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1 **High interannual variability of a climate-driven amphibian**
2 **community in a seasonal rainforest**

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21

22 **Abstract**

23 Seasonality exerts strong pressures on biodiversity patterns. Yet, temporal beta-diversity is
24 poorly studied in tropical systems, and the drivers of variability in amphibian activity and
25 seasonality remain largely unknown. We quantified intra- and interannual variation in temporal
26 beta-diversity relying on a nine-year, year-round survey (51 species, $n > 23\ 000$) performed in
27 a protected area (Betampona, Madagascar). We assessed the dependence on climate of beta-
28 diversity and abundance using a distance-based redundancy analysis and generalised linear
29 mixed models, respectively. Despite the majority of species being preferentially active during
30 one specific period, beta-diversity and abundance were more variable between years than within
31 years. Temporal variation in beta-diversity was best explained by temperature (but climate
32 accounted for only 2% of variation). Species abundance was best explained by temperature (for
33 32% of the tested species), monthly humidity (30%) and monthly rainfall (24%). We found no
34 climatic dependence for 24% of the species. Our results suggest that studies focusing on species
35 phenology can be misleading when based on single-year surveys even in seasonal systems. The
36 high interannual variability in diversity may be due to an adaptive responses to an important
37 regime of stochastic events. Given the direction of the relationships between weather and
38 abundances, we predict that a large proportion of amphibians would suffer from climate change
39 in Madagascar. We emphasise the need to account for multiple temporal scales in studies of
40 tropical species composition and abundance to better understand species phenology and their
41 response to climate change, and make targeted conservation actions more effective.

42

43 **Key-words:** Madagascar, Phenology, Rainforest anurans, *Reserve Naturelle Intégrale de*
44 *Betampona*, Temporal beta-diversity, Weather.

45 **Introduction**

46 Seasonality, the cyclical predictability of temperature, rainfall and available resources, is a
47 major component of environmental variation which strongly shapes many aspects of
48 biodiversity such as community structure and composition (Tonkin et al. 2017), and
49 population dynamics (Sparks and Carey 1995). While spatial patterns of Beta-diversity (i.e.,
50 the component of regional diversity that accumulates as a result of differences between sites)
51 are comparatively well studied (Socolar et al. 2016), the patterns of temporal beta-diversity
52 (i.e., differences between species assemblages at different periods) is still poorly known both
53 in temperate and in tropical areas. This is due, in part, to studies examining temporal
54 variability in species composition focusing on within-year variability (i.e., seasonality).
55 Although community composition can exhibit substantial variation between years (e.g.,
56 Gómez-Rodríguez et al. 2010), most surveys in tropical systems are limited to one year (e.g.,
57 Andreone 1994, 1996, Bertoluci and Rodrigues 2002, Gottsberger and Gruber 2004, Lopez et
58 al. 2011, Heinermann et al. 2015).

59 Ectothermic organisms such as amphibians mostly rely on external conditions for their
60 physiological state and hence, their seasonal activity patterns, reproductive periods, and
61 population dynamics (Wells 2010; Segev et al. 2012). Understanding species' activity
62 patterns and phenology is crucial for planning targeted conservation and management actions
63 (e.g., Heinermann et al. 2015), but also allows for the detection of putative shifts in response
64 to unusual weather events and/or climate change (e.g., Visser and Both 2005, Moussus et al.
65 2009). Despite its importance for research and conservation, there have been few long-term
66 studies assessing amphibian seasonality (see also Prado et al. 2005, Saenz et al. 2006) and
67 little is known about between-year variability in species' activity patterns and community
68 composition on tropical amphibian activity patterns, particularly in biodiversity-rich places
69 such as Madagascar (Gross 2019).

70 The impact of environmental conditions on amphibian temporal diversity can be
71 observed at two levels: the community level (through changes in species composition; Tonkin
72 et al. 2017), and the population level (through effects on species activity; Segev et al. 2012).
73 Most studies identified temperature (Bertoluci and Rodrigues 2002, Saenz et al. 2006, Schalk
74 and Saenz 2016, Segev et al. 2012), rainfall (Duellman 1995; Bevier 1997; Gottsberger and
75 Gruber 2004; Schalk and Saenz 2016) and humidity (Heinermann et al. 2015) as important
76 drivers of amphibian species activity. Temporal activity may also be driven by intrinsic
77 factors, with species exhibiting consistent peaks of activity between years (Duellman and
78 Trueb 1994). Activity peaks of Malagasy amphibians are often centred within the warm and
79 wet season (Glaw and Vences 2007), which in Madagascar extends from October to April and
80 coincides with breeding events for most species. Amphibian activity patterns are often
81 characterised by strong variations between and within species. For instance, several species
82 may exhibit a peak of activity during the dry-cold season (Glaw and Vences 1996), while
83 others are active and breed continuously through the year (Crump 1974). To better understand
84 the phenology of amphibians that inhabit Madagascar's eastern rainforests, there is an urgent
85 need to formally assess the (1) timing, (2) duration, and (3) climatic dependence of each
86 species' activity.

87 Here we present our analysis of temporal variations in (a) species composition and
88 abundance at the community level, and (b) individual species abundances (population level),
89 based on nine years of a year-round survey carried out at the “*Réserve Naturelle Intégrale de*
90 *Betampona*” (from here onwards “Betampona”), in eastern Madagascar (Rosa et al., 2012).
91 As the climate in our system follows a seasonal rhythm in terms of temperature and
92 precipitation (Fig. 1c, d), we expected a marked seasonality in species composition and
93 abundance, with little variation between years. We propose a classification of species through
94 selection of aspects of their activity patterns (i.e., period, duration, and climatic drivers), and
95 provide recommendations for the development of monitoring and management programs.
96

97 **Material and Methods**

98 STUDY SITE

99 Most of Madagascar’s amphibian diversity is found on the eastern rainforest coastal
100 band (Green and Sussman 1990; Brown et al. 2016). Betampona is an isolated 2,228 hectare
101 lowland rainforest fragment located approximately 40 km northwest of Toamsina (Fig. S1). It
102 extends from 92 to 571 m above sea level (Ghulam 2014) and is characterised by a tropical
103 rainforest climate (Peel et al. 2007). Betampona is managed by Madagascar National Parks
104 (MNP) and the Madagascar Fauna and Flora Group (MFG) serves as MNP’s research partner.
105 In that role, the MFG has encouraged and facilitated long-term research focused on the
106 reserve’s incredibly rich frog community, which has led to an increasing number of scientific
107 contributions over the past decade (Andreone et al. 2010; Rosa et al. 2011; Rosa et al. 2012;
108 Rosa et al. 2014; Bellati et al. 2018). More recent surveys have revised Betampona’s species
109 list that now includes over 80 frog species (A. Crottini, pers. obs.). Based on previous
110 inventory efforts in Betampona, we selected two amphibian-rich sites to establish long-term
111 monitoring transects for amphibians, locally known as “Sahabefoza” (S 17° 54’ 51.2”; E 049°
112 12’ 27.7”) and “Sahambendrana” (S 17° 53’ 54.2”; E 049° 12’ 55.4”).
113

114 CLIMATIC DATA

115 Betampona’s tropical climate is characterised by a marked seasonality in terms of temperature
116 and precipitation (Fig. 1c, d), with lower temperatures ($23.0^{\circ}\text{C} \pm 3.0$ SD) and precipitation
117 ($5.2 \text{ mm}\cdot\text{day}^{-1} \pm 10.2$ SD) during winter (May to August, included) and higher temperatures
118 ($28.3^{\circ}\text{C} \pm 1.7$ SD) and precipitation ($10.1 \text{ mm}\cdot\text{day}^{-1} \pm 17.0$ SD) during summer (October to
119 April). We define two additional seasons, following Heinermann et al. (2015): early spring
120 (September – October), characterised by intermediate temperatures ($24.3^{\circ}\text{C} \pm 2.1$ SD) and
121 low precipitation ($3.4 \text{ mm}\cdot\text{day}^{-1} \pm 6.0$ SD); and late spring (November – December),
122 characterised by high temperatures ($27.6^{\circ}\text{C} \pm 2.4$ SD) and low precipitation ($3.8 \text{ mm}\cdot\text{day}^{-1} \pm$
123 7.6 SD).

124 We obtained daily maximum and minimum records of temperature and humidity, and daily
125 rainfall from the MFG field station at the southwest entrance of the reserve, locally known as
126 “Rendrirendry”. We computed daily mean temperature and humidity as the average between
127 the maximum and minimum of daily records. To avoid collinearity, we only included

128 uncorrelated variables (Pearson's $|r| < 0.70$; Table S1a in supporting information). For
129 temperature, mean values were highly correlated to minimum and maximum values ($r > 0.85$),
130 so hence we excluded the latter two. We also discarded maximum humidity, because this
131 parameter showed little variation (mean = $0.93\% \pm 0.04$ SD). Because there may be a lag
132 between trait expression and environmental variability (van de Pol and Cockburn 2011), we
133 computed weekly (i.e., the seven preceding days) and monthly temperature and humidity as
134 the mean of daily records, and weekly and monthly precipitation as the sum of daily records.
135 We finally excluded daily, and monthly temperature, because they were highly correlated
136 with weekly temperature ($r > 0.90$), and we kept the latter variable because it showed the
137 highest variability. We also excluded weekly humidity (correlated with monthly humidity; $r =$
138 0.85). The variables included in our analyses were: weekly mean temperature (referred to as
139 "temperature"), daily and monthly mean humidity, and daily, weekly, and monthly sum
140 precipitation (Fig. 1; Table S1b). To enable comparisons of their relative effects, all climatic
141 variables were centred and scaled.

142

143 SURVEYS

144 We established six 500 m long transects regularly sampled during the period 2009 – 2017,
145 with each transect being completed three to 23 times per year. All transects were
146 approximately equally represented throughout the dataset (between 55 and 61 sampling
147 sessions per transect). Both "Sahabefoza" and "Sahambendrana" have a forest stream running
148 through with a slope alongside. Three transects were installed at each site: (1) along the edge
149 of the forest stream (hereafter "stream"), (2) parallel to the first transect but 30 – 50 m uphill
150 ("slope") and (3) on the ridge top of the same slope ("ridge"). For each site a different transect
151 was surveyed each night (between 6:30 pm and 9:30 pm) for three consecutive nights by one
152 to four trained observers equipped with head-lamps and flashlights. The observers were all
153 long-term employees of MFG with many years' proven experience at reliably identifying
154 *Betampona* amphibian species. Initially (from July 2009 to September 2012) transects
155 searches were carried out at both sites most months, but from October 2012 onwards, searches
156 were limited to one site only per month. We noted date, observers, weather conditions, start,
157 and end time of the surveys. Transects were walked at a steady speed of ca. 200 m per hour,
158 taking note of all encountered amphibians.

159 In *Betampona*, twelve taxa are significantly genetically distinct from one or more species that
160 are morphologically and ecologically very similar, and, therefore, are very difficult to
161 distinguish from each other in the field (these are listed in supporting information; Appendix
162 1). Additionally, these complexes of species present similar activity patterns and thus, for
163 survey and analysis purposes, we treated them as a single morpho-species (taxa marked with
164 "£" in Table S2). Species identification follows Vieites et al. (2009) and Rosa et al. (2012).

165

166 STATISTICAL ANALYSES

167 We cross-tabulated field count data by species and day. As transects were not performed on
168 the same dates, one cross-table was computed for each transect individually to limit zero-
169 inflation. All statistical analyses were carried out under R version 3.5.2 (R Core Team 2018).

170

171 *Community level – quantifying temporal variability*

172 We assessed temporal changes in species composition and abundance (i.e. temporal beta-
173 diversity) of amphibian communities using two indices of dissimilarity: Jaccard' index for
174 presence-absence data and Bray-Curtis for abundance data. Here we assume that one
175 community corresponds to one transect at one site for one date, resulting in 350 communities.
176 We first used Metric Multidimensional Scaling (MDS) ordinations to visualise pairwise
177 dissimilarities of communities within each transect. Visualising beta-diversity within each
178 transect separately enabled us to disentangle temporal patterns from topographical and spatial
179 factors and allowed us to identify whether some ecological contexts induce more temporal
180 variations in community composition. Secondly, we assessed whether community
181 composition and abundance differed according to seasons and years, using Permutational
182 Multivariate Analysis of Variance (PERMANOVAs). We performed marginal tests to
183 determine the individual contribution of each variable to variation in community composition
184 and abundance.

185 We then quantified the mean temporal beta-diversity within and between years by focusing on
186 strict species turnover, calculated by multiple-site dissimilarities following the framework of
187 Baselga (2010). The turnover index was independent of differences in species richness
188 (Leprieur and Oikonomou 2013), so we strictly focused on species turnover in beta-diversity
189 changes. To test for temporal differences in beta-diversity, we used linear mixed-effect
190 models (LMMs), with sites and transects as random factors to account for spatial design.
191 Beta-diversity analyses were performed using the “betapart” and “vegan” R packages
192 (Baselga and Orme 2012; Oksanen et al. 2015).

193

194 *Community level – climatic drivers of species composition and abundance*

195 We examined the influence of the six climatic variables selected (see above) on the Jaccard
196 and the Bray-Curtis dissimilarity matrices using distance-based redundancy analysis (db-
197 RDA). To improve the statistical power, we ran the db-RDAs over the entire dataset after
198 removing communities for which we did not have climate data ($350 - 37 = 313$ communities
199 studied). To account for spatial design and to focus on temporal beta-diversity, we
200 constrained our model by two spatial factors (sites and transects).

201

202 *Population level - Activity duration*

203 We estimated species monthly abundances to classify species' activity duration following
204 three categories: continuous, prolonged and sporadic (adapted from Wells 1977, Prado et al.
205 2005, Heinermann et al. 2015). Species activity duration was defined on the basis of the
206 temporal dispersion of the number of observations (p), following Heinermann et al. (2015).

207 The temporal dispersion of observations was computed as the variance of monthly counts,
208 expressed as the proportion of species total counts to control for differences in species
209 abundance. As our survey encompassed several years, we computed p only for the year with
210 the highest number of recorded individuals, for each species separately. We defined activity
211 duration classes according to the modalities found in the distribution frequency of species
212 coefficients of variation. We assumed that the first modality represented species that are
213 continuously active throughout the year, the second one represented species with prolonged
214 activity, and the third one represented species for which the detection is sporadic (i.e.,
215 exhibiting a clear peak of activity). The low percentage of observations of some species
216 during one sampling session —relative to the total number of observations— can produce
217 high variances and impede characterisation of their overall activity pattern. Species, whose
218 total number of observations during the year was fewer than 10, were classified as “rare
219 species”.

220

221 *Population level - Preferred activity period*

222 We tested the effect of a four-level season factor (early spring, late spring, summer, winter;
223 Heinermann et al. 2015) on species abundances. For each species separately, we used
224 generalised linear mixed models (GLMMs; lme4 R package, version 1.1.12; Bates et al.
225 2015), assuming a Poisson distribution, with daily count as a response variable, and the
226 season as the explanatory variable. A preferential season of activity was identified on the
227 basis of the significance of parameter estimates. We controlled for confounding effects using
228 the following adjustment variables: site and transect topography as factorial fixed effects, and
229 observer groups and the year of observation as random effects.

230

231 *Population level - Climatic drivers of species abundance*

232 We investigated the relationships between species abundances and climatic variables using a
233 multi-model inference approach (Johnson and Omland 2004). For each species individually,
234 we used GLMMs assuming a negative binomial distribution, with daily count as a response
235 variable, and the selected environmental variables (see above) as explanatory variables. We
236 first built a full model that included all candidate variables. We accounted for the possibility
237 of a non-linear effect of temperature by adding a quadratic effect. We then performed a model
238 selection process, based on second order Akaike Information Criterion (AICc; Burnham and
239 Anderson 2002). The model containing the effects with the highest statistical support receives
240 the lowest value of AICc. Multi-model inference was implemented using the MuMIn R
241 package version 1.42.1 (Barton 2018). The MuMIn function enables to build one model for
242 each possible combination of all tested variables. The statistical support of a model i was
243 assessed by their AICc weight (w_i). We retained all models where $\Delta\text{AICc} < 2$, to account for
244 model selection uncertainty. We then used model averaging to produce the averaged
245 parameter estimates and relative importance ($\sum w_i$) of each parameter (Burnham and Anderson
246 2002). Models that are included in the best model set could include both the linear and the
247 quadratic effect of a given variable, which can be misleading as the coefficient estimates

248 would have a different biological meaning when the quadratic term is present or absent
249 (Grueber et al. 2011). To account for this possibility, we re-performed the model selection
250 process while removing the quadratic term for each of the ‘best model sets’ that included only
251 a linear effect of temperature. We controlled for confounding effects by including the
252 aforementioned adjustment variables in all models.

253

254 **Results**

255 We recorded a total of 23,427 individuals assigned to 51 taxa between 2009 and 2017 (Table
256 S2). No data were collected for 18 species known to occur in Betampona. Those mostly
257 correspond to species that are only occasionally found in the Reserve or are found only
258 occasionally along the chosen transects.

259

260 COMMUNITY LEVEL

261 *Shifts in temporal beta-diversity*

262 Our analyses showed that amphibian community composition and abundance varied within
263 and between the nine survey years (Figs 2 – 3, Table. 1). On average, the shift in overall
264 community composition (Jaccard dissimilarity) reached 0.64 ± 0.18 (mean \pm Standard
265 deviation SD) within years and 0.70 ± 0.08 between the years; whereas the shift in overall
266 community abundances (Bray-Curtis dissimilarity) reached 0.54 ± 0.14 and 0.59 ± 0.10 ,
267 respectively (Fig. S2). Partitioning of temporal beta-diversity revealed that these changes
268 were largely due to strict turnover rather than shifts in species richness: turnover and balanced
269 variation accounted for 81% and 68% of the Jaccard and the Bray-Curtis within-year
270 dissimilarities, and for 80% and 73% of between-years dissimilarities, respectively (Fig. S2).

271 Within years, no clear pattern of seasonality emerged onto the MDS spaces of the six
272 studied transects (i.e., communities are not clustered by seasons; Fig. 2). Indeed, the
273 PERMANOVA enabled the identification of significant variation in amphibian communities
274 among seasons in only 1/6 transects for species composition (i.e., a stream transect; Table 1).
275 In contrast, for abundance PERMANOVA identified significant variation in 4/6 transects. On
276 the other hand, we found significant (or quasi-significant; $p < 0.1$) differences between-years
277 in community composition and abundance in most transects (5/6 and 6/6, respectively).
278 Overall, the “year” factor explained a much larger proportion of variation in community
279 composition and abundance compared to the ‘season’ factor (R^2 ranged from 0.16 to 0.27 and
280 0.04 to 0.13, respectively; Table 1). This is consistent with our assessment of changes in
281 temporal beta-diversity: interannual variations in community composition and abundance
282 were significantly higher than intra-annual variations (Wald’s test, $p < 0.05$; Fig. S2). The
283 MDS summarised 20.1 – 29.0 % of the variance in the Jaccard dissimilarity matrices and 25.9
284 – 38.5 % in the Bray-Curtis dissimilarity matrices (Fig. 2). Overall, the pairwise distances
285 plotted onto the ordination space were proportional to the observed ones (indicated by the
286 important alignment of data points; see Fig S3).

287

288 *Climatic drivers of community composition and abundance*

289 The climatic variables explained only a small amount of variation of community composition
290 and abundance (< 2% of the total variation in both cases according to the db-RDAs). Out of
291 the six climatic variables tested, only “weekly temperature” was significantly related to
292 variation in community composition and abundance; nevertheless, “Monthly humidity” and
293 “Monthly rain” were quasi-significantly related to variation in community composition (Table
294 2).

295

296 POPULATION LEVEL

297 *Activity duration*

298 Among the 51 amphibian taxa, 23 (45%) were active year-round, 11 (22%) showed prolonged
299 activity, one (*Boophis albilabris*; 2%) was observed sporadically (Fig. 3, S2; Table S2) and
300 16 (25%) were considered rare species.

301

302 *Activity period*

303 We modelled the abundances of 38 species (models could not converge for 13 species, with
304 the lowest number of observations; Table S2). Nine species were significantly more present in
305 a unique season (five during winter, one during early spring and three during summer),
306 relative to all other seasons (Table S2; Fig. 3). The remaining 29 species were active during
307 more than one season. During winter, early spring, late spring and summer respectively, 12,
308 10, 5 and 7 taxa were significantly more abundant relative to another season. No difference in
309 abundance was detected between seasons for 16 species (see Fig. 3 for more details).

310

311 *Climatic drivers*

312 Temperature was the most important predictor of the abundance of 12 (32%) species
313 (negative effect for seven species, positive effect for five species), including nine for which
314 the effect was robust ($\Sigma wi = 1.00$; negative for six species, positive for three species). Monthly
315 humidity affected the abundances of 11 (30%) species (negative for four species and positive
316 for seven species), including nine for which the effect was robust (negative for two species
317 and positive for seven species). Monthly rainfall affected nine (24%) species (negative for
318 three species and positive for six species), including six for which the effect was robust
319 (negative for two species and positive for four species). Daily rainfall affected six (16%)
320 species, the effect was robust for three species. Daily humidity affected five (14%) species
321 (robust for four species). Nine (24%) species did not appear to be affected by any of the
322 climatic variables included in this study.

323

324 **Discussion**

325 *Within-year variability versus between-year variability*

326 The majority of species showed clear fluctuations in abundance between seasons (Fig. 3).
327 However, there is more variation in composition and abundance between years than between
328 seasons. We only found a slight seasonality in beta-diversity along streams. This weak
329 seasonality contrasts with previous studies performed in tropical seasonal environments where
330 clearer patterns of amphibian activity emerged (Duellman 1995; Marques et al. 2001;
331 Bertoluci and Rodrigues 2002; Kupfer et al. 2005; Prado et al. 2005; Gardner et al. 2007; dos
332 Santos et al. 2009; Lopez et al. 2011; Vasconcelos et al. 2011; Segev et al. 2012; Schalk and
333 Saenz 2016). Those studies were mostly performed in regions with marked seasonal
334 precipitation. Although the average rainfall in Madagascar's eastern rainforests, including
335 Betampona, is higher in the summer, precipitation is less variable within the year, with no real
336 period of drought (Fig. 1). The marked seasonality in temperatures affects beta-diversity to a
337 limited extent (Table 2), suggesting that variation in species composition is mainly driven by
338 factors other than climate such as lunar phases (Grant et al. 2009; Vignoli et al., 2014) or
339 stochastic processes (Baselga et al. 2015) such as extreme weather events. The high
340 interannual variability in beta-diversity is consistent with previous studies performed in
341 environments with low seasonality (Tonkin et al. 2017), or in environments that are
342 characterised by highly unpredictable climatic conditions (Gómez-Rodríguez et al. 2010).
343 Despite cyclones being more frequent in the austral summer, their occurrence is highly
344 variable during the year (Ho et al. 2006). The high frequency of cyclonic disturbances
345 influencing the eastern rainforest belt may constitute an important stochastic factor that
346 shapes patterns of amphibian activity (Riemann et al. 2017). A weak expression of seasonality
347 in rainforest amphibians may reflect an adaptive response to a high frequency of cyclones,
348 towards more opportunistic strategies (Frederiksen et al. 2008; Tökölyi et al. 2012). In the
349 absence of a consistent season associated with severe weather conditions, evolutionary
350 pressure may not have selected for strategies of avoidance of unfavourable seasons such as
351 hibernation or migration. Instead, unpredictable environments may rather select for adaptive
352 plasticity, and the development of traits such as non-seasonal hibernation or opportunistic
353 reproduction (Canale and Henry 2010). Another possible factor that could explain why
354 species composition is more variable between years than within years is an asynchrony
355 between species in biotic interactions. For some species, population dynamics may be
356 regulated by density-dependent predator-prey, or pathogen-/parasite-host interactions
357 (Whiteman and Wissinger 2005). Uncoupled fluctuations within the amphibian community
358 would have driven important interannual variation in beta-diversity.

359

360 *Activity duration*

361 We found a high proportion of species with continuous activity (45%), which strongly differs
362 from Neotropical systems (i.e., between 11 and 16%; Bertoluci and Rodrigues 2002; Prado et
363 al. 2005). This is presumably due to the absence of a severe dry season in the eastern
364 rainforest belt of Madagascar, enabling a large number of species to remain active year-round.

365 This is consistent with the low proportion of sporadically active species (only one species out
366 of 51, with a unique peak of activity: 41 individuals of *B. albilabris* recorded in only one
367 day). This activity peak probably coincides with an explosive breeding event of this species
368 and suggests that the proportion of explosive breeders is low compared to other amphibian
369 communities in Madagascar (e.g., Glos 2003) or in other tropical areas (Bertoluci and
370 Rodrigues 2002; Gottsberger and Gruber 2004; Prado et al. 2005). It is feasible that other
371 explosive breeders were not detected during our surveys, and some of the species that here are
372 classified as “rare” may be explosive breeders instead. Although activity can be related to
373 breeding events, some species known as explosive breeders (e.g., *Aglyptodactylus inguinalis*)
374 showed prolonged activity in this study (Table S2), suggesting that the proportion of
375 explosive breeders may be underestimated. The formal identification of breeding strategies
376 should be better assessed using calling activity, exhibition of secondary sexual characters, and
377 observation of amplexus and tadpoles (e.g., Schalk and Saenz 2016). Hence, comparisons
378 with other studies focusing on amphibian breeding activity must be treated with caution. Even
379 taking into account this likely underestimation, the proportion of explosive breeders seems to
380 be lower along the eastern rainforest of Madagascar in comparison with other tropical sites
381 (e.g. Pantanal, Brazil; Prado et al. 2005). Heinermann et al. (2015) found a higher proportion
382 of sporadically active species in eastern Madagascar, but they recorded only one clear peak of
383 activity, and the remaining species were rather rare (≤ 10 individuals). Explosive breeding
384 strategies are usually driven by the presence of non-permanent ponds (Hero et al. 1998),
385 and/or unpredictable weather conditions (Prado et al. 2005). The putative low proportion of
386 explosive breeders in Betampona can presumably be explained by weather conditions (e.g.,
387 rainfall events) that—apart from cyclones—are less unpredictable in eastern Madagascar,
388 where the precipitation regime would enable streams to flow and side pools to be filled for
389 longer periods.

390

391 *Activity period*

392 The majority of species showed a preferred period of activity. Yet, a relatively large
393 proportion (46%) is active year-round. Winter and early spring are the seasons with the
394 highest amphibian activity, which differs from other studies conducted on the eastern belt
395 where species richness was evenly distributed throughout the year (Heinermann et al. 2015),
396 or during the warm-wet season (Strauß et al. 2016). This also contrasts with other studies
397 performed in tropical environments, where most amphibian activity was concentrated in the
398 warm season (e.g., Lopez et al. 2011, Schalk et al. 2016). This suggests that surveys in
399 Betampona could be concentrated during winter and early spring for more cost-effective
400 monitoring.

401

402 *Environmental drivers*

403 The activity of a large majority of species (76%) is driven by climatic and weather conditions.
404 The high importance of temperature on species activity contrasts with Heinermann et al.
405 (2015) data from Analamazaotra forest (central eastern Madagascar). In Analamazaotra

406 rainfall is the best predictor of species richness. The dependence on temperature is
407 presumably related to its impact on prey availability (i.e., invertebrate activity), but also on
408 physiology and metabolic rates and characteristics of breeding sites (e.g., Gómez-Rodríguez
409 et al. 2010).

410 When looking at the population level we observed more complex dynamics, with climatic
411 factors driving species' activity patterns in different directions. The most abundant amphibian
412 taxa, which were detected continually throughout the year, did not respond to climatic
413 fluctuations, in accordance with Duellman and Trueb (1994). However, a number of species
414 with continuous activity were still dependent on climatic and weather fluctuations. This
415 suggests that, even if breeding of continuously active species may not be triggered by specific
416 weather conditions, their activity and abundance can still be influenced by meteorology and
417 climatic variation, presumably through effects on larval development (Benard 2015; Thurman
418 and Garcia 2017) or juvenile survival (Bernal-bautista et al. 2017). All species with
419 continuous activity that were affected by temperature were less numerous in warmer
420 conditions (with the exception of *Mantidactylus biporus*); potentially a response to reducing
421 the risk of desiccation (Shoemaker 1992).

422 Rainfall was also an important driver of activity in continuously active taxa, probably because
423 high precipitation reduces the risk of desiccation. Higher temperature and precipitation can
424 indirectly affect amphibian populations through degradation of their breeding habitat (e.g.,
425 changes in the hydroperiod; Daszak et al. 2005) or facilitation of infectious disease
426 transmission (Carey and Alexander 2003).

427 The only species with observed sporadic activity (*Boophis albilabris*) clearly responded to
428 weekly precipitation, likely due to its explosive breeding strategy (Wells 1977; Prado et al.
429 2005; Heinermann et al. 2015). Despite its peak of activity being in summer, this species was
430 also strongly dependent on low daily humidity and low temperatures. The observation of the
431 dependence on daily humidity is probably the result of the unique detection of the peak of
432 activity of this species during a particularly dry day, five days after a heavy rainfall episode
433 that may have induced an explosive breeding event. The activity of this species is probably
434 triggered by rain, but mainly during the coldest days of summer, as previously observed for a
435 closely related species (i.e., *B. tsilomaro*; Andreone et al. 2002).

436

437 **Directions for research and conservation**

438 Species activity varies throughout the year, but varies even more between years.
439 Studies of amphibian activity patterns that are not based on long-term sampling schemes may
440 lead to erroneous or incomplete assumptions, even in seasonal tropical systems.

441 The high proportion of species with continuous activity and the higher number of
442 species detected during winter and early spring indicate that sampling campaigns may be
443 concentrated during this period for cost-effective monitoring of the community as a whole.
444 Because of the high interannual variability in activity, studies focussed on single species are
445 challenging. Nevertheless, we identified a significant proportion of species that exhibit a

446 higher activity during one season, with a strong dependence on climatic variables. Therefore,
447 studies focusing on single species along the eastern rainforest belt can be concentrated during
448 specific periods for cost-effective surveys. This is also true for species that expressed weak
449 seasonality but were dependent on weather and climate. Targeted surveys can be planned
450 when suitable weather conditions are met.

451 Climate warming is expected to shift species activity and community composition and
452 structure in the near future (Bellard et al. 2012). We showed that species with continuous
453 activity can still have activity patterns which largely depend on weather conditions, contrary
454 to former assumptions (Duellman and Trueb 1994). This emphasises the need to carefully
455 monitor population trends in regard to future climate change, regardless of species
456 seasonality. Given the climatic trends (Bellard et al. 2012) and the important isolation of the
457 Betampona forest, we fear that most amphibian species will be strongly affected. Studies
458 focussing on single species should be prioritised on those most sensitive to temperature and
459 precipitation variation.

460 The unique amphibian community of Betampona is facing a host of conservation
461 threats. Betampona, like much of Madagascar, suffers from increasing rates of habitat
462 alteration and fragmentation (Vallan 2000; Harper et al. 2007; Allnutt et al. 2008; Ghulam
463 2014; McConnell et al. 2015; Vieilledent et al. 2018), a trend which is likely to continue in
464 the near future, even in formally protected areas (e.g., Piludu et al. 2015). The positive report
465 of amphibian chytrid fungus on the island (Bletz et al. 2015), the presence (and ongoing
466 expansion) of the invasive Asian toad *Duttaphrynus melanostictus* (Pearson 2015,
467 McClelland et al. 2015, Licata et al. 2019) and other invasive species such as the day geckoes
468 *Phelsuma grandis* and *P. laticauda* (Dubos 2013; Dubos et al. 2014), *Hoplobatrachus*
469 *tigerinus* (Goodman et al. 2017) also represent a threat for this imperiled community.

470 Better targeting and prioritisation of conservation action heavily relies on the detection
471 of putative phenological shifts and population declines, which aligns well with
472 recommendations reported in the action plan for amphibian conservation in Madagascar
473 (Andreone et al. 2016). Understanding the whole picture of species assemblages in
474 Madagascar (and other seasonal tropical systems) represents an important challenge and is
475 still far from being achieved. Making use of technology such as automated sound loggers with
476 the establishment of bioacoustics surveys, enabling reliable identification of cryptic or
477 polytypic species (Vieites et al. 2009; Köhler et al. 2017), may support not only the
478 monitoring of populations and communities but also the description of new species (Rosa et
479 al. 2012), and could facilitate continuous, long-term surveys.

480 The study of temporal patterns of species diversity while accounting for multiple
481 temporal scales will enable the identification of suitable monitoring periods, the assessment of
482 species' sensitivity to climate-change, and setting optimal conditions for captive breeding or
483 translocation for the most endangered species (Andreone and Randriamahazo 2008). Long-
484 term, comparable monitoring in several key forests of Madagascar, as well as in any tropical
485 systems with apparent seasonality, could provide a powerful tool to monitor community and
486 population changes and highlight possible ecological crises in amphibian and other vertebrate
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488

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504

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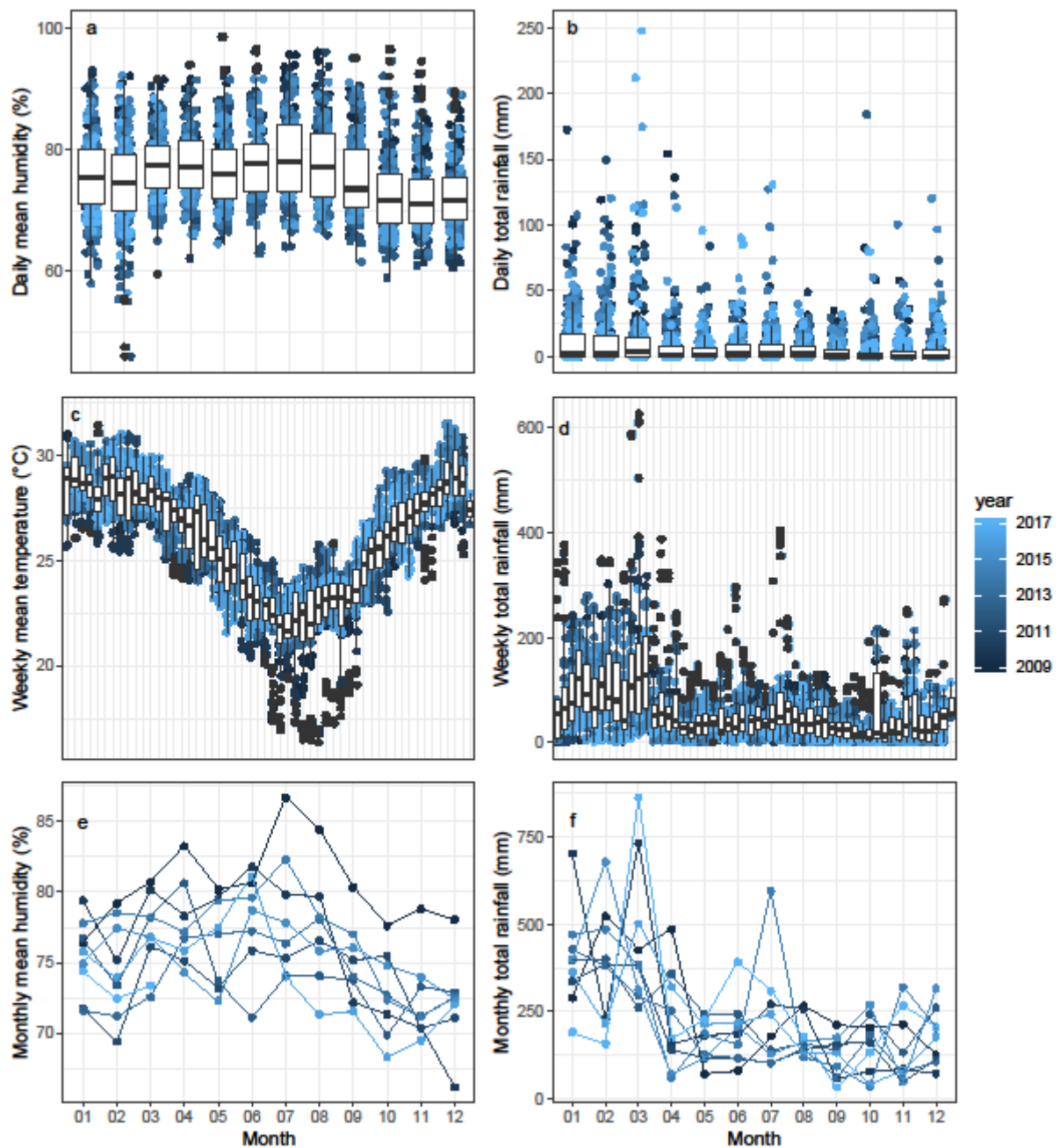
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741

742

743 **Data Accessibility Statement**

744 The data used in this study is available online as an R object in the supporting information.



746

747 **Figure 1** Temporal variation in the six selected weather variables, recorded at Betampona,

748 Madagascar, between 2009 and 2017. Within-year variation is represented along the x axis while

749 between-year variation is represented by the colour gradient. Dark-blue points represent the

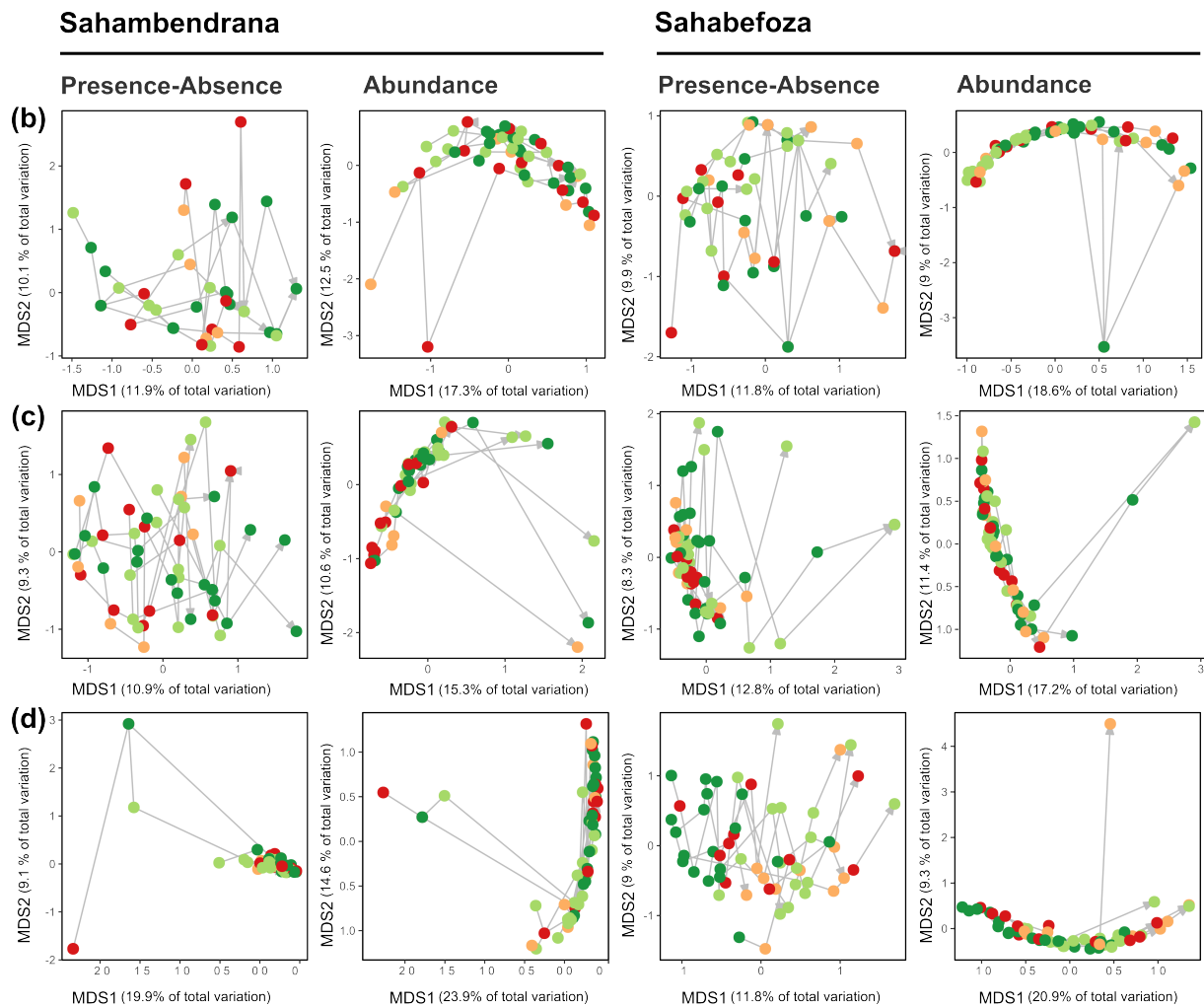
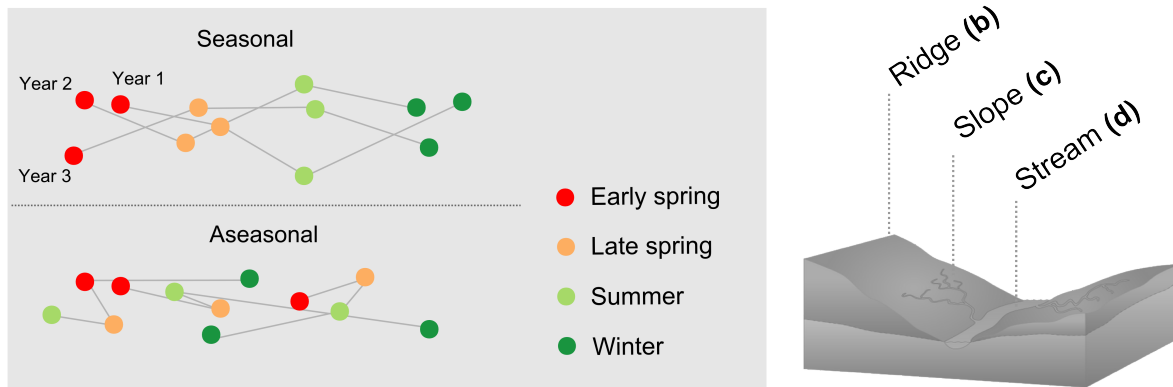
750 oldest records (2009) while light-blue points represent the most recent ones (2017). Boxplots

751 represent 25% and 75% quartiles, bars represent the median (per month for daily variables; per

752 week for weekly variables)

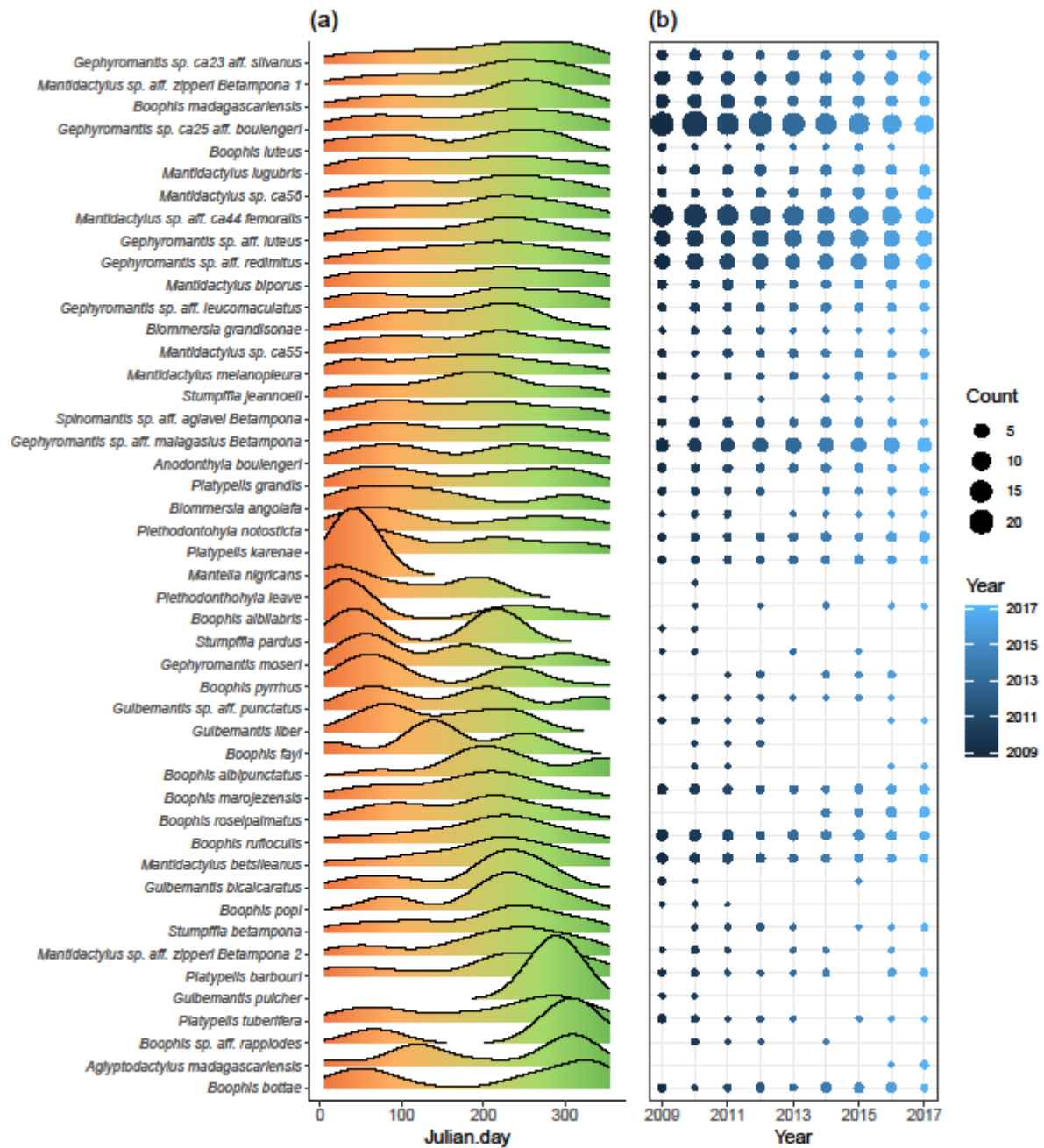
753

(a) Hypothetical patterns



754

755 **Figure 2** Patterns of temporal beta diversity of amphibian communities at Betampona. We
 756 show hypothetical patterns of community structure according to seasonal variability (a), and
 757 ordinations (MDS) of amphibian communities studied within each of the six transects (b to d).
 758 The lines connecting the dots represent trajectories of community composition across the years.



759

760 **Figure 3** Within-year (a), and between-year (b) variation in abundances of 47 amphibian taxa
 761 from Betampona Strict Nature Reserve, eastern Madagascar. Abundances are expressed as (a)
 762 the proportion of total abundances at a given date and (b) the mean number of individuals
 763 counted per day of observation. The more abundant the higher the curve (a) and the larger the
 764 circle (b). We excluded species with less than three individuals recorded ($n = 4$).

Table 1. Results of PERMANOVAs (999 permutations) testing the marginal effects (i.e. individual contribution of each variable in the overall model) of seasons and years in each of the 6 transects for both community composition (Jaccard dissimilarity) and abundance (Bray-Curtis dissimilarity).

Jaccard dissimilarity

	<i>df</i>	<i>R</i> ²	<i>F</i>	<i>P</i>		<i>df</i>	<i>R</i> ²	<i>F</i>	<i>P</i>
Sahabendrana					Sahabefoza				
Ridge					Ridge				
Season	3	0.05	1.02	0.44	Season	3	0.05	1.01	0.44
Year	8	0.17	1.25	0.07(*)	Year	8	0.17	1.28	0.09(*)
Residual	48	0.72			Residual	49	0.78		
Slope					Slope				
Season	3	0.04	0.69	0.81	Season	3	0.05	1.03	0.44
Year	8	0.16	1.12	0.28	Year	8	0.18	1.39	0.02*
Residual	43	0.79			Residual	47	0.78		
Stream					Stream				
Season	3	0.05	1.12	0.29	Season	3	0.13	3.07	0.001***
Year	8	0.20	1.66	0.007**	Year	8	0.21	1.83	0.001***
Residual	48	0.72			Residual	46	0.65		

Bray-Curtis dissimilarity

Ridge					Ridge				
Season	3	0.07	1.45	0.1	Season	3	0.10	2.12	0.02*
Year	8	0.25	2.06	0.003**	Year	8	0.20	1.67	0.02*
Residual	43	0.65			Residual	47	0.71		
Slope					Slope				
Season	3	0.07	1.48	0.08(*)	Season	3	0.04	0.88	0.61
Year	8	0.19	1.48	0.03*	Year	8	0.17	1.34	0.07(*)
Residual	45	0.71			Residual	49	0.78		
Stream					Stream				
Season	3	0.07	1.7	0.07(*)	Season	3	0.13	3.34	0.001***
Year	8	0.18	1.6	0.03*	Year	8	0.27	2.65	0.001***
Residual	48	0.70			Residual	46	0.58		

(*) $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 2. Results of distance-based RDAs testing the influence of climatic variables into variation of community composition (Jaccard dissimilarity) and abundance (Bray-Curtis dissimilarity); type II tests.

Proportion of variation	Jaccard		Bray-Curtis	
	R ²		R ²	
Conditional variation (Site + transect)	0.24		0.166	
Constrained variation (Climatic variables)	0.017		0.018	
Unconstrained variation	0.743		0.816	
Climatic variables	F	<i>P</i>	F	<i>P</i>
Daily humidity	1.11	0.202	1.07	0.121
Monthly humidity	1.22	0.061(*)	10.07	0.141
Daily rain	0.93	0.642	0.97	0.617
Weekly rain	0.91	0.725	0.96	0.696
Monthly rain	1.21	0.076(*)	1.01	0.433
Weekly temperature	1.33	0.018*	1.51	0.001***

(*) $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$