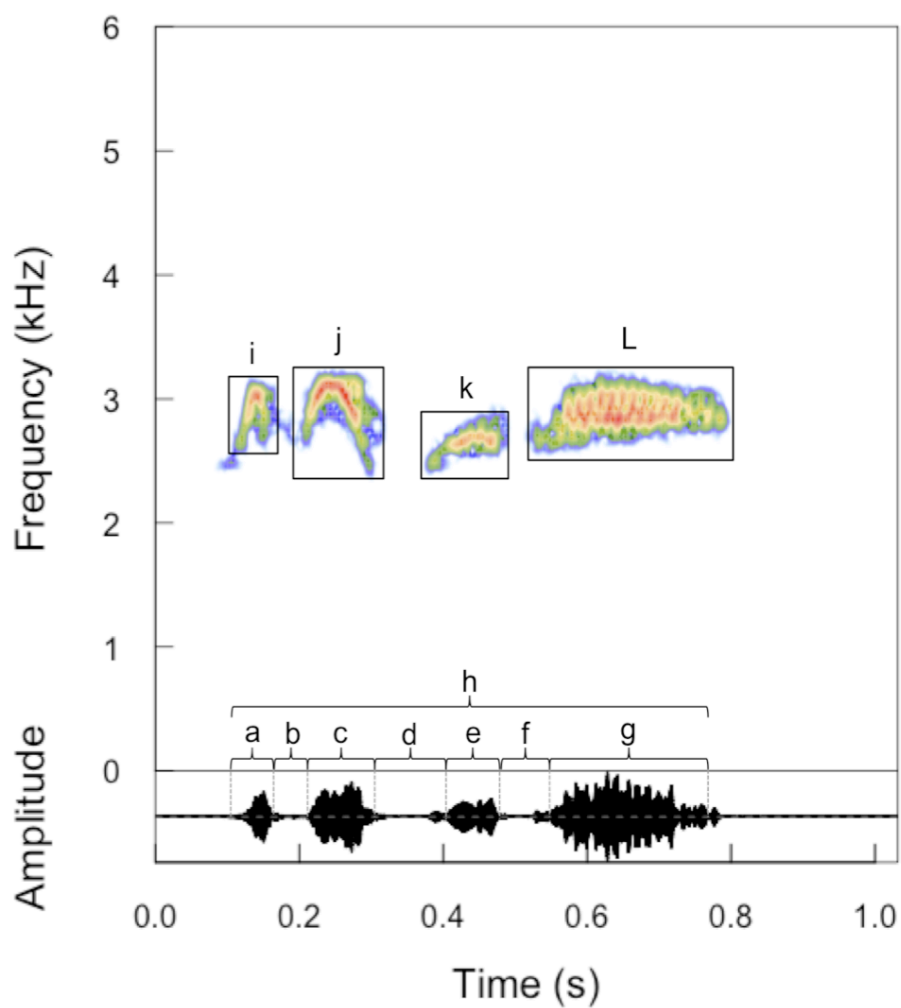
DN3	0.17	0.51
PF3	0.87	-0.35
IN _{N3N4}	0.03	-0.58
LFN4	0.71	-0.59
HFN4	0.89	-0.37
BWN4	0.91	-0.13
D4	-0.15	0.49
PF4	0.87	-0.27
SD	-0.14	0.36
Eigenvalues	9.95	5.71
% Explained variation	37.67	22.35



- a** - Duration introductory note
- b** - Inter-note silent intervals Introductory and 1st note
- c** - Duration 1st note
- d** - Duration Ascending portion 2nd note
- e** - Duration Descending portion 2nd note
- f** - Duration Terminal portion 2nd note
- g** - Duration Entire song
- h** - Highest frequency, Lowest frequency, Bandwidth, Peak frequency introductory note
- i** - Highest frequency, Lowest frequency, Bandwidth, Peak frequency 1st note
- j** - Highest frequency, Lowest frequency, Bandwidth, Peak frequency Ascending portion 2nd note
- k** - Highest frequency, Lowest frequency, Bandwidth, Peak frequency Descending portion 2nd note
- L** - Highest frequency, Lowest frequency, Bandwidth, Peak frequency Terminal portion 2nd note

651

652 Figure S1.



- a** - Duration 1st note
- b** - Inter-note silent intervals between 1st and 2nd note
- c** - Duration 2nd note
- d** - Inter-note silent intervals between 2nd and 3rd note
- e** - Duration 3rd note
- f** - Inter-note silent intervals between 3rd and 4th note
- g** - Duration 4th note
- h** - Duration Entire song
- i** - Highest frequency, Lowest frequency, Bandwidth, Peak frequency 1st note
- j** - Highest frequency, Lowest frequency, Bandwidth, Peak frequency 2nd note
- k** - Highest frequency, Lowest frequency, Bandwidth, Peak frequency 3rd note
- L** - Highest frequency, Lowest frequency, Bandwidth, Peak frequency 4th note

653

654 Figure S2.

655



Ministério da
Ciência, Tecnologia
e Inovação



ATA DA DEFESA PÚBLICA DA
DISSERTAÇÃO DE MESTRADO DO
PROGRAMA DE PÓS-GRADUAÇÃO EM
ECOLOGIA DO INSTITUTO NACIONAL
DE PESQUISAS DA AMAZÔNIA.

Aos 22 dias do mês de maio do ano de 2015, às 08:30 horas, no Auditório do PPG/ATU/ECO, Campus III, INPA/V8, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a) **Fabrizio Beggiato Baccaro**, da Universidade Federal do Amazonas - UFAM, o(a) Prof(a). Dr(a) **Renato Cintra Soares**, do Instituto Nacional de Pesquisas da Amazônia - INPA e o(a) Prof(a). Dr(a) **Igor Luis Kaefer**, da Universidade Federal do Amazonas - UFAM, tendo como suplentes o(a) Prof(a). Dr(a) Albertina Pimentel Lima, do Instituto Nacional de Pesquisas da Amazônia - INPA, e o(a) Prof(a). Dr(a) Cintia Cornelius Fische, da Universidade Federal do Amazonas - UFAM, sob a presidência do(a) primeiro(a), a fim de proceder a arguição pública do trabalho de **DISSERTAÇÃO DE MESTRADO de THIAGO BICUDO KREMPEL SANTANA**, intitulado: "Efeitos da insularização sobre a comunicação acústicas em aves do reservatório da usina hidrelétrica de Balbina, Amazonas" orientado pelo(a) Prof(a). Dr(a) Marina Anciães do Instituto Nacional de Pesquisas da Amazônia - INPA, e coorientado pelo(a) Prof(a) Dr(a). Pedro Ivo Simões da Pontifícia Universidade Católica do Rio Grande do Sul - PUCRS.

Após a exposição, o(a) discente foi arguido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

APROVADO(A) REPROVADO(A)
 POR UNANIMIDADE POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a). Fabrizio Beggiato Baccaro

Prof(a).Dr(a). Renato Cintra Soares

Prof(a).Dr(a). Igor Luis Kaefer

Prof(a).Dr(a). Albertina Pimentel Lima

Prof(a).Dr(a). Cintia Cornelius Fische


Coordenação PPG-ECO/INPA



AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): THIAGO BICUDO KREMPPEL SANTANA
 Curso: ECOLOGIA
 Nível: Mestrado
 Orientador(a): Dra. Marina Anciães (INPA)
 Co-orientador (a): Dr. Pedro Ivo Simões (INPA)

Título

"EFEITOS DA INSULARIZAÇÃO SOBRE A COMUNICAÇÃO ACÚSTICA EM AVES DO RESERVATÓRIO DA USINA HIDRELÉTRICA DE BALBINA, AMAZONAS"

BANCA JULGADORA:

TITULARES:

MARIO COHN-HAFT (INPA)
 SÉRGIO HENRIQUE BORGES (FVA)
 TÂNIA MARGARETE SANAIOTTI (INPA)

SUPLENTE:

ALAN FECCHIO (UFAM)
 RENATO CINTRA SOARES (INPA)

PARECER	ASSINATURA
MARIO COHN-HAFT (INPA) <input checked="" type="checkbox"/> Aprovado <input type="checkbox"/> Reprovado	
SÉRGIO HENRIQUE BORGES (FVA) <input checked="" type="checkbox"/> Aprovado <input type="checkbox"/> Reprovado	
TÂNIA MARGARETE SANAIOTTI (INPA) <input checked="" type="checkbox"/> Aprovado <input type="checkbox"/> Reprovado	
ALAN FECCHIO (UFAM) <input type="checkbox"/> Aprovado <input type="checkbox"/> Reprovado	_____
RENATO CINTRA SOARES (INPA) <input type="checkbox"/> Aprovado <input type="checkbox"/> Reprovado	_____

Manaus(AM), 24 de fevereiro de 2014

OBS: Enfatizar os aspectos biológicos da vocalização e das espécies; Serão esperadas
insights sobre variações entre ambiente insularizado e não insularizado; atenção às
colocadas e às variações independentes, eventualmente focar o trabalho como um caso
de bioacústica.

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA INPA
 PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA PPG-ECO
 Av. Efigênio Sales, 2239 - Bairro: Aleixo - Caixa Postal: 2223 - CEP: 69.060-020, Manaus/AM
 Fone/Fax: (+55) 92 3643-1909 / 1838

site: <http://pg.inpa.gov.br>

e-mail: pgecologia@gmail.com

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661 Anexo 2 - Ata qualificação