

# Local-scale Seasonality Shapes Anuran Community Abundance in a Cloud Forest of the Tropical Andes

Pedro M. Villa<sup>1,\*</sup>, Antonio J. Pérez-Sánchez<sup>2,\*</sup>, Francisco Nava<sup>3</sup>, Aldemar Acevedo<sup>4</sup>, and Diego A. Cadenas<sup>5</sup>

<sup>1</sup>Fundación para la Conservación de la Biodiversidad, Puerto Ayacucho, Amazonas, Venezuela. \*Correspondence: E-mail: villautana@gmail.com

<sup>2</sup>Thünen Institute of Biodiversity, Braunschweig, Germany. \*Correspondence: E-mail: antonio.perez@thuenen.de

<sup>3</sup>Laboratorio de Ecología Sensorial, Centro Multidisciplinario de Ciencias, Instituto Venezolano de Investigaciones Científicas, Mérida, Venezuela

<sup>4</sup>Laboratorio de Biología Evolutiva, Pontificia Universidad Católica de Chile, Santiago, Chile

<sup>5</sup>Instituto de Ciencias, Ambientales y Ecológicas, Universidad de Los Andes, 5101, Mérida, Venezuela

Received 18 November 2018 / Accepted 5 June 2019 / Published 17 July 2019  
Communicated by Yeong-choy Kam

Analysing how seasonality shapes abundance patterns fosters understanding of the processes related to amphibian community assemblies. In this study we analyse the relationship between local seasonal patterns of abundance within the anuran community of the Monte Zepa Cloud Forest, Mérida Mountain Range (Cordillera de Mérida), in the Venezuelan Andes. We hypothesized that variation in precipitation, temperature, and relative humidity affects the temporal abundance patterns of anurans. Data collection was performed through nocturnal biweekly inspections from 2002 to 2003. Air temperature, relative humidity, and monthly precipitation were considered as variables of climatic seasonality. Generalized linear models were used to evaluate the effect of climatic variables on anuran abundance across seasons. Overall, 542 individuals and four anuran species were recorded in stream tributaries only. The local anuran community was comprised of *Hyalinobatrachium durantei*, *Hyloscirtus platydactylus*, *Hyloscirtus jahni*, and *Pristimantis vanadisae*. The most abundant species were *H. durantei* (288 individuals) and *H. platydactylus* (145 individuals), representing 53% and 27% of the total anuran abundance, respectively. Differences in abundance between species were observed. Although the total abundance of anurans was higher during the low precipitation season, no significant differences between the two seasons were detected. The variation in anuran abundance was explained by relative humidity and temperature. Our results suggest that the highest abundance of anurans can be expected when temperatures reach favourable levels (15–17°C), relative humidity increases, and precipitation remains constant.

**Key words:** Anuran assemblages, Centrolenidae, Cordillera de Mérida, Craugastoridae, Hylidae, Hydroperiod.

## BACKGROUND

Understanding how species richness, composition, and abundance patterns respond to different environmental drivers has been fundamental to the analysis of processes related to amphibian community assemblies (Duellman and Trueb 1994; Santos-Pereira

et al. 2011; Ficetola and Maiorano 2016). Fluctuations in the abundance of amphibians have also been considered a key indicator of environmental variability (Duellman and Trueb 1994; Alford and Richards 1999; Buckley et al. 2012). Such variations have proven to be relevant to the evaluation of anthropogenic impacts on modified landscapes and the prediction

of climate change scenarios (Cole et al. 2014; While and Uller 2014; Almeida-Gomes et al. 2015; Pacifici et al. 2015), especially tropics, some amphibian populations have declined and gone extinct (Pounds et al. 1999; Stuart et al. 2004; Menéndez-Guerrero and Graham 2013). In addition, monitoring of amphibian abundance has been fundamental in establishing a reference for wildlife conservation criteria (Young et al. 2001; Wiens 2016). Besides, spatial and temporal variations in species abundance strongly determine the amphibian communities' structure (Duellman and Trueb 1994; Marsh 2001). Studies have shown that amphibian abundance patterns can change over time due to multiple climatic factors; for example, changes in precipitation and temperature (Pounds et al. 1999; Stuart et al. 2004; Menin et al. 2011; Pacifici et al. 2015). For this reason, identification of those factors that regulate temporal variation in amphibian abundance remains necessary in order to understand the processes that govern species diversity and overall abundance in this critical group, and thereby to establish appropriate levels of conservation for the ecosystems they occupy.

Abiotic variables such as temperature, precipitation, and relative humidity are considered the critical climatic variables shaping abundance patterns along environmental gradients (Pounds et al. 1999; Ficetola and Maiorano 2016). Despite the high degree of covariation between environmental variables, it is possible that each of them influences anuran abundance at the local scale in different ways (Brooke et al. 2000). However, the amphibian environment relationship has generally been evaluated using temperature and precipitation, or their simultaneous effect, as the main determinants of abundance (Alexander and Eischeid 2001; Saenz et al. 2006; Pacifici et al. 2015). Furthermore, it has been demonstrated that abrupt changes in temperature and humidity have a remarkable influence on the decrease in abundance of amphibians in different habitats (Pounds and Crump 1994; Pacifici et al. 2015), mainly because temperature and water play an essential role in the biological cycles of these vertebrates (Carey et al. 2001; Buckley et al. 2012; Ficetola and Maiorano 2016; Barbosa et al. 2017).

The Andes is considered as a hotspot for conservation with high biological diversity and high endemism levels per unit area (Myers et al. 2000). Moreover, the mountainous regions of the tropical Andes and Central America have a high risk of species loss and constitute a focal zone for studies regarding the dynamics and processes of amphibian communities (Myers et al. 2000; Hutter et al. 2017). In fact, most of the amphibian species with declining populations are located in Andean regions (Lips et al. 2005 2008). In Venezuela, most of the species suffering critical

population decline are found in Mérida Mountain Range (Cordillera de Mérida) and Coast Mountain Range (Cordillera de La Costa), where anuran species such as *Atelopus carbonerensis*, *A. pinangoi*, and *A. sorianoi* seem to have reached the brink of extinction over the last two decades (La Marca et al. 2005). In general, the anuran species found in the Mérida Mountain Range have a restricted distribution, which increases their vulnerability to extinction (La Marca et al. 2005). To date, most of the research developed in the region has been focused on taxonomic reports, habitat descriptions, and the impact of chytridiomycosis disease (La Marca 1992, Piñero and Durant 1993, Sánchez et al. 2008, Cadenas et al. 2019). Against this background, further research based on small-scale and temporal analysis (*i.e.*, local seasonal and inter-annual) of the variability in amphibian populations is necessary in these ecosystems susceptible to global climate change.

Tropical montane cloud forests represent the main habitats for amphibians along Mérida Mountain Range (La Marca 1992). These ecosystems are characterized by a high cloudiness, high humidity, and low temperatures without dry months in terms of precipitation, which confers to them high climatic stability (Ataroff and Sarmiento 2004, Bruijnzeel et al. 2010). However, such climatic stability for ectothermic species (*i.e.*, amphibians) may depend on local seasonality. Herein, we aimed to assess how local-scale seasonality, namely on precipitation, temperature and humidity, affect anuran community abundance in Monte Zepa Cloud Forest of Mérida Mountain Range (Venezuelan Andes). Since changes in climatic variables are often hypothesized to influence variation in anuran community abundance (Pacifici et al. 2015; Ficetola and Maiorano 2016), it would be expected that local anuran communities show a temporal variation associated with local seasonality. Based on this anuran community–local climate relationship hypothesis, we tested whether seasonal variation in climatic variables promotes changes in species composition and abundance within the anuran community. Herein, we address the following questions: i) Is there a temporal pattern within the anuran abundance? ii) Does local seasonality shapes the anuran abundance? and iii) What are the main effects of climatic variables on anuran abundance?

## MATERIALS AND METHODS

### Study area

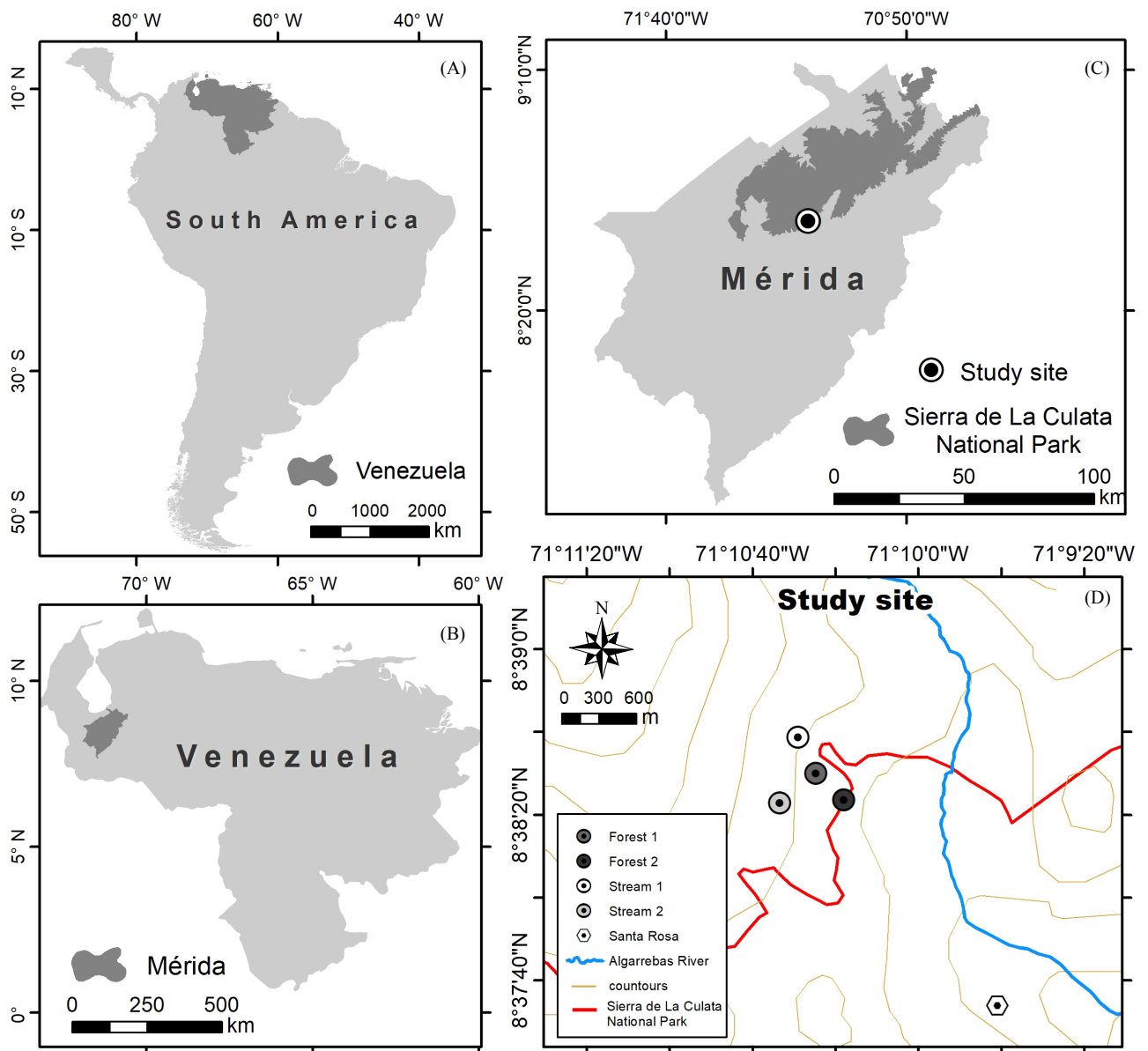
The study was performed in the area of Monte Zepa, in the municipality of Libertador, Mérida State, Venezuela (Fig. 1). The Monte Zepa Cloud Forest is

located at the Sierra de La Culata National Park border and includes the sub-basins of Alto Albarregas and Milla (Fig. 1). The vegetation and environmental conditions are characteristic of tropical mountain cloud forests (Piñero and Durant 1993; Cadenas et al. 2009). Climate is characterized by a bimodal pattern of precipitation (Fig. S1, Appendix in Electronic Supplementary Material, ESM hereafter) with two defined low precipitation seasons (December–March and June–August) and two high precipitation seasons (April–May and September–November; Piñero and Durant 1993; Cadenas et al. 2009). Mean annual precipitation is 2125 mm, mean annual temperature is 16°C, and

relative humidity is about 85% all year (Cadenas et al. 2009).

**Data collection**

Data collection was limited to four fixed 500 m long transects distributed within two stream tributaries of the Albarregas River and two forest areas, each at ≈ 2100 m high (Fig. 1). Anuran sampling was performed by biweekly nocturnal inspections from November 2002 to November 2003. Each session consisted of eight hours of active search using headlamps from before sunset to midnight (17:00-24:00 h). Anuran abundance



**Fig. 1.** Geographic location of the study area in relation to South America (A), Venezuela (B), Mérida State (C), and the Monte Zerpa Cloud Forest (D). Points indicate sampled areas.

per species was determined by conventional visual encounter sampling methods (Lips et al. 2001). Three people searched for individuals along the entire transect using a constant pace and spatially aligned up to five meters from the transect core (*i.e.*, 5 m perpendicularly from the stream channel or central line in a forested area). Visual encounter records were assisted by tracking acoustic encounters, but a compromise on the number recorded individuals was reached by the collectors *in situ* in order to avoid overcounting. The total sampling effort per transect for one night session was 24 hours of active search (3 people  $\times$  8 hours each), yielding a sampling effort of 576 hours over a year (2304 hours for the entire study area). Additionally, air temperature and relative humidity were recorded at each transect during each night session. Mean monthly precipitation records were obtained from the Santa Rosa weather station, located 1 km from the study area (Fig. 1).

## Data analysis

All analyses were performed using the R platform (R Core Team 2018). Climate charts revealed the same distribution pattern of precipitation as reported in previous studies, with high and low precipitation seasons (see Cadenas et al. 2009). A principal components analysis (PCA) was used to assess variation in precipitation (Pp), air temperature (Temp), and relative humidity (RH) among sampling seasons. For that, all variables were centred and standardized. We also calculated Pearson correlations among the climate variables and the PCA ordination axes (Fig. S2 in Electronic Supplementary Material- ESM). The PCA was performed using the 'FactoMineR' package (Le et al. 2008). Patterns in species composition were explored using the Principal Coordinates Analysis (PCoA) based on the original abundance sampled per month. Species data were standardized by marginal rows and column totals, and a similarity measure based on Bray-Curtis was used. Betadisper function (PERMDISP, 9999 permutations) from vegan package was implemented in order to test potential differences in centroid groups and dispersion (measures of central tendency and variance in multivariate space) among the two seasons (Anderson 2006; Oksanen et al. 2018).

Overall, normality on anuran data was tested with the Shapiro-Wilk test and a Q-Q plot (Crawley 2012). Relative abundance was analysed following three approaches. First, a Kruskal-Wallis test with *a posteriori* Dunn's test was used to evaluate differences among the total abundance of species. Second, the mean abundance of the whole assemblage was compared between high and low precipitation seasons using a *t*-test for normally-distributed data. Third, the Mann-Whitney

*U* test for non-normal distributed data was used in order to evaluate the abundance variation of each separate species between seasons.

Generalized Linear Models (GLMs) were fitted following the parsimonious approach to explain the main effect of climatic variables on the total anuran abundance (community) and each species across seasons. Models were fitted using Poisson distribution family since the response variables were counts. The identity link was identified for each model through the normality confirmed by the Shapiro-Wilk test and Q-Q graph (Crawley 2013). Abundance of anurans (total and per species) was used the response variable, while precipitation, temperature, and humidity relative were used as continues explanatory variables. Based on PCA results the Spearman correlation coefficients analysis ( $r \geq 0.6$ ), only univariate models were fitted (Fig. S3). To assess the best models, we applied a multi model inference approach (Burnham and Anderson 2002) with the dredge function from the MuMIn package (Barton 2013), which gives all possible combinations of the explanatory variables included in the global model (Barton 2013). To determine which of these variables best explained the changes in abundance, we used an information theoretical approach based on the Akaike's Information Criterion with a correction for finite sample sizes (AICc) and model weights based on AICc (AICc<sub>w</sub>; Burnham and Anderson 2002). We defined the "best" model with the lowest AICc and those models with different AICc than the best model were fewer than four units ( $\Delta\text{AICc} < 4$ ; Burnham et al. 2011). GLMs were calculated and compared using the MASS package (Ripley et al. 2017). All graphical outputs were constructed using the ggplot2 package (Hadley 2015).

## RESULTS

Overall, 542 individuals and four anuran species were recorded in the study area. The local community was comprised of *Hyalinobatrachium durante* (Centrolenidae), *Hyloscirtus platydactylus* and *Hyloscirtus jahni* (Hylidae), and *Pristimantis vanadisae* (Craugastoridae) (Fig. 2). The species with highest abundance were *H. durante* (288 individuals) and *H. platydactylus* (145 individuals), representing 53% and 27% of the total anuran abundance, respectively. *P. vanadisae* (7%, 39 individuals) was the only rare species within the assemblage.

Principal components analysis showed a pronounced separation between precipitation seasons, with more than 90% of the climatic variation explained by the first two principal components (Fig. 3A). The first axis (PCA1) explained 65.4% of the variation in



climate data and was positively correlated with relative humidity ( $R = 0.93$ ,  $p < 0.05$ ) and precipitation ( $R = 0.79$ ,  $p < 0.05$ ), but negatively with temperature ( $R = -0.58$ ,  $p < 0.05$ ). The second axis (PCA2) explained 27.6% of the variation in climate data and was mainly correlated with temperature ( $R = -0.80$ ,  $p < 0.05$ ). Overall, climatic variation between seasons is explained by precipitation. Similarly, the PCoA ordination showed a strong clustering of the temporal sampling (months) into both precipitation seasons based on species composition and abundance (Fig. 3B). In this analysis, the first two axes explain the 67% of the total variance in the composition data, but only the first axis captured seasonality. According to this, most of the sample points from the low precipitation season are clustered together in the multidimensional space with less distance from the centroid in comparison with the high precipitation season sample points, which had a more disperse pattern (Fig. 3B). Significant differences between the two ordination groups were detected (PERMDISP,  $F_{1,11} = 3.4$ ;  $p = 0.01$ ).

Differences were observed in the total abundance among anuran species (Fig. 4A;  $\chi^2 = 22.42$ ,  $d.f. = 3$ ,  $p = 0.001$ ). Although the total abundance of anurans

(at the community level) was higher during the low precipitation season, no statistical differences between the two seasons were detected (Fig. 4B;  $t = 1.13$ ,  $d.f. = 7.9$ ,  $p = 0.28$ ). At the species level, only *H. platydactylus* abundance varied significantly between seasons (Fig. 3C;  $W = 2$ ,  $p = 0.01$ ); no significant variation between seasons was observed in the relative abundance of *H. durantei* ( $W = 12$ ,  $p = 0.37$ ), *H. jahni* ( $W = 5$ ,  $p = 0.10$ ), or *P. vanadisae* ( $W = 28$ ,  $p = 0.12$ ; Fig. 4C).

Models including a single climatic variable consistently explained more variation in the anuran abundance (Table 1). Overall, our GLM suggested that total anuran abundance (community level) was affected mainly by precipitation (Table 1). According to the best specific models fitted at species level, the variation in *H. durantei* abundance was positively explained by relative humidity (GLM:  $z = 0.29$ ,  $p < 0.001$ ) and negatively with temperature (GLM:  $z = -0.11$ ,  $p < 0.05$ ). Conversely, *P. vanadisae* abundance presented a significant negative relation with precipitation and temperature (Table 1). No significant changes were detected in *H. jahni* or *H. platydactylus* abundance regarding climatic variables (Table 1, Fig. 5).

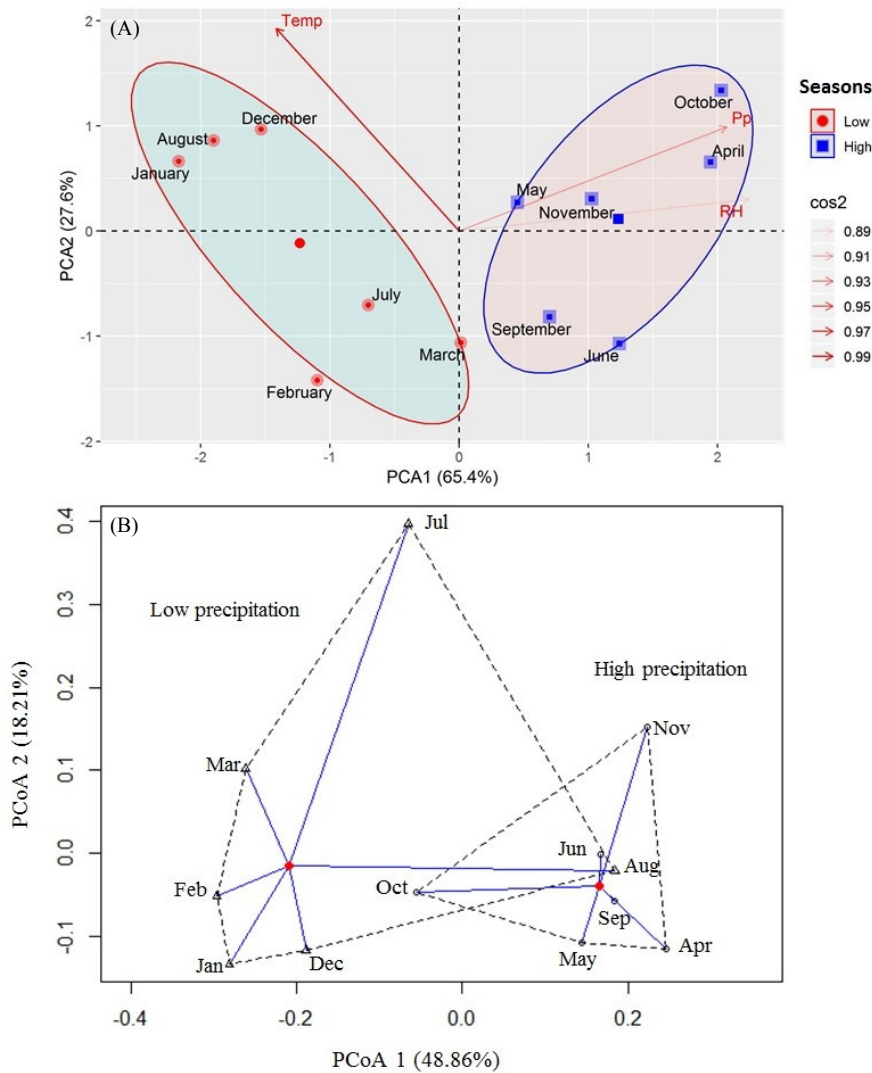


**Fig. 2.** Anuran species recorded in the Monte Zerpa Cloud Forest. *Hyalinobatrachium durantei* (A), *Hyloscirtus platydactylus* (B), *Hyloscirtus jahni* (C), and *Pristimantis vanadisae* (D). Photos: Francisco Nava (A, C, D) and Pascual Soriano (B).

**DISCUSSION**

Temperature and relative humidity are fundamental factors governing the amphibian life cycle (Duellman and Trueb 1994; Marsh 2001; Alexander and Eischeid 2001). Still, it is not entirely clear how climatic factors influence important parameters at the population level, such as abundance at a local scale (Blaustein et al. 2010; Ficetola and Maiorano 2016). Our results showed that changes in total anuran abundance within the Monte Zerpa Cloud Forest were strongly influenced by seasonal variations in precipitation, although the effect of these variables varies among species. These results are in accordance with the pattern reported by Ficetola and Maiorano (2016), where the effect of

precipitation on species abundance is stronger than the effect of temperature in tropical ecosystems. These authors revealed that, while phenological changes are mostly linked to temperature changes, population dynamics are most strongly determined by the variation in precipitation. However, seasonality variation on climate is not the only direct cause of drastic changes in anuran abundances (Duellman and Trueb 1994; Carey et al. 2001; Ochoa-Ochoa and Whittaker 2014), and the indirect effect of multiple widely-studied drivers (*e.g.*, resource availability, pathogenic disease) could also have a strong influence on anuran population dynamics at different scales (Blaustein and Kiesecker 2002; Gottsberger and Gruber 2004; Cortés et al. 2008; Lampo et al. 2008; Cole et al. 2014; Bower et al. 2017). This

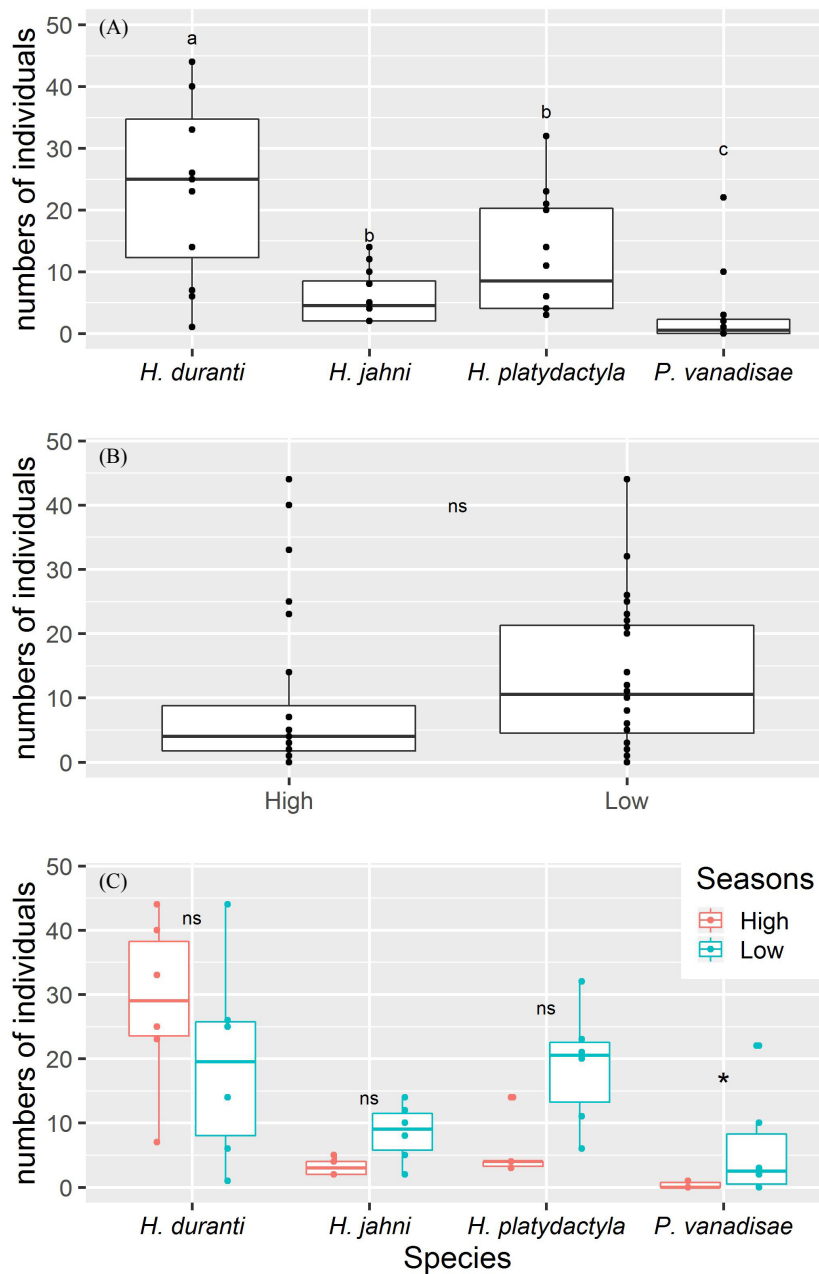


**Fig. 3.** Seasonal climatic and anuran variation among sampling sessions. (A) Principal Component Analysis (PCA) for all individual climate variables measured in 24 sampling sessions. The analysis included precipitation (Pp), relative humidity (RH) and air temperature (Temp). The level of Pearson correlation of each vector is indicated (cos2). (B) Principal Coordinate Analysis (PCoA) for the anuran assemblage based on species composition and abundance during the high and low precipitation seasons. The centroid points represent the average precipitation each month.

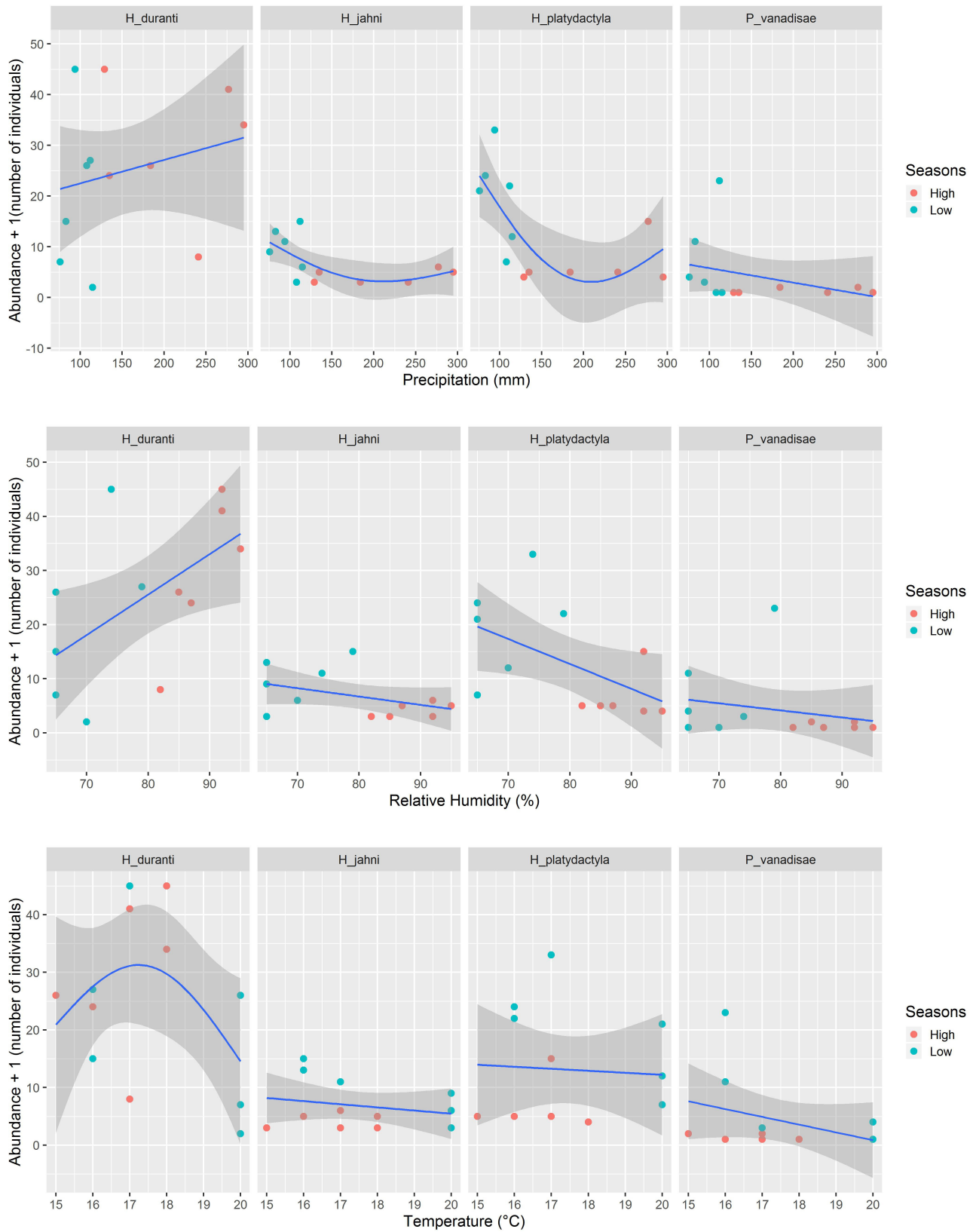
highlights the importance of identifying individuals and joint effects of climatic variables on the amphibian's abundance at the local scale before analysing density-dependent processes.

Our results suggest that seasonally climatic variables promote changes in total and species abundance within the anuran community. However, the sampling techniques used in our investigation (transects along the streams) resulted in the highest

representativeness of species in the low precipitation season, when anurans may be aggregated in the surrounding streams. This increased abundance pattern during the low precipitation season has previously been reported in tropical anuran assemblages, generally associated with their use of water sources for reproduction (e.g., Santos-Pereira et al. 2011; Rodríguez-Mendoza and Pineda 2010), regulation of body temperature (Navas et al. 2013), and calling



**Fig. 4.** Abundance variation of anurans in the Monte Zerpa Cloud Forest. Differences in overall abundances among species (A), total anuran abundance between precipitation seasons (B), abundances by species between seasons (C) are presented. Letters indicate significant differences among groups according to *post hoc* tests ( $p < 0.05$ ), while ns indicates non-significant differences between samples.



**Fig. 5.** Relationship between species abundance and climatic predictors according to the generalized linear models. Solid lines represent the fitted values (prediction) of the models, and the shaded area shows the 95% confidence interval of the predicted values of each model. Colour-code points indicate data by precipitation season (low and high).

activity (Steen et al. 2013). In this sense, this result may be explained by such species aggregation in the streams peripheries as a consequence of a favourable microclimate. Water might be a limiting factor during low precipitation season, and it could be expected that anurans move towards the streams to help them tolerate lower levels of relative humidity. Different studies have shown that riparian habitats are determinants of amphibian survival in tropical forests because many species maintain their life cycles closely linked to nearby water sources (Ficetola et al. 2009; Todd et al. 2009; Almeida-Gomes et al. 2015). However, some groups of neotropical amphibians, such as the Craugastoridae family, do not depend directly on waterbodies for reproduction, although optimal levels of relative humidity and temperature are essential for skin respiration (Duellman and Trueb 1994; von May et al. 2017). Thus, our results indicate that during the high precipitation season some species of the community such as *H. durantei*, maintained similar abundance levels while *P. vanadisae* abundance decreased considerably. This pattern suggests greater dispersion of anurans when there is higher relative humidity, which perhaps expedites mobility through the forest and allows the anuran's to occupy an extended vertical stratum (up

to 1.5 m, Barrio-Amorós et al. 2013), lessening direct dependence on the streams during this season.

The most abundant species found was *H. durantei*, whose relative abundance responded positively to higher precipitations and relative humidity, the reproductive mode of this species may explain the pattern detected. Like other species of Centrolenidae (e.g., *Centrolene savagei*, Vargas-Salinas et al. 2014), *H. durantei* lays eggs on the surface of plant leaves located over streams and the male protects the egg cluster until the eggs hatch (Duellman and Trueb 1994; Crump 2015). Relatively higher humidity and water inlets by horizontal precipitation may favour sexual encounters and therefore increase the overall abundance of *H. durantei* through seasons of higher precipitation in comparison to the relatively drier conditions obtaining during the low precipitation season (Duellman and Trueb 1994; Crump 2015). Conversely, *H. platydactylus* and *H. jahni* showed higher relative abundance during the low precipitation season. In this case, both species require streams to spawn and for tadpole development (La Marca 1985). The higher relative abundance observed during the low precipitation season may be a consequence of the weaker stream flow, which produces less disturbance for mating, oviposition, and

**Table 1.** Candidate generalized linear models predicting the effects of climatic variables on anuran abundance at community and species level (Family distribution: Poisson). The Akaike's Information Criterion corrected for small samples (AICc), difference AICc between one estimated AICc and the lowest AICc the best model ( $\Delta$ AICc), model weights (AICcwt) are presented. Only models with values of  $\Delta$ AICc < 4 are presented

Response variable (Abundance)	Candidate models	Estimate	z-value	LogLik	AICc	$\Delta$ AICc	AICcwt
Community level	~ Pp	-0.02	0.19**	-31.27	69.27	0	0.76
	~ HR	-0.03	0.04*	-33.28	71.89	2.61	0.21
	~ Temp	-0.10	0.25	-35.28	75.89	6.62	0.03
<i>H. durantei</i>	~ HR	0.39	0.001***	-71.30	147.92	0	0.90
	~ Temp	-0.11	0.02**	-83.33	171.99	24.06	0.09
	~ Pp	0.02	0.04*	-85.12	175.58	27.66	0.01
<i>H. platydactylus</i>	~ HR	-0.04	0.03	-39.22	87.43	0	0.55
	~ Pp	-0.01	0.07	-39.57	88.15	0.71	0.39
	~ Temp	-0.02	0.84	-41.47	91.50	4.50	0.06
<i>H. jahni</i>	~ Pp	-0.01	0.10	-30.23	69.47	0	0.53
	~ HR	-0.02	0.13	-30.67	70.34	0.87	0.34
	~ Temp	-0.09	0.46	-31.59	72.18	2.71	0.14
<i>P. vanadisae</i>	~ Pp	-0.01	0.001**	-47.82	100.97	0	0.61
	~ Temp	-0.54	0.02***	-48.27	101.87	0.90	0.38
	~ HR	-0.04	0.18*	-55.36	116.05	15.08	0.01

Predictors are: Relative humidity, HR; Temperature, Temp; Precipitation, Pp. The *p*-value of each predictor is given as: \**p* < 0.05; \*\**p* > 0.01; \*\*\**p* < 0.001.

development of the larvae. There is evidence for this pattern in other Neotropical species where a greater abundance has been observed when precipitation rates decreased (Watling and Donnelly 2002).

Precipitation and relative humidity determine anuran population dynamics and their distribution patterns (Ochoa-Ochoa and Whittaker 2014; Dabés et al. 2012; Ficetola and Maiorano 2016). For example, greater spatial dispersion of anuran species have been found in forest interiors that are distantly located from any water source based on acoustic surveys (Marsh 2001; Santos-Pereira et al. 2011). Such a spatial distribution pattern might lead to biased estimations of relative abundance that arose because the sampling techniques were restricted to water sources (e.g., streams, ponds). Although a similar situation can be applied to our study, acoustic sampling was a complementary tool in our surveys and sampling transects employed in our study were representative of both forest interiors and water streams habitats. In this sense, comparative studies on amphibian abundance between seasons should take into account the wide sampling effort and spatial distribution in addition to environmental variation (Lips et al. 2005). Furthermore, to analyse the effect of climatic variables on amphibian abundance, comparisons within years are recommended (i.e., seasonality) and not only inter-annual variability patterns although long-term monitoring efforts in the tropics are not always affordable in terms of economics or logistics (Alexander and Eischeid 2001; Ochoa-Ochoa and Whittaker 2014). On the other hand, some studies in leaf-litter frog communities (e.g., Brachycephalidae, Leptodactylidae, Leiuperidae, Craugastoridae families) have reported contrasting patterns where abundance is affected by temperature or its variation along elevational gradients rather than humidity (Santos-Pereira et al. 2011; Siqueira et al. 2014). In any case, abundance of anurans is strongly affected by relative humidity and precipitation in tropical forests with strong seasonality (Ficetola and Maiorano 2016), a pattern that has been previously observed in our study area with high values of amphibians abundance associated with streams during the low precipitation season (Cadenas et al. 2009).

We suggest that other environmental drivers (e.g., horizontal precipitation, stream flow dynamics), local spatial distribution, and fluctuations in anuran populations, and their potential interaction with pathogenic diseases (e.g., *Batrachochytrium dendrobatidis*), should also be considered when evaluating abundance patterns within and between anuran communities in the region. It should be noted that a negative relationship between *H. platydactylus* and *B. dendrobatidis* has been reported in Venezuela (Lampo

et al. 2008; Sánchez et al. 2008), which should be further explored for in other amphibians with restricted distribution in the Venezuelan Andes. We emphasize that the species found in this study have a restricted geographic distribution in the Merida Mountain Range, except *H. platydactylus*, which is distributed along the Venezuelan Andes (Táchira, Mérida, Trujillo, and *H. durante* which has been detected about eight kilometres from Boconó, Trujillo State (La Marca 1992). The small-scale monitoring of anuran abundance fluctuation found in this study becomes more important since these species, with insufficient data about population levels, are threatened by extinction (La Marca et al. 2005; Sánchez et al. 2008). In addition, it should be noted that *P. vanadisae* and *H. jahni* are included in the category “near threatened”, while *H. platydactylus* has been catalogued as “vulnerable to extinction” (Sánchez et al. 2008). In contrast, the information required to define the conservation status of *H. durante* is limited, which highlights the importance of the results obtained in this study. Furthermore, it is important to mention that there are limited studies evaluating the relationship between local climatic drivers and species abundance within anuran communities in cloud forests of the Mérida mountain chain. Therefore, this research represents a relevant contribution which may act as a starting point to define short- and long-term monitoring plans and the development of conservation criteria in the region.

## CONCLUSIONS

Our study showed that local seasonally in terms monthly precipitation, temperature and relative humidity variations shape the temporal abundance pattern of anurans in the Monte Zerpa Cloud Forest. Total abundance of anurans communities vary between high and low precipitation seasons. However, each species may respond differently to variations in precipitation, temperature and relative humidity. During low precipitation season, the relative abundances are broadly similar between species, but higher overall; while during the high precipitation season, only species such as *H. durante* showed increased abundance. Models confirmed this pattern and indicated that *H. platydactylus* and *H. durante* are more sensitive to changes in relative humidity, while *H. jahni* and *P. vanadisae* are more sensitive to variations in precipitation.

**Acknowledgments:** We thank the Department of Animal Ecology, Faculty of Sciences, University of Los Andes; Pascual Soriano; and Enrique La Marca for their valuable comments and ideas on the early version of this article and project development. We also thank all



our colleagues for their voluntary support during data collection.

**Authors' contributions:** DC and FN designed the research approach. All authors performed the field work. PV and AP performed the statistical analyses. PV and AP contributed to drafting and revising the manuscript. All authors read, revised, and approved the final manuscript.

**Competing interests:** All authors declare that they have no conflict of interests regarding the publication of this paper.

**Availability of data and materials:** We do want to make our data available.

**Consent for publication:** Not applicable.

**Ethics approval consent to participate:** Not applicable. Data were collected in field work and with approval from the Los Andes University.

## REFERENCES

- Alexander MA, Eisechid JK. 2001. Climate variability in regions of amphibian declines. *Conserv Biol* **15**:930–942. doi:10.1046/j.1523-1739.2001.015004930.x.
- Alford RA, Richards SJ. 1999. Global Amphibian Declines: A problem in Applied Ecology. *Annu Rev Ecol Syst* **30**:133–165. doi:10.1146/annurev.ecolsys.30.1.133.
- Almeida-Gomes M, Duarte CF, Vieira MV. 2015. Anuran community composition along two large rivers in a tropical disturbed landscape. *Zoologia* **32**:9–13. doi:10.1590/S1984-46702015000100002.
- Anderson MJ. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* **62**:245–253. doi:10.1111/j.1541-0420.2005.00440.x.
- Ataroff M, Sarmiento L. 2004. Las unidades ecológicas de los Andes de Venezuela. In: La Marca E, Soriano P. eds. *Reptiles de Los Andes de Venezuela*. Fundación Polar, Codepre-ULA, Fundacite-Mérida, Biogeos, Mérida.
- Barbosa FG, Both C, Araújo MB. 2017. Invasive American bullfrogs and African clawed frogs in South America: high suitability of occurrence in biodiversity hotspots. *Zool Stud* **56**:28. doi:10.6620/ZS.2017.56-28.
- Barton K. 2013. MuMIn: multi-model inference. <http://CRAN.R-project.org/package=MuMIn>. Accessed 10 June 2018.
- Barrio-Amorós CL, Heinicke MP, Hedges SB. 2013. A new tuberculated *Pristimantis* Anura, Terrarana, Strabomantidae from the Venezuelan Andes, redescription of *Pristimantis pleurostriatus*, and variation within *Pristimantis vanadisae*. *Zootaxa* **3647**:43–62. doi:10.11646/zootaxa.3647.1.2.
- Bower DS, Lips KR, Schwarzkopf L, Georges A, Clulow S. 2017. Amphibians on the brink. *Science* **357**:454–455. doi:10.1126/science.aao0500.
- Buckley LB, Hurlbert AH, Jetz W. 2012. Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Glob Ecol Biogeogr* **21**:873–885. doi:10.1111/j.1466-8238.2011.00737.x.
- Burnham KP, Anderson DR. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. Springer, New York.
- Burnham KP, Anderson DR, Huyvaert KP. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav Ecol Sociobiol* **65**:23–35. doi:10.1007/s00265-010-1029-6.
- Blaustein AR, Kiesecker JM. 2002. Complexity in conservation: lessons from the global decline of amphibian populations. *Ecol Lett* **5**:597–608. doi:10.1046/j.1461-0248.2002.00352.x.
- Blaustein AR, Walls SC, Bancroft BA, Lawler JJ, Searle CL, Gervasi SS. 2010. Direct and indirect effects of climate change on amphibian populations. *Diversity* **2**:281–313. doi:10.3390/d2020281.
- Brooke PN, Alford RA, Schwarzkopf L. 2000. Environmental and social factors influence chorusing behavior in a tropical frog: examining various temporal and spatial scales. *Behav Ecol Soc* **49**:79–87. doi:10.1007/s002650000256.
- Bruijnzeel LA, Kappelle M, Mulligan M, Scatena FN. 2010. Tropical montane cloud forests: state of knowledge and sustainability perspectives in a changing world. In: Bruijnzeel LA, Scatena F.N., Hamilton, L.S. eds. *Tropical Montane Cloud Forests*. Science for Conservation and Management, Cambridge University Press: Cambridge, UK, pp. 691–740.
- Cadenas DA, Pérez-Sánchez AJ, Villa PM, De Ascensão A. 2009. Abundancia relativa, uso del hábitat y dieta de *Bolitoglossa orestes* Urodela: Plethodontidae en una Selva Nublada Andina Venezolana. *Ecotropicos* **22**:99–109.
- Carey C, Heyer R, Wilkinson J. 2001. Amphibians declines and environmental change: Use of remote-Sensing Data to Identify Environmental Correlates. *Conserv Biol* **15**:903–913. doi:10.1046/j.1523-1739.2001.015004903.x.
- Cole EM, Bustamante MR, Almeida-Reinoso D, Funk WC. 2014. Spatial and temporal variation in population dynamics of Andean frogs: Effects of forest disturbance and evidence for declines. *Glob Ecol Conserv* **1**:60–70. doi:10.1016/j.gecco.2014.06.002.
- Cortés AM, Ramírez-Pinilla MP, Suárez HA, Tovar E. 2008. Edge effects on richness, abundance and diversity of frogs in Andean cloud forest fragments. *S Am J Herpetol* **3**:213–222. doi:10.2994/1808-9798-3.3.213.
- Crawley MJ. 2013. *The R Book*, second ed. Wiley, London.
- Crump ML. 2015. Anuran Reproductive Modes: Evolving Perspectives. *J Herpetol* **49**:1–16. doi:10.1670/14-097.
- Dabés L, Bonfim VM, Napoli MF, Klein W. 2012. Water balance and spatial distribution of an anuran community from Brazil. *Herpetologica* **68**:443–455. doi:10.1655/HERPETOLOGICA-D-10-00058.
- Duellman WE, Trueb L. 1994. *Biology of Amphibians*. New York, McGraw-Hill, 670 p.
- Ficetola GF, Maiorano L. 2016. Contrasting effects of temperature and precipitation change on amphibian phenology, abundance and performance. *Oecologia* **3**:673–683. doi:10.1007/s00442-016-3610-9.
- Ficetola GF, Padoa-Schioppa E, Bernardi F. 2009. Influence of landscape elements in riparian buffers on the conservation of semiaquatic amphibians. *Conserv Biol* **23**:114–123. doi:10.1111/j.1523-1739.2008.01081.x.
- Gottsberger B, Gruber E. 2004. Temporal partitioning of reproductive activity in a Neotropical anuran community. *J Trop Ecol* **20**:271–280. doi:10.1017/S0266467403001172.
- Hadley W. 2015. R ggplot2 package: an implementation of the grammar of graphics. Available at <http://ggplot2.org>, <https://>



- github.com/hadley/ggplot2. Accessed 10 June 2018.
- Hutter CR, Lambert SM, Wiens JJ. 2017. Rapid Diversification and Time Explain Amphibian Richness at Different Scales in the Tropical Andes, Earth's Most Biodiverse Hotspot. *Am Nat* **6**:828–843. doi:10.1086/694319.
- La Marca E. 1985. Systematics and ecological observations on the Neotropical frogs *Hyla jahnii* and *Hyla platydactyla*. *J Herpet* **19**:227–237.
- La Marca E. 1992. Catálogo taxonómico, biogeográfico y bibliográfico de las ranas de Venezuela. Universidad de los Andes, Mérida.
- La Marca, E Lips, KR Lötters S, Puschendorf R, Ibáñez R, Rueda-Almonacid JV, Schulte R, Marty C, Castro F, Manzanilla-Puppo J, García-Pérez JE, Bolaños F, Chaves G, Pounds JA, Toral E, Young BE. 2005. Catastrophic Population Declines and Extinctions in Neotropical Harlequin Frogs Bufonidae: Atelopus. *Biotropica* **37**:190–201. doi:10.1111/j.1744-7429.2005.00026.x.
- Lampo MA, Sánchez DI, Nicolás AN, Márquez MA, Nava-González FR, García CZ, Rinaldi MI, Rodríguez-Contreras AR, León F, Han BA, Chacón-Ortiz AN. 2008. *Batrachochytrium dendrobatidis* in Venezuela. *Herpet Rev* **39**:449.
- Le S, Josse J, Husson F. 2008. FactoMineR: An R Package for Multivariate Analysis. *J Statist Soft* **25**:1–18. doi:10.18637/jss.v025.i01.
- Lips KR, Reaser JK, Young BE, Ibañez R. 2001. Amphibian monitoring in Latin America: a protocol manual/Monitoreo de Anfíbios en América Latina: Manual de protocolos. SSAR Herpetological Circular **30**:1–11.
- Lips KR, Burrowes P, Mendelson J, Parra-Olea G. 2005. Amphibian declines in Latin America: widespread population decline, extinctions, and impacts. *Biotropica* **37**:163–165. doi:10.1111/j.1744-7429.2005.00023.x.
- Lips KR, Diffendorfer J, Mendelson J, Sears MW. 2008. Riding the wave: Reconciling the roles of disease and climate change in Amphibian declines. *PLoS Biol* **6**:441–453. doi:10.1371/journal.pbio.0060072.
- Marsh DM. 2001. Fluctuations in amphibian populations: a meta-analysis. *Biol Conserv* **101**:327–335. doi:10.1016/S0006-3207(01)00076-3.
- Menéndez-Guerrero PA, Graham CH. 2013. Evaluating multiple causes of amphibian declines of Ecuador using geographical quantitative analyses. *Ecography* **36**:756–769. doi:10.1111/j.1600-0587.2012.07877.x.
- Menin M, Waldez F, Lima AP. 2011. Effects of environmental and spatial factors on the distribution of anuran species with aquatic reproduction in central Amazonia. *Herpet J* **21**:255–261.
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**:853–858. doi:10.1038/35002501.
- Navas CA, Carvajalino-Fernández JM, Saboyá-Acosta LP, Rueda-Solano LA, Carvajalino-Fernández MA. 2013. The body temperature of active amphibians along a tropical elevation gradient: patterns of mean and variance and inference from environmental data. *Funct Ecol* **27**:1145–1154. doi:10.1111/1365-2435.12106.
- Ochoa-Ochoa LM, Whittaker RJ. 2014. Spatial and temporal variation in amphibian metacommunity structure in Chiapas, Mexico. *J Trop Ecol* **30**:537–549. doi:10.1017/S0266467414000388.
- Oksanen J, Blanchet JG, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens HH, Szoecs E, Wagner H. 2018. *vegan*: Community Ecology Package. R package version 2.5-2. <https://CRAN.R-project.org/package=vegan>. Accessed 10 June 2018.
- Pacifici M, Foden WB, Visconti P, Watson JE, Butchart SH, Kovacs KM, Scheffers BR, Hole DG, Martin TG, Akçakaya HR, Corlett RT, Huntley B, Bickford D, Carr JA, Hoffmann AA, Midgley GF, Pearce-Kelly P, Pearson RG, Williams SE, Willis SG, Young B, Rondinini C. 2015. Assessing species vulnerability to climate change. *Nat Clim Change* **5**:215–224. doi:10.1038/nclimate2448.
- Piñero B, Durant P. 1993. Dieta y hábitat de una comunidad de anuros de selva nublada en los Andes meridionales. *Ecotropicos* **62**:1–9.
- Pounds JA, Crump ML. 1994. Amphibians declines and climate disturbance: the case the golden toad and the harlequin frog. *Conserv Biol* **8**:72–85.
- Pounds JA, Fogden L, Campbell J. 1999. Biological response to climate change on a tropical mountain. *Nature* **398**:611–615. doi:10.1038/19297.
- R Core Team. 2018. R: A language and environment for statistical computing R Foundation for Statistical Computing, Vienna, Austria. Available <https://www.r-project.org/>. Accessed 10 June 2018.
- Ripley B, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D. 2017. R Package 'MASS'. Available: <http://cran.r-project.org/web/packages/MASS/MASS.pdf>. Accessed 10 June 2018.
- Rodríguez-Mendoza C, Pineda E. 2010. Importance of riparian remnants for frog species diversity in a highly fragmented rainforest. *Biol Let* **6**:781–784. doi:10.1098/rsbl.2010.0334.
- Sánchez D, Chacón-Ortiz A, León F, Han B, Lampo M. 2008. Widespread occurrence of an emerging pathogen in amphibian communities of the Venezuelan Andes. *Biol Conserv* **141**:2898–2905. doi:10.1016/j.biocon.2008.08.009.
- Saenz D, Fitzgerald L, Baum K, Conner R. 2006. Abiotic Correlates of Anuran Calling Phenology: The Importance of Rain, Temperature, and Season. *Herpet Monog* **20**:64–82. doi:10.1655/0733-1347(2007)20[64:ACOACP]2.0.CO;2.
- Santos-Pereira M, Candaten A, Milani D, Oliveira FB, Gardelin JD, Rocha CF. 2011. Seasonal variation in the leaf-litter frog community Amphibia: Anura from an Atlantic Forest Area in the Salto Morato Natural Reserve, southern Brazil. *Zoologia* **28**:755–761. doi:10.1590/S1984-46702011000600008.
- Siqueira CC, Vrcibradic D, Nogueira-Costa P, Martins AR, Dantas L, Gomes V, Bergallo HGD, Rocha CF. 2014. Environmental parameters affecting the structure of leaf-litter frog Amphibia: Anura communities in tropical forests: A case study from an Atlantic Rainforest area in southeastern Brazil. *Zoologia* **31**:147–152. doi:10.1590/S1984-46702014000200005.
- Steen DA, McClure CJ, Graham SP. 2013. Relative influence of weather and season on anuran calling activity. *Can J Zool* **91**:462–467. doi:10.1139/cjz-2012-0266.
- Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Fischman DL, Waller RW. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* **306**:1783–1786. doi:10.1126/science.1103538.
- Todd BD, Luhring TM, Rothermel BB, Gibbons W. 2009. Effects of forest removal on amphibian migrations: implications for habitat and landscape connectivity. *J Appl Ecol* **46**:554–561. doi:10.1111/j.1365-2664.2009.01645.x.
- Vargas-Salinas F, Quintero-Ángel A, Osorio-Domínguez D, Rojas-Morales JA, Escobar-Lasso S, Gutiérrez-Cárdenas PDA, Amézquita A. 2014. Breeding and parental behaviour in the glass frog *Centrolene savagei* Anura: Centrolenidae. *J Nat Hist* **48**:1689–1705. doi:10.1080/00222933.2013.840942.
- von May R, Catenazzi A, Corl A, Santa-Cruz R, Carnaval AC, Moritz C. 2017. Divergence of thermal physiological traits in terrestrial breeding frogs along a tropical elevational gradient. *Ecol Evol* **7**:3257–3267. doi:10.1002/ece3.2929.
- Watling JI, Donnelly MA. 2002. Seasonal patterns of reproduction and abundance of leaf litter frogs in a Central American rainforest. *J Zool* **258**:269–276. doi:10.1017/S0952836902001371.

- Wiens JJ. 2016. Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species. *PLoS Biol* **14**:e2001104. doi:10.1371/journal.pbio.2001104.
- While GM, Uller T. 2014. Quo vadis amphibia? Global warming and breeding phenology in frogs, toads and salamanders. *Ecography* **37**:921–929. doi:10.1111/ecog.00521.
- Young B, Lips K, Reaser J, Ibañez R, Salas A, Cedeño R, Coloma L, Ron A, La Marca E, Meyer J, Muñoz A, Bolaños F, Chaves G, Romo D. 2001. Population declines and priorities for amphibian conservation in Latin America. *Conserv Biol* **15**:1213–1223. doi:10.1111/j.1523-1739.2001.00218.x.

## Supplementary materials

**Table S1.** Number of individuals of anuran species recorded during different precipitation seasons (low and high seasons) through visual encounter surveys in Monte Zerp Cloud Forest, Mérida Venezuela. Species: *Hyloscirtus platydactylus*, H pla; *Hyloscirtus jahni*, H jah; *Pristimantis vanadisae*, P van; and *Hyalinobatrachium durante*, H dur. Mean values of climatic variables are indicated: Stream flow, Q (cm<sup>3</sup>/s); relative humidity, HR (%); temperature, Temp (°C); and precipitation, Pp (mm). (download)

**Fig. S1.** Climate chart of the Monte Zerp Cloud Forest during the survey period (2002–2003). (download)

**Fig. S2.** Significance levels are based on Pearson correlation coefficients between climate variables and principal components of PCA from 24 sampling sessions. For analysis, precipitation (Pp), relative humidity (RH) and air temperature (Temp) were included. (download)

**Fig. S3.** Pearson correlation among all individual variables measured in 24 sampling session. For analysis, precipitation (Pp), relative humidity (RH) and air temperature (Temp) were included. (download)