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**Climatic breadth of calling behaviour in two widespread
Neotropical frogs: insights from humidity extremes**

Running title: Climatic breadth of calling frogs

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33 **ABSTRACT**

34 Climate change is severely altering precipitation regimes at local and global scales,
35 yet the capacity of species to cope with these changes has been insufficiently
36 examined. Amphibians are globally endangered and particularly sensitive to
37 moisture conditions. For mating, most amphibian species rely on calling behaviour,
38 which is a key weather-dependent trait. Using passive acoustics, we monitored the
39 calling behaviour of two widely distributed Neotropical frogs in 12 populations
40 located at the humidity extremes but thermal mean of the species distribution.
41 Based on 2,554 hours of recordings over a breeding season, we found that both the
42 arboreal species *Boana raniceps* and the aquatic species *Pseudis paradoxa* exhibited
43 calling behaviour at a wide range of relative humidity. Calling humidity was
44 significantly lower in conspecific populations subjected to drier conditions, while
45 calling temperature did not differ between populations or species. Overall, no
46 variation in climatic breadth was observed between large and small choruses, and
47 calling behaviour was scarcely detected during the driest, hottest and coldest
48 potential periods of breeding. Our results showed that calling humidity of the
49 studied species varies according to the precipitation regime, suggesting that
50 widespread Neotropical anurans may have the capacity to exhibit sexual displays in
51 different climatic environments. Regardless of the underlying mechanism (plasticity
52 or local adaptation), which should be determined by common garden experiments,
53 a wide and population-specific climatic breadth of calling behaviour may assist
54 species to deal with changing humidity conditions. To our knowledge, this is the first
55 study to explore the response capacity of anurans to perform calling behaviour
56 under contrasting precipitation regimes.

INTRODUCTION

Human-induced climate change is severely altering both thermal and precipitation regimes worldwide (e.g. Huntington, 2006; IPCC, 2013; IPCC, 2007; Zhang et al., 2007), modifying average temperatures and the volume and temporal patterns of rainfall at local and global scales (Coffel, Horton & Sherbinin, 2018; New, Todd, Hulme & Jones, 2001; Río, Herrero, Fraile & Penas, 2011; Smith, Yin & Gruber, 2006). The environmental changes that species are facing potentially impact their distribution (Araújo, Thuiller & Pearson, 2006; Hickling, Roy, Hill, Fox & Thomas, 2006; Wilson, Gutiérrez, Gutiérrez, Martínez, Agudo & Monserrat, 2005), phenology (Dunn & Møller, 2014; Llusia, Márquez, Beltrán, Moreira & Amaral, 2013a; Oseen & Wassersug, 2002), trophic interactions (Gilman, Urban, Tewksbury, Gilchrist & Holt, 2010; Ockendon et al., 2014; Thackeray et al., 2010) and, in turn, survival (Cowley & Siriwardena, 2005; Shrader, Pimm & van Aarde, 2010; Sinervo et al., 2010). The effects of global warming on animals have received growing attention (Angilletta, 2009; Gunderson & Stillman, 2015; Huey et al., 2012; Sinervo et al., 2010), yet the consequences of changing precipitation regimes are still largely unknown (Weltzin et al., 2003).

Amphibians are particularly vulnerable to changes in rainfall and moisture conditions given their high dependence to water at various stages of their life cycle (Feder & Burggren, 1992; Wells & Schwartz, 2007), and climate-driven population declines in several taxa have been documented by long-term studies (e.g. Burrowes, Joglar & Green, 2004; Scheele, Driscoll, Fischer & Hunter, 2012). Despite the remarkable diversity of reproductive modes, amphibians mostly rely on freshwater availability for reproduction and larval development (Crump, 2015; Haddad &

81 Prado, 2005). Moreover, in adults, water balance is a major environmental
82 constraint due to their water-permeable skin. Indeed, multiple adaptations have
83 evolved in this group to reduce the risk of dehydration in terrestrial environments
84 (McDiarmid, 1994; Wells & Schwartz, 2007). However, extreme droughts, shortened
85 hydroperiods, reduced soil moisture and shifts in rainfall patterns can lead to
86 population-level changes in abundance (Burrowes et al., 2004; Stewart, 1995),
87 activity level (Jansen, Schulze, Werding & Streit, 2009) and structure (McMenamin
88 & Hadly, 2010) or even to local extinctions (Scheele et al., 2012).

89 Predicting the impact of climate change on amphibians is a pressing
90 challenge for biologists. Global population declines make amphibians the most
91 endangered vertebrate class, with more than 40% of the described species classified
92 as threatened on the IUCN Red List (Hoffmann et al., 2010). In addition to habitat
93 loss and emerging diseases (Collins & Storfer, 2003; Hecnar, 1997; O'Hanlon et al.,
94 2018), climate change is another driver that may produce synergistic deleterious
95 effects on amphibian populations (Bosch, Carrascal, Duran, Walker & Fisher, 2007;
96 D'Amen & Bombi, 2009; Hof, Araujo, Jetz & Rahbek, 2011). However, the link
97 between climate change and global amphibian declines is still unclear (Beebee &
98 Griffiths, 2005; Li, Cohen & Rohr, 2013; Lips, Diffendorfer, Mendelson & Sears, 2008;
99 Rohr, Raffel, Romansic, McCallum & Hudson, 2008), indicating the need for new
100 approaches and metrics for its investigation (Beebee & Griffiths, 2005; Carey &
101 Alexander, 2003; Lips et al., 2008). Mechanistic models offer a promising
102 framework, though the shortage of eco-physiological information on species
103 constrains their application (Bovo, Navas, Tejedo, Valença & Gouveia, 2018).

104 Calling behaviour is a key component of the mating strategy of most anuran

amphibians, and is directly involved in sexual selection (Gerhard & Huber, 2002; Narins, Feng, Fay & Popper, 2007). Males typically produce advertisement and territorial calls, often forming loud choruses at breeding sites, to attract potential mates and deter competitors. Several environmental factors regulate calling and chorusing behaviour including rainfall and relative humidity (Brooke, Alford & Schwarzkopf, 2000; Donnelly & Guyer, 1994; Hatano, Rocha & Sluys, 2002; Llusia et al., 2013a; Steelman & Dorcas, 2010), temperature (Llusia et al., 2013a; Murphy, 2003; Steelman & Dorcas, 2010), barometric pressure (Henzi, Dyson, Piper, Passmore & Bishop, 1995; Oseen & Wassersug, 2002) and light intensity (Almeida-Gomes, Van Sluys & Duarte Rocha, 2007; Steelman & Dorcas, 2010, Grant, Halliday & Chadwick, 2013). In addition to being a widespread and weather-dependent trait and playing a crucial role in species survival, calling behaviour can also be used to monitor populations. By using emerging techniques (Sueur & Farina, 2015) such as passive acoustic monitoring (Sugai, Silva, Ribeiro & Llusia, 2019), phenological patterns and their relationship with weather conditions can be explored to shed light on the effects of climate on populations (Krause & Farina, 2016; Llusia, Márquez, Beltrán, Benítez & Amaral, 2013b; MacLaren, McCracen & Forstner, 2018; Sueur et al., 2019).

Widespread species generally experience a broad range of climatic conditions across their geographic distribution, making them suitable models to investigate the capacity of the species to cope with changing climatic environments. By monitoring populations located at the thermal or humidity extremes of the species range, we can estimate the climatic breadth of key traits such as calling behaviour to better understand how species respond to distinct climatic regimes. Recently, Llusia et al. (2013b) used acoustic monitoring to estimate the thermal

breadth of calling behaviour in temperate anurans and showed that the studied species have the capacity to display calling behaviour at a wide range of temperatures. To our knowledge, no previous study has explored the breadth of calling behaviour in relation to moisture conditions and how anurans respond to distinct precipitation regimes.

The effect of precipitation changes may be particularly severe in open environments, such as tropical savannahs, which are largely exposed to fluctuating humidity conditions. Climate change velocity is predicted to be highest in flooded grasslands and tropical savannahs (Loarie et al., 2009), the latter of which are considered biodiversity hotspots (Silva & Bates, 2002) and particularly threatened (Overbeck et al., 2015; Roque et al., 2016). Despite this, the impact of climate change has been less investigated in these environments compared with other tropical biomes (e.g. tropical forests).

Here, we examined the climatic breadth of calling behaviour in two widespread Neotropical anurans inhabiting savannahs, the arboreal frog *Boana raniceps* and the aquatic frog *Pseudis paradoxa*. Using passive acoustic monitoring during an entire breeding season, we recorded the calling activity of 12 populations located at the humidity extremes but thermal mean of the species distribution. Specifically, we hypothesized that widespread Neotropical frogs can perform calling behaviour under different climatic environments. According to this hypothesis, we tested the following three predictions: (i) the studied species will show calling behaviour across a wide overall range of humidity; (ii) populations located at humidity extremes will show different ranges of calling humidity; and (iii) daily and seasonal patterns of calling activity will reveal differences in calling humidity and

calling temperature across species and populations. Finally, we discuss to what extent the observed responses imply mechanisms (plasticity or local adaptation) allowing species to cope with changing precipitation regimes, providing insight on the role of moisture conditions on the capacity of widespread species to respond to climate change.

METHODS

Study species

Pseudis paradoxa (Linnaeus, 1758) and *Boana raniceps* (Cope, 1862) (previously identified as *Hypsiboas raniceps* but changed to *B. raniceps* after Dubois, 2017) are Neotropical hylid frogs commonly found in open areas such as savannahs and grasslands. They are distributed across the Amazon basin and surrounding regions including Bolivia, Paraguay and northern Argentina. As geographically widespread species, they are subjected to a broad range of climatic conditions across their distribution ranges (Figs 1 and 2). Both species are sizeable frogs (Lescure & Marty, 2000; Haddad, Toledo, Prado, Loebmann, Gasparini & Sazima, 2013) and prolonged breeders (i.e. breeding season lasting for more 3 consecutive months), with similar reproductive mode, characterized by laying eggs in lentic water and the development of exotrophic tadpoles (Prado, Uetanabaro & Haddad, 2005), particularly large in *P. paradoxa* (Emerson, 1988). Low genetic distances have been recorded among populations of *B. raniceps* throughout the range of the species (Fouquet et al., 2007; Jansen, Bloch, Schulze & Pfenninger, 2011; Lyra, Haddad, & Azeredo-Espin, 2017). The conspecificity of *P. paradoxa* populations from French Guiana and Pantanal was confirmed based on call similarity (Santana et al. 2010).

Although subspecies within *P. paradoxa* were formerly considered to be full species (Aguiar et al., 2007), geographic and morphological data are still required to propose any taxonomical change based on genetic evidence (Aguiar et al., 2007; Garda & Cannatella, 2007; Garda et al., 2010).

Microhabitat use

Pseudis paradoxa and *Boana raniceps* belong to distinct subfamilies within Hylidae, namely Pseudinae and Cophomantinae, respectively (Frost et al., 2006). Both species exhibit sharp differences in microhabitat preference. *Pseudis paradoxa* is an aquatic frog that inhabits marshy areas and flooded plains with stagnant water and abundant aquatic vegetation (Angulo & Baldo, 2010; Lescure & Marty, 2000). Males of *P. paradoxa* can be found at the edges of ponds and swamps, preferentially calling over water surfaces near floating vegetation (Bosch, De la Riva & Márquez, 1996). *Boana raniceps* is an arboreal frog found on emergent macrophytes and terrestrial vegetation that surround ponds, lagoons and large river banks (La Marca, 2004). The usual calling sites of this species are branches and leaves at the top part of aquatic vegetation (Márquez, De la Riva & Bosch, 1993; Prado, Uetanabaro & Haddad, 2005).

Advertisement calls

Acoustic communication plays a key role in the sexual selection of the two species (Bosch et al., 1996; Höld, 1977; Márquez et al., 1993). During the breeding season, males of both species produce advertisement calls within loud choruses to attract females. The advertisement call of *P. paradoxa* is composed of pulsed notes, emitted

in series of 8 notes on average, with a mean duration of 301 ms and a mean dominant frequency between 2,540 and 2,711 Hz (Bosch et al., 1996; Tárano, 2010). The advertisement call of *B. raniceps* is composed of pulsatile notes (note-centred approach; Köhler et al., 2017) emitted in series ranging from 2 to 10 notes, with a mean duration of 163 ms and a mean dominant frequency between 761 Hz and 901 Hz (Guimarães & Bastos, 2003; Márquez et al., 1993).

Study areas

Calling activity of the studied species was monitored in two areas located at the humidity extremes of the species range (Fig. 1): (i) the littoral region between the cities of Cayenne and Kourou in French Guiana (hereafter FG) for the humid extreme and (ii) the Pantanal wetlands in the state of Mato Grosso do Sul in the central-southern region of Brazil (hereafter BR) for the dry extreme. Due to distinct climatic regimes (Peel, Finlayson & McMahon, 2007) and hydrogeologic dynamics (Assine, 2005; Davidson et al., 2012), FG and BR are located in two different tropical biomes, the Amazonian and the Pantanal, respectively. Annual precipitation strongly differs between the two areas, reaching on average 3,075 mm in FG and 1,312 mm in BR (Fick & Hijmans, 2017; Fig. 1). Annual mean temperature, in contrast, differs only by 0.4°C between the two areas (25.5°C in FG and 25.1°C in BR; Fig. 2).

To estimate the extremity of the precipitation and thermal regimes of each study area, IUCN polygons (IUCN et al., 2008a; IUCN et al., 2008b) and WorldClim layers (version 2.0, 5 arc-minute resolution, ~10 x 10 km grid cells; Fick & Hijmans, 2017) were used to determine, respectively, the distribution range of each species and the annual precipitation and mean temperature within each range. With the R

packages *raster*, *sp* and *rgdal*, we extracted temperature and precipitation values for all raster cells from the WorldClim layers using the IUCN polygons as masks to obtain the frequency distribution of these values within the range of the studied species. We then calculated the level of precipitation and thermal extremity of the two study areas (Figs 1 and 2). Precipitation extremity was defined as the proportion of the species range with an annual precipitation below and above the annual precipitation of each study area. For both species, between 96% and 98% of their distribution range (occurrence grids) had a lower annual precipitation than that of FG (i.e. <3,075 mm; humid extreme) and between 77% and 84% had a higher annual precipitation than that of BR (i.e. >1,312 mm; dry extreme; Fig. 1, Table 1). Therefore, FG and BR show a high level of precipitation extremity. Conversely, the annual mean temperature of both study areas was similar to the overall average temperature of each species range (i.e. 25.7°C for *P. paradoxa* and 24.8°C for *B. raniceps*). The level of thermal extremity of the areas was very low, ranging between 32% and 60% (Fig. 2, Table 1).

The monitored sites within each study area are located within vast open landscapes known as tropical or subtropical savannahs and are characterized by the predominance of grasslands, shrubs and open woodlands. Ponds and seasonally flooded fields therein serve as breeding habitats for the anuran species. In addition to the climatic criteria, the study areas were selected based on accessibility to private or restricted sites that facilitated fieldwork and reduced potential sources of human disturbance and damage to the equipment.

249 ***Monitored populations***

250 A total of seven sites were monitored, four in FG and three in BR (Fig. 3),
251 corresponding to 7 and 5 populations of *P. paradoxa* and *B. raniceps*, respectively.
252 All populations were sympatric, except for two in FG, where *B. raniceps* was absent
253 (FG1 and FG2; Fig. 3). The monitored populations in FG were located across two
254 agricultural zones, locally known as “Guatemala” (5°06'58.2"N 52°36'41.4"W) and
255 “Matiti” (5°02'06.1"N; 52°33'51.4"W). The populations in BR were within the limits
256 of the “Barranco Alto” farm (19°34'38.0"S; 56°09'09.6"W). Water was present in the
257 breeding habitats for the duration of the monitoring period. Surrounding areas
258 included livestock farms and were composed of a mosaic of native grasslands and
259 cultivated pastures, with woodland patches present up to 1 km from the monitored
260 water bodies.

261

262 ***Data collection***

263 Calling activity of the populations and weather conditions were monitored for 6–9
264 months in 2016–2017. The total monitoring period covered 295 consecutive days
265 from 7/10/2016 to 29/07/2017 (Table 1) and encompassed an entire breeding
266 season for both species, including the peak of calling activity and several weeks
267 before and after the expected calling season.

268 Advertisement calls were recorded through passive acoustic monitoring
269 using automated digital sound recorders (SM2 in FG and SM2, SM3 and SM4 in BR;
270 Wildlife Acoustics, Inc.). One recorder was deployed at each breeding site. Each
271 recorder was tied 1.5–2 m above ground to either a tree or a wooden stake located
272 1–15 m from the pond shore. All recorders were equipped with two omnidirectional

condenser microphones (SMX-II, Wildlife Acoustics, Inc.) and set to record sounds for 2 minutes every 20 minutes (i.e. 6 minutes per hour) from 1–2 hours before sunset until 0–1 hour after sunrise. This time period comprises the expected calling period of both species. The recording schedule was double the sampling effort shown to be adequate to record calling activity of temperate anurans (i.e. 3 minutes per hour; Shiroye et al., 1997; and also see Alquezar & Machado, 2015; Dorcas, Price, Walls & Barichivich, 2009). The schedule was designed to increase both temporal resolution of sampling and species detectability in complex soundscapes, such as those found in tropical environments.

Audio settings were adjusted to record sounds in WAV stereo format at a sampling rate of 44.1 kHz and 16-bit audio depth. Hourly measurements of precipitation (in mm), air temperature (in °C) and relative air humidity (in %) were obtained via the closest meteorological stations to the study areas, namely *Mornand* station in French Guiana (4°55'10.1"N; 52°31'38.3"W; approximately 20 km from the study area) and *Aquidauana* station in Brazil (20°28'31.5"S; 55°47'02.4"W; approximately 100 km from the study area).

Sound analysis

Sound analysis consisted of two main stages: (i) pre-processing for standardization of passive recordings (track selection, frequency filtering and amplitude normalization; see below) and (ii) detection and recognition of each species' signals through a semi-automated procedure. First, sound quality was manually checked from a random selection of recordings within each site for signal-to-noise ratio and microphone dysfunction in order to select the most suitable track. The sound

recordings were then transformed from stereo to mono using the package “seewave” (Sueur et al., 2008) in R.3.2.5 (R Core Team, 2016). Second, to enhance species detection, recordings were standardized to increase overall quality and frequency resolution. A high-pass filter set at 500 Hz (roll-off of 36 dB) and a low-pass filter set at 5,000 Hz (roll-off of 48 dB) were applied to all recordings by batch processing in Audacity 2.1.2. (Audacity Team, 2014). The high-pass filter was chosen to reduce environmental noise and enhance signal-to-noise ratio while keeping the focal signals unaltered (Brumm, 2004; Penna, Pottstock & Velasquez, 2005). The low-pass filter was chosen to remove other animal signals while preserving the highest spectral components of the advertisement call of the studied species (Lescure & Marty, 2000). Finally, the sound amplitude in all recordings was normalized to maximum peak amplitude by batch processing in Audacity 2.1.2.

After the standardization procedure, audio files were processed to detect the calling activity of each species along the time series of passive recordings. We employed a semi-automated signal recognition procedure involving two steps (Llusia et al., 2013b). The first step consisted of searches based on spectrogram cross-correlation using a data template detector available in the XBAT R9 software (Figuerola & Robbins, 2007). For this task, spectrograms of all recordings were created using a short-term Fourier transform (STFT) algorithm set to a window size of 512 points, an overlap of 96% and a “Hann” tapering window. To build a signal detector for each species, species-specific call templates were selected from the whole dataset with an emphasis on representing overall variability in advertisement calls and acoustic conditions. Then, automated scans of the recorded time series were run using a correlation threshold of 50% (i.e. the required correlation rate between any call template and a potential call event for it to be considered a positive

detection) to control for false positives and false negatives. The second step involved manual audio-visual inspection of all spectrograms to validate each detected call event and to include new candidates, thus eliminating all false positives and significantly reducing false negatives.

Furthermore, a relative abundance index of the number of calling individuals was assigned to each 2-min recording. We used an adapted version of the Amphibian Calling Index (ACI) of the North American Amphibian Monitoring Program (NAAMP) protocol (Weir & Mossman, 2005). In contrast with the original index that ranges from 0 to 3, here the ACI values ranged from 0 to 5, thus allowing a finer characterization of calling activity, and were defined as the following: 0, absence of calling; 1, seldom vocalizations from one or two isolated individuals; 2, few vocalizations from countable individuals interspersed with non-calling periods; 3, distinct calls from uncountable individuals and with only a few overlapping calls; 4, intermittent chorus, with discontinuous calls and some overlapping; and 5, full chorus, with continuous calls and constant overlapping. The first author (A.B.) assigned all ACI values to avoid potential deviations due to inter-observer effects (Pierce & Hall, 2013).

Data analysis

A set of variables characterizing the calling activity of each species was obtained from the sound analysis of the passive audio recordings. First, presence (ACI>0) and absence (ACI=0) of calling activity was determined at a resolution of 20 minutes, which was then used to determine daily and seasonal activity patterns. Second, a maximum ACI value (hereafter maxACI) was calculated for each hour and then

346 associated with corresponding hourly measurements of relative humidity and
347 temperature. Thus, four variables per species were determined according to the
348 intensity of calling activity: (i) calling humidity and (ii) calling temperature (i.e.
349 relative humidity and temperature for hourly recordings with a maxACI between 1
350 and 3), and (iii) chorusing humidity and (iv) chorusing temperature (i.e. relative
351 humidity and temperature for hourly recordings with a maxACI>3). Furthermore,
352 (v) potential calling humidity and (vi) potential calling temperature were also
353 estimated. These variables were defined as the relative humidity and temperature,
354 recorded hourly, of the entire monitoring period at night (one hour before sunset to
355 one hour before sunrise), i.e. the expected calling period of the species. Wilcoxon
356 tests were used to check for regional differences in potential calling humidity and
357 potential calling temperature between precipitation extremes. Daily averages of
358 these variables were used in the analysis to prevent data autocorrelation associated
359 with hourly-collected data (Llusia et al., 2013a).

360 To investigate the variation in climatic breadth of calling behaviour between
361 species and populations, we used two generalized linear mixed models (GLMMs).
362 The first model included calling humidity (% of relative humidity) as the response
363 variable, coded as a binomial response via a two-column matrix composed of the
364 relative humidity at the time of calling (i.e. the percentage of saturated water
365 vapour) and the percentage of unsaturated water vapour (i.e. 100 minus the relative
366 humidity at the time of calling). A binomial error structure and the logit link function
367 were applied to this model. The second GLMM included calling temperature (°C) as
368 the response variable, using a Gaussian error structure and the identity link
369 function. The two models also included species (*P. paradoxa* and *B. raniceps*) and
370 study area (FG and BR) as fixed factors, and sites (FG1–4 and BR1–3), recording day

and recording hour as random factors.

Statistical analyses were performed using R 3.2.5 (R Core Team, 2016) and significance levels were set to a nominal type-I error of 5%. The *glmer* and *lmer* functions in the R package *lme4* (Bates, Mächler, Bolker & Walker, 2015) were used to build the two respective models. To keep the type-I error at 5%, five random slopes (study area within recording day, study area within recording hour, species within population, species within recording day and species within recording hour) were included in each model (Barr, Levy, Scheepers & Tily, 2013). For model inference, we performed likelihood-ratio tests through the *anova* function, which allows for a full-null model comparison. Null models comprised all predictor terms except for the fixed factors. To test for a potential interaction between species and areas, we compared models with and without this interaction term but found no significant differences and, thus, it was removed from the model. The effect of individual predictors on the response variable was also assessed through a full-null model comparison and a likelihood ratio test using the *drop1* function.

Concerning test assumptions, the variance inflation factor was used to confirm absence of collinearity between fixed factors in all models, using the R *gvif* and *vif* functions. The first GLMM showed a dispersion parameter close to 1, revealing no over- or under-dispersion. The residuals of the second GLMM were inspected by distribution probability plots that indicated no obvious deviations from the assumptions of normality and homoscedasticity. Confidence intervals of model coefficients were computed through 1,000 bootstrap iterations. Additionally, the daily and seasonal patterns of calling activity were compared graphically between species, study areas and populations.

395

396 **RESULTS**

397 ***Calling activity***

398 A total of 76,629 2-min audio files (2,554 hours) was obtained from passive acoustic
399 monitoring over 247 days of sampling in FG and 266 days in BR, with a mean of
400 3,649 hourly monitoring data per population (Table 1). Using a semi-automated
401 procedure for signal recognition, we detected 9,488 calling events (i.e. number of
402 hours with presence of calling activity from either of the studied species; Table 2),
403 which were paired with local measurements of relative air humidity and
404 temperature. The calling phenology differed between the study areas, and started 8
405 and 10 weeks in advance at the dry extremes for *Pseudis paradoxa* and *Boana*
406 *raniceps*, respectively (S1). However, the calling activity of both species lasted
407 similarly, with an average of 20 weeks for the season and 5 hours per night (Table
408 2). Among populations, the seasonal and daily duration of calling activity were
409 highly variable, ranging from a total of 53 to 200 calling nights over the season and
410 from 1 to 15 hours per day. When comparing the two areas located at the humidity
411 extremes, the activity period only varied 5–10 nights and 0–2 hours per night
412 between conspecific populations in FG and BR (Table 2).

413

414 ***Weather conditions***

415 During the monitoring period, precipitation was as much as 4.5-fold higher in the
416 humid (FG; 2,237 mm) than in the dry extreme (BR, 494 mm), and the potential
417 calling humidity was significantly different between the two areas ($W=1,109.5$,

$p < 2.2 \cdot 10^{-16}$; Fig. 4), which averaged 94% in FG and 74% in BR (Table 3). In contrast, the potential calling temperature was similar ($W=35,220$, $p=0.136$; Fig. 4), with an average of 24.7°C for both areas (Table 3). Overall, FG populations had narrower ranges of potential calling humidity and temperature than those in BR, where the weather conditions were highly variable across the breeding season (Table 2; Fig. 4).

Calling humidity and calling temperature

As shown by the full-null model comparison, the calling humidity of *P. paradoxa* and *B. raniceps* was significantly influenced by the model predictors (likelihood-ratio test: $\chi^2=42.1$, $df=2$, $p\text{-value}=7.3 \cdot 10^{-10}$). The calling activity of conspecific populations of the two species located at the humidity extremes occurred at significantly different ranges of relative humidity ($\chi^2=37.9$, $df=1$, $p\text{-value}=7.5 \cdot 10^{-10}$; Table 3), up to 21% higher in the humid (FG) than the dry extreme (BR) (Table 3). Moreover, both species showed similar responses ($\chi^2=1.2$, $df=1$, $p=0.26$) and no obvious interaction between species and study areas was found ($\chi^2=3.4$, $df=1$, $p=0.064$). Over the study period, *P. paradoxa* and *B. raniceps* were recorded calling at relative humidities ranging from 75% to 100% in FG and from 31% to 97% in BR (Table 2; Fig. 4). In contrast, calling temperature did not differ between humidity extremes or species (likelihood-ratio test: $\chi^2=0.7$, $df=2$, $p\text{-value}=0.69$) and no interaction between these predictors was found ($\chi^2=1.2$, $df=1$, $p\text{-value}=0.27$). Calling activity occurred at temperatures ranging from 15°C to 34°C in BR and from 22°C to 30°C in FG, and the mean calling temperature for both species and areas was around 25°C (Table 3). Moreover, the recorded climatic breadth of calling behaviour did not

encompass the whole range of potential calling humidity and temperature observed at the study areas. Overall, calling activity was scarcely detected during the driest, hottest and coldest nights of the breeding season (Table 3; Fig. 4).

Amphibian calling index

According to the ACI, calling activity was not equally intense over the duration of the night and the breeding season (Fig. 5, S1), with marked differences in the number of calling individuals. However, the climatic breadth did not vary notably across ACI levels (Table 3). The mean and range of both relative humidity and temperature during chorusing activity ($\text{maxACI} > 3$) were similar to those during calling activity ($1 \leq \text{maxACI} \leq 3$). Only the chorusing activity of *P. paradoxa* occurred under more restricted humidity conditions in the dry extreme (i.e. the minimum relative humidity was 12% higher than that at the humid extreme, Table 3).

The daily calling activity of all populations progressively increased after sunset, peaking just before midnight (Fig. 5). However, while the maximum abundance of calling individuals occurred at the same time in *B. raniceps* populations located at the humidity extremes, it occurred at a different time in those of *P. paradoxa* (i.e. 4 hours later at the dry extreme than at the humid one). As shown in Figure 5, despite these divergent temporal patterns, *P. paradoxa* did not perform calling behaviour under similar humidity conditions between the study areas. Thus, conspecific populations of both species exhibited a distinct calling humidity during the period of maximum abundance of calling individuals. In contrast, calling temperature at the peak of calling activity was similar across species and study areas

(Fig. 5), in agreement with the general trend observed in overall calling humidity and calling temperature.

Regarding the breeding season, *P. paradoxa* started calling slightly after *B. raniceps*, and both species exhibited high levels of calling abundance even late in the season, particularly in the dry extreme (S1). However, the onset of calling activity was different between the two study areas: *P. paradoxa* and *B. raniceps* populations both started calling around mid-December in FG but approximately two months earlier in BR. Once the breeding season started, calling activity occurred mostly on a daily basis. However, the level of calling activity varied along the season, being higher at periods of intense precipitation. Toward the end of monitoring period, calling activity had greatly decreased in FG but was still occurring at high levels in BR (S1).

DISCUSSION

Passive acoustic monitoring of distant Neotropical populations under contrasting humidity conditions demonstrates that the studied frog species (*Boana raniceps* and *Pseudis paradoxa*) can perform calling behaviour across a broad range of relative humidity. In addition, a divergent pattern was observed between conspecific populations located at the humidity extremes of the species geographic distribution, indicating that calling humidity is not a fixed species trait and may potentially vary according to the precipitation regime experienced by populations. Although *B. raniceps* and *P. paradoxa* show distinct ecological and behavioural features, individuals of both species were reproductively active even under dry conditions,

suggesting an extensive capacity in widespread Neotropical anurans to exhibit their sexual displays in different climatic environments.

The pattern of calling humidity observed here is congruent with the one found for calling temperature in populations of five temperate anurans located at the thermal extremes of their distribution (Llusia et al., 2013b). Both sets of studied species, i.e. temperate and widely distributed Neotropical anurans, showed a broad and population-specific climatic breadth of calling behaviour. The capacity to maintain calling activity under variable weather conditions may reflect genetic or plastic responses associated with climatic tolerance (Angilletta, 2009; Duarte, Tejedo, Katzenberger, Marangoni, Baldo, Beltrán, Martí, Richter-Boix & Gonzalez-Voyer, 2011), which might confer species some mechanisms to mitigate the effects of climate change. Moreover, the monitoring of calling behaviour and its abiotic determinants provides important eco-physiological information (Bovo et al., 2018) that can improve models forecasting climate change impacts on anurans (Araújo et al., 2006).

Divergent ranges of calling humidity across species distribution can be explained by either local adaptation or phenotypic plasticity (Corlett, 2011). On the one hand, local climatic conditions can generate selective pressures on species traits through adaptation, especially for species occupying habitats more vulnerable to climate changes, such as savannah biomes (Loarie et al., 2009). The observed differences in calling behaviour could reflect a process of disruptive selection, as the populations are geographically distant, favouring adaptation to local climatic regimes. Although evolutionary processes often require large time scales, rapid genetic adaptation driven by climate change has also been reported for specific

phenotypic traits (Karell, Ahola, Karstinen, Valkama & Brommer, 2011). Nevertheless, in the studied species, there is no clear support for these processes. Low genetic differentiation has been reported between the studied conspecific populations of *B. raniceps* (Fouquet et al., 2007; Jansen et al., 2011; Lyra et al., 2017) and most of the temperate species monitored so far (Llusia et al. 2013b), while subspecies can be recognized in both *P. paradoxa* (Aguar et al., 2007; Garda & Cannatella, 2007; Garda et al., 2010) and the temperate species *Alytes obstetricans* (Martínez-Solano, Gonçalves, Arntzen & García-París, 2004).

On the other hand, phenotypic plasticity driven by environmental acclimation is a well-documented phenomenon that has been largely associated with temperature (Angilletta, 2009; Calosi, Bilton, Spicer & Atfield, 2008; Gvoždík, 2012; Rome, Loughna & Goldspink, 1984). The interannual variation in thermal breadth observed in the same populations of temperate anurans (Llusia et al. 2013b) supports acclimation as a potential mechanism that may lead to divergence in climatic breadth of calling behaviour. Yet, such responses associated with relative humidity remains mostly unexplored. Further investigations, such as common garden experiments (De Villemereuil, Gaggiotti, Mouterde, & Till-Bottraud, 2016), are required to attribute the observed patterns to evolutionary or acclimation processes and to provide a better understanding of the potential role of relative humidity in the climatic tolerance of animal populations.

Identifying the underlying mechanisms determining a species response to climate change is a daunting task (Merilä & Hendry, 2014). Regardless of the specific mechanism, both selection and phenotypic plasticity might supply amphibians with key abilities under climate changes, although the potential of tolerance plasticity to

buffer overheating risk in ectotherms has recently been questioned (Gunderson & Stillman, 2015). The broad climatic breadth of calling behaviour in anurans might allow these animals to better cope with the effects of variations in humidity and temperature, especially during the performance of sexual displays.

Our findings were based on cross-sites comparisons across latitudinal gradient, a suitable approach to examine species responses to variation in climatic conditions (Weltzin et al. 2003). However, manipulative experiments are needed to fully assess the climatic tolerance of species. Innovative facilities based on mesocosms (Lawton et al., 1993) have recently been developed to recreate natural microhabitats under the control of abiotic factors (Gao, Jin, Llusia & Li, 2015; Stewart et al., 2013). Such facilities can also be used in the experimental study of climatic tolerance of calling behaviour. Despite this, calling behaviour is a complex phenomenon, challenging to be reproduced under experimental settings, which hinders the determination of the limits of climatic tolerance, in comparison with physiological metrics as CT_{max}, and hence appropriated experimental designs must still to be developed.

Calling activity of both studied species was seldom recorded under the driest, coldest and hottest weather conditions during the breeding season. This partly corresponded to the onset of the season, when individuals emerge from estivation searching for suitable breeding sites, and the end, when they retreat to refuges (Brooke et al. 2000, Gao et al., 2015; Prado et al. 2005). Moreover, these low levels of calling activity may also reflect potential limits on the species climatic tolerance. Thermal limits associated with high-energy behaviours in adults, such as calling, are likely narrower than those associated with sub-lethal endpoints in larvae

(Lutterschmidt & Hutchison, 1997). Predictive models of climate change impacts on anurans should, therefore, consider to apply smaller ranges than the lethal thermal limits, otherwise, forecasts would presumably overestimate the response capacity of the species. In tadpole populations in Argentina, the critical thermal maximum (CTmax) was determined to be 42.25°C for *P. paradoxa* and 41.18°C for *B. raniceps* (Nava, 2009), while the maximum calling temperature recorded for the same species in our study was 33.9°C and 32.7°C, respectively. The calling temperatures found here were estimated from populations subjected to average thermal conditions; therefore, we hypothesize that populations at the thermal extremes of the studied species' ranges would have higher calling temperatures.

The variation in climatic conditions that species experience in their habitats is expected to influence their eco-physiological tolerance to climate change (Ghalambor, Huey, Martin, Tewksbury & Wang, 2006; Janzen, 1967). Thus, tropical ectotherms are likely more sensitive to temperature changes than temperate-zone species (Bonetti & Wiens, 2014; Deutsch et al., 2008; Duarte et al., 2011; Sunday, Bates & Dulvy, 2011). Although variation in thermal tolerance at different latitudes may be negligible, the degree of seasonality has an effect on the plasticity of thermal responses (Gunderson & Stillman, 2015). Climate change is expected to drive significant shifts in the magnitude and concentration of seasonal rainfall in the tropics (Feng, Porporato, & Rodriguez-Iturbe, 2013). Additionally, local abiotic factors play a major role in restraining the warming tolerances of tropical amphibians, and behavioural adjustments associated with habitat-use can help certain ectotherms cope with increasing climatic variation (Duarte et al., 2011).

Our thorough analysis of the temporal patterns of calling activity between species and study areas revealed particular aspects of the climatic breadth of calling behaviour. Conspecific populations of *P. paradoxa* showed different daily patterns of calling activity at the humidity extremes, suggesting that the temporal shift in peak calling activity in this species is not driven by hydric conditions, as relative humidity ranges differed between the distant regions at the daily activity peaks. Multiple factors can influence the daily pattern of calling activity in anurans, such as weather condition, competitive exclusion, social facilitation and predator pressure (Brooke et al., 2000; Llusia et al., 2013a; Oseen & Wassersug, 2002). The period of breeding season is closely linked to seasonal precipitation, particularly at the humid extremes, and the period observed in our study is consistent with those observed in previous studies of the same species (Prado et al., 2005). Seasonal patterns of anuran calling activity are strongly related to rainfall, especially in the tropics, which have heavy rainy seasons (Donnelly & Guyer, 1994; Ulloa, Aubin, Llusia, Courtois, Fouquet, Gaucher, Pavoine & Sueur, 2019). In temperate regions, these patterns have mostly been linked to the joint effect of temperature and rainfall (Caldwell, 1987; Llusia et al., 2013a; Oseen & Wassersug, 2002). However, seasonal patterns of calling activity may be less closely related to rainfall at dry extremes given that they are located at higher latitudes and are characterized by a subtropical climate (i.e. a different amplitude range of temperature and drier conditions).

Climate change impacts on habitats may also affect species persistence, directly or in combination with other identified drivers of amphibian population decline (Carey & Alexander, 2003; Hof et al., 2011). Changes in rainfall volume and seasonality greatly alter the availability of breeding sites and the hydroperiod of amphibians, thus compromising reproduction, larval development and population

survival (Burrowes et al., 2004; Stewart, 1995). Habitat changes or loss due to precipitation extremes that produce torrents can also lead to an increase in amphibian mortality at all life stages (Bickford, Howard, Ng & Sheridan, 2010). The tropical savannahs inhabited by many amphibian species are also particularly threatened at both global and local scales (Overbeck et al., 2015; Roque et al., 2016; Silva & Bates, 2002). In French Guiana, where savannahs represent only 0.3% of the territory, savannah habitats are jeopardized by land-use transformation and urbanization. Population decline has been the trend in both of the studied species over the last 10 years, and a recent regional red list assessment has classed *B. raniceps* as endangered and *P. paradoxa* as near threatened (UICN France et al., 2017). In the Pantanal, the continuous removal of native vegetation in the uplands is so severe that it has led to changes in the population dynamics and persistence of species in the lowlands (Roque et al., 2016).

As shown here and in previous studies (Krause & Farina, 2016; Llusia et al., 2013b; Sueur et al., 2019), automated acoustic monitoring techniques (Sugai et al., 2019) can provide important information on species behaviour under different climatic conditions, thus assisting climate change research. With these new techniques, the thermal breadth of calling activity can also be further investigated and provide a complementary view on the response capacity of anuran amphibians to climate change. For instance, monitoring the sexual displays of populations that experience similar precipitation regimes but contrasting thermal conditions will shed light on the extent to which certain tropical species are vulnerable to global warming. Automated acoustic monitoring can also be used to compare the climatic breadth of calling behaviour between narrowly distributed species and widely distributed species. Other aspects of the acoustic communication systems of the

studied species, such as variations in call parameters or hearing sensitivity, may also be affected by climatic conditions and should be further explored. Since temporal features of calls (e.g. call rate, call duration or duty cycle) are temperature-dependent (Narins et al., 2007) as well as key selected traits in female choice (Gerhardt & Huber, 2002), it is expected that climate change cause indirect effects on physiology of calling males, calling performance and sexual selection in anurans, among other consequences. Finally, future experimental studies should focus on determining the climatic tolerance of calling behaviour in anurans and clarifying the underlying mechanisms driving species responses.

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DATA AVAILABILITY STATEMENT

The dataset that supports the findings of this study is archived in the Universidad
Autónoma de Madrid and available from the corresponding author upon reasonable
request. A subset of this database is available from e-cienciaDatos in
<<https://doi.org/10.21950/LHESKW>> (Bonnefond et al. 2020).

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TABLES

Table 1. General features of the study areas and monitored sites. Study areas correspond to the French Guiana coast (FG) and the southern Pantanal wetlands in the state of Mato Grosso do Sul, Brazil (BR). Weather conditions (Fick & Hijmans, 2017), level of precipitation and thermal extremity within each species range (*Pp* = *Pseudis paradoxa*; *Br* = *Boana raniceps*), geographic coordinates and monitoring period are shown. *Boana raniceps* is absent at sites FG1 and FG2.

Table 2. Calling activity of *Pseudis paradoxa* and *Boana raniceps* in sites from the French Guiana coast (FG) and the southern Pantanal wetlands in Brazil (BR). Species activity was recorded by passive acoustic monitoring and detected with a semi-automated procedure of signal recognition.

Table 3. Relative humidity (%) and temperature (°C) during calling behaviour of two widespread Neotropical frogs. Data were compiled from seven populations of *Pseudis paradoxa* and five populations of *Boana raniceps* monitored in the French Guiana coast (FG) and the southern Pantanal wetlands in Brazil (BR). Weather conditions are shown separately for: (i) the entire monitoring period at night, one hour before sunset to one hour before sunrise, when species could potentially exhibit calling behaviour (potential); and (ii) when calling or (iii) chorusing behaviour was actually recorded.

Table 4. Regression coefficients and standard errors from generalized linear mixed-effects models on calling humidity and calling temperature. Models included localities (the French Guiana coast, FG; and the southern Pantanal wetlands in Brazil, BR) and species (*Pseudis paradoxa*, *Pp*; and *Boana raniceps*, *Br*) as fixed factors, and sites, nights and hours as random factors. Reference values are based on *Br* and BR. Lower and Upper CL correspond to the confidence intervals of GLMM coefficients obtained through 1,000 bootstrap iterations.

FIGURES

Figure 1. Annual precipitation across the distribution range of *Pseudis paradoxa* (a, b) and *Boana raniceps* (c, d). Arrows on the histograms show the annual precipitation (mm, Fick & Hijmans, 2017) in the two study areas: the French Guiana coast (FG) and the southern Pantanal wetlands in Brazil (BR). Dashed lines indicate the average annual precipitation of each species range (IUCN et al., 2008a; IUCN et al., 2008b).

Figure 2. Annual mean temperatures across the distribution range of *Pseudis paradoxa* (a, b) and *Boana raniceps* (c, d). Arrows on the histograms show the annual mean temperature (°C, Fick & Hijmans, 2017) in the French Guiana coast (FG) and the southern Pantanal wetlands in Brazil (BR). Dashed lines show the average annual mean temperature of each species range (IUCN et al., 2008a; IUCN et al., 2008b).

Figure 3. Habitat characterization and distribution of study sites in areas located at the humidity extremes of the distribution range of *Pseudis paradoxa* and *Boana raniceps*, namely the French Guiana coast (a) and the southern Pantanal wetlands in Brazil (b).

Figure 4. Relative humidity and temperature during calling activity of *Pseudis paradoxa* (a, c) and *Boana raniceps* (b, d) from sites in the French Guiana coast (FG1–4) and the southern Pantanal wetlands in Brazil (BR1–3). Boxplots represent median (horizontal line), 1st–3rd quartile range (box), and range (whiskers). Squares (FG) and diamonds (BR) depict average calling humidity and temperature for each study area. Grey rectangles represent the total breadth of relative humidity (a, b) and temperature (c, d) during the nights of the breeding season.

Figure 5. Daily calling activity, potential relative humidity (a-d) and potential temperature (e-h) in monitored populations of *Pseudis paradoxa* (first and third row) and *Boana raniceps* (second and fourth row) from the French Guiana coast (FG, left panels) and the southern Pantanal

1076 wetlands in Brazil (BR, right panels). Boxplots represent median (horizontal line), 1st–3rd
1077 quartile range (box), and range (whiskers) of relative humidity (a–d) and temperature (e–h).
1078 Dashed lines depict mean calling humidity or mean calling temperatures in FG (long-dashed)
1079 and BR (short-dashed). Calling activity is represented by the hourly average of the maximum
1080 Amphibian Calling Index (maxACI; based on an adapted version of the index ranging from 0 to
1081 5, see Methods) and its standard deviation. Grey rectangles highlight the relative humidity and
1082 temperature at the peak of calling activity.

| Area | Annual precipitation (mm) | Annual Mean Temp (°C) | Level of precipitation extremity (%) | | Level of thermal extremity (%) | | Site | Latitude, Longitude (W) | Altitude (m.a.s.l.) | Monitoring perio (dd/mm/yy) | |
|--------------------|---------------------------|-----------------------|--------------------------------------|-----------|--------------------------------|-----------|------|-------------------------|---------------------|-----------------------------|-------|
| | | | <i>Pp</i> | <i>Br</i> | <i>Pp</i> | <i>Br</i> | | | | start | end |
| French Guiana (FG) | 3,075 | 25.5 | 95.9 | 98.4 | 60.1 | 46.8 | FG1 | 05° 02'N, 52° 33' | 9 | ##### | ##### |
| | | | | | | | FG2 | 05° 01'N, 52° 34' | 23 | ##### | ##### |
| | | | | | | | FG3 | 05° 06'N, 52° 35' | 11 | ##### | ##### |
| | | | | | | | FG4 | 05° 07'N, 52° 36' | 12 | ##### | ##### |
| Brazil (BR) | 1,312 | 25.1 | 83.8 | 76.8 | 31.9 | 44 | BR1 | 19° 33'S, 56° 06' | 110 | ##### | ##### |
| | | | | | | | BR2 | 19° 31'S, 56° 09' | 110 | ##### | ##### |
| | | | | | | | BR3 | 19° 29'S, 56° 09' | 110 | ##### | ##### |

nd

days

236

187

205

239

266

266

266

| Species | Area | Populations | Calling nights per population | | | Calling hours per night | | |
|--------------------|------|-------------|-------------------------------|---------|--------|-------------------------|-------|-------|
| | | | Mean \pm SD | Range | Nights | Mean \pm SD | Range | Hours |
| <i>P. paradoxa</i> | FG | 4 | 136 \pm 34.2 | 86–162 | 545 | 5.2 \pm 3.0 | 1–15 | 2797 |
| | BR | 3 | 138 \pm 76.1 | 53–200 | 414 | 5.4 \pm 2.7 | 1–13 | 2525 |
| <i>B. raniceps</i> | FG | 2 | 131 \pm 7.8 | 126–137 | 263 | 4.2 \pm 1.9 | 1–10 | 1087 |
| | BR | 3 | 148 \pm 34.2 | 79–189 | 444 | 6.0 \pm 2.7 | 1–12 | 3079 |

| Species | Locality | Relative Humidity (%) | | | | | |
|--------------------|----------|-----------------------|--------|----------------|--------|----------------|--------|
| | | Potential | | Calling | | Chorusing | |
| | | Mean \pm SD | Range | Mean \pm SD | Range | Mean \pm SD | Range |
| <i>P. paradoxa</i> | FG | 94 \pm 6 | 65–100 | 93 \pm 6 | 75–100 | 94 \pm 4 | 75–100 |
| | BR | 74 \pm 17 | 15–100 | 77 \pm 13 | 31–97 | 80 \pm 11 | 43–96 |
| <i>B. raniceps</i> | FG | 94 \pm 6 | 65–100 | 95 \pm 5 | 81–100 | 95 \pm 4 | 82–100 |
| | BR | 74 \pm 17 | 15–100 | 74 \pm 13 | 31–97 | 71 \pm 12 | 31–96 |
| Temperature (°C) | | | | | | | |
| <i>P. paradoxa</i> | FG | 24.7 \pm 1.6 | 20–30 | 25.3 \pm 1.3 | 22–30 | 25.5 \pm 1.0 | 22–29 |
| | BR | 24.7 \pm 3.3 | 9–37 | 24.6 \pm 2.1 | 15–34 | 24.6 \pm 1.5 | 18–31 |
| <i>B. raniceps</i> | FG | 24.7 \pm 1.5 | 20–30 | 24.7 \pm 0.9 | 22–27 | 24.7 \pm 1.0 | 22–27 |
| | BR | 24.7 \pm 3.3 | 9–37 | 25.5 \pm 2.3 | 16–33 | 26.0 \pm 2.0 | 20–31 |

| Variable | Predictor | Coefficient | Std.error | Lower CL | Upper CL |
|----------------------------|-----------------------|-------------|-----------|----------|----------|
| Relative humidty (%) | Intercept | 1.32 | 0.17 | 0.91 | 1.53 |
| | Locality (FG) | 2.12 | 0.09 | 1.55 | 2.86 |
| | Species (<i>Pp</i>) | -0.05 | 0.04 | -0.09 | 0.16 |
| Temperature (°C) | Intercept | 25.55 | 0.70 | 24.22 | 26.92 |
| | Locality (FG) | -0.95 | 0.43 | -1.75 | -0.12 |
| | Species (<i>Pp</i>) | -0.05 | 0.07 | -0.17 | -0.09 |

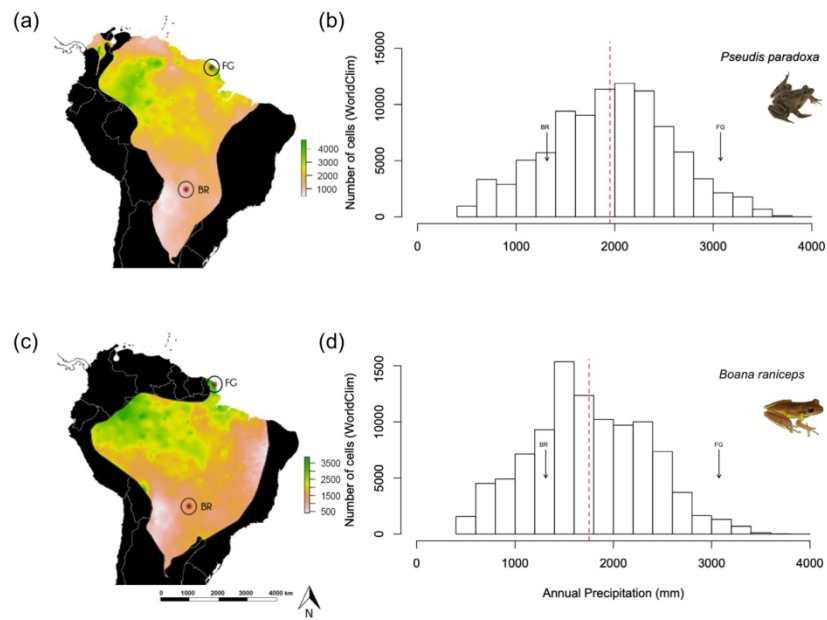


Fig. 1_color (JPEG)

190x236mm (242 x 242 DPI)

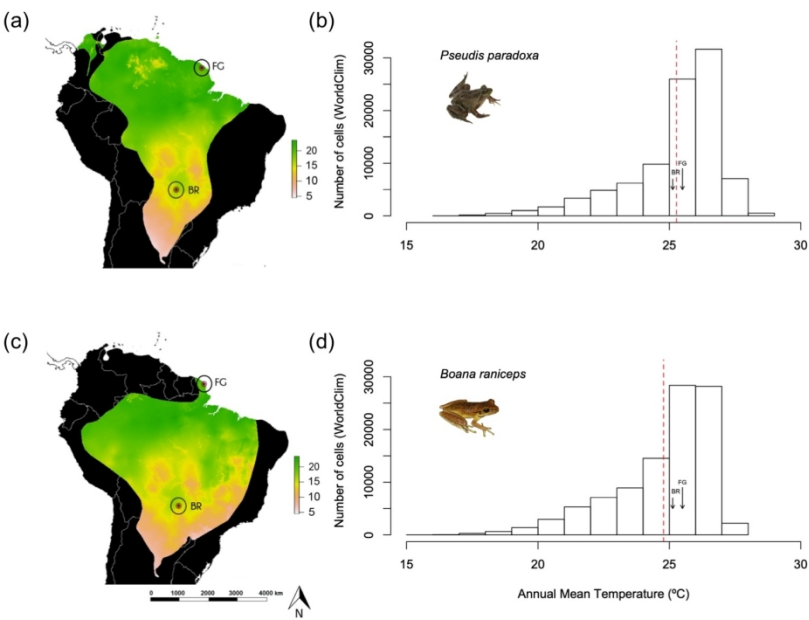


Fig. 2_color (JPEG)

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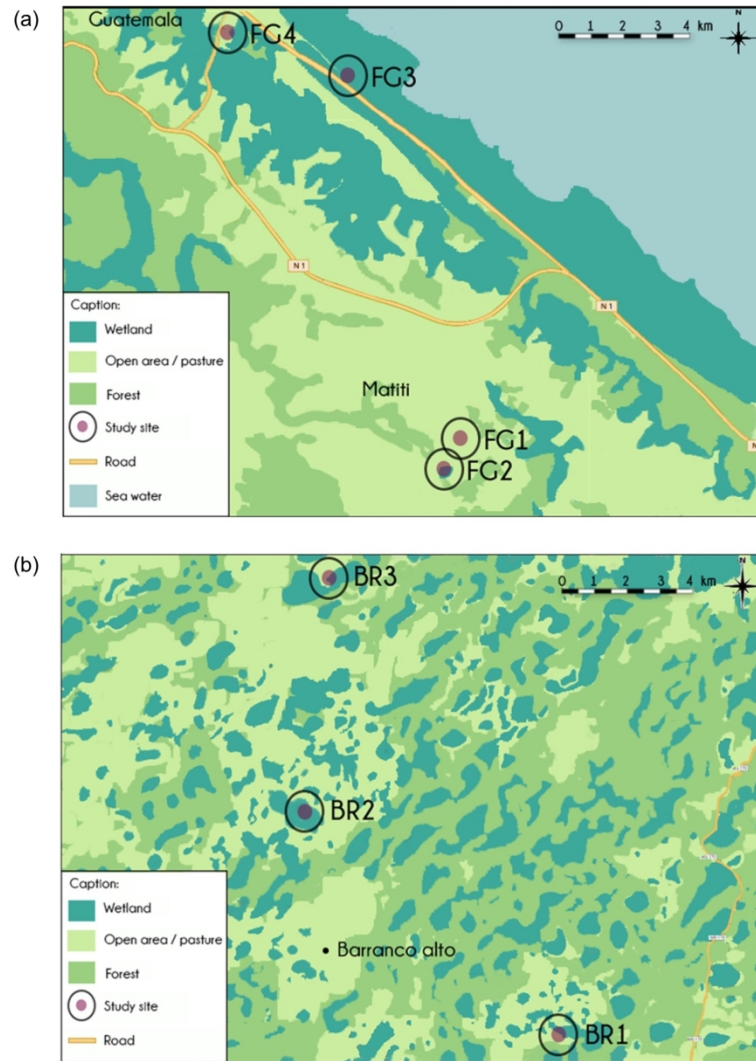


Fig. 3_color (JPEG)

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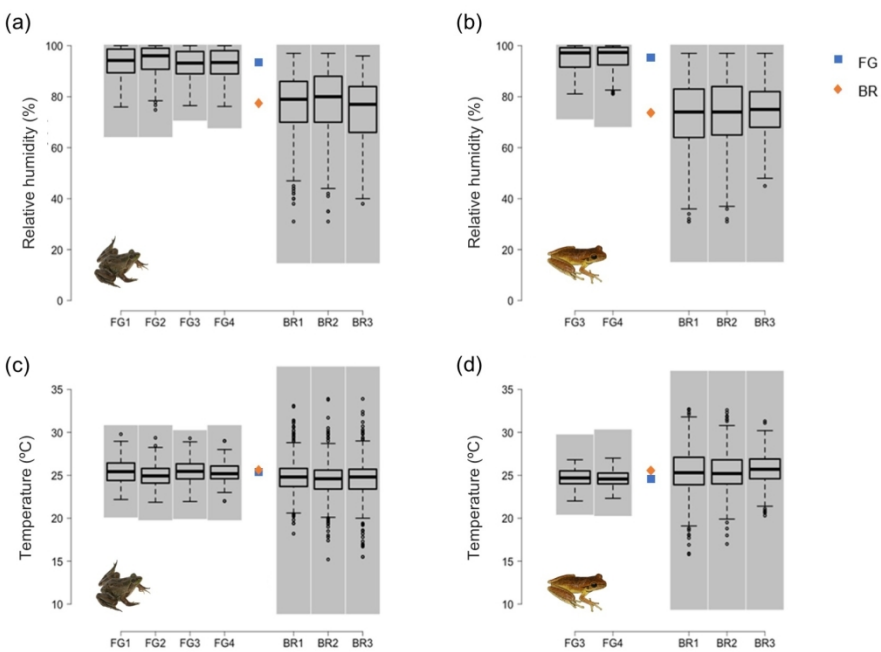


Fig. 4_color (JPEG)

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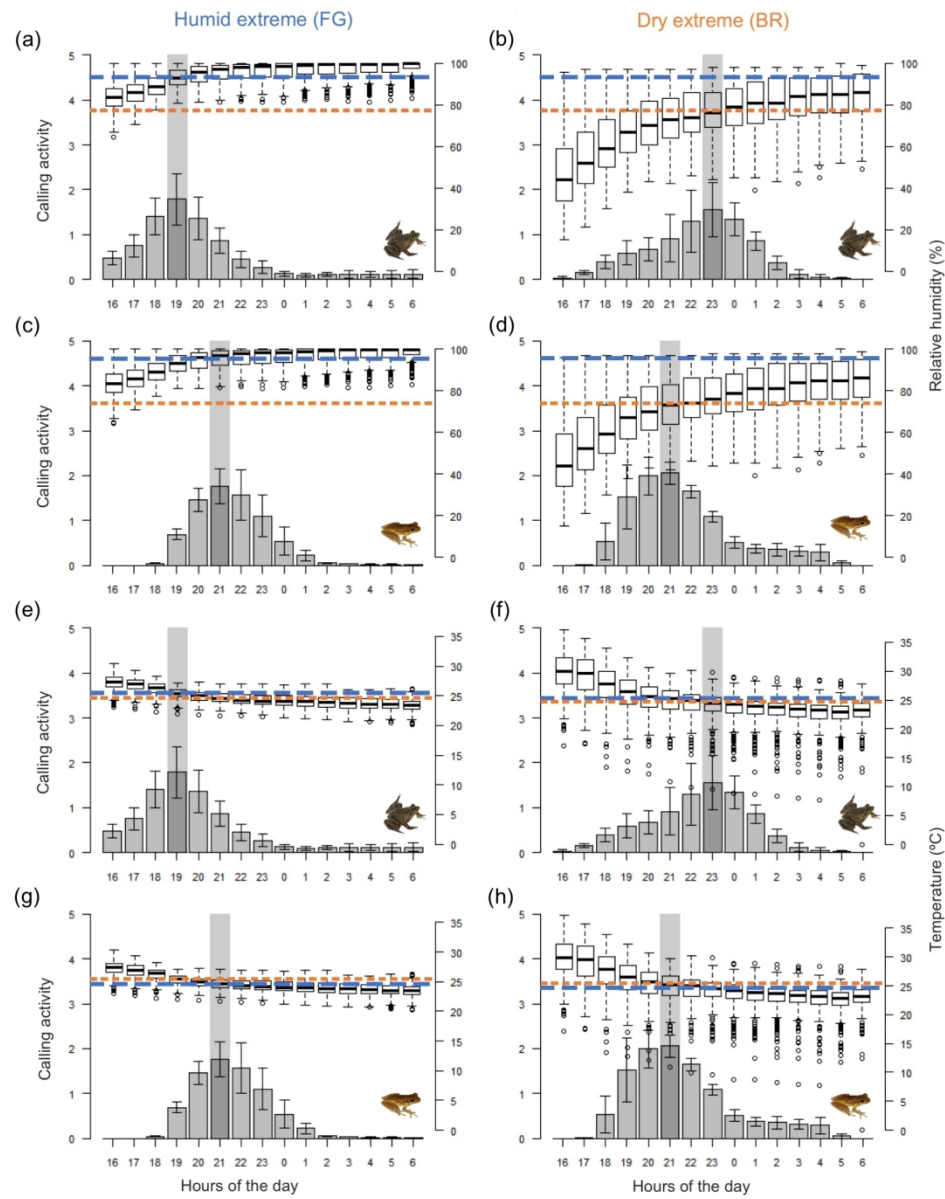
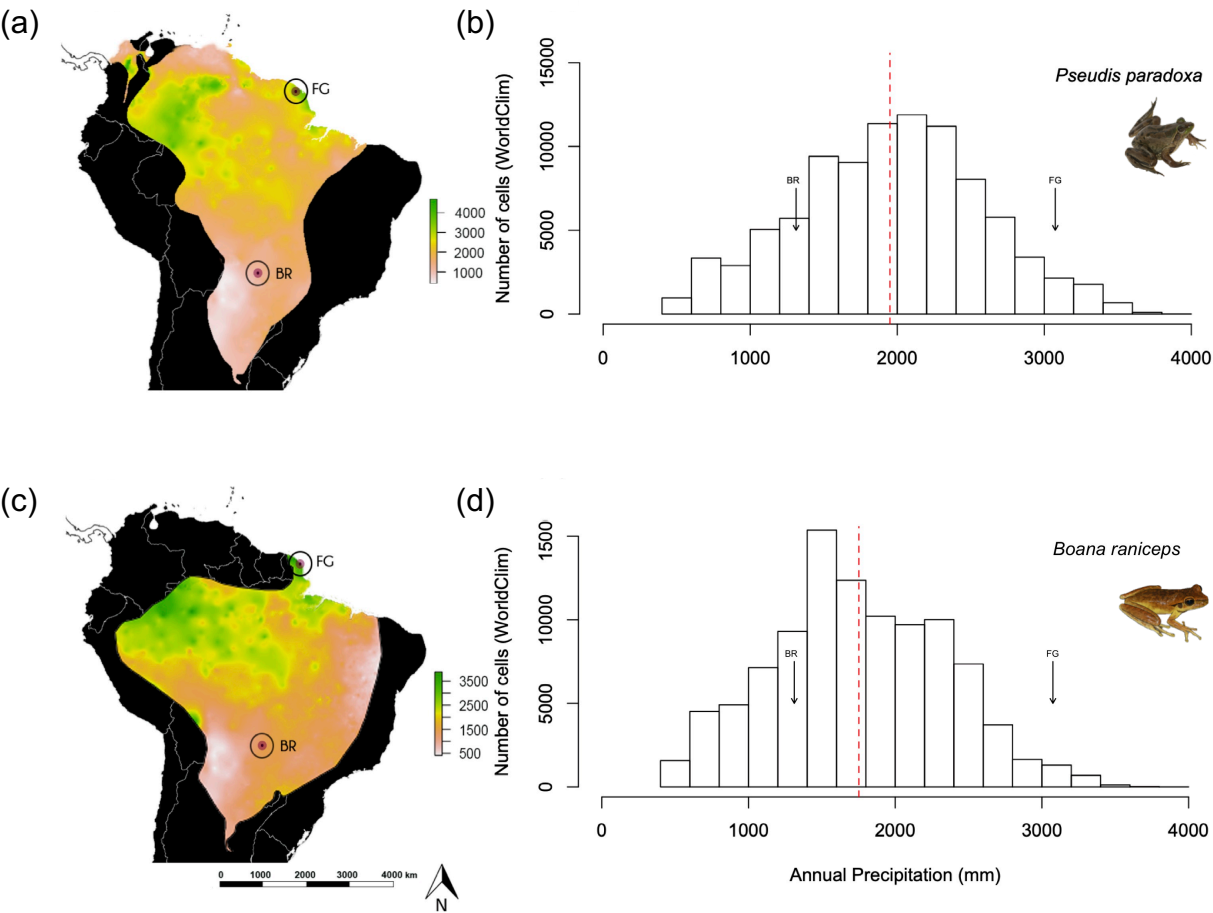
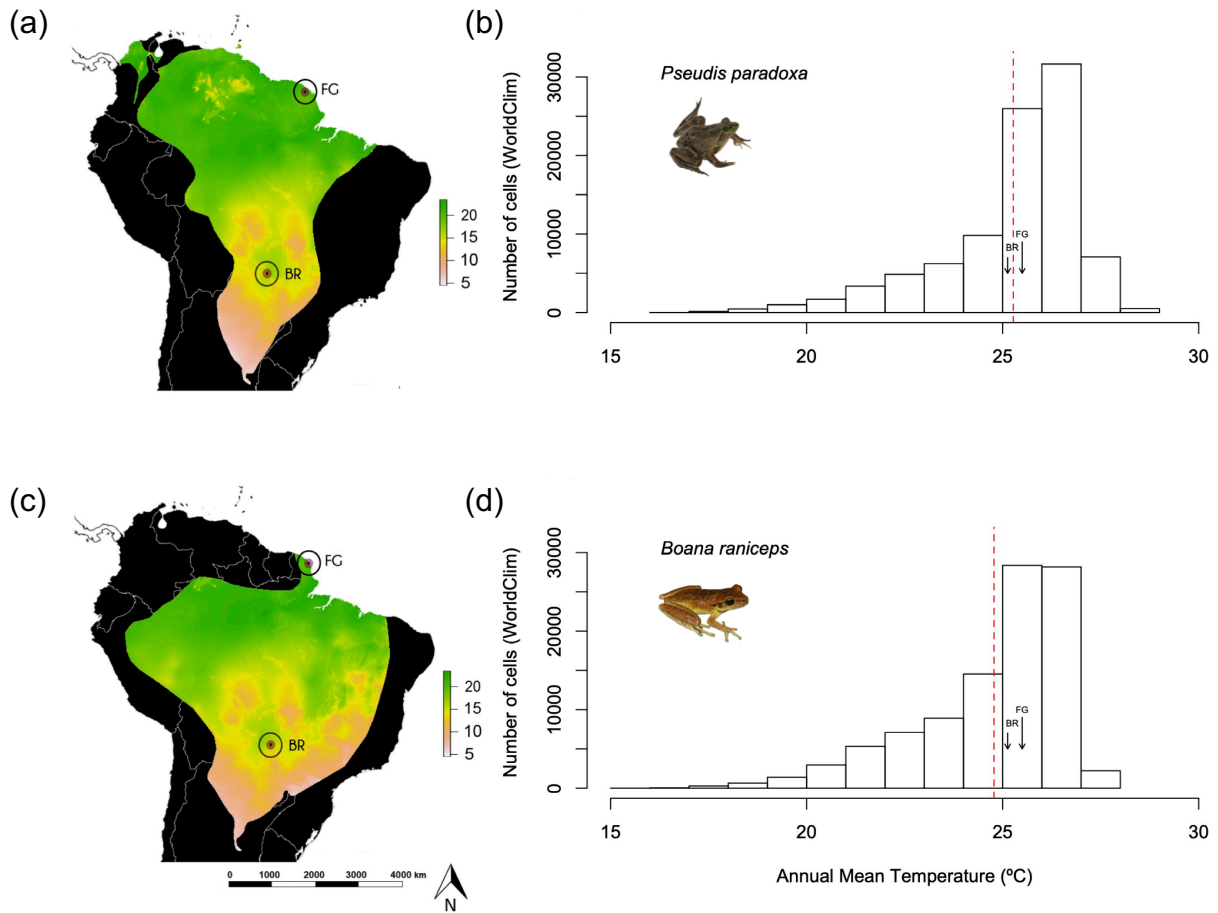
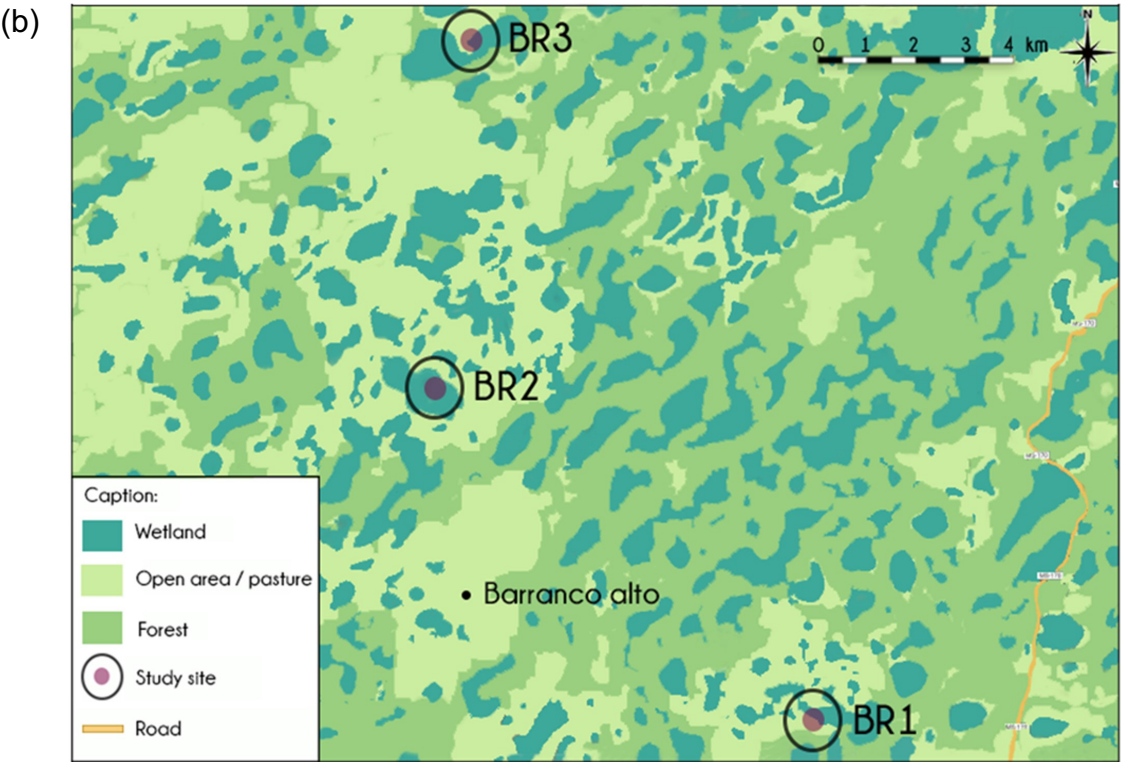


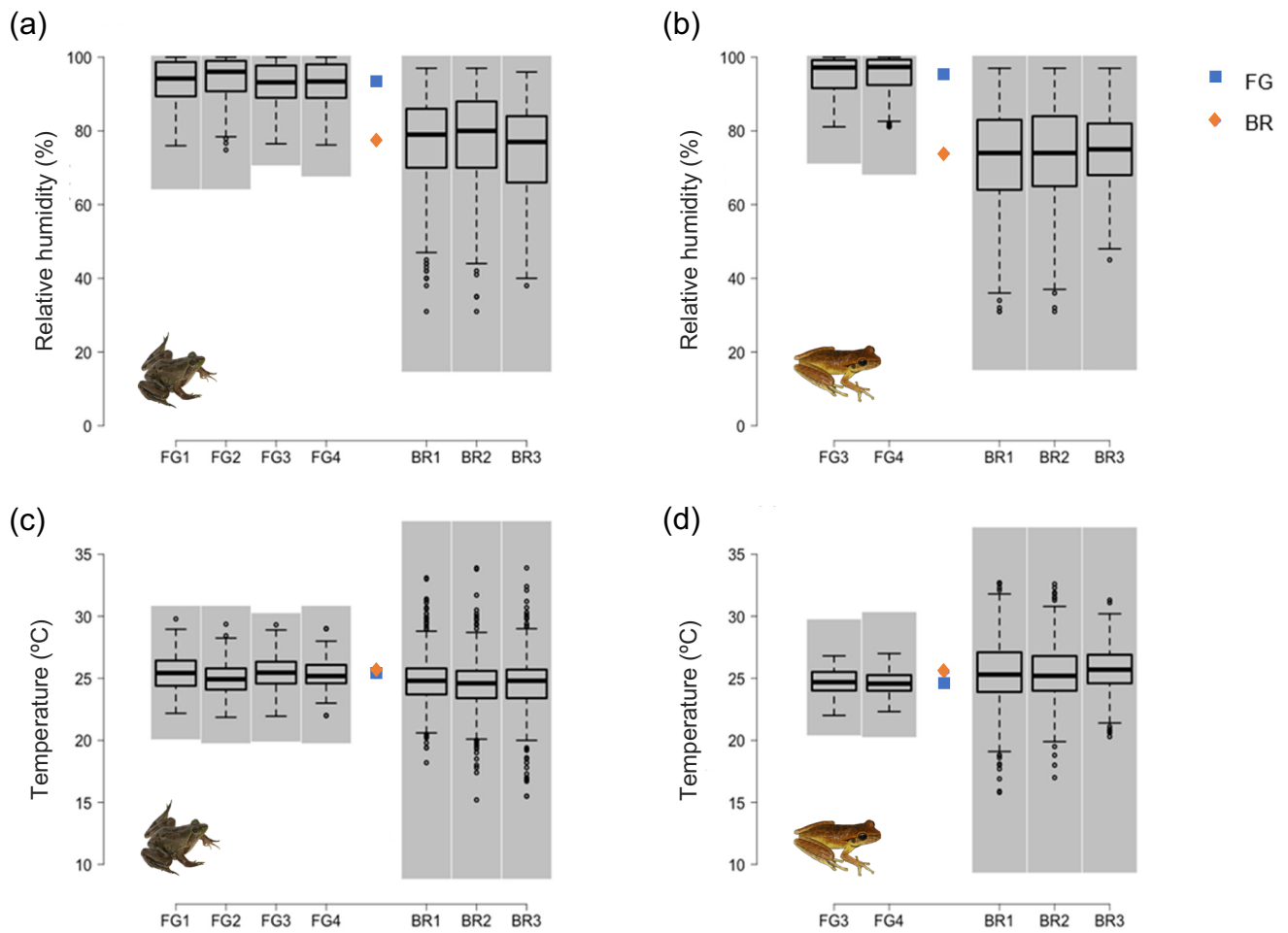
Fig. 5_color (JPEG)

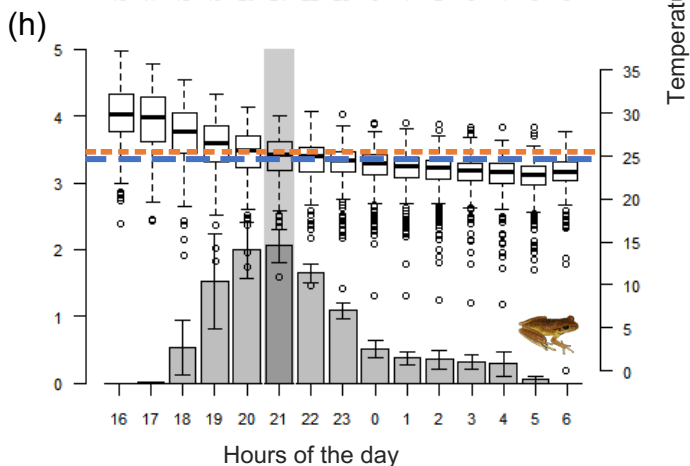
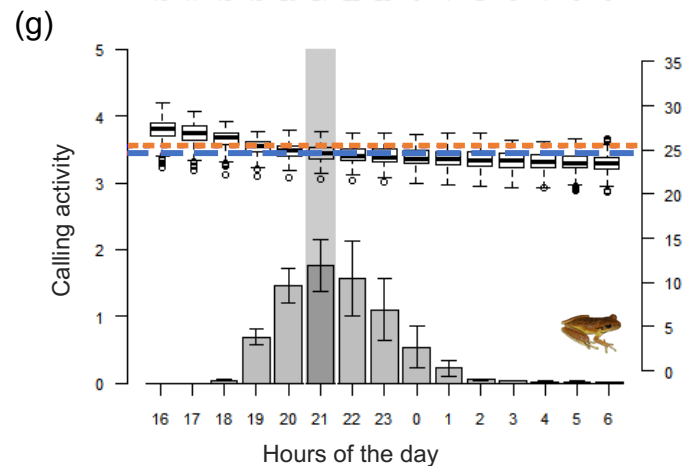
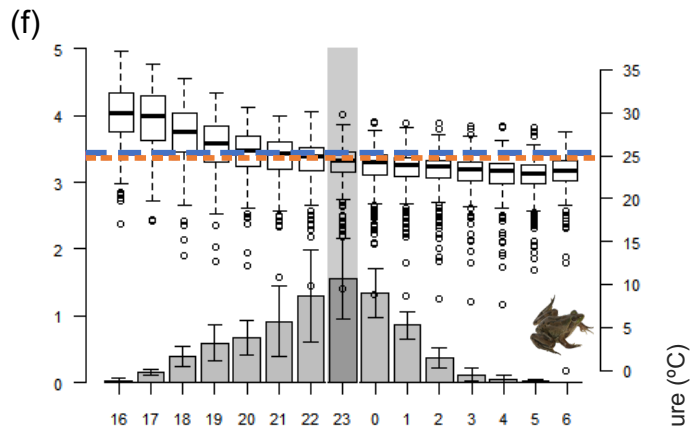
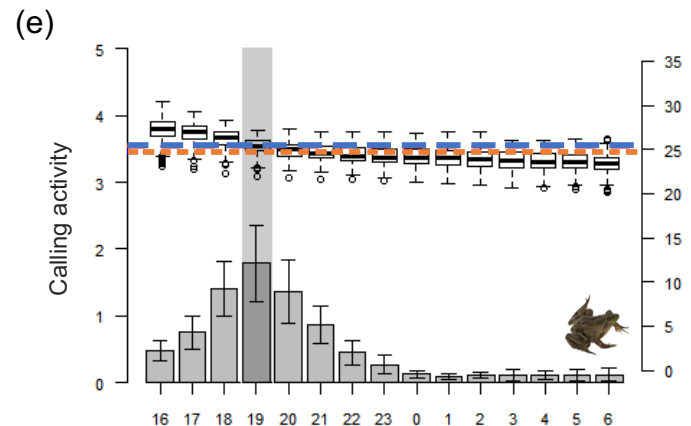
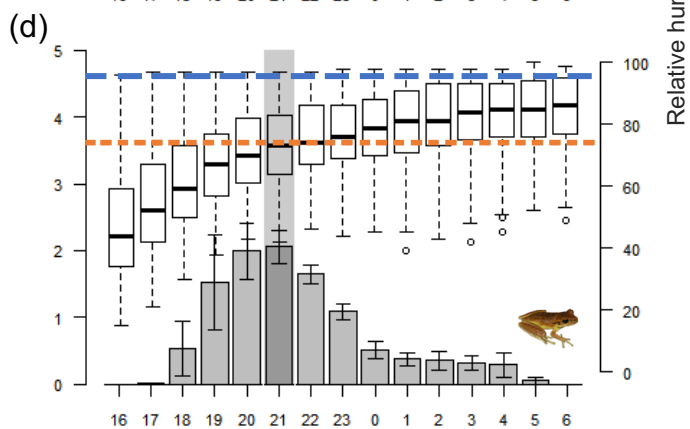
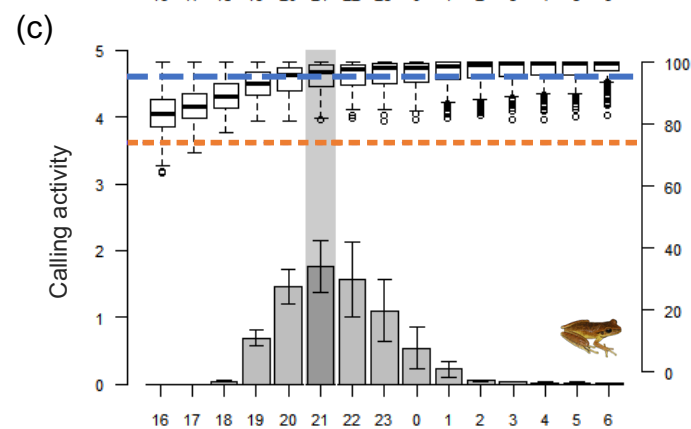
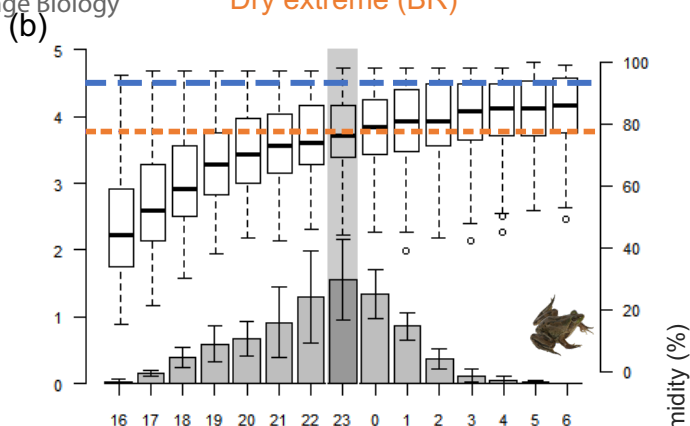
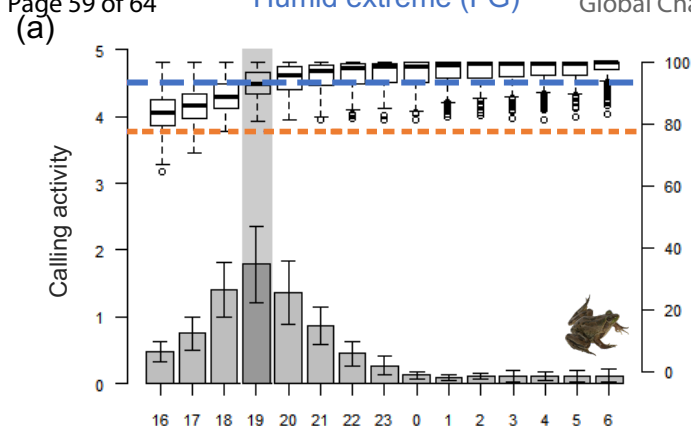
190x236mm (242 x 242 DPI)











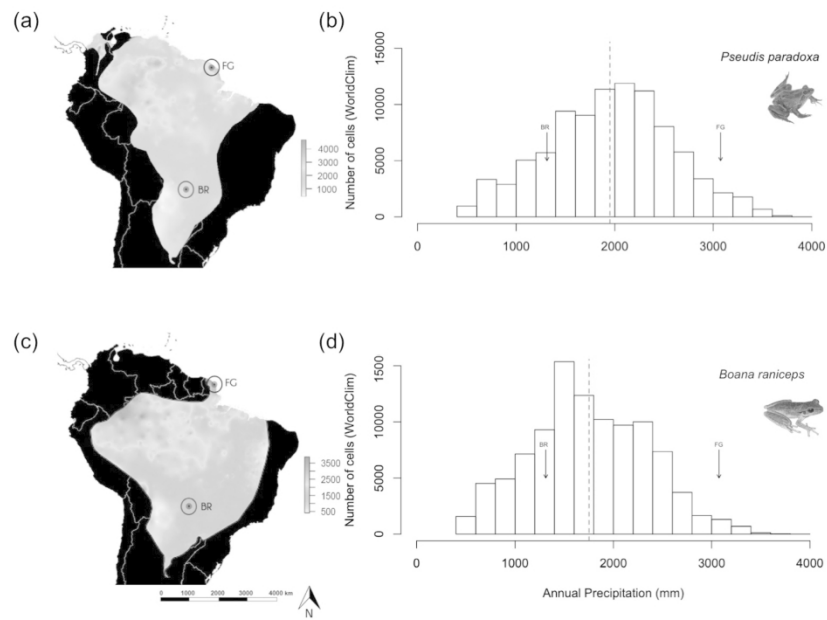


Fig. 1_b&w (JPEG)

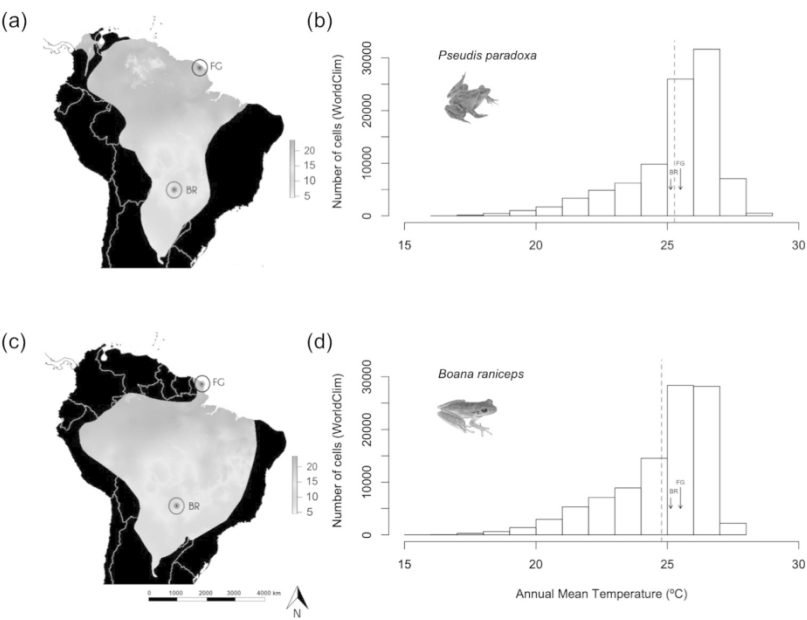


Fig. 2_b&w (JPEG)



Fig. 3_b&w (JPEG)

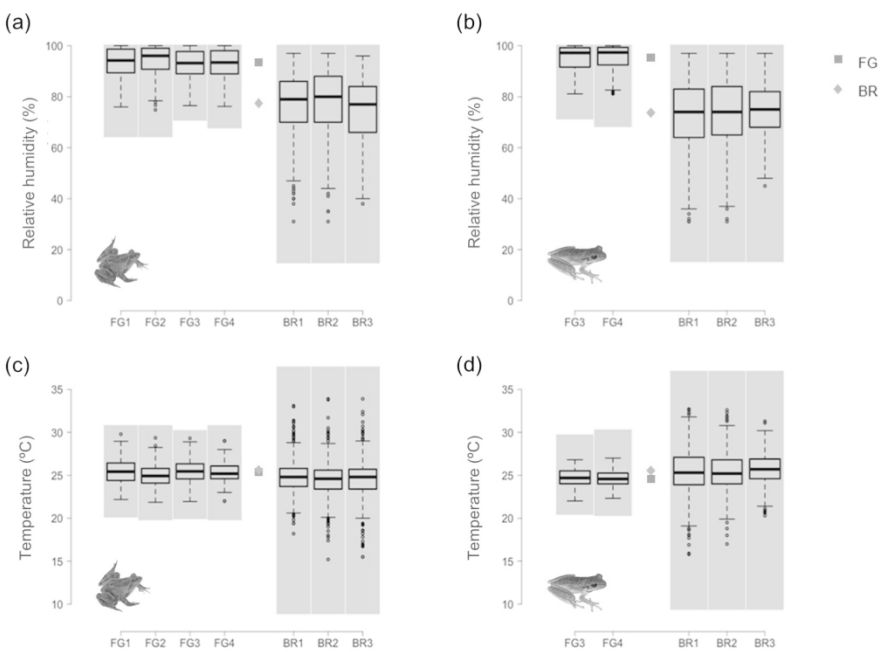


Fig. 4_b&w (JPEG)

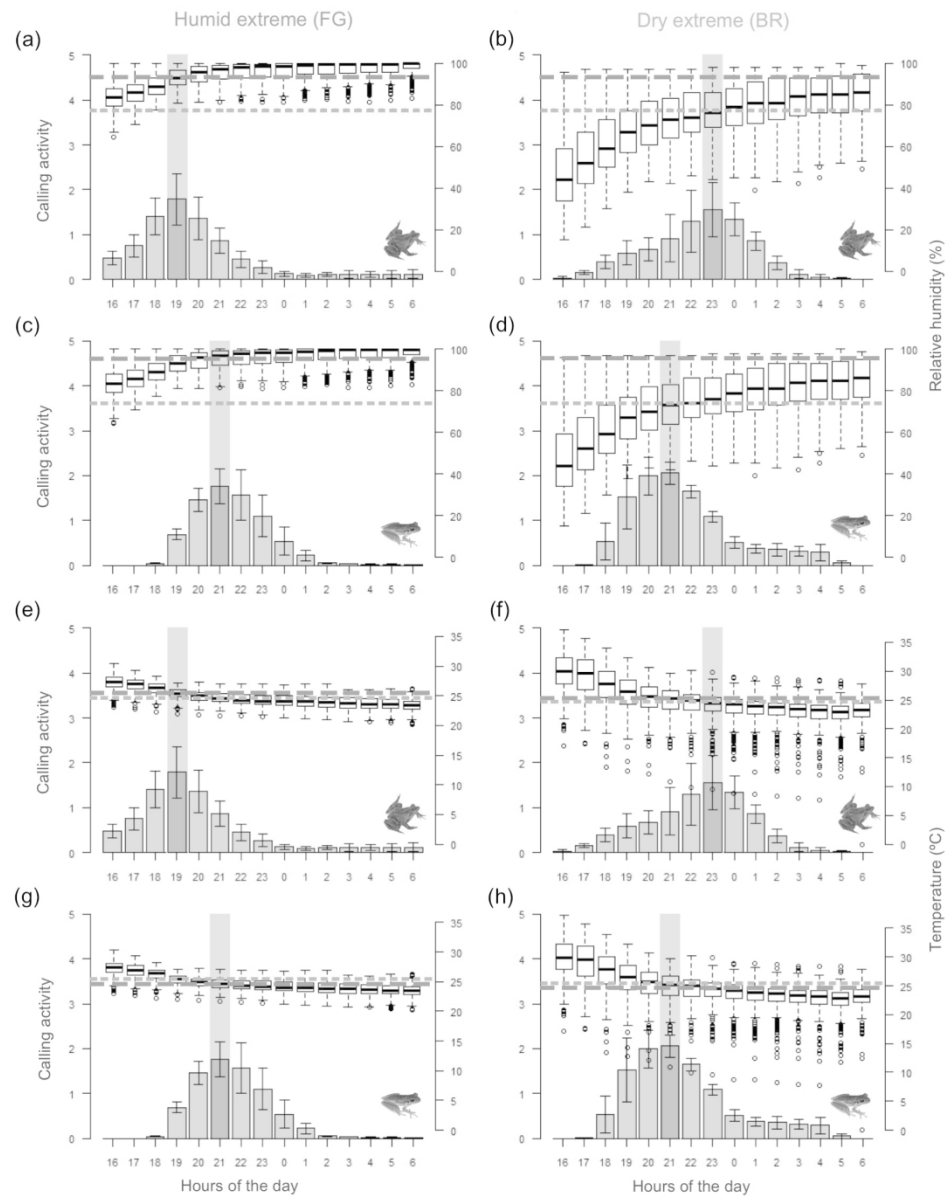


Fig. 5_b&w (JPEG)