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## **Explosive breeding in tropical anurans: environmental triggers, community composition and acoustic structure**

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1 **Explosive breeding in tropical anurans: environmental triggers,**  
2 **community composition and acoustic structure**

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33

34 **Abstract**

35

36 **Background**

37 Anurans largely rely on acoustic communication for sexual selection and reproduction. While  
38 multiple studies have focused on the calling activity patterns of prolonged breeding  
39 assemblages, species that concentrate their reproduction in short-time windows, explosive  
40 breeders, are still largely unknown, probably because of their ephemeral nature. In tropical  
41 regions, multiple species of explosive breeders may simultaneously aggregate leading to  
42 massive, mixed and dynamic choruses. To understand the environmental triggers, the  
43 phenology and composition of these choruses, we collected acoustic and environmental data  
44 at five ponds in French Guiana during a rainy season, assessing acoustic communities before  
45 and during explosive breeding events.

46

47 **Results**

48 We detected in each pond two explosive breeding events, lasting between 24 and 70 hours.  
49 The rainfall during the previous 48 hours was the most important factor predicting the  
50 emergence of these events. During explosive breeding events, we identified a temporal factor  
51 that clearly distinguished pre- and mid-explosive communities. A common pool of explosive  
52 breeders co-occurred in most of the events, namely *Chiasmocleis shudikarensis*,  
53 *Trachycephalus coriaceus* and *Ceratophrys cornuta*. Nevertheless, the species composition  
54 was remarkably variable between ponds and for each pond between the first and the second  
55 events. The acoustic structure of explosive breeding communities had outlying levels of  
56 amplitude and unexpected low acoustic diversity, significantly lower than the communities  
57 preceding explosive breeding events.

58

59 **Conclusions**

60 Explosive breeding communities were tightly linked with specific rainfall patterns. With  
61 climate change increasing rainfall variability in tropical regions, such communities may  
62 experience significant shifts in their timing, distribution and composition. In structurally  
63 similar habitats, located in the same region without obvious barriers, our results highlight the  
64 variation in composition across explosive breeding events. The characteristic acoustic  
65 structure of explosive breeding events stands out from the circadian acoustic environment  
66 being easily detected at long distance, probably reflecting behavioural singularities and  
67 conveying heterospecific information announcing the availability of short-lived breeding

68 sites. Our data provides a baseline against which future changes, possibly linked to climate  
69 change, can be measured, contributing to a better understanding on the causes, patterns and  
70 consequences of these unique assemblages.

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72 **Keywords**

73 acoustic diversity, anuran community, ecoacoustics, biodiversity monitoring.

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## 102 **1. Background**

103 Amphibians are currently the most endangered group of vertebrates, with more than 32% of  
104 species classified as at risk of extinction [1–3]. Recent investigations on the causes of  
105 amphibian declines have identified the role of climate change on a global scale [4–7]. In  
106 addition to the climate-linked epidemic hypothesis, research has focused on the effect of  
107 climate change on behaviour, reproduction and distribution of amphibians [8,9]. As  
108 ectotherms, alterations on temperature and rainfall regimes might strongly affect key aspects  
109 of amphibian life cycles, even jeopardizing their survival [10]. Both theoretical and  
110 experimental studies suggest that low latitude ectothermic species are more vulnerable to  
111 climate changes than their higher latitude counterparts [11]. Tropical species indeed tend to  
112 have narrower thermal tolerance [12] and their actual habitat temperatures are closer to their  
113 upper thermal limit [10,13]. Even slight changes in environmental conditions might therefore  
114 have a strong effect on these tropical species [14].

115 Anurans largely rely on acoustic communication for sexual selection and reproduction  
116 [15,16]. Studies have revealed that temporal patterns of calling and breeding activity of  
117 anurans are influenced by multiple environmental factors, such as temperature, humidity or  
118 light intensity [17–19]. Moreover, recent findings have also shown that photoperiod might be  
119 an important driver of the calling activity of numerous anuran species [20–23]. The response  
120 to abiotic environmental factors may vary between species and according to the reproduction  
121 strategy [18,24]. While some anurans show long periods of calling activity and mating,  
122 known as prolonged breeders, others concentrate their reproduction during short time  
123 windows, even a few hours per year, and are known as explosive breeders [24]. In tropical  
124 regions, massive aggregations of explosive breeders generally involve multiple species  
125 simultaneously, leading to highly-diverse anuran communities [25–28]. Such phenomena  
126 typically occur in ephemeral ponds, which are sparsely distributed in tropical forests and are  
127 likely triggered under particular weather conditions.

128 Yet, the structure and dynamics of these unique acoustic communities are still largely  
129 unknown probably because of their ephemeral nature, density and complexity. To our best  
130 knowledge, few studies have documented broad and generic patterns in explosive neotropical  
131 anurans, observing correlations between peaks of activity and the occurrence of heavy rainfall  
132 at the beginning of the rainy season [25,26,28], and only two studies have analysed their fine  
133 scale dynamics [23,27]. In the former study, the data collection was done by human calling  
134 surveys through a four-month fieldwork in French Guiana. Gottsberger and Gruber in 2004  
135 identified temporal partitioning within the anuran community according to their reproductive

136 modes [27]. In particular, the group of species with aquatic oviposition presented sporadic  
137 acoustic activity following heavy rainfall, a phenomenon that occurred twice during the study.  
138 But their study focused on two close-by ponds, less than 240 m apart, limiting the  
139 interpretation of the results. Replications at spatial and temporal dimensions are crucial to  
140 examine the constitution and diversity of these communities, to decipher their dynamics and  
141 to identify their link with environmental factors. In the later study, Schalk and Saenz in 2016  
142 examined the calling phenology of anurans in the Gran Chaco ecoregion at seven ponds  
143 during nine months with passive acoustic sensors. For explosive breeding species they found  
144 that calling activity was positively and significantly correlated with at least two abiotic  
145 factors, rainfall and photoperiod [23]. Calling individuals gathering around breeding points  
146 form dense choruses characterized by a complex acoustic structure, broad masking  
147 interference and high sound pressure level [29]. Choruses formed by tropical anurans in  
148 explosive breeding events are extreme on these features due to the extraordinary species  
149 diversity and density of calling males [27]. Such assemblages constitute unique examples of  
150 multi-species choruses presumably eliciting complex interspecific interactions.

151         The technical difficulty in monitoring simultaneously these ephemeral communities  
152 has been one of the reasons for the lack of a wider geographic coverage. Traditional field-  
153 based observations are not scalable, thus it is crucial to adapt and test cost-effective methods.  
154 More than 20 years ago the idea of using automated data acquisition methods to monitor  
155 amphibians was already proposed [30], but it is only recently, thanks to the development of  
156 reliable passive acoustic sensors, that this method has gain popularity [31–36]). These  
157 acoustic sensors can be programmed to record for days or even months in a non-invasive and  
158 cost-efficient way, so that replication in time and space is now possible. Most anuran  
159 amphibians produce loud, stereotyped, and species-specific advertisement calls for mate  
160 attraction. These acoustic signals can be therefore remotely recorded to monitor populations  
161 as testified by several studies on temperate (e.g. [8,18,37]) and tropical species (e.g. [17,38–  
162 40]).

163         Using automated sensors, we collected for the first time acoustic and environmental  
164 data to monitor simultaneously and regularly explosive breeding events in tropical anuran  
165 communities, at five temporary ponds located along the Kaw Mountain in French Guiana.  
166 This systematic passive acoustic monitoring allowed us to tackle key ecological questions  
167 related to the patterns, causes and consequences of such a striking phenomenon. We  
168 specifically addressed four questions: (1) What are the main meteorological factors that  
169 trigger the emergence of explosive breeders? (2) Which species co-occur before and during

170 explosive breeding events? (3) What is the variation in the acoustic community composition  
171 within and between sites? (4) What are the main acoustic patterns, spectral characteristics and  
172 diversity before and during explosive breeding events? Answering these questions may shed  
173 light on the potential selective pressures shaping these complex acoustic communities.

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## 176 **2. Methods**

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### 178 *2.1. Study site*

179 We monitored explosive breeding assemblages in the lowland tropical rainforest of French  
180 Guiana, along the Kaw Mountain (4°36'N; 52°16'W). As in most regions located close to the  
181 equator, seasonal climatic variations in the study site were primarily due to changes in rainfall  
182 and humidity. The climate regime is characterized by two periods of rainfall: the main rainy  
183 season takes place from mid-November to the end of February and a less marked rainy season  
184 occurs from April to July. For this study, we collected acoustic and environmental data from  
185 the end of the dry season (10 November 2015) to the end of the main rainy season (16  
186 February 2016).

187 We focused the sampling on five seasonal ponds along a 30.4 km transect  
188 corresponding to the departmental road D6 (Fig. 1). These temporary shallow water bodies  
189 are flooded during the rainy seasons and then dry out predictably during periods of low  
190 rainfall, July to November. The ponds were surrounded by dense tropical forest, located  
191 between 236 and 313 meters above the sea level, and had distinct sizes, from 224.8 m<sup>2</sup> to  
192 2240.2 m<sup>2</sup> (Table 1).

193

194 **Table 1.** Altitude, location, and area of the five study ponds. Altitude is given in meters above  
195 sea level (m a.s.l.) and area in m<sup>2</sup>.

196

Local name	Code name	Altitude	GPS coordinates	Area
Caïman	Ca	313	4°34'10"N; 52°13'11"W	1192.3
Blanc	Bl	236	4°40'14"N; 52°18'22"W	399.5
Patawa	Pa	295	4°31'41"N; 52°07'14"W	2240.2
Arlesienne	Ar	269	4°32'44"N; 52°14'11"W	672.0
Petite	Pe	289	4°35'59"N; 52°15'59"W	224.8

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198

## 199 *2.2. Sampling protocol*

200 We monitored anuran calling activity and weather conditions simultaneously in each pond  
201 using automated sensors with a regular sampling schedule. To record the acoustic  
202 communities, we placed on the edge of each pond at breast height an automated sound  
203 recorder equipped with an omnidirectional microphone (SM2, Wildlife Acoustics, Inc.,  
204 Concord, MA, USA). The device was set up to record data 1 minute every 29 minutes, at 44.1  
205 kHz and 16 bit resolution, so that we obtained 5,616 recordings for each pond.

206 To register local abiotic environmental data, we placed next to the sound recorder a data  
207 logger (H21-002, Onset) equipped with sensors to measure three weather variables: rainfall  
208 (Onset, S-RGB-M002), temperature, and relative humidity (Onset, S-THB-M008). In  
209 addition, we retrieved two global environmental variables, atmospheric pressure (PTB220,  
210 Vaisala) and solar radiation (CMP6, Kipp and Zonen), from the nearest weather station at the  
211 Félix Eboué airport (4°50'N; 52°22'W), 19 km from the study site.

212

## 213 *2.3. Time-series analysis*

214 Because of the emergence of a great number of males from multiple amphibian species,  
215 explosive breeding events are known to produce a remarkably loud chorus. Therefore, we  
216 identified the occurrence of explosive breeding events in the audio recordings by searching  
217 for outlier amplitude peaks. The overall amplitude of each recording was measured by  
218 computing the root-mean-square of the signal amplitude envelope. Then, we applied a median  
219 filter with a 24-hour window and we searched for outliers in the resulting smoothed time  
220 series. The outliers were defined as values distributed one-and-a-half times the inter-quartile  
221 range (IQR) above the third quartile ( $Q3 + 1.5 \times IQR$ ). Every outlier event was inspected by  
222 listening to the recordings to confirm the presence of an explosive breeding event.

223 Preliminary analyses showed clear and steep increase on the sound pressure level during  
224 explosive breeding events resulting from the increase in calling activity from anuran  
225 communities. While the beginning of the explosive breeding events exhibited constant and  
226 exceptionally high call rate for around 24 hours, calling activity later presented multiple  
227 oscillations before ceasing or returning to common levels. In order to have comparable  
228 sections for each event and compare pre- and mid-explosive breeding communities, we  
229 focused our subsequent analysis on a 48 h window, starting 24 h before the onset and ending  
230 24 h after the onset of explosive breeding events.

231 We used a machine-learning framework to test whether the occurrence of the explosive  
232 breeding events could be predicted by abiotic factors. Weather conditions were considered as  
233 predictor variables and the triggering dates of the explosive breeding events as a binary  
234 response variable. The abiotic variables comprised low-level and high-level features. Low-  
235 level features were the raw quantitative meteorological measurements from the on-site  
236 sensors and the weather station, namely temperature, temperature variation, relative humidity,  
237 rainfall, atmospheric pressure, atmospheric pressure variation, photoperiod and solar  
238 radiation. Since the emergence of the breeding events can also be due to previous  
239 environmental conditions, we also included high-level features in the statistical analyses  
240 calculated based on the raw climatic data. These high-level features were the lagged-  
241 variables, previous 24, 48, and 72 hours, and past-cumulative variables from the previous 48  
242 and 72 hours. The final predictor matrix included 48 variables with 466 observations. We  
243 measured prediction accuracy and variable importance on classification using the Random  
244 Forest statistical classifier [41]. We assessed the importance of the predictor variables by  
245 comparing the difference in misclassification error (mean decrease accuracy) between the  
246 original data and a permuted set of data. The modified data for each predictor variable  
247 consisted in randomly permuted observations that are passed down the Random Forest. The  
248 higher the decrease in accuracy between the original and the modified data, the higher the  
249 importance of the predictor variable [42].

250

#### 251 *2.4. Community diversity analysis*

252 We investigated temporal and spatial variation on the diversity and composition of the  
253 acoustic communities of explosive breeding events. We define a community as the set of  
254 species heard at a given time interval before or after a specified explosive event, on a given  
255 pond. For each event, we systematically discretized the temporal gradient of 48 hours into  
256 four temporal periods of 12 hours. A first period (t1) ranged from 24 to 12 hours before the  
257 explosive breeding event, a second period (t2) ranged from 12 hours before to the onset of the  
258 event, a third period (t3) enclosed the first 12 hours of the event, and a fourth period (t4)  
259 ranged from 12 to 24 hours after the onset of the event.

260 We then sub-sampled our database by choosing one recording every two hours, for a  
261 total of 240 recordings of 60 seconds. Three of us (EC, AF and PG), who are highly trained in  
262 aural identification of anuran species of French Guiana, scrutinized each recording and  
263 annotated the occurrence of calling species. A final presence-absence vector was derived for  
264 each recording by majority voting, thereby, potential observer bias was prevented while the

265 accuracy of the annotations enhanced. This phase led to the identification of a total of 25  
266 species.

267 We used the crossed-DPCoA [43], an ordination method that provides an approach for  
268 analysing the effects of crossed factors on the diversity of communities, to identify the effects  
269 of external factors on community composition. Here we analysed the effect on the species  
270 composition of amphibian communities of the time period before or after the event (t1, t2, t3,  
271 t4), and the event (an event is one of the two breeding explosions observed at a given pond).  
272 The time period and the event are two crossed factors. The aim of crossed-DPCoA is to  
273 visualize the pattern of diversity due to a factor A knowing the existence of a crossed factor  
274 B. DPCoA helps to visualize the main effect of factor A, here species composition, and the  
275 effect of the interaction between A and B, removing the main effect of factor B. The method  
276 first defines a space where species, communities and the levels of the two factors are  
277 visualized as points. Then, the communities are positioned at the centroid of their constitutive  
278 species, and the levels of the factors at the centroid of communities associated with them. The  
279 method then searches for principal axes of the levels of factor A, retaining potential effects of  
280 the interaction between A and B, but removing the main effect of factor B. In particular, we  
281 used the first version of DPCoA, which eliminates the effect of factor B by moving this factor  
282 to the centre of the space. We analysed first the effect of the events on the species  
283 composition of amphibian communities given the time period and then the effect of the time  
284 periods given the event.

285

### 286 *2.5. Acoustic diversity analysis*

287 To further compare the anuran acoustic assemblages of the pre- and mid-explosive breeding  
288 events, we followed the same previous procedure while adding information related to the  
289 acoustic dissimilarities between species. We used the same community data and repeated the  
290 ordination analysis. However, here we did not consider species as equidistant in the space of  
291 the crossed-DPCoA, we used the acoustic properties of the calls of the species to define  
292 acoustic dissimilarities between pairs of species. In this defined space, the distance between  
293 two species-specific points is a measure of the acoustic dissimilarity.

294 We estimated the acoustic dissimilarity between two species using focal recordings of  
295 each species-specific call available from personal field recordings (PG, EC, AF, JSU; n=17)  
296 and from commercial recordings ([44], n=8). We selected recordings that met two criteria: (1)  
297 the call had to be emitted by an isolated individual, and (2) the signal-to-noise-ratio (SNR) of  
298 the signal had to be higher than 30, where  $SNR = 20 \log_{10}(RMS_{signal}/RMS_{noise})$  and RMS is

299 the root-mean-square amplitude of the signal. Then, the spectral composition of each call was  
300 quantified by computing a short-time Fourier transform (FFT length of 512, no overlap,  
301 Hanning window), averaging the columns of the subsequent matrix (the temporal dimension),  
302 and applying a log-transformation. The acoustic dissimilarity between the species call was  
303 assessed by computing the cumulative dissimilarity of the spectral distributions or index  $D_{cf}$   
304 [45].

305 In addition, we analyzed the spectral profiles of the recordings collected in the field to  
306 investigate the changes in the acoustic environment before and during explosive breeding  
307 events. We first calculated the mean spectrum of each file. Then, we compared the spectral  
308 profiles at different moments of the explosive breeding event using a Random Forest  
309 procedure. We quantified and evaluated the classification accuracy and the importance of  
310 each feature, here each spectral profile, for the classification using the Random Forest  
311 importance measure [42].

312 Finally, we estimated the  $\alpha$  diversity of each acoustic community by computing the  
313 species richness, the Gini-Simpson coefficient, and the quadratic entropy. The richness is the  
314 number of species in the community. The Gini-Simpson index takes into account the number  
315 of species and their proportions [46,47]. The quadratic entropy, or Rao's diversity coefficient  
316 [48], is based on the number of species, their proportions and incorporates a between-species  
317 dissimilarity matrix (here the pair-wise acoustic dissimilarities). For each diversity index, we  
318 tested the differences among periods of the explosive breeding event (i.e. t1, t2, t3 and t4) and  
319 between events (i.e. the first and second event per site), as well as the interaction between  
320 both factors, with repeated-measures ANOVA. Shapiro-Wilk and Mauchly tests revealed no  
321 violation of the assumptions of normality and sphericity, respectively, when using ANOVA  
322 tests (in all cases:  $W > 0.76$ ,  $df = 5$ ,  $p > 0.05$ ;  $X^2 < 0.02$ ,  $df = 5$ ,  $p > 0.05$ ). Tukey test with  
323 Bonferroni correction was finally performed as post-hoc procedure to examine pairwise  
324 comparisons between time periods. The type I error was set at a nominal level of 5%.

325 Acoustic and statistical analyses were computed using the R software [49]. In particular,  
326 spectral audio features and dissimilarity matrices were computed using the seewave R-  
327 package [50], community and diversity ordination analyses were calculated with the adiv R-  
328 package [51], and statistical classification was computed with the randomForest R-package  
329 [52].

330

331

332 **3. Results**

333

### 334 *3.1. Time series analysis*

335 Sound pressure level showed regular 24-hour cycles during the study (Fig. 2). Yet, this  
336 regularity was interrupted by abrupt and steep increases in the amplitude lasting between 24  
337 and 70 hours that occurred at the end of December 2015 and the beginning of February 2016.  
338 Rainfall was irregularly distributed during the study showing two major rainfall events, the  
339 first one between 19 December 2015 and 4 January 2016, and the second one from 23 January  
340 to 15 February 2016. During those periods, daily fluctuations in temperature were less  
341 pronounced, solar radiation was lower, and relative humidity remained close to 100% (Fig. 2).

342 Applying an amplitude filter, we detected in each pond two major explosive events,  
343 i.e. 10 in total, lasting between 24 and 70 hours, later confirmed by aural evaluation. Using  
344 the combined meteorological variables (instant, lagged and past-cumulative) and the Random  
345 Forest classifier, we were able to accurately predict the emergence of all (100%) explosive  
346 breeding events with a low false positive rate of 9.6 % for out-of-the-bag estimates, that is  
347 using observations that were not used to build the predictive model. Variable importance  
348 ranking showed that rainfall was the most influential weather determinant, in particular, the  
349 amount of rain during the previous 24 hours and most importantly the past-cumulative rainfall  
350 during the previous 48 to 72 hours (Fig. 3). The rest of the variables (temperature, relative  
351 humidity, atmospheric pressure, photoperiod and solar radiation) had minor predictive power.

352

### 353 *3.2. Community diversity analysis*

354 We first analysed the species composition of explosive breeding events using crossed-  
355 DPCoA, which allowed to focus on the explosive breeding events removing the effect of the  
356 crossed factor linked to the time period before or after the event. The first two principal axes  
357 expressed respectively 34.8% and 30% of the main effect variability of the factor site (Fig.  
358 4A). Neither the first nor the second axis presented a particular pattern, the explosive breeding  
359 events having largely overlapping communities. Nevertheless, some sites (Patawa, Arlesienne  
360 and Petite) presented high between-event diversity, each explosive breeding event having a  
361 particular and unique combination of species (Fig. 4B). Inter-site and intra-site variability of  
362 the explosive breeding events for these sites had the same order of magnitude.

363 Then, to reveal the temporal variability in the communities, we eliminated the crossed  
364 effect of factor 'event' with the DPCoA. The calling activity of the anuran communities was  
365 structured along the temporal dimension (Fig. 5A). The first axis of the DPCoA, with 84.3 %  
366 of variance explained, clearly discriminated two assemblages: the pre-explosive community

367 (t1 and t2 on the negative side) and a characteristic explosive breeding community (t4 on the  
368 positive side). A transitional community with species from both sides appeared near the origin  
369 (t3). While the pre-explosive communities (t1 and t2) were partly similar in their species  
370 composition, t3 and t4 had clear and unique species composition. The species that  
371 characterized the pre-explosive community (t1 and t2) were *Phyllomedusa tomopterna*,  
372 *Leptodactylus mystaceus*, and *Dendropsophus counani* (Fig. 5B). Because they had positive  
373 coordinates on the first axis, the species that characterized the explosive breeding community  
374 (t4) were *Chiasmocleis shudikarensis*, *Trachycephalus coriaceus* and *Ceratophrys cornuta*  
375 (Fig. 5B). The transitional community (t3) showed an intermediate place on the ordination;  
376 these communities had a balanced mixed of pre-explosive and explosive breeding species.

377

378

### 379 3.3. Acoustic diversity analysis

380 As in the previous community analysis, we initially removed the effect of the crossed  
381 factor time. The first principal axis, with 87.6 % of variance explained, was strongly  
382 correlated with the peak frequency of the calls ( $r = 0.96$ , Pearson correlation; Fig 6). The  
383 crossed-DPCoA ordered the species with low frequency sounds on the left of the axis and  
384 species with high-pitched calls on the right. Distributed in this new space, the sites presented  
385 largely overlapping acoustic communities with a balance between high and low frequencies.  
386 Yet, the ponds Patawa, and Arlesienne had a high between-event acoustic diversity (Fig. 6A).  
387 At both ponds, the first explosive breeding event was characterized with lower frequencies  
388 than the second one.

389 Subsequently, we removed the effect of the cross factor event to show the temporal  
390 variability of the acoustic signals. Again, the first and second axes were strongly correlated  
391 with the peak frequency of the calls ( $r = 0.91$  and  $r = 0.96$ , Pearson correlation). For both  
392 axes, low frequency calls lied on the negative side of the axis and high frequency calls on the  
393 positive one (Fig. 7). In this bi-dimensional space the acoustic community was structured  
394 along the temporal dimension (Fig. 7A). The first axis of the ordination analysis, with 60.1 %  
395 of explained variance, showed a progression from t1 (negative side) to t4 (positive side), a  
396 progression toward mid-frequencies dominance. The levels t1 and t2 presented elongated  
397 ellipses, showing a dispersed range of frequency calls, with low and high-pitched sounds (Fig.  
398 7A). This elongated shape was much less pronounced for levels t3 and t4, which was mainly  
399 characterized by calls in the mid-frequency range. The sounds that characterized, by their  
400 higher proportions, the explosive breeding event acoustics were the calls of *C. shudikarensis*

401 and *T. coriaceus* (Fig. 7B). The calls of these anurans were in the middle range of the acoustic  
402 community, 3.4 kHz and 1.8 kHz for *C. shudikarensis* and *T. coriaceus* respectively.

403 Further spectral analyses at the soundscape level supported the previous results obtained  
404 with isolated vocalisations. Using a statistical classifier we were able to classify explosive  
405 breeding recordings with high accuracy, using only their spectral profile (Random Forest,  
406 89% out-of-the-bag accuracy). The feature importance analysis showed that mid frequencies,  
407 between 2 and 4.4 kHz, were clearly the most important predictor variables (Fig 8).

408 The temporal pattern observed using the species richness and the Gini-Simpson index  
409 was similar, with maximal values during the first hours of the explosive breeding event  
410 (period t3; Fig. 9). Differences in acoustic diversity among periods were statistically  
411 significant when measured as species richness (ANOVA,  $F_{3,12} = 5.86$ ,  $p = 0.010$ ) and  
412 marginally significant when measured by Gini-Simpson index (ANOVA,  $F_{3,12} = 3.21$ ,  $p =$   
413  $0.062$ ). Post-hoc test revealed that the period t3 showed significantly higher species richness  
414 ( $2.8 \pm 0.8$ ) than the previous period t2 ( $Z = 3.51$ ,  $p = 0.003$ ), being others not statistically  
415 different. Rao's diversity coefficient, which includes the acoustic dissimilarity matrix, also  
416 varied according to the time periods (ANOVA,  $F_{3,12} = 5.72$   $p = 0.011$ ). This index was  
417 significantly higher at t1 than at t4 ( $0.15 \pm 0.05$ ;  $Z = 3.24$ ,  $p = 0.007$ ), indicating a progressive  
418 decrease in acoustic diversity as the explosive breeding community predominates (Fig. 9). No  
419 effect of the season nor its interaction with the periods of the event were identified in all cases  
420 (ANOVA,  $F_{1,4} < 4.48$ ,  $p > 0.101$ ), and hence the two explosive breeding events recorded per  
421 site, during each of the two rainy seasons, were equivalent in terms of acoustic diversity.

422

423

#### 424 **4. Discussion**

425

##### 426 *Time series analysis*

427 We found that environmental variables could predict the emergence of explosive  
428 breeding events, with rain as the most important predictor variable. While rain is abundant  
429 during the whole season, it is relevant to note that explosive breeding species respond to two  
430 specific patterns of rain: consistency during the previous 48 to 72 hours and amount during  
431 previous 24 hours. Our results are in agreement with those of Gottsberger and Gruber [27]  
432 who found that rainfall for the previous 24 hours contributed the best, among other  
433 environmental variables, to explain the calling activity of the explosive breeding species. As  
434 we included more derived variables of the rain in our analyses, we complement previous

435 results asserting that the consistency of the rain is also crucial. Having replicated this  
436 observation at several sites, we confirm that species participating in explosive breeding events  
437 are highly tuned to specific rainfall patterns. Recent studies have identified the photoperiod as  
438 an important predictor of anuran activity [20–23], but our statistical analyses showed no clear  
439 links between this factor and explosive breeding events. Our study site was very close to the  
440 equator (4°36'N), where the difference between maximum and minimum day length across the  
441 year is less than 32 minutes. Former studies on photoperiod were conducted at latitudes where  
442 the difference in day length are much more pronounced (at least 4.4 times stronger), which  
443 probably explains why this factor was so important.

444 This apparently high dependency of explosive breeders' reproduction not only to the  
445 amount of precipitation but also to the timing of rain events raises the question of the  
446 vulnerability of explosive breeders to climate changes. While other factors such as  
447 programmed annual migration might be involved in triggering explosive breeding events, our  
448 study suggests that the two specific patterns of rain (i.e. consistency during the previous 48 to  
449 72 hours and amount during previous 24 hours) are key parameters for the initiation of  
450 reproduction. With climate change increasing rainfall variability in tropical regions [53],  
451 reproductive events might be shifted or disrupted. Moreover, these species rely on very  
452 specific habitats (temporary reproductive ponds) for their reproduction that are very fragile  
453 and particularly vulnerable to climate changes [14]. Finally, the high number of individuals  
454 from several species at the time of reproduction might increase probability of intra and inter-  
455 species infection at the breeding ponds and therefore increase the sensitivity of these species  
456 to emerging infectious disease, in particular the fungus *Batrachochytrium dendrobatidis* [54].  
457 These combined factors, may lead to significant shifts in the timing, distribution and  
458 composition of explosive breeding communities, which may desynchronize phenology and  
459 other biological responses throughout several trophic levels in the ecosystem [55].

460

#### 461 *Community diversity analyses*

462 In structurally similar habitats, located in the same region without obvious barriers, we  
463 expected to have homogeneous amphibian communities. Yet, our results highlight the  
464 variability of species composition in explosive breeding events. The ordination diagram  
465 showed differences in species composition both between ponds and for a given pond, between  
466 the two observed events. In other words, each explosive breeding event, while often sharing a  
467 common pool of species, had a unique combination of species. When controlling for the  
468 differences between explosive breeding communities, a clear temporal factor structured the

469 acoustic community during explosive breeding events, showing pronounced differences  
470 between pre-explosive and explosive breeding communities. The main species characterising  
471 the explosive breeding event, *C. shudikarensis*, *T. coriaceus* and *C. cornuta*, were also found  
472 as predominant species in explosive breeding events in the Aratai river, more than 100 km  
473 away from our study site [27]. While other species are also present during these aggregations,  
474 these species seem particularly representative of the acoustic community.

475         It remains to explain the species turnover between events in space (ponds) and time  
476 (for each pond between the first and the second event). This turnover could be due to  
477 stochastic factors or related to multiple combined determinants, such as ecological and  
478 behavioural traits. As in many other sampling techniques in ecology, rare and elusive species  
479 are difficult to detect. It is also possible that the dense chorus of the louder species masked the  
480 vocalisations of more silent species, inducing detection errors and causing community  
481 variations in space and time.

482

#### 483 *Acoustic diversity analyses*

484 Regarding the acoustic environment of explosive breeding events, we found outlying levels of  
485 activity with a characteristic spectral signature. This signature stands out from the circadian  
486 acoustic environment and can be easily detected at long distance. Acoustic signatures convey  
487 information that could be exploited by conspecifics (or heterospecific) for general orientation  
488 within a landscape [56]. Fish and crustacean larvae [57], birds [58], and frogs [59,60] are  
489 known to use sounds in the environment for spatial orientation. Indeed, acoustic cues might  
490 gain importance for anuran explosive breeding species since sounds may signal availability,  
491 in space and time, of short-lived breeding sites [60,61].

492         Alpha diversity indices, measured with species richness and Gini-Simpson, showed  
493 temporal communities with similar values between pre-explosive (t1-t2) and the explosive  
494 breeding community (t4). The transitional community (t3) had higher values, probably  
495 because it had species from both communities, pre- and explosive breeding. More  
496 surprisingly, Rao's diversity coefficient showed a significant diminution of the spectral  
497 diversity during explosive breeding events (t4). Even when the number of calling species was  
498 similar, we observed more frequency overlap in signals for the explosive breeding community  
499 than for the pre-explosive community.

500         Species belonging to a community may compete to access acoustic resources, that is to  
501 a free acoustic channel. It has been therefore hypothesized that species calling in a chorus  
502 should exhibit frequency dispersion. Formulated under the acoustic niche hypothesis,

503 organisms would have evolved to occupy specific spectro-temporal 'niches', decreasing the  
504 risk of heterospecific mating and information masking [62]. Acoustic partitioning has been  
505 observed in multiple taxa, such as insects [63,64], birds [65] and amphibians [66]. However,  
506 recent studies also presented limitations of such hypothesis, showing no significant spectral  
507 divergence in cricket assemblages [67] and more similarity in signal design that expected by  
508 chance for tropical forest birds [68]. Our results are in line with these last studies; contrary to  
509 our prediction, the species did not show frequency dispersion but frequency overlap.

510 Multiple hypotheses might explain this observation. First, the study ponds had similar  
511 habitat characteristics and hence similar acoustic properties that might have an effect on the  
512 features of anuran sounds. Following the Acoustic Adaptation Hypothesis [69–71], the habitat  
513 might impose limits (e.g. signal attenuation and degradation) for sound propagation at high  
514 and low frequencies, resulting in an adaptation of explosive breeding species to produce  
515 sounds at mid frequencies, where they can maximize propagation. Indeed, for sounds  
516 produced at ground level, a window suitable for acoustic long range communication have  
517 been found at mid-frequencies (1-4 kHz) during experiments in an Amazonian rainforest in  
518 southern Venezuela [72]. Second, compared to prolonged breeders that show long periods of  
519 calling activity, explosive breeders share the acoustic space for very brief moments. As  
520 discussed by Wells [24], due to the short time window for exchanging vocal signals between  
521 individuals, males would rather compete physically and not acoustically. The selective  
522 pressures acting on the acoustic space of these species might be weaker, which could explain  
523 the high frequency overlap of the explosive breeding events. Finally, a convergence of  
524 signals, not only in time but also in frequency, could serve to better synchronise the sporadic  
525 emergence of multiple anuran species. A signal with common features across taxa would  
526 allow recruiting a larger number of individuals at precise location and time, aggregating  
527 organisms at densities that exceed the potential number of local predators. Indeed, studies on  
528 a variety of animals [73–75] and plants [76,77] have shown that sporadic synchronous  
529 reproduction within a population significantly reduces levels of predation. However, to  
530 confirm a convergence on the signal, additional data should be included in the analysis, such  
531 as phylogenetic and functional traits. Moreover, sound propagation and playback experiments  
532 should be performed to shed light on the selective pressure driving widespread chorusing  
533 behaviour.

534

535 **Conclusions**

536

537 In this study, we coupled biotic and abiotic variables, revealing community changes at  
538 multiple spatiotemporal scales and their tight link with the environment. Such data provides a  
539 baseline against which future changes can be measured, contributing to a better understanding  
540 and hopefully to a better management of such unique communities. Acoustic signatures could  
541 be used as a suitable way to monitor wildlife, not only at the individual or population level,  
542 but also at the community level, one of the main task of ecoacoustics [78]. A more  
543 widespread use of standardized methods combining passive acoustic recorders with a  
544 monitoring of key environmental parameters would become a comprehensible and cost-  
545 efficient framework to improve our knowledge and manage rich animal communities of  
546 tropical forests.

547

548

549

## 550 **Abbreviations**

551

552 ANOVA: Analysis of Variance

553 Ar: Arlesienne

554 Bl: Blanc

555 Ca: Caïman

556 DPCoA: Double Principle Coordinate Analysis

557 FFT: Fast Fourier Transform

558 GIS: Geographic Information System

559 IQR: Inter Quartile Range

560 m a.s.l: meters above sea level

561 Pa: Patawa

562 Pe: Petite

563 RMS: Root Mean Square

564 SNR: Signal to Noise Ratio

565

## 566 **Declarations**

567

568 *Ethics approval and consent to participate*

569 There was no requirement to seek ethical approval to carry out the work described above.

570

571 *Consent for publication*

572 Not applicable

573

574 *Availability of data and material*

575 The environmental audio recordings were deposited at the sound library of the Muséum  
576 national d'Histoire naturelle (<https://sonotheque.mnhn.fr/>).

577

578 *Competing interests*

579 The authors declare that they have no competing interests

580

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589

590 *Authors' contributions*

591 JSU, JS, EC and PG participated in the deployment and maintenance of acoustic sensors for  
592 data acquisition. EC, PG and AF manually scrutinised audio recordings and provided personal  
593 recordings for the analyses. JSU, JS and TA made substantial contributions on the conception  
594 and design of the acquisition of data, analysis of the data and drafting of the manuscript. DLL  
595 and SP assisted in the analysis and interpretation of the community diversity data. All authors  
596 participated in revising critically the article contents. All authors read and approved the final  
597 manuscript.

598

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## 608 **References**

609

610 [1] Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Fischman DL, et al. Status  
611 and Trends of Amphibian Declines and Extinctions Worldwide. *Science*  
612 2004;306:1783–6. doi:10.1126/science.1103538.

613 [2] Hoffmann M, Hilton-Taylor C, Angulo A, Böhm M, Brooks TM, Butchart SHM, et al.  
614 The Impact of Conservation on the Status of the World’s Vertebrates. *Science*  
615 2010;1194442. doi:10.1126/science.1194442.

616 [3] Alroy J. Current extinction rates of reptiles and amphibians. *Proc Natl Acad Sci*  
617 2015;112:13003–8. doi:10.1073/pnas.1508681112.

618 [4] Carey C, Alexander MA. Climate change and amphibian declines: is there a link? *Divers*  
619 *Distrib* 2003;9:111–21. doi:10.1046/j.1472-4642.2003.00011.x.

620 [5] Pounds JA, Bustamante MR, Coloma LA, Consuegra JA, Fogden MPL, Foster PN, et al.  
621 Widespread amphibian extinctions from epidemic disease driven by global warming.  
622 *Nature* 2006;439:161–7. doi:10.1038/nature04246.

623 [6] Lips KR, Diffendorfer J, Iii JRM, Sears MW. Riding the Wave: Reconciling the Roles of  
624 Disease and Climate Change in Amphibian Declines. *PLOS Biol* 2008;6:e72.  
625 doi:10.1371/journal.pbio.0060072.

626 [7] Bellard C, Thuiller W, Leroy B, Genovesi P, Bakkenes M, Courchamp F. Will climate  
627 change promote future invasions? *Glob Change Biol* 2013;19:3740–8.  
628 doi:10.1111/gcb.12344.

629 [8] Llusia D, Márquez R, Beltrán JF, Benítez M, do Amaral JP. Calling behaviour under  
630 climate change: geographical and seasonal variation of calling temperatures in  
631 ectotherms. *Glob Change Biol* 2013;19:2655–74. doi:10.1111/gcb.12267.

632 [9] Araújo MB, Thuiller W, Pearson RG. Climate warming and the decline of amphibians  
633 and reptiles in Europe. *J Biogeogr* 2006;33:1712–28. doi:10.1111/j.1365-  
634 2699.2006.01482.x.

635 [10] Duarte H, Tejedo M, Katzenberger M, Marangoni F, Baldo D, Beltrán Juan Francisco, et  
636 al. Can amphibians take the heat? Vulnerability to climate warming in subtropical and

- 637 temperate larval amphibian communities. *Glob Change Biol* 2011;18:412–21.  
638 doi:10.1111/j.1365-2486.2011.02518.x.
- 639 [11] Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, et al.  
640 Impacts of climate warming on terrestrial ectotherms across latitude. *Proc Natl Acad Sci*  
641 2008;105:6668–6672.
- 642 [12] Bonetti MF, Wiens JJ. Evolution of climatic niche specialization: a phylogenetic  
643 analysis in amphibians. *Proc R Soc B Biol Sci* 2014;281:20133229–20133229.  
644 doi:10.1098/rspb.2013.3229.
- 645 [13] Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, Longino JT, et al.  
646 Thermal-safety margins and the necessity of thermoregulatory behavior across latitude  
647 and elevation. *Proc Natl Acad Sci* 2014;111:5610–5. doi:10.1073/pnas.1316145111.
- 648 [14] Foden WB, Butchart SHM, Stuart SN, Vié J-C, Akçakaya HR, Angulo A, et al.  
649 Identifying the World’s Most Climate Change Vulnerable Species: A Systematic Trait-  
650 Based Assessment of all Birds, Amphibians and Corals. *PLoS ONE* 2013;8:e65427.  
651 doi:10.1371/journal.pone.0065427.
- 652 [15] Gerhardt HC, Huber F. Acoustic communication in insects and anurans: common  
653 problems and diverse solutions. Chicago: University of Chicago Press; 2002.
- 654 [16] Narins PM, Feng AS, Fay RR, Popper AN, editors. Hearing and Sound Communication  
655 in Amphibians. vol. 28. Springer New York; 2006. doi:10.1007/978-0-387-47796-1.
- 656 [17] Brooke PN, Alford RA, Schwarzkopf L. Environmental and social factors influence  
657 chorusing behaviour in a tropical frog: examining various temporal and spatial scales.  
658 *Behav Ecol Sociobiol* 2000;49:79–87. doi:10.1007/s002650000256.
- 659 [18] Oseen KL, Wassersug RJ. Environmental factors influencing calling in sympatric  
660 anurans. *Oecologia* 2002;133:616–25. doi:10.1007/s00442-002-1067-5.
- 661 [19] Llusia D, Márquez R, Beltrán JF, Moreira C, Amaral JP do. Environmental and social  
662 determinants of anuran lekking behavior: intraspecific variation in populations at  
663 thermal extremes. *Behav Ecol Sociobiol* 2013;67:493–511. doi:10.1007/s00265-012-  
664 1469-2.
- 665 [20] Both C, Kaefer ÍL, Santos TG, Cechin STZ. An austral anuran assemblage in the  
666 Neotropics: seasonal occurrence correlated with photoperiod. *J Nat Hist* 2008;42:205–  
667 22. doi:10.1080/00222930701847923.
- 668 [21] Canavero A, Arim M. Clues supporting photoperiod as the main determinant of seasonal  
669 variation in amphibian activity. *J Nat Hist* 2009;43:2975–84.  
670 doi:10.1080/00222930903377539.

- 671 [22] Iwai N. Relationship between chorusing activity and number of oviposition events in the  
672 Otton frog. *Anim Biol* 2018;68:105–11. doi:10.1163/15707563-17000143.
- 673 [23] Schalk CM, Saenz D. Environmental drivers of anuran calling phenology in a seasonal  
674 Neotropical ecosystem: Anuran Temporal Partitioning. *Austral Ecol* 2016;41:16–27.  
675 doi:10.1111/aec.12281.
- 676 [24] Wells KD. The social behaviour of anuran amphibians. *Anim Behav* 1977;25:666–93.  
677 doi:10.1016/0003-3472(77)90118-X.
- 678 [25] Aichinger M. Annual activity patterns of anurans in a seasonal neotropical environment.  
679 *Oecologia* 1987;71:583–592.
- 680 [26] Duellman WE. Temporal Fluctuations in Abundances of Anuran Amphibians in a  
681 Seasonal Amazonian Rainforest. *J Herpetol* 1995;29:13. doi:10.2307/1565080.
- 682 [27] Gottsberger B, Gruber E. Temporal partitioning of reproductive activity in a neotropical  
683 anuran community. *J Trop Ecol* 2004;20:271–80. doi:10.1017/S0266467403001172.
- 684 [28] Prado C, Uetanabaro M, Haddad C. Breeding activity patterns, reproductive modes, and  
685 habitat use by anurans (Amphibia) in a seasonal environment in the Pantanal, Brazil.  
686 *Amphib-Reptil* 2005;26:211–21.
- 687 [29] Gerhardt HC, Huber F. Causes and Consequences of Chorusing. *Acoust. Commun.*  
688 *Insects Anurans Common Probl. Diverse Solut.*, Chicago: University of Chicago Press;  
689 2002.
- 690 [30] Peterson CR, Dorcas ME. Automated data acquisition. *Meas. Monit. Biol. Divers. Stand.*  
691 *Methods Amphib.* R.W. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and  
692 M.S. Foster (eds.), Smithsonian Institution Press, Washington DC, USA; 1994, p. 47–57.
- 693 [31] Browning E, Gibb R, Glover-Kapfer P, Jones KE. Passive acoustic monitoring in  
694 ecology and conservation. Woking, United Kingdom: WWF; 2017.
- 695 [32] Saenz D, Fitzgerald LA, Baum KA, Conner RN. Abiotic correlates of anuran calling  
696 phenology: the importance of rain, temperature, and season. *Herpetol Monogr*  
697 2006;20:64–83. doi:10.1655/0733-1347(2007)20[64:ACOACP]2.0.CO;2.
- 698 [33] Gibb R, Browning E, Glover-Kapfer P, Jones KE. Emerging opportunities and  
699 challenges for passive acoustics in ecological assessment and monitoring. *Methods Ecol*  
700 *Evol* 2018;1–17. doi:10.1111/2041-210X.13101.
- 701 [34] Acevedo MA, Villanueva-Rivera LJ. Using automated digital recording systems as  
702 effective tools for the monitoring of birds and amphibians. *Wildl Soc Bull* 2006;34:211–  
703 4.

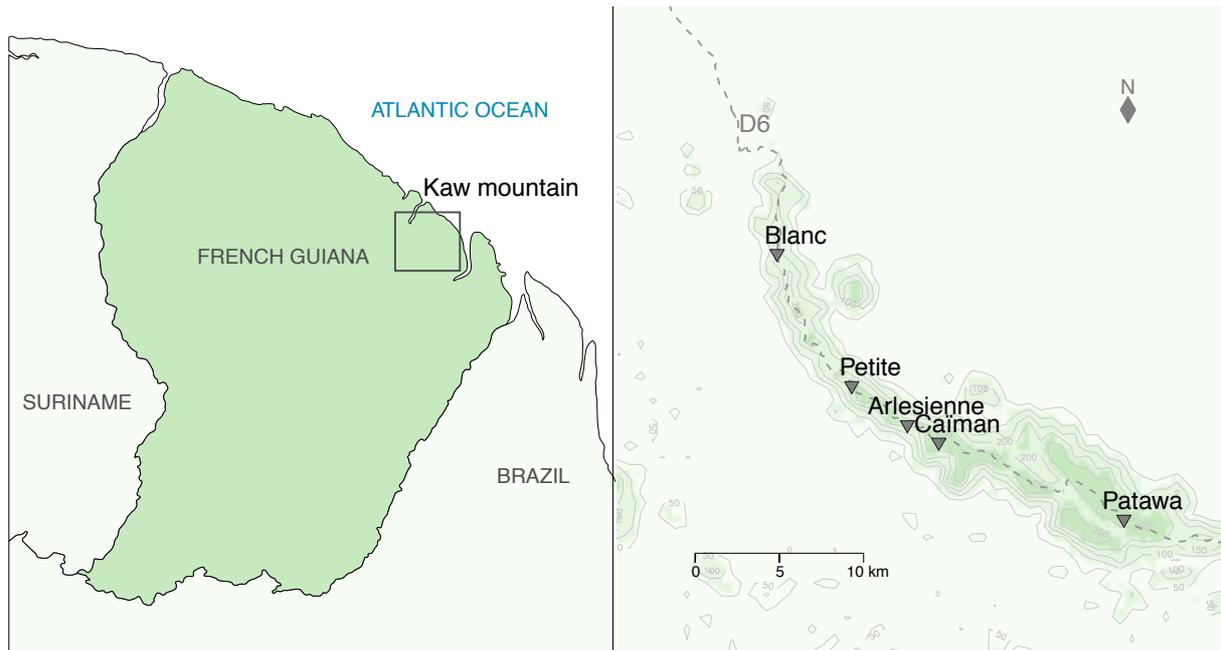
- 704 [35] Obrist MK, Pavan G, Sueur J, Riede K, Llusia D, Márquez R. Bioacoustics approaches  
705 in biodiversity inventories. In: Eymann J, Degreef J, Häuser C, Monje JC, Samyn Y,  
706 Vandenspiegel YD, editors. *Man. Field Rec. Tech. Protoc. Taxa Biodivers. Invent.*  
707 *Monit.*, vol. 8, ABC Taxa; 2010, p. 18–48.
- 708 [36] Servick K. Eavesdropping on Ecosystems. *Science* 2014;343:834–7.  
709 doi:10.1126/science.343.6173.834.
- 710 [37] Bridges AS, Dorcas ME. Temporal variation in anuran calling behavior: implications for  
711 surveys and monitoring programs. *Copeia* 2000;2000:587–92. doi:10.1643/0045-  
712 8511(2000)000[0587:TVIACB]2.0.CO;2.
- 713 [38] Hilje B, Aide TM. Recovery of amphibian species richness and composition in a  
714 chronosequence of secondary forests, northeastern Costa Rica. *Biol Conserv*  
715 2012;146:170–6. doi:10.1016/j.biocon.2011.12.007.
- 716 [39] Jansen M, Plath M, Brusquetti F, Ryan MJ. Asymmetric frequency shift in  
717 advertisement calls of sympatric frogs. *Amphib-Reptil* 2016;37:137–52.  
718 doi:10.1163/15685381-00003038.
- 719 [40] Pereyra LC, Akmentins MS, Sanabria EA, Vaira M. Diurnal? Calling activity patterns  
720 reveal nocturnal habits in the aposematic toad *Melanophryniscus rubriventris*. *Can J*  
721 *Zool* 2016;94:497–503. doi:10.1139/cjz-2015-0197.
- 722 [41] Breiman L. Random Forests. *Mach Learn* 2001;45:5–32.  
723 doi:10.1023/A:1010933404324.
- 724 [42] Cutler DR, Edwards TC, Beard KH, Cutler A, Hess KT, Gibson J, et al. Random forests  
725 for classification in ecology. *Ecology* 2007;88:2783–92. doi:10.1890/07-0539.1.
- 726 [43] Pavoine S, Blondel J, Dufour AB, Gasc A, Bonsall MB. A New Technique for  
727 Analysing Interacting Factors Affecting Biodiversity Patterns: Crossed-DPCoA. *PLoS*  
728 *ONE* 2013;8:e54530. doi:10.1371/journal.pone.0054530.
- 729 [44] Marty C, Gaucher P. Sound guide to the tailless amphibians of French Guiana. France:  
730 Ceba (Centre Bioacoustique Alpin); 1999.
- 731 [45] Lellouch L, Pavoine S, Jiguet F, Glotin H, Sueur J. Monitoring temporal change of bird  
732 communities with dissimilarity acoustic indices. *Methods Ecol Evol* 2014;5:495–505.  
733 doi:10.1111/2041-210X.12178.
- 734 [46] Gini C. Variabilità e mutabilità. *Contrib. Allo Studio Delle Distrib. E Delle Relazioni*  
735 *Stat.*, C. Cuppini, Bologna; 1912.
- 736 [47] Simpson EH. Measurement of Diversity. *Nature* 1949;163:688.

- 737 [48] Rao CR. Diversity and dissimilarity coefficients: A unified approach. *Theor Popul Biol*  
738 1982;21:24–43. doi:10.1016/0040-5809(82)90004-1.
- 739 [49] R Core Team. *R: A Language and Environment for Statistical Computing*. Vienna,  
740 Austria: R Foundation for Statistical Computing; 2017.
- 741 [50] Sueur J, Aubin T, Simonis C. Seewave: a free modular tool for sound analysis and  
742 synthesis. *Bioacoustics* 2008;18:213–26.
- 743 [51] Pavoine S. *adiv: Analysis of Diversity*, version 1.1. 2017.
- 744 [52] Liaw A, Wiener M. Classification and Regression by randomForest. *R News* 2002;2:18–  
745 22.
- 746 [53] Feng X, Porporato A, Rodriguez-Iturbe I. Changes in rainfall seasonality in the tropics.  
747 *Nat Clim Change* 2013;3:811–5. doi:10.1038/nclimate1907.
- 748 [54] O’Hanlon SJ, Rieux A, Farrer RA, Rosa GM, Waldman B, Bataille A, et al. Recent  
749 Asian origin of chytrid fungi causing global amphibian declines. *Science* 2018;360:621–  
750 7. doi:10.1126/science.aar1965.
- 751 [55] Schwartz MD. *Phenology: an integrative environmental science*. 2013.
- 752 [56] Slabbekoorn H, Bouton N. Soundscape orientation: a new field in need of sound  
753 investigation. *Anim Behav* 2008;76:e5–8. doi:10.1016/j.anbehav.2008.06.010.
- 754 [57] Montgomery JC, Jeffs A, Simpson SD, Meekan M, Tindle C. Sound as an orientation  
755 cue for the pelagic larvae of reef fishes and decapod crustaceans. *Adv Mar Biol*  
756 2006;51:143–96. doi:10.1016/S0065-2881(06)51003-X.
- 757 [58] Mönkkönen M, Helle P, Soppela K. Numerical and behavioural responses of migrant  
758 passerines to experimental manipulation of resident tits (*Parus* spp.): heterospecific  
759 attraction in northern breeding bird communities? *Oecologia* 1990;85:218–25.  
760 doi:10.1007/BF00319404.
- 761 [59] Gerhardt HC, Klump GM. Phonotactic responses and selectivity of barking treefrogs  
762 (*Hyla gratiosa*) to chorus sounds. *J Comp Physiol A* 1988;163:795–802.  
763 doi:10.1007/BF00604056.
- 764 [60] Bee MA. Selective phonotaxis by male wood frogs (*Rana sylvatica*) to the sound of a  
765 chorus. *Behav Ecol Sociobiol* 2007;61:955–66. doi:10.1007/s00265-006-0324-8.
- 766 [61] Swanson EM, Tekmen SM, Bee MA. Do female frogs exploit inadvertent social  
767 information to locate breeding aggregations? *Can J Zool* 2007;85:921–32.  
768 doi:10.1139/Z07-074.
- 769 [62] Krause BL. The niche hypothesis: a virtual symphony of animal sounds, the origins of  
770 musical expression and the health of habitats. *Soundscape Newsl* 1993;6:4–6.

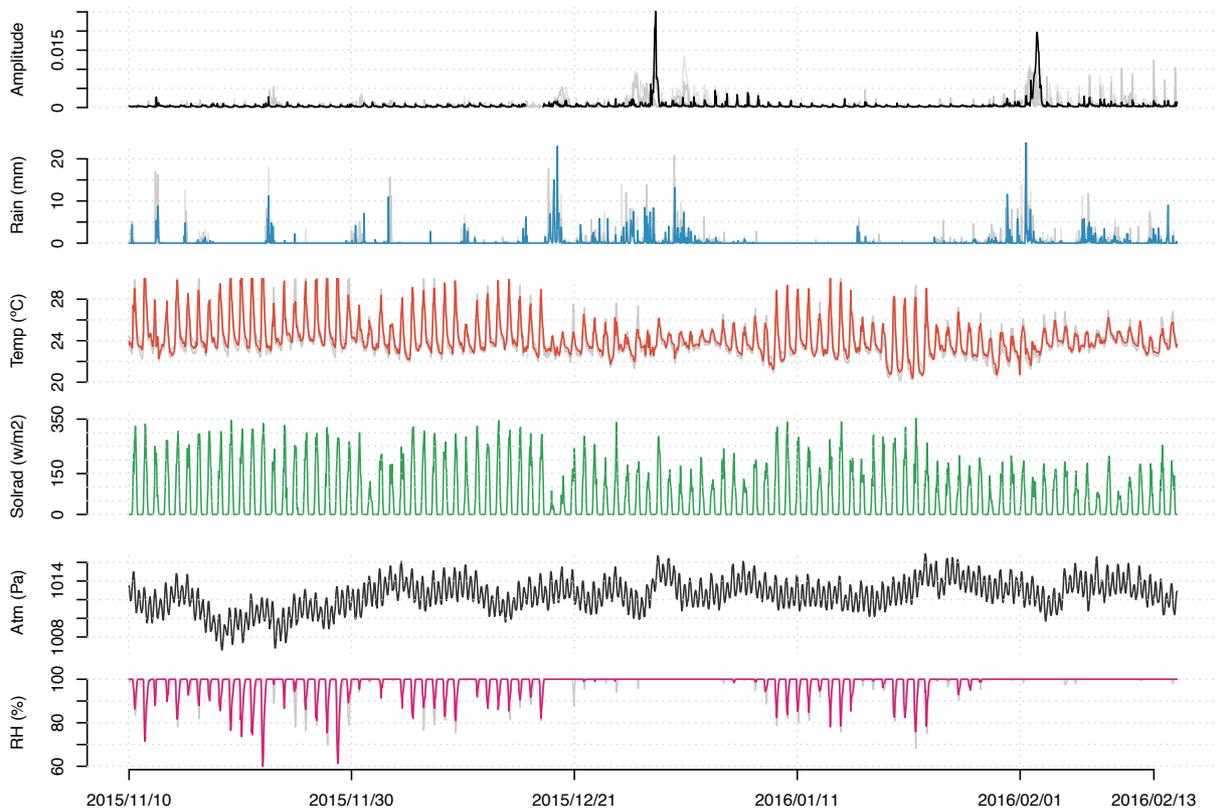
- 771 [63] Sueur J. Cicada acoustic communication: potential sound partitioning in a multispecies  
772 community from Mexico (Hemiptera: Cicadomorpha: Cicadidae). *Biol J Linn Soc*  
773 2002;75:379–94. doi:10.1046/j.1095-8312.2002.00030.x.
- 774 [64] Schmidt AKD, Römer H, Riede K. Spectral niche segregation and community  
775 organization in a tropical cricket assemblage. *Behav Ecol* 2013;24:470–80.  
776 doi:10.1093/beheco/ars187.
- 777 [65] Planqué R, Slabbekoorn H. Spectral Overlap in Songs and Temporal Avoidance in a  
778 Peruvian Bird Assemblage. *Ethology* 2008;114:262–71. doi:10.1111/j.1439-  
779 0310.2007.01461.x.
- 780 [66] Villanueva-Rivera LJ. Eleutherodactylus frogs show frequency but no temporal  
781 partitioning: implications for the acoustic niche hypothesis. *PeerJ* 2014;2:e496.  
782 doi:10.7717/peerj.496.
- 783 [67] Schmidt AKD, Riede K, Römer H. No phenotypic signature of acoustic competition in  
784 songs of a tropical cricket assemblage. *Behav Ecol* 2016;27:211–8.  
785 doi:10.1093/beheco/arv141.
- 786 [68] Tobias JA, Planqué R, Cram DL, Seddon N. Species interactions and the structure of  
787 complex communication networks. *Proc Natl Acad Sci* 2014;111:1020–5.  
788 doi:10.1073/pnas.1314337111.
- 789 [69] Morton ES. Ecological sources of selection on avian sounds. *Am Nat* 1975;109:17–34.
- 790 [70] Marten K, Marler P. Sound transmission and its significance for animal vocalization.  
791 *Behav Ecol Sociobiol* 1977;2:271–90. doi:10.1007/BF00299740.
- 792 [71] Ey E, Fischer J. The “acoustic adaptation hypothesis” - a review of the evidence from  
793 birds, anurans and mammals. *Bioacoustics* 2009;19:21–48.
- 794 [72] Ellinger N, Hödl W. Habitat acoustics of a neotropical lowland rainforest. *Bioacoustics*  
795 2003;13:297–321.
- 796 [73] Sweeney BW, Vannote RL. Population Synchrony in Mayflies: A Predator Satiation  
797 Hypothesis. *Evolution* 1982;36:810–21. doi:10.1111/j.1558-5646.1982.tb05447.x.
- 798 [74] Williams KS, Smith KG, Stephen FM. Emergence of 13-Yr Periodical Cicadas  
799 (Cicadidae: Magicicada): Phenology, Mortality, and Predators Satiation. *Ecology*  
800 1993;74:1143–52. doi:10.2307/1940484.
- 801 [75] Santos RG, Pinheiro HT, Martins AS, Riul P, Bruno SC, Janzen FJ, et al. The anti-  
802 predator role of within-nest emergence synchrony in sea turtle hatchlings. *Proc R Soc B*  
803 2016;283:20160697. doi:10.1098/rspb.2016.0697.

- 804 [76] Donaldson JS. Mast-seeding in the cycad genus *Encephalartos*: a test of the predator  
805 satiation hypothesis. *Oecologia* 1993;94:262–71. doi:10.1007/BF00341326.
- 806 [77] Xiao Z, Zhang Z, Krebs CJ. Long-term seed survival and dispersal dynamics in a rodent-  
807 dispersed tree: testing the predator satiation hypothesis and the predator dispersal  
808 hypothesis. *J Ecol* 2013;101:1256–64. doi:10.1111/1365-2745.12113.
- 809 [78] Farina A, Gage SH, editors. *Ecoacoustics: The Ecological Role of Sounds*. Chichester,  
810 UK: John Wiley & Sons, Ltd; 2017. doi:10.1002/9781119230724.
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815 **Figures**

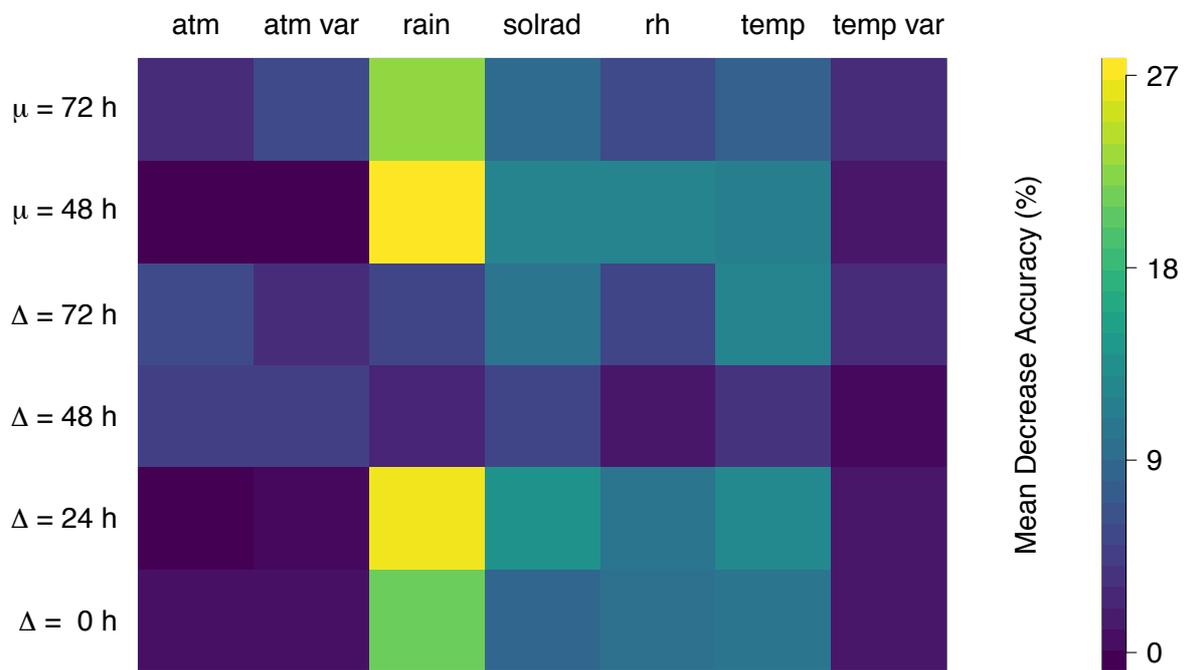


816  
817 **Fig. 1** Location of the study area. On the left, location of the Kaw mountain in French Guiana.  
818 On the right, location of the five study sites along a 30.4 km transect next to the departmental  
819 road D6. GIS shape files were obtained from the National Institute of Geographic and  
820 Forestry Information (<http://professionnels.ign.fr/>).  
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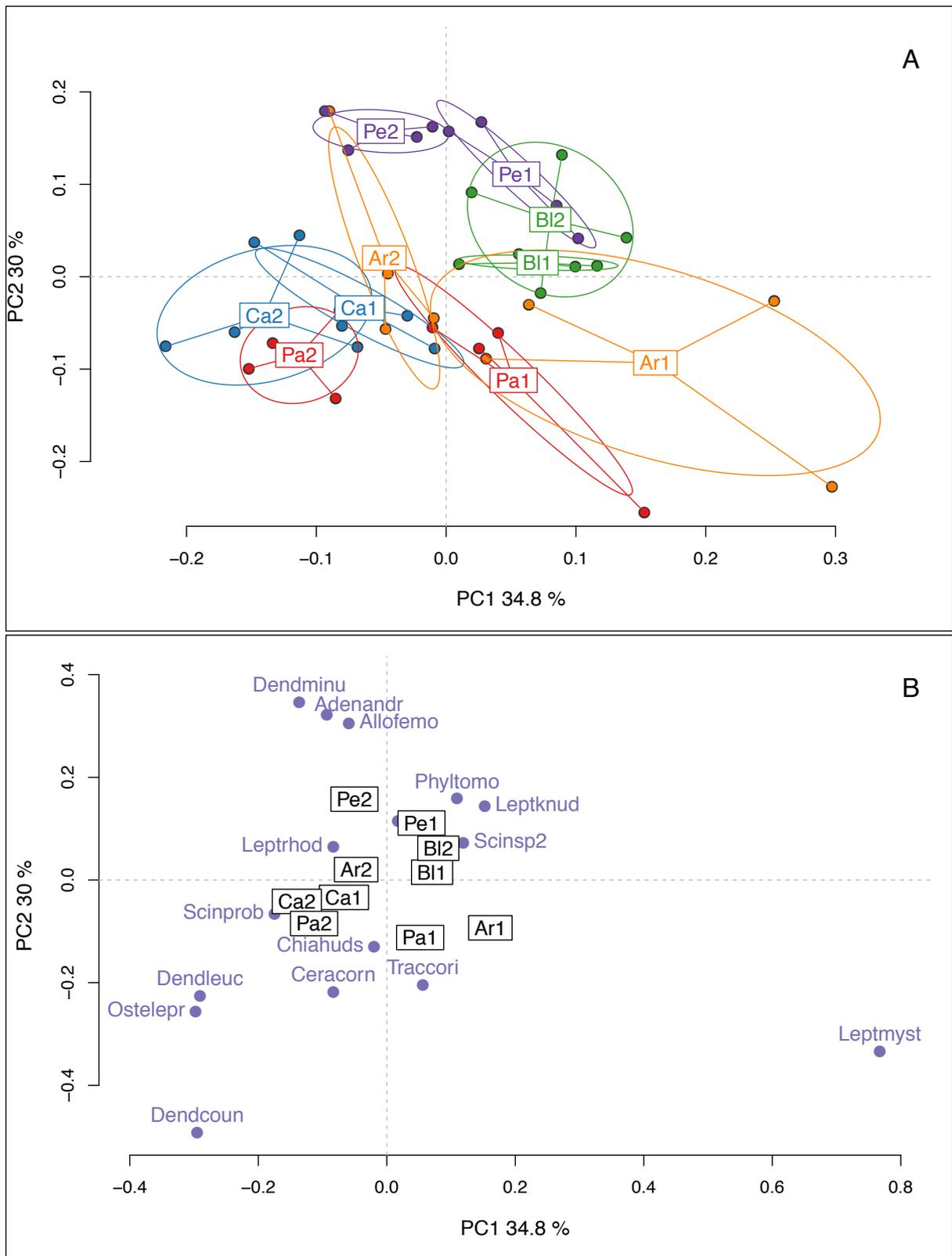


822

823 **Fig. 2** Temporal fluctuation of the measured environmental variables: sound pressure  
 824 amplitude (root mean square of the signal amplitude envelope), rainfall (mm), temperature  
 825 ( $^{\circ}\text{C}$ ), solar radiation ( $\text{w}/\text{m}^2$ ), atmospheric pressure (Pa) and relative humidity (%). The  
 826 acoustic amplitude plot shows two clear peaks that are related to explosive breeding events.  
 827 For illustration purposes, only the variables measured at a single pond (Blanc) are highlighted  
 828 in dark colours, the data collected at the other four ponds are plotted as light grey lines in the  
 829 background. Dates are given as year/month/day.  
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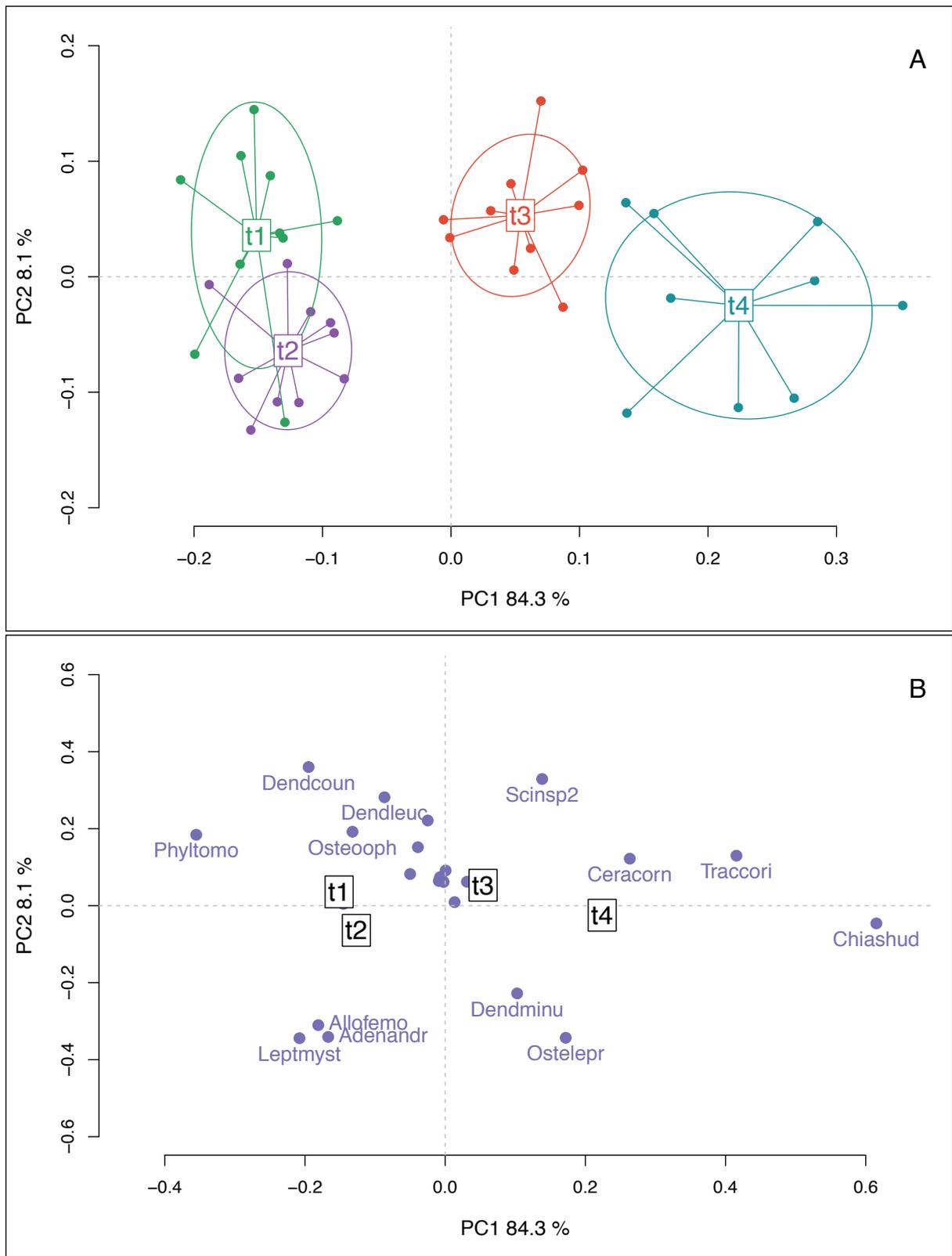


831  
 832 **Fig. 3** Variable importance measure (mean decrease accuracy) from Random Forest  
 833 classification used for predicting the start of the explosive breeding events. Variables with  
 834 higher values were more important for the classification. A total of 48 environmental  
 835 variables were evaluated based on the combination of eight measurements and six derived  
 836 variables. The variables measured were: photoperiod (phper), atmospheric pressure (atm),  
 837 atmospheric pressure variance (atm var), rainfall (rain), solar radiation (solrad), relative  
 838 humidity (rh), temperature (temp) and temperature variance (temp var). The derived variables  
 839 were based on their delay ( $\Delta$ ) and persistence ( $\mu$ ) along the time (0, 24, 48 and 72 hours).



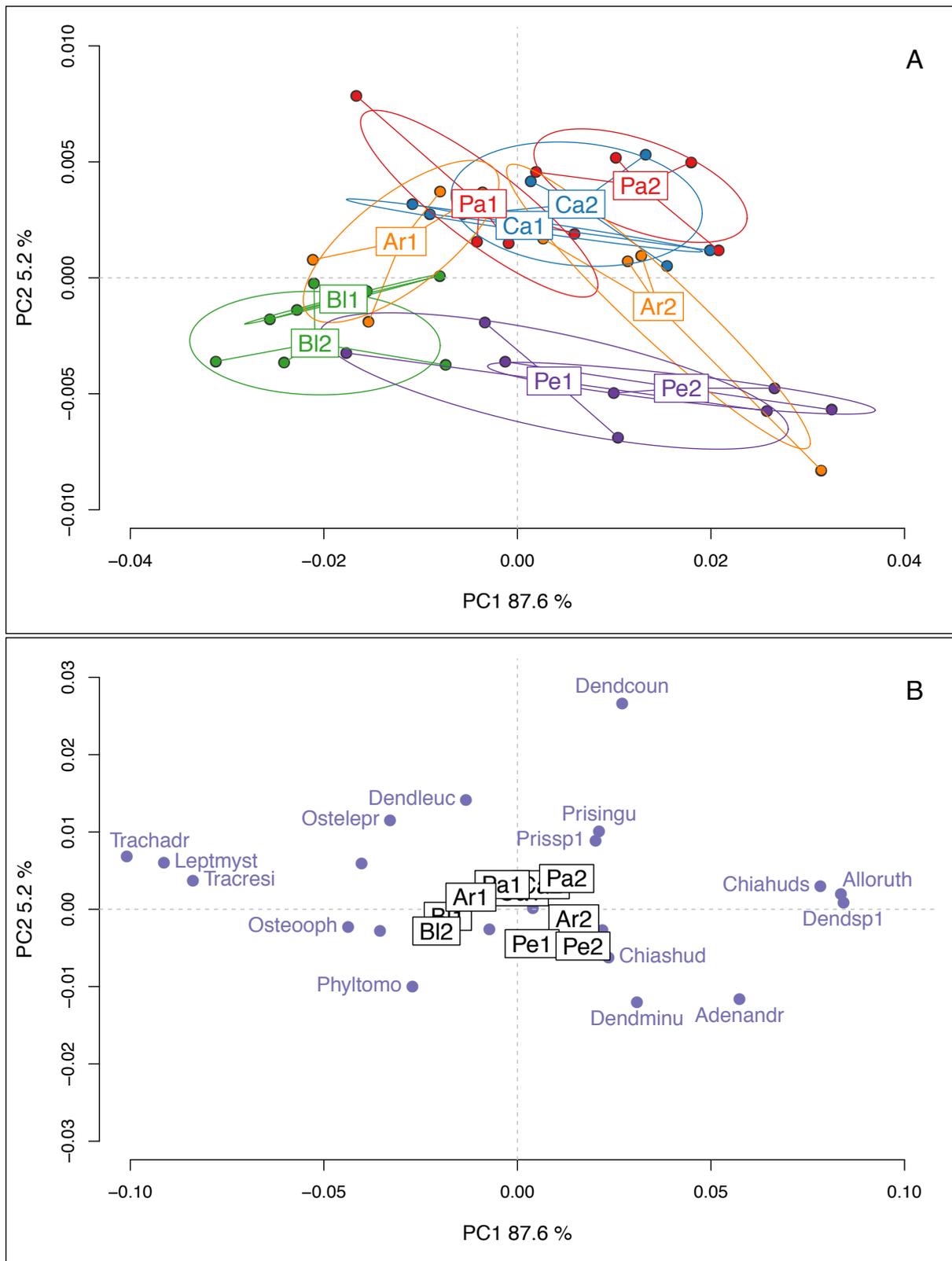
840  
 841 **Fig. 4** Diversity of the species composition in explosive breeding events across sites. The two  
 842 principal axes (64.8 % of variance explained) of the crossed DPCoA analysis are plotted. (A)  
 843 Diversity between and within communities. Each point is a community. The communities  
 844 were color-coded with the levels of the factor event. Code names for events are: Ar =

845 Arlesienne, Bl = Blanc, Ca = Caïman, Pa = Patawa, Pe = Petite. The number that follows the  
846 code name distinguishes the explosive breeding event in each site, for instance Ar1 is for the  
847 first event on site Arlesienne, and Ar2 is for the second event on the same site. (B)  
848 Coordinates of the constitutive species in the axes. Each point is a species. Only the species  
849 that had the highest values on the axes were named. Code names for the species are:  
850 *Adenomera andreae* = Adenandr, *Allobates femoralis* = Allofemo, *Ceratophrys cornuta* =  
851 Ceracorn, *Chiasmocleis hudsoni* = Chiahuds, *Dendropsophus counani* = Dendcoun,  
852 *Dendropsophus leucophyllatus* = Dendleuc, *Dendropsophus minutus* = Dendminu,  
853 *Leptodactylus knudseni* = Leptknud, *Leptodactylus mystaceus* = Leptmyst, *Leptodactylus*  
854 *rhodomystax* = Leptrhod, *Osteocephalus leprieurii* = Ostelepr, *Phyllomedusa tomopterna* =  
855 Phyltomo, *Scinax sp2* = Scinsp2, *Trachycephalus coriaceus* = Traccori.



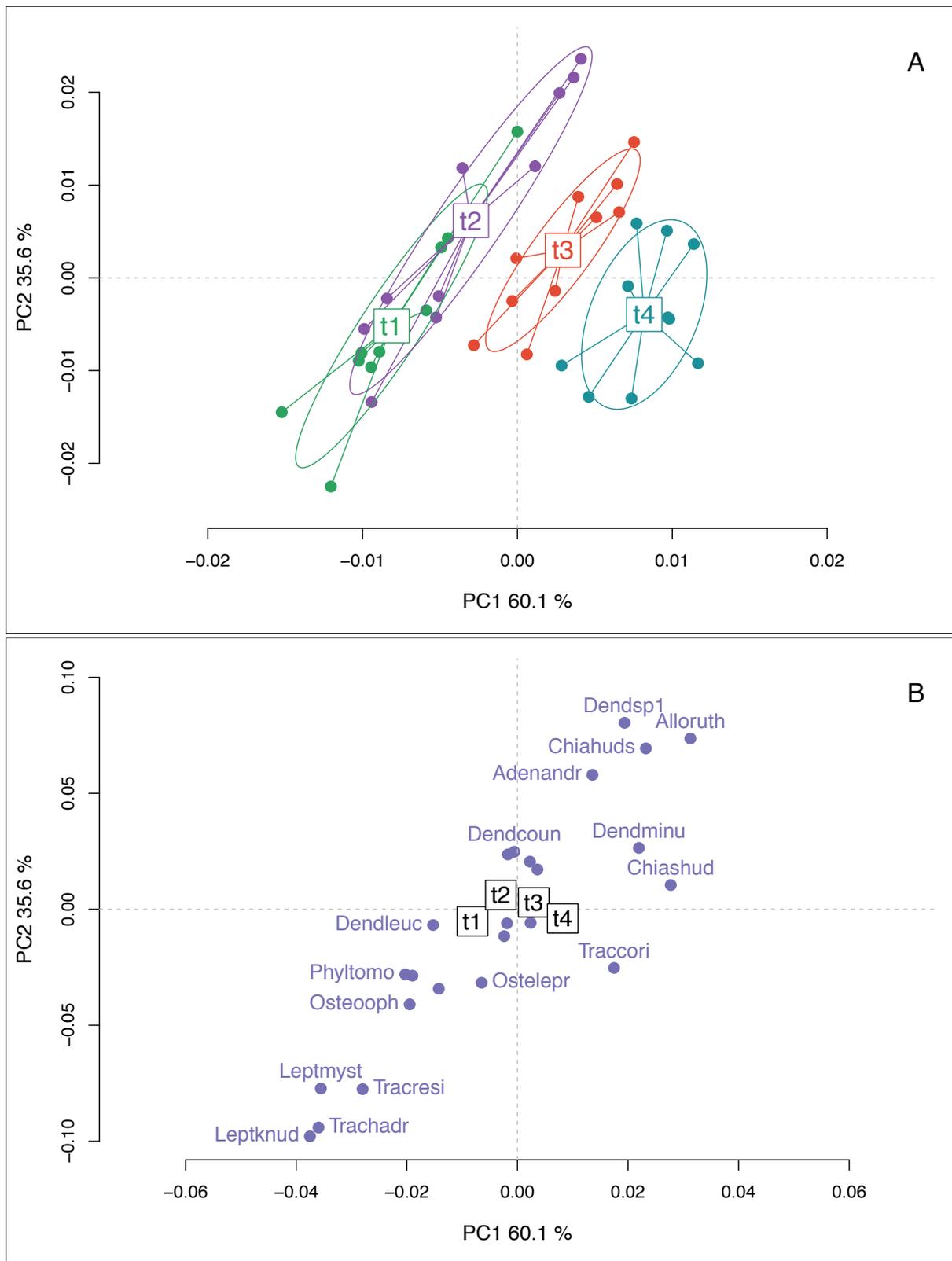
856  
 857 **Fig. 5** Diversity of the species composition in explosive breeding events across time. The two  
 858 principal axes (92.4 % of variance explained) of the crossed DPCoA analysis are plotted. (A)  
 859 Diversity between and within communities along the time. Each point is a community. The  
 860 communities are color-coded with the levels of factor time: t1, t2 ,t3, and t4. Pre-explosive

861 and mid-explosive communities are clearly discriminated along the first axis. (B) Coordinates  
862 of the constitutive species in the axes. Each point is a species. Only the species that had the  
863 highest values on the axes were named: *Adomera andreae* = Adenandr, *Allobates femoralis*  
864 = Allofemo, *Ceratophrys cornuta* = Ceracorn, *Chiasmocleis shudikarensis* = Chiashud,  
865 *Dendropsophus counani* = Dendcoun, *Dendropsophus leucophyllatus* = Dendleuc,  
866 *Dendropsophus minutus* = Dendminu, *Leptodactylus mystaceus* = Leptmyst, *Osteocephalus*  
867 *leprieurii* = Ostelepr, *Osteocephalus oophagus* = Osteooph, *Phyllomedusa tomopterna* =  
868 Phyltomo, *Scinax sp2* = Scinsp2, *Trachycephalus coriaceus* = Traccori.  
869



870  
 871 **Fig. 6** Diversity of the acoustic composition in explosive breeding events across sites. The  
 872 two principal axes (92.8 % of variance explained) of the crossed DPCoA analysis are plotted.  
 873 (A) Diversity between and within communities. Each point is a community. The communities  
 874 were color-coded with the levels of the factor event. Code names for events are: Ar =

875 Arlesienne, Bl = Blanc, Ca = Caïman, Pa = Patawa, Pe = Petite. The number that follows the  
876 code name distinguishes the explosive breeding event in each site, for instance Ar1 is for the  
877 first event on site Arlesienne, and Ar2 is for the second event on the same site. (B)  
878 Coordinates of the constitutive species in the axes. Each point is a species. Only the species  
879 that had the highest values on the axes were named. Code names for the species are:  
880 *Adomera andreae* = Adenandr, *Allophryne ruthveni* = Alloruth, *Chiasmocleis hudsoni* =  
881 Chiahuds, *Chiasmocleis shudikarensis* = Chiashud, *Dendropsophus counani* = Dendcoun,  
882 *Dendropsophus leucophyllatus* = Dendleuc, *Dendropsophus minutus* = Dendminu,  
883 *Dendropsophus sp1* = Dendsp1, *Leptodactylus mystaceus* = Leptmyst, *Osteocephalus*  
884 *leprieurii* = Ostelepr, *Osteocephalus oophagus* = Osteoph, *Phyllomedusa tomopterna* =  
885 Phyltomo, *Pristimantis inguinalis* = Prisingu, *Pristimantis sp1* = Prissp1, *Trachycephalus*  
886 *coriaceus* = Traccori, *Trachycephalus hadroceph* = Trachadr, *Trachycephalus resinifictrix* =  
887 Tracresi



888

889 **Fig. 7** Diversity of the acoustic composition in explosive breeding events across time. The

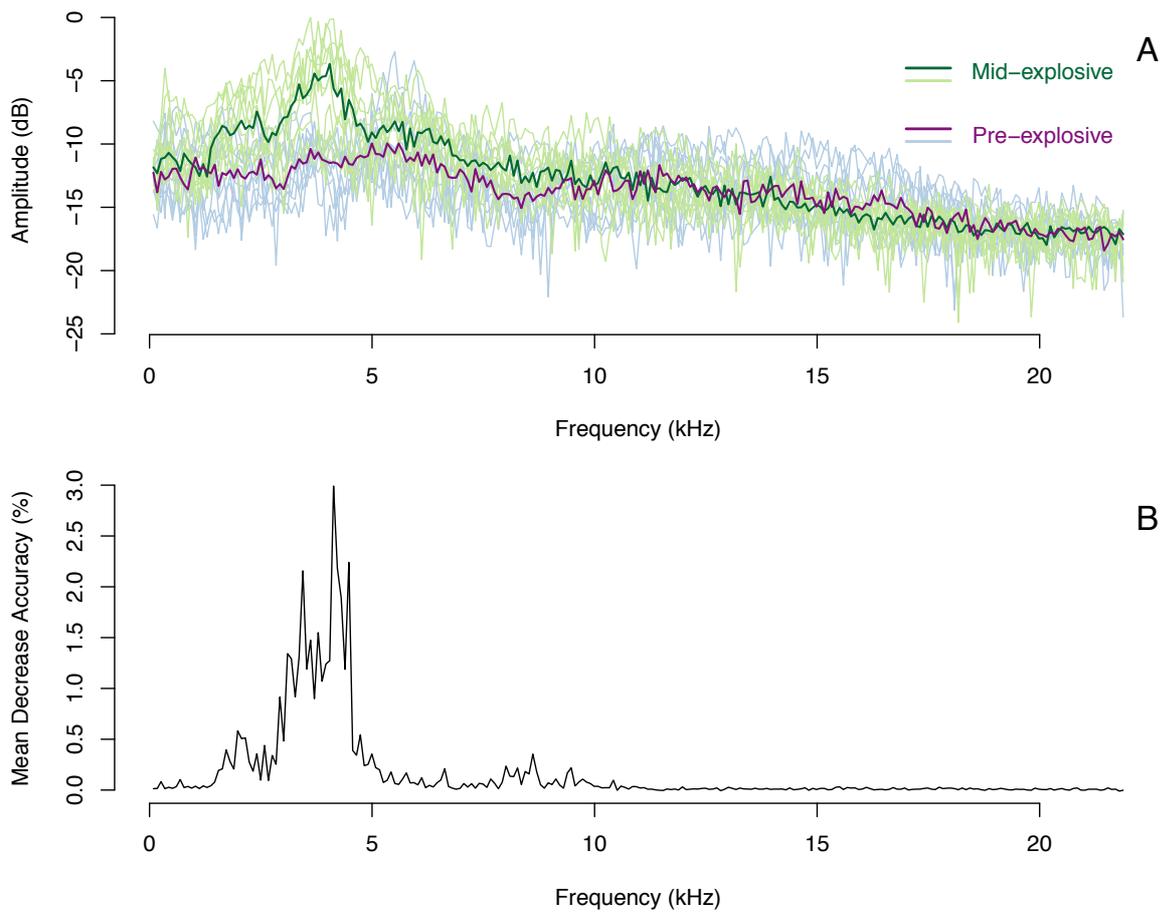
890 two principal axes (95.7 % of variance explained) of the crossed DPCoA analysis were

891 plotted. (A) Diversity between and within communities. Each point is a community.

892 Communities were color-coded with levels of factor time: t1, t2, t3, t4. Time periods t1 and t2

893 range 24-12 hours and 12-0 hours respectively before the onset of explosive breeding events,  
 894 t3 and t4 range 0-12 hours and 12-24 hours respectively after the onset. (B) Coordinates of the  
 895 constitutive species-specific calls in the principal axes. Each point is a species. Only the calls  
 896 with higher values on the axes were named: *Adenomera andreae* = Adenandr, *Allophryne*  
 897 *ruthveni* = Alloruth, *Chiasmocleis hudsoni* = Chiahuds, *Chiasmocleis shudikarensis* =  
 898 Chiashud, *Dendropsophus counani* = Dendcoun, *Dendropsophus leucophyllatus* = Dendleuc,  
 899 *Dendropsophus minutus* = Dendminu, *Dendropsophus spl* = Dendsp1, *Leptodactylus*  
 900 *knudseni* = Leptknud, *Leptodactylus mystaceus* = Leptmyst, *Osteocephalus leprieurii* =  
 901 Ostelepr, *Osteocephalus oophagus* = Osteooph, *Phyllomedusa tomopterna* = Phyltomo,  
 902 *Trachycephalus coriaceus* = Traccori, *Trachycephalus hadroceph* = Trachadr,  
 903 *Trachycephalus resinifictrix* = Tracresi

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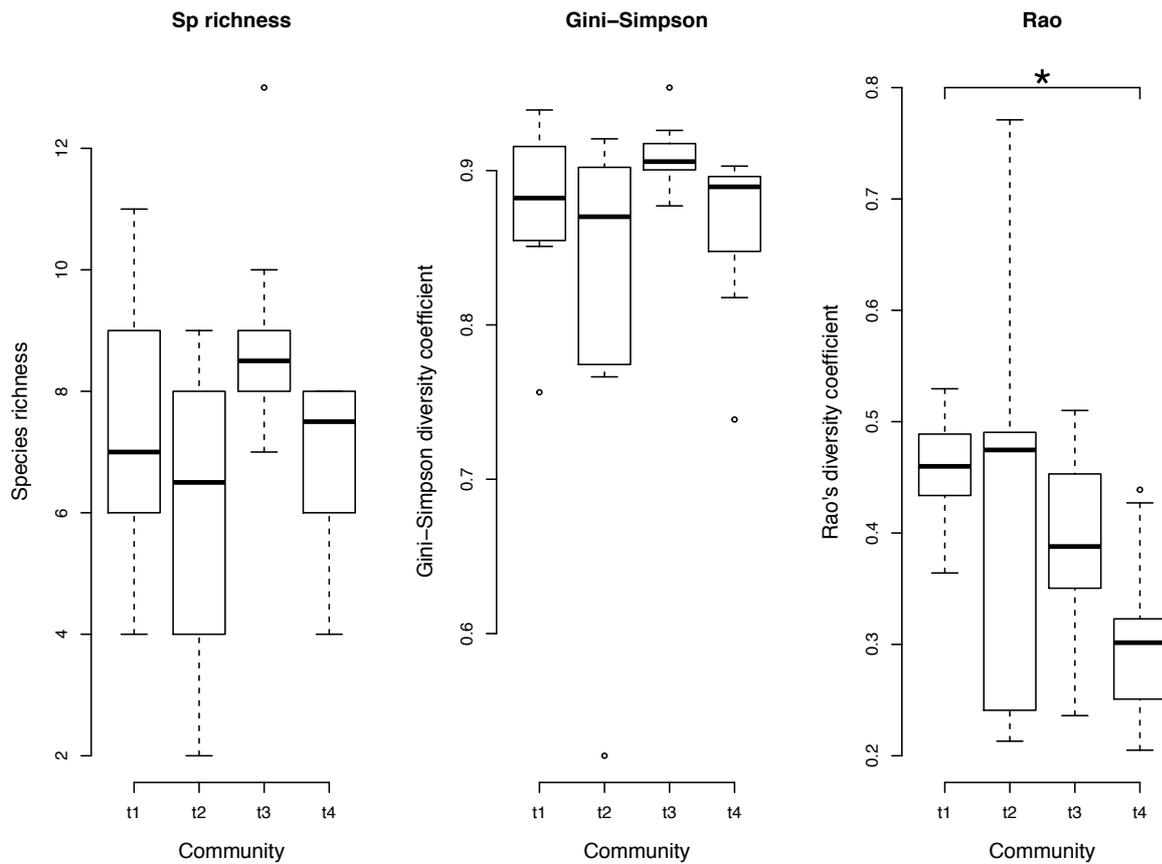


905

906 **Fig. 8** Comparison between spectral profiles of the acoustic communities before (pre) and  
907 during (mid) explosive breeding events. (A) In light colours, 10 random samples of each  
908 acoustic community, in dark blue (pre-explosive) and black (mid-explosive), the median  
909 spectrum of these communities. (B) Variable importance measure (mean decrease accuracy)  
910 from Random Forest classification used for discriminating the acoustics of explosive breeding  
911 events. Mid frequencies, between 3 and 4.4 kHz were the most important predictor variables.

912

913



915

916 **Fig. 9** Diversity measures within each of the temporal community (t1, t2, t3 and t4) at each  
 917 explosive breeding event (n=10). Three diversity indices are compared: species richness,  
 918 Gini-Simpson diversity and Rao's diversity coefficient. While alpha diversity indices (species  
 919 richness and Gini-Simpson index) showed similar values for pre-explosive (t1-t2) and  
 920 explosive breeding communities (t4), Rao's diversity index, which includes spectral distances  
 921 between species, showed a significant diminution during explosive breeding events. Asterisk  
 922 indicates significant differences between time periods.