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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.

174

175

176 **2. Methods**

177

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 m² to
192 2240.2 m² (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 m².

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°15'59W	224.8

197

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 α 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 ± 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 ± 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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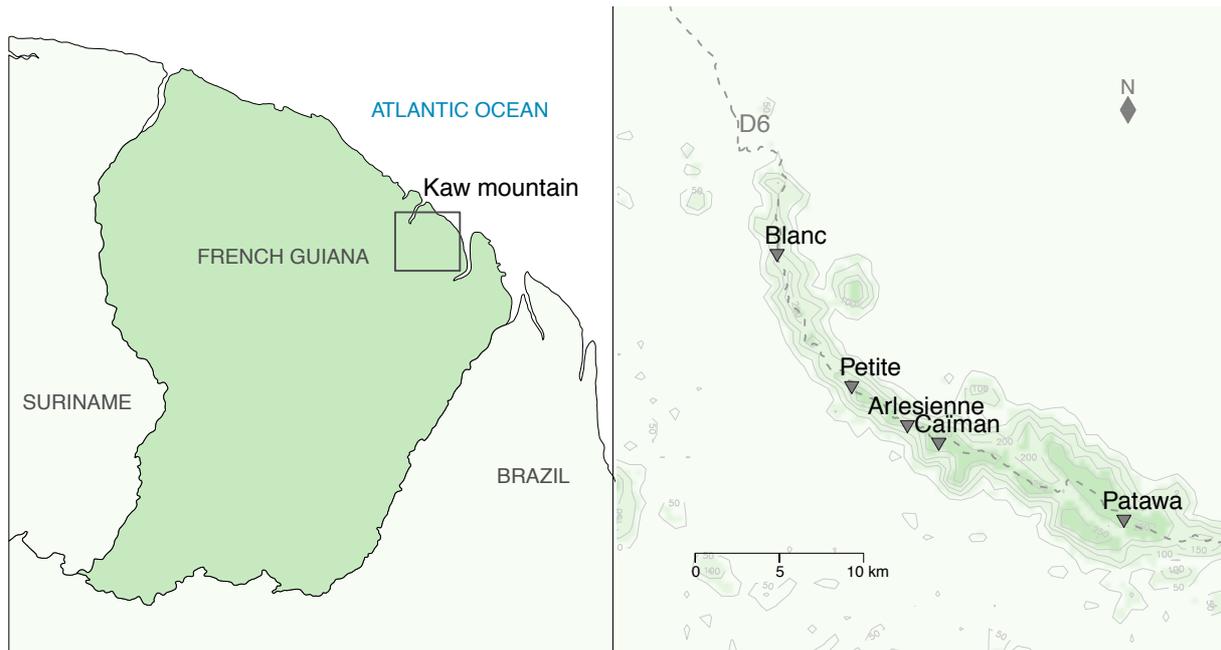
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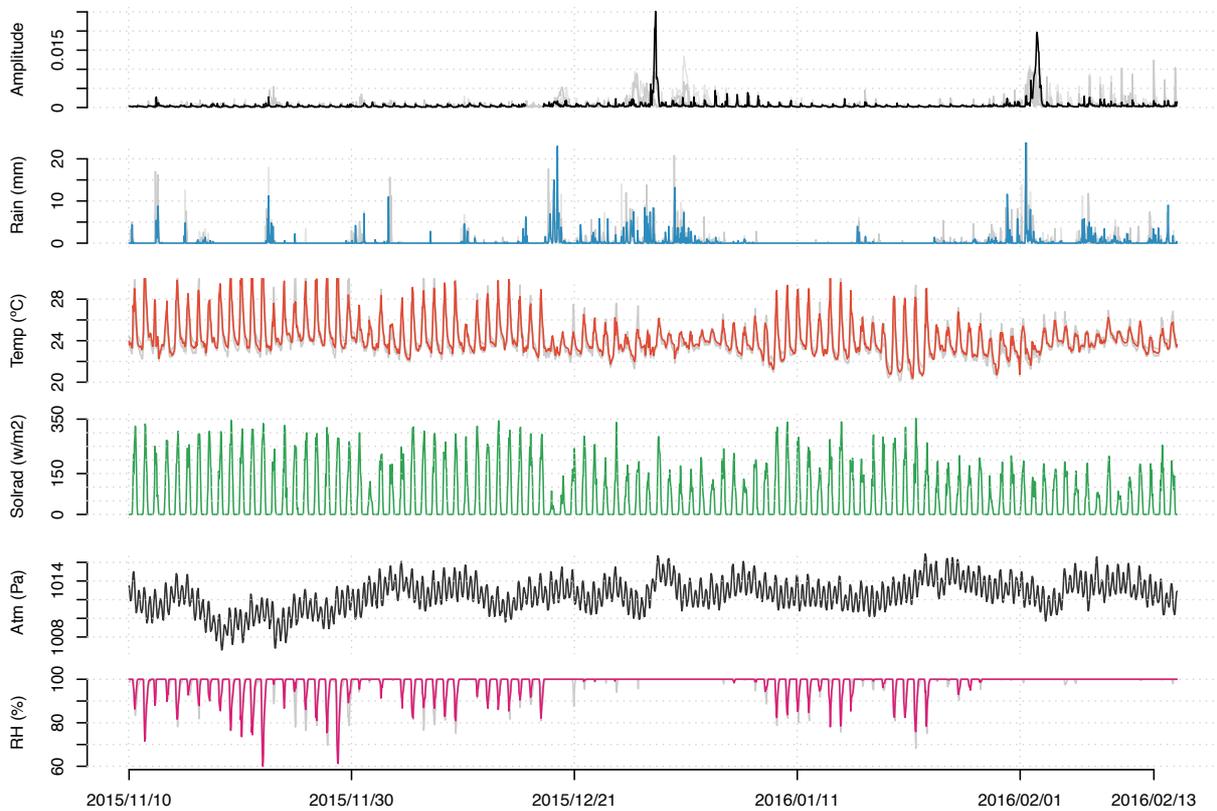
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815 **Figures**

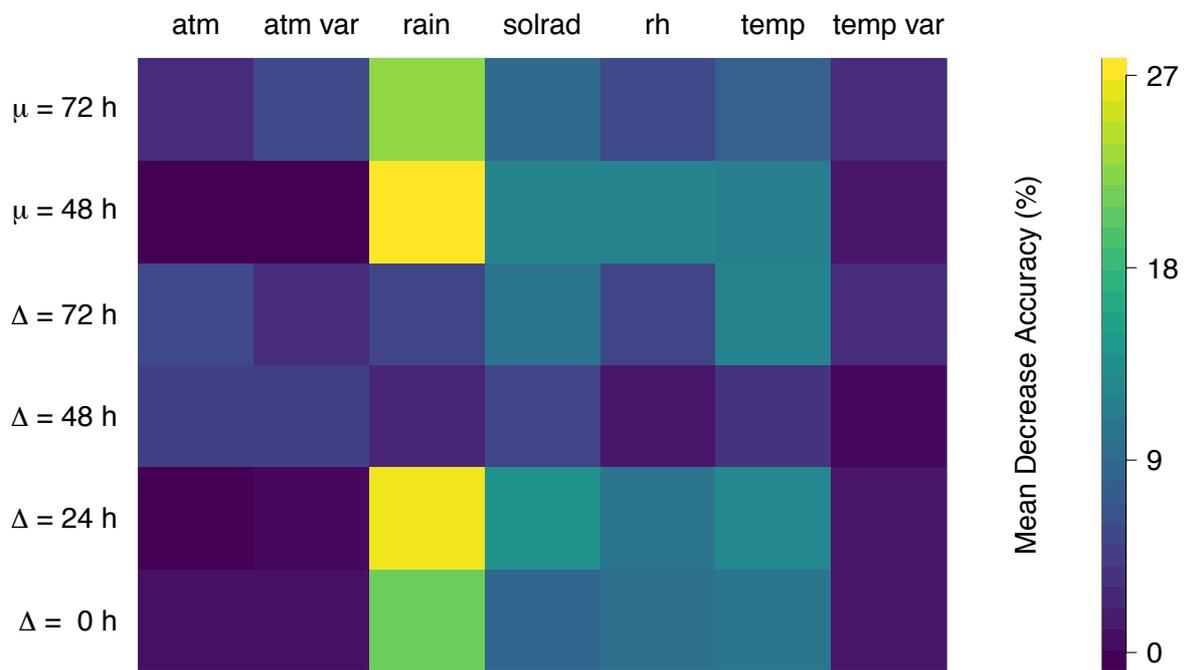


816
817 **Fig. 1** Location of the study area. On the left, location of the Kaw mountain in French Guiana.
818 On the right, location of the five study sites along a 30.4 km transect next to the departmental
819 road D6. GIS shape files were obtained from the National Institute of Geographic and
820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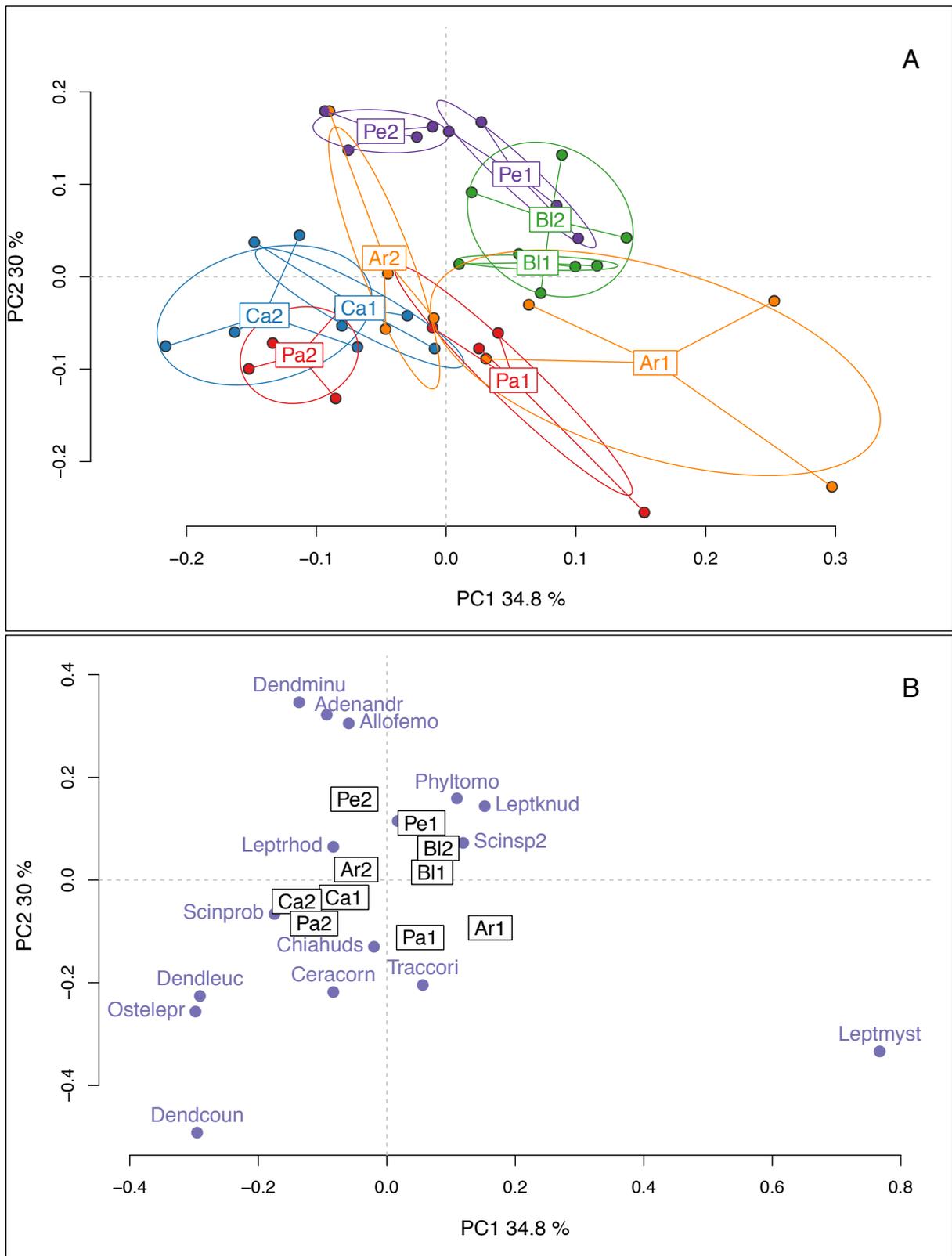


822

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 (w/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.
 830



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 (Δ) and persistence (μ) along the time (0, 24, 48 and 72 hours).



840

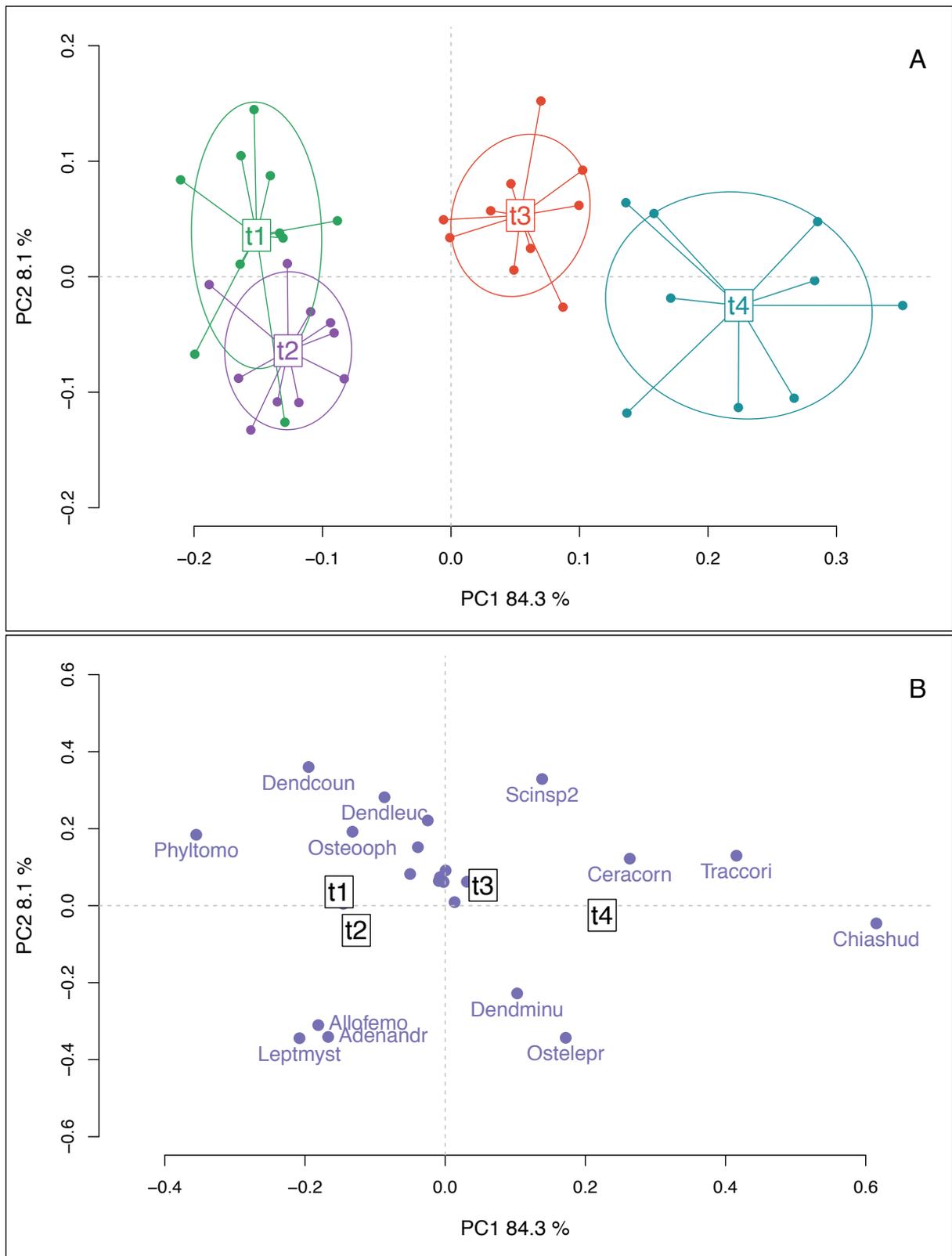
841 **Fig. 4** Diversity of the species composition in explosive breeding events across sites. The two

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

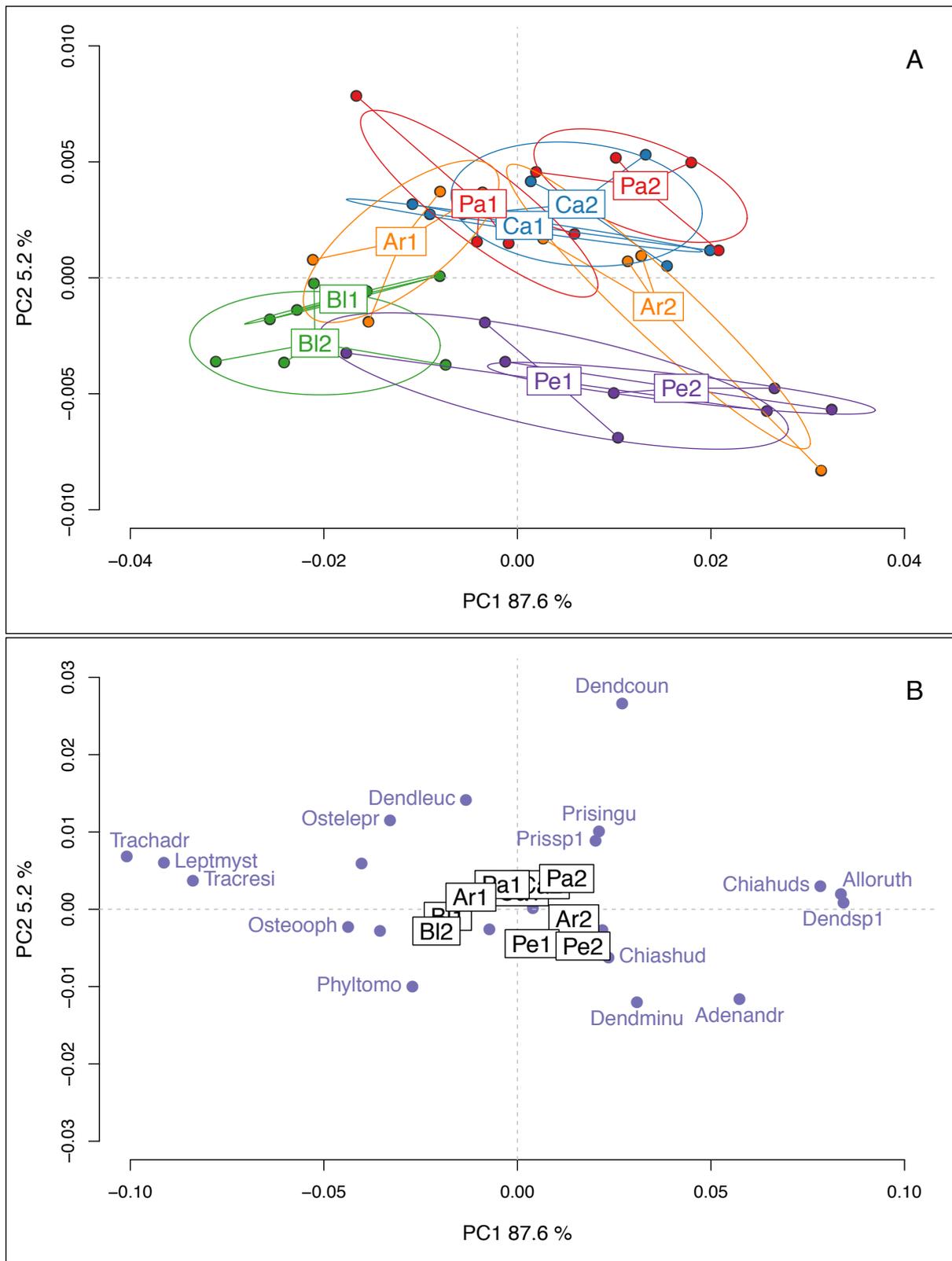
844 were color-coded with the levels of the factor event. Code names for events are: Ar =

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.



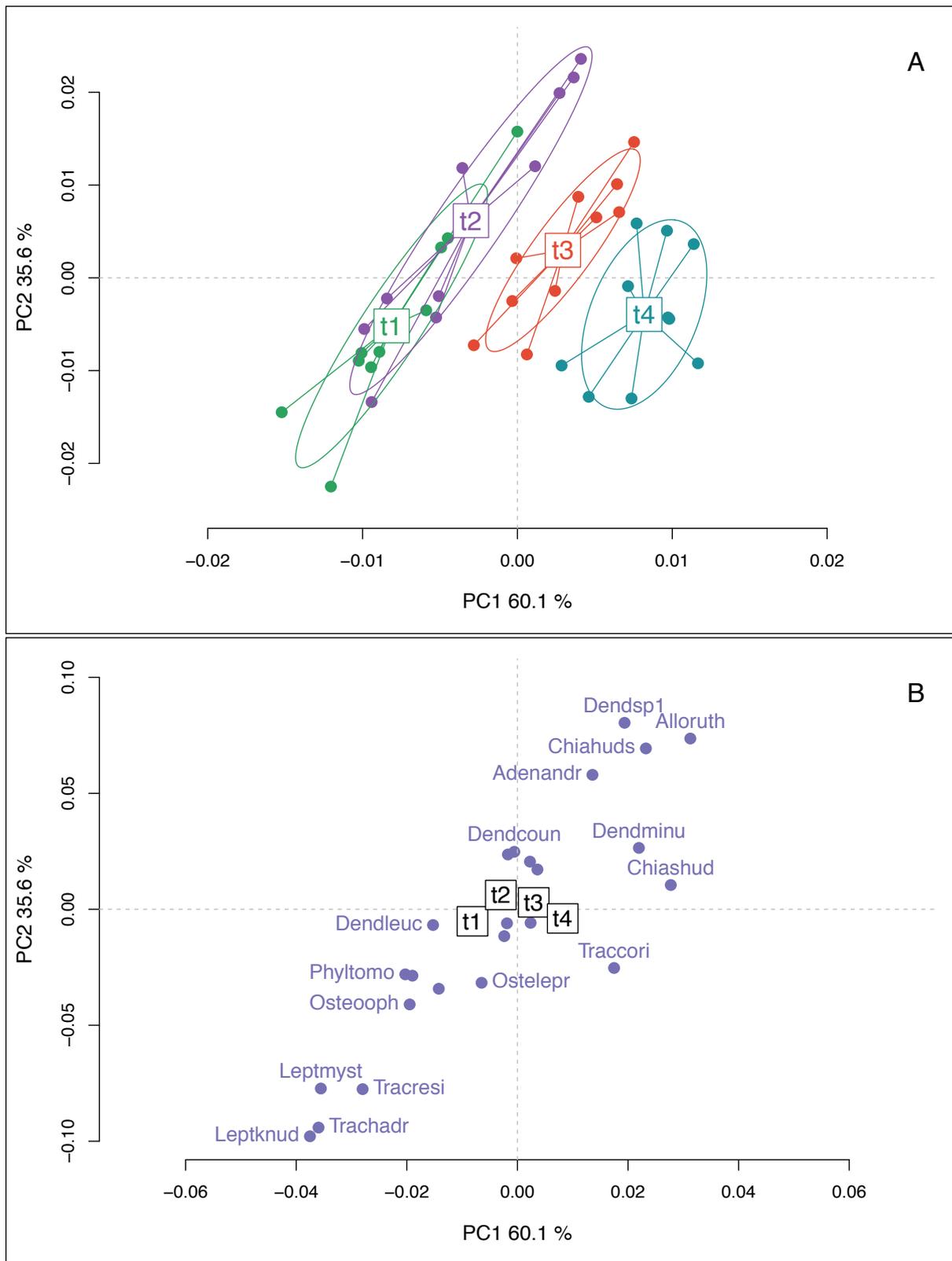
856
 857 **Fig. 5** Diversity of the species composition in explosive breeding events across time. The two
 858 principal axes (92.4 % of variance explained) of the crossed DPCoA analysis are plotted. (A)
 859 Diversity between and within communities along the time. Each point is a community. The
 860 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

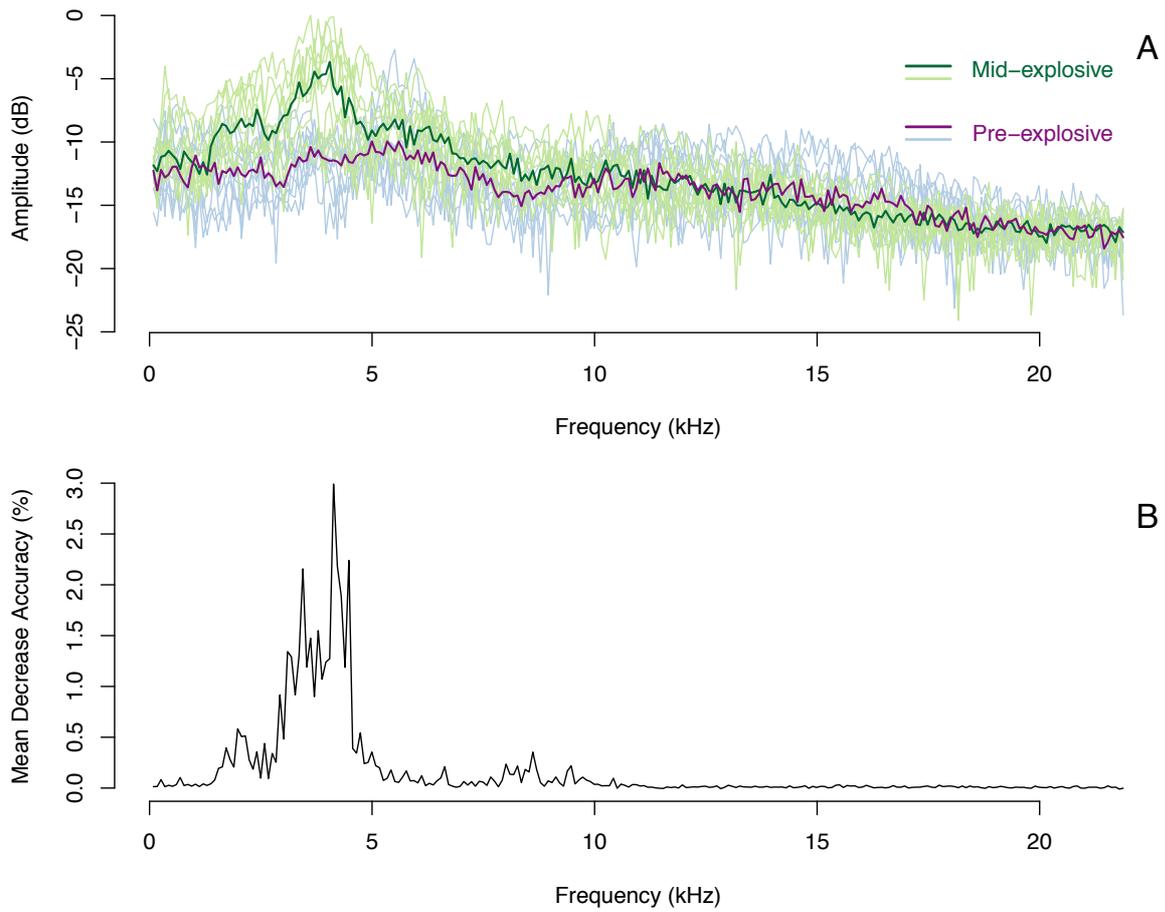
890 two principal axes (95.7 % of variance explained) of the crossed DPCoA analysis were

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 hadroceps* = Trachadr,
903 *Trachycephalus resinifictrix* = Tracresi

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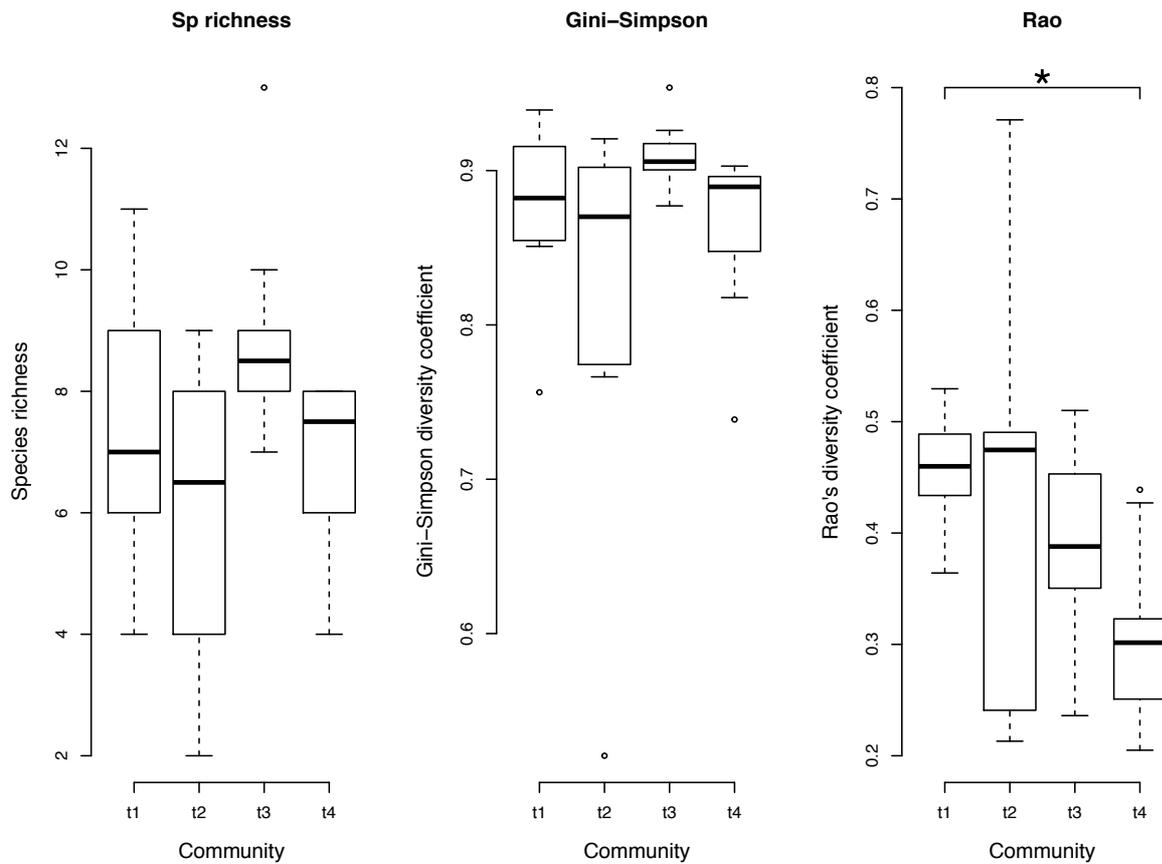


905

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.