

PONTIFICIA UNIVERSIDAD CATÓLICA DE CHILE Facultad de Ciencias Biológicas Programa de Doctorado en Ciencias Biológicas Mención Ecología

TESIS DOCTORAL

PHENOLOGY, AS A COMPONENT AND DETERMINANT OF

ANURAN COMMUNITY STRUCTURE

Por

ANDRÉS CANAVERO RODRÍGUEZ

AGOSTO 2015



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Esta tesis está dedicada a mis abuelos Nélida Irigoyen y Jacinto Rodríguez. Han sido ellos quienes fueron ejemplo de sensibilidad y asombro por la naturaleza, así como de respeto por el conocimiento.

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PHENOLOGY, AS A COMPONENT AND DETERMINANT OF ANURAN COMMUNITY STRUCTURE

GENERAL INTRODUCTION

Time is an axis along which communities are structured (Chesson 2000, Kronfeld-Schor and Dayan 2003, Bradshaw and Holzapfel 2007), which is manifested in its recognition as one of the three major niche axes (Pianka 1973, Schoener 1974, Jaksic 1982, Morin 1999, Sandvik et al. 2002). Organisms have evolved by coupling their vital activities to specific times of year, resulting in annual or seasonal temporal patterns of life history and abundance called phenologies (Emerson et al. 2008, Forrest and Miller-Rushing 2010, Donnelly et al. 2011). In this sense, phenologies are associated with seasonal resource tracking, to avoid predators, to the success of pollination, to physiological restrictions, and/or to temporal resource partitioning (Morin 1999, Sandvik et al. 2002, Kronfeld-Schor and Dayan 2003, Bradshaw and Holzapfel 2007, Canavero et al. 2008). A current challenge for ecology is to predict the phenological changes and their consequences at different levels of organization associated to global warming, a phenomenon that has already manifested its effects mainly at the population level (Walther 2010, Jenouvrier and Visser 2011, Pau et al. 2011). One of the main components of ecological theory, the metabolic theory of ecology (MTE), links the effects of environmental temperature with organism metabolism and its scaling through organization levels (Brown et al. 2004). Although the MTE has described and predicted an important amount of biological phenomena, the phenological phenomenon has not been considered yet.

A major component of communities is the seasonal variation in the number of species that are observed performing a particular behavior, i.e. community phenology (e.g. Canavero et al. 2009, Aizen and Rovere 2010). The identification of temporal modules of species can be used as a tool to explore possible functional roles of modules at community level, and to infer historical processes on community assembly (Hooper et al. 2002, Wiens et al. 2006, Cadotte et al. 2009, Wiens et al. 2011, Cavender-Bares et al. 2012). The analysis of local community phenologies and its variation at geographical scale, due to either changes in conditions and environmental factors or to phylogenetic composition, allows to infer eco-evolutionary mechanisms of assembly (Maurer 1999, Marquet et al. 2004).

Amphibians are a classic model to analyze the connection between environmental conditions, individual behavior, and community structure (Blair 1961, Inger 1969, Crump 1974, Canavero et al. 2009). As ectotherms, amphibian metabolic rate is directly related to temperature of its environment (Angilletta and Sears 2011). Furthermore, they are dependent on the availability of water to preserve homeostasis, due to their highly permeable skin, and for reproduction (Zug et al. 2001). In fact, many studies have reported associations between richness of amphibians in activity, and environmental conditions (e.g. Oseen and Wassersug 2002, Saenz et al. 2006, Both et al. 2008, Canavero et al. 2008, Steen et al. 2013). An energetically expensive behavior of anurans is mating calls (Wells 2007), for which metabolic theory of ecology (MTE) was able to predict its frequency, power, and duration (Gillooly and Ophir 2010, Ophir et al. 2010). Thus, anurans represent a suitable group to explore ideas about the phenological phenomenon at community level and its geographical variation through the new energetics perspective of the MTE (Brown et al. 2004), incorporating new metrics for analyzing community structure (Marquitti et al. 2013,

Schleuning et al. 2014), including the historical component of evolution (Wiens et al. 2011, Pyron and Wiens 2013), all factors operating in the process of community assembly.

This thesis work, presents in three chapters the analysis of phenological data from 52 communities of Neotropical anurans using a deconstructive perspective: from the structure of local communities, through geographic patterns, to phenological modules and species, and returning to community assembly (sensu Maurer 1999, Marquet et al. 2004). In Chapter 1 MTE predictions are analyzed in relation to the phenological phenomenon: the richness of calling species and its connection with environmental temperature. I include in this chapter a description of the geographical variation in temperature dependence and its relationship with the phylogenetic composition of communities. In Chapter 2, I analyze three core components of community structure: phylogenetic diversity, phenological modularity (i.e. species coexistence over time), and temperature dependence of species richness. In order to explore the putative effects of global warming, I explore the latitudinal trend in community structure and its relationship to environmental variables in 34 communities presenting thermal dependence. In Chapter 3, through the analysis of 22 modular communities of Neotropical anurans I describe the phenological modular structure and its relationship with seasonality, richness, and phylogenetic relationships. The relevance of seasonality and phenological modules on the history of the assembly of Neotropical communities is discussed.

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CHAPTER I: A metabolic view of amphibian local community structure: the role of activation energy

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ABSTRACT

In the context of the Metabolic Theory of Ecology (MTE), the activation energy (E) reflects the temperature dependence of metabolism and organism performance in different activities such as calling behavior. In this contribution we test the role of temperature in affecting local amphibian community structure, particularly the number of species engaged in calling behavior across a temperature gradient. Toward this aim, we compiled 52 published databases of phenological calling activity of Neotropical anuran communities. E was estimated and the performance of MTE predictions evaluated for each community. We found values of activation energy that were significantly higher than previous reports, attributable to the energetically expensive nature of calling. The distribution of activation energies was contrasted with previous reports, and its variation among communities related to their phylogenetic structure, local environmental conditions, richness, and phenology. In this sense, organisms couple what the environment offers with its own metabolic demands for calling, diminishing the activation energy at high latitudes, where phenologies are more seasonal and environments less energetic. We also found a main role of niche conservatism and community filtering in the ensemble of amphibian communities. Our results consolidate the view of activation energy as an important parameter of biodiversity organization, which unravels the effects of ecological and evolutionary processes on biodiversity structure and function.

INTRODUCTION

One of the major challenges of the Metabolic Theory of Ecology (MTE) is to provide understanding of local community patterns [1]. Indeed, although metabolic approaches have been used to understand the local community patterns associated to size distributions and density scaling relationships [e.g. 2, 3-6] the fundamental questions of the regulation of species richness, distribution of abundance and coexistence still remain elusive.

One of the fundamental parameters of MTE is the activation energy of metabolism (E) that expresses the temperature dependence of metabolic rates $B_T \approx \exp(-E/kT)$, where k is Boltzmann's constant [8.62x10-5eV/K, 7] and T is temperature in degrees Kelvin. Using MTE's canonical equation it has been possible to link changes in environmental temperature with a variety of biologically important processes such as metabolism [7], mutation rate [8-10], speciation rate [8], species lifetime [11], and species richness [12]. Empirical evidence suggests that the activation energy (E) could capture relevant information about the energetic relationship between organisms and their environment [7, 13] by making explicit the temperature dependence of organism performance, constrained by their physiology and environment [14-16]. In this sense, the analysis of changes in *E* along natural gradients, as well as across populations and species, could provide novel insights about the determinants of biodiversity structure and function, and its dependence on ambient temperature [15]. Indeed, the recently reported variation in E among higher taxa [17, 18] suggests that a species' evolutionary history could affect how sensitive a species is to environmental temperature variation.

A main component of community structure closely related with ambient temperature is the seasonal variation in the number of species that are observed performing some behavior—i.e. phenology. Organisms have evolved vital activities coupled to specific times of year [19]. Specifically, phenologies were proposed to originate for seasonal resource tracking, predator avoidance, pollination success, physiological constraints, and/or temporal partitioning of resources [20-23]. The recognition of the roles of phenology on ecosystem diversity and functioning, as well as the limitations of ecological theory to account for observed patterns, has positioned its study as a frontier topic in the context of global change [24-29]. Indeed, the environmental temperature dependence of phenological activities associated to, for example, breeding and migration has received increasing attention in association with climate change [e.g. 25, 28, 30, 31, 32].

The phenological trends in anuran calling activity have been thoroughly studied for over half a century [33-35] and as expected for ectotherms, environmental temperature is considered as one of the main drivers of anuran phenologies [20, 29]. In consequence, different authors have explored correlation between the mean monthly ambient temperature and the number of species engaged in calling activities [see 36, 37-39]. The mating call of anurans is an energetically costly behavior whose frequency, power and duration conform to predictions of MTE [40-42]. Thus, we considered anurans as an appropriate group to obtain insights on this community-level phenological phenomenon through the novel perspective provided by the MTE [13].

In this article, we compiled information on the phenological calling activity of Neotropical anuran local communities, and for each one we estimated the activation energy of calling behavior E from a metabolic model. Then we analyzed the relationship between the activation energy E connecting the richness of calling

amphibians with environmental gradients related to available energy (e.g. latitude, NDVI, PET), and the phylogenetic divergence of the species conforming the local communities. We found relatively high activation energies, which were related with communities' phylogenetic structure, local environmental conditions, richness, and seasonality. Our results indicate that organisms' physiology couples available energy (temperature and resources) with calling metabolic demands, diminishing the activation energy at higher latitudes and less productive environments. Further, niche conservatisms, community filtering, and flexibility in activation energy could also be accounting for the environment-activation energy relationship herein reported.

MATERIAL AND METHODS

We compiled 52 published databases of phenological activity patterns of Neotropical anuran communities. This compilation includes 361 species from 50 genera, with species richness of communities ranging between 9 and 39 species, periods of activity lasting between 10 and 28 months, and a latitudinal gradient varying between 7° and 34°S (Fig. 1 and Table 1). The methodologies and scales used to generate each database are similar: surveys of one to five nights per month registering the presence of anuran species based on their calling behavior [43]. For each community, we obtained information about environmental productivity (NDVI, normalized difference vegetation index), potential evapotranspiration (PET), coefficient of variation in annual precipitation (P_{CV}), annual precipitation (Rain), coefficient of variation in mean monthly temperature (T_{CV}), annual mean temperature

 (T_{amean}) , maximum temperature of hottest month (T_{max}) , and minimum temperature of coldest month (T_{min}) from Hijmans et al. [44] and Rangel et al. [45].

Model fitting

We fit a metabolic model, $\ln(S) = -E^* 1/kT + C$ [see 12], to anuran phenological data (species richness of calling males each month). We added 1 to species richness values to perform the log transformation. The analysis of the model fit follows three stages. First, the global information about temperature dependence of species richness was assessed with a mixed effects model in which the source community was modeled as a random effect. Second, the local performance of the metabolic prediction was evaluated. Third, considering the previous detection of local variation on activation energy and the good performance of the metabolic model, trends in activation energy among communities were related with their phylogenetic composition and biotic and abiotic conditions.

Three linear mixed effects models were fitted by restricted maximum likelihood estimation (REML) with 717 observations (number of species that call in a specific month) of 52 groups (communities) [46]. These three linear models included as an independent variable the reciprocal temperature in Kelvin multiplied by Boltzmann's constant (*k*), and as dependent variables the natural logarithm of the number of species that call per month. Models included community identity as a random effect, considering a random intercept, a random intercept and slope, and in which all variation in richness originated from community identity without effect of temperature. Models were ranked on the basis of their Akaike's Information Criterion values (AIC) [46]. Model performances were contrasted with the AIC and judging

differences in AIC values greater than two as significant [47, 48]. All linear mixed effects models were done using the nlme package in R v. 2.15.2 [49].

In order to explore the local performance of the metabolic model [12] and the distribution of the estimated parameter *E* (i.e. activation energy), we assessed the independence of residuals of each fitted metabolic model with Pearson's correlation. In order to compare the distribution of *E* values calculated from our database (see Table 1) with those calculated by recent reviews [see Table S3 in 14, Supporting Information], we performed a two-sample Kolmogorov-Smirnov test. We also fit a sinusoidal function of month (S=S_{mean}+S_{amp} sin [2*Pi (month + c)/12]) to each of the 52 vectors of S (S, number of species that call in a particular month). This sinusoidal model has parameters with biological interpretation, which can be used to describe the seasonal trend of the number of species in calling activity (S_{amp}, amplitude of the function) [see 39, 50].

Evaluating the variation in the community activation energy

We performed a path analysis in order to evaluate a causal connection between environment, diversity and the activation energy. We included the biological parameters estimated by the metabolic and sinusoidal models, and the set of environmental variables obtained for each locality. We used Structural Equation Modeling (SEM) to test the overall path diagram and the significance of each single connection between couples of variables. Path analysis was used with maximum likelihood methods and standardized coefficient. To assess the significance of the overall path model, we used a χ^2 statistic computed from the departure between the observed and expected covariance matrix from the proposed path model. A significant

 χ^2 (P < 0.05) indicates that the data do not support the model. The explained variance for each endogenous variable is estimated as one minus the path coefficient between its associated error variable [51]. Because our data matrix does not present multivariate normality based on kurtosis (using the mynorm.kur.test function of the ICS package in R v. 2.15.2, W = 27.0852, w1 = 0.625, df1 = 20.000, w2 = 1.000, df2= 1.000, p-value<0.01), we develop the Satorra–Bentler robust estimations of the Chisquared statistic and standard errors. It corrects excessive kurtosis, problems in which the errors are not independent of their causal non-descendants and is important for models with latent variables. We performed a SEM, which represents the effect of the environment (latent variable constructed by NDVI, PET, and latitude) on the activation energy (E) and on community seasonality (S_{amp}, amplitude of the sinusoidal function), and the latter is also determined by the activation energy and local richness (Sloc). We also evaluated alternative path models, including the putative role of environment on the local species richness (Sloc), but this path connection was rejected as a plausible causal explanation of data (see Supporting Information). All SEM models were fitted using the R-Package lavaan [52].

To incorporate community phylogenetic distances in our analysis, we reconstructed the phylogeny of 361 species of Neotropical anurans (for methodological details and tree image see Supporting Information). Then we estimated the mean pairwise phylogenetic distance (MPD). This index finds for each taxon in a community the average phylogenetic distance to all taxa in the other community, and calculates the mean using the COMDIST module of PHYLOCOM software [53]. Next, we compared the environmental (Euclidean distances of community environment measured as: NDVI, PET, and latitude ordered by the two first axes of a Principal Component Analysis) and MPD distance matrices with the

matrix of community activation energy distances (each distance was calculated as the activation energy of community A minus the activation energy of community B) using a simple Mantel test (10,000 permutations). Finally, we explored the link between the community activation energy, and phylogeny or environment using partial Mantel test (10,000 permutations). In order to describe the activation energy matrix, we calculated the partial correlation with phylogeny after removing the effect of environment, and then calculated the partial correlation with environment after removing the contribution of phylogeny [see 54].

RESULTS

The number of species engaged in calling activities was better explained by the random intercept and slope model, which had the lowest AIC value (AIC=1407.65) in comparison with the random intercept model (AIC=1440.66) and the random effects model (AIC=1621.17). The former model presents high values of standard deviation of the intercept (28.62) and of the slope (0.74eV) showing the relevance of community idiosyncrasy (Fig. 2). This variation in slope highlights the importance of analyzing the activation energy as a biological variable. Of the 52 phenological community data-series we analyzed, 35 fit significantly the metabolic model, with a percentage of the explained variance ranging from 27.5 to 87.4%. We considered the case 5 [55] as an outlier because it presents an extreme value of *E* (-1.033eV). The mean and median of *E* values estimated is 1.80eV (standard error=0.14eV) and 1.67eV respectively (n=34). The distribution of the activation energy shows significant differences with the right skewness distribution presented by

Dell *et al.* [14] of the responses of traits corresponding to positive motivations (e.g. attack body velocity) (two-sample Kolmogorov-Smirnov test: D=0.648, p-value<0.001) and no significant deviation from a normal distribution (Shapiro-Wilk test of normality: W=0.957, p-value=0.204) (Fig. 3). The 95% confidence interval of the mean activation energy of the calling activity (1.53 to 2.08eV) excludes the empirical value of approximately 0.65eV [56] and also the range of values 0.2 to 1.2eV proposed by Downs *et al.* [57].

The analysis of residuals reported a significant autocorrelation in 17 of the 52 cases. So we included a temporal component to the equation $(\ln(S)=-E*1/kT+month+C)$ and estimated the slope (i.e. the activation energy *E*). In this case eighteen models had a significant fit (alpha=0.05) and twenty-eight a marginal fit (alpha=0.1). We did not find differences between mean values of *E* estimated from both models and total data (Welch two sample t-test, N₁=N₂=52, t=0.966, df=101.06, p-value=0.337) or only the significant fits (Welch two sample t-test, N₁=34, N₂=28, t=0.560, df=51.484, p-value=0.578, mean₁=1.804, mean₂=1.675). When comparing the *E* values distribution, we did not find significant differences (Two-sample Kolmogorov-Smirnov test, D=0.132, p-value=0.910). Based on this result, where *E* does not differ significantly on their mean and distribution no matter if it is estimated considering residual autocorrelation or not, we opted for the initial estimates.

Path analysis and simple and partial Mantel tests were performed with the 34 communities data that fit significantly the metabolic model. The path analysis revealed a putative role of the environment (represented by a latent variable constructed by NDVI, PET, and latitude) and diversity (represented by S_{loc} , and S_{amp}) on calling activation energy. This structural model was able to explain 55% of the variance of *E*, reporting the connection between the variance of the calling activation

energy, environment and community seasonality (Fig. 4). The latent variable shows a positive correlation with productivity variables (NDVI and PET) and calling activation energy, and negative correlation with latitude and calling seasonality (S_{amp}). This means that with an increase in latitude we find a decrease in system productivity, greater calling seasonality, and smaller calling activation energy. We also found positive connection between calling activation energy and calling seasonality. Latitude also presented significant correlation with T_{amean} (R²=0.31, p<0.001, b=-0.34), T_{CV} (R²=0.72, p<0.001, b=0.78), T_{min} (R²=0.48, p<0.001, b=-0.46), Rain (R²=0.32, p<0.001, b=36.00), P_{CV} (R²=0.63, p<0.001, b=-3.76).

The simple Mantel test reported a significant association between the environmental and the MPD matrix ($r_{pearson}=0.47$, p<0.0001) (Fig. 5 top). The partial Mantel tests with the environment similarity matrix after removing the effect of phylogeny was significant ($r_{pearson}=0.35$, p<0.0001), but for phylogeny after removing the effect of environment the correlation was no significant ($r_{pearson}=0.08$, p=0.154) (Fig. 5 top). When we explore a simple Mantel test between phylogeny and activation energy matrix we found a significant association ($r_{pearson}=0.26$, p=0.002) (Fig. 5 bottom).

DISCUSSION

Understanding the observed variation in E among organisms and environments represents a novel challenge for the MTE [14-16]. In this contribution we show that variance in E is associated to ecological and evolutionary processes. Unlike previous estimation of variability in E, which combine data from different locations that differ in area, community abundance, and phylogenetic ensembles [58], that could bias the estimation of activation energy and its determinants [see 58, 59], our analysis focused on local communities to assess seasonal trends in activity. Thus, we overcome previous criticisms to MTE because it involves: i) changes in community richness (i.e. number of species in activity) with temperature but without changes in area [60]; ii) a reasonable constancy in total community abundance changing the proportion of individuals in activity [58]; iii) a single species pool, and thus no change in the phylogenetic structure of communities potentially active at different temperatures [generally geographical, see 61, 62, 63]; and iv) changes in richness with temperature are decoupled from mutation and speciation rates, which is an alternative metabolic connection between temperature and richness [9, 64, 65]. The seasonal variation in richness of ectotherm activity represents an ideal model system to study the connection between organismal energetics and community structure.

Phenological patterns could be addressed as a temporal version of the moreindividuals hypothesis [66], where an increase of energy availability in some months of a year would lead to higher abundances of individuals (via increased reproduction and migration) and consequently more species [58, 66]. An alternative hypothesis considers that ectothermic species have different activation thresholds or differential tolerances to the harsh period (e.g. lower temperatures) and alternate between reduction on vital activities in unfavorable conditions and activation during favorable ones [67, 68].

Our results showed values of E (mean=1.80eV) significantly higher than what was expected by the MTE for the geographical patterns of richness [i.e. 0.65eV or the interval 0.2–1.2 eV, 7, 57, 69, 70] meaning that it is highly sensitive to temperature variation. This difference in activation energies could be reflecting the nature of the

traits used to estimate model parameters [14, 16] and its relationship to fitness. Reproduction, more than growth and usual activities, is the largest component of the entire annual energy budget of anurans. The calling behavior is tightly coupled to individual fitness [42] and is the most expensive behavior performed by anuran males during their entire life, being 6 to 20 times more expensive than resting metabolic rates in the field [41, 42]. The morphological and biochemical basis of this ability is centered in the muscles of call production: trunk and laryngeal muscles. They have differences with the leg muscles, allowing anurans to have an intense aerobic metabolism (more aerobic fiber types, higher concentrations of mitochondria, capillary densities, and activities of enzymes) [42]. In this context, it is not surprising that our estimations exceed twice the activation energies values proposed by the MTE, reflecting the energy expenditure of an expensive behavior.

Environment-diversity relationship is the result of the interplay between environmental conditions, organisms' attributes, and the effect of evolutionary history on these attributes [71]. Calling is an energetically expensive activity that pushes anurans to their limits and brings an opportunity to explore their physiological constraints [42]. We found that at higher latitudes, where phenologies are more seasonal and environments less energetic, communities tend to show lower E values. Apparently organisms are coupling what the environment offers with their own metabolic demands for calling. Dell et al. [14] found that individuals under attack maximize effort at low temperature to survive even though it is energetically costly [68]. And there is evidence that amphibians expand their thermal tolerance breadths with latitude mostly by decreasing the lower thermal limit [72]. In our case, anurans may call at higher latitudes with lower temperatures simply because if they do not, they fail to reproduce. The observed trend of reduction in E with latitude raises

questions: How do anurans call in less energetic environments? or How do anurans reduce the energetic demands of calling? In this vein, a correlation has been observed between the metabolic demand to call and the size of the muscular system of calling [41, 42]. So we hypothesize that as latitude increases, there is a reduction in calling parameters [e.g. sound frequency, call rate, call duration, sound power, see 40, 41] associated with the downsizing of the muscular system of calling [e.g. anuran trunk muscles, see 41, 42]. Our results also show that an increase in the activation energy result in phenologies with stronger seasonality, when other abiotic variables (i.e. NDVI, PET, latitude) are fixed. If the activation energy is low, organisms can be active with little energy and are relatively insensitive to environmental seasonality, determining low seasonality in calling phenologies. On the other hand, organisms that have high activation energies are more sensitive to the environment, which should result in high variation in the number of active species and therefore high seasonality in calling phenologies.

The detected connections among communities' phylogenetic structure, environmental conditions, and activation energy relate major blocks of biodiversity structure and their determinants with a cornerstone of the MTE. The environmentalphylogeny association (see the Mantel tests results) herein observed is congruent with previous results and with a main role of niche conservatisms and community filtering in the ensemble of amphibian communities [73-75]. Further, the environmentactivation energy association supports the view of activation energy as a parameter that encapsulates main components of the relationship between energy use, environmental conditions, and organisms physiology, being a meaningful biological parameter at different biological levels [13, 14]. Thus, the environmentactivation

actively filtered depending on their activation energies and the local environments [76]. On the other hand, individuals' flexibility in activation energy could also account for this association. It was recently shown that amphibian calls are flexible and not fixed as is usually assumed [77]. Among the several attributes composing mating calls, individuals could potentially modulate the cost of calls and required temperature to activate the associated physiological processes—activation energy. As was pointed out above, structural changes could also take place in response to environmental conditions, allocating more or fewer resources to production of muscle and structures used in calls [41]. These changes could determine the metabolic scope—increase from resting to calling metabolic rate—and the activation energy involved in the processes [41].

The ecological concept of activation energy is being reconsidered from a fixed attribute of higher taxa (e.g. amphibians) to a parameter that depends of the species involved and the traits considered [14, 16]. If activation energy proves to be a flexible parameter, it should be further pondered, implicating that its represents a set of individual traits that can be modulated by single genotype in order to endure different environments.

The significant correlation with phylogeny in simple Mantel test but a lack of a phylogenetic effect when environment is taken into account strongly suggests that niche conservatism could be the mechanism involved in the evolution of activation energy [78]. The exploration of phylogenetic signal and the evidence for selection of activation energy among lineages were beyond the aim of the present study. However, relevant hypotheses for testing emerge from our results because patterns of niche conservatism could be the result of adaptation to phylogenetically-structured niches or to genuine phylogenetic inertia [i.e, evolutionary stasis, 79], and appropriate

comparative phylogenetic methods are available to distinguish between these alternatives [80].

Moving from the existence of a universal thermal dependence controlling the biological processes [13, 56] to address the activation energy as a biological trait represents a challenge but also an opportunity of research [15, 81], because this variation may reflect the ecological and evolutionary nature of the trait [14, 16, 56]. The MTE has been combined with other theories in order to reach new insights and the understanding of the biological complexity at different levels and scales [e.g. life-history theory, the neutral theory of biodiversity, food web theory 59]. In this vein, we found that incorporating the MTE to the phenological framework makes a contribution to improving the understanding of a phenomenon that has a community nature [1].

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Table 1.

Reference of the Neotropical data series and their geographic locations. The fit of the
metabolic and the S_{amp} parameter sinusoidal model is included. *E*, calling activation
energy; S_{loc}, total number of species that call at least once in the study period; NDVI,
normalized difference vegetation index; PET, potential evapotranspiration. 34 of the 52
data series with a significant fit are marked with asterisk.

Deference	Locality	c	Match alia was dal			c	NDVI	DET
Kelefence	Locality	Sloc	$F = \mathbf{P}^2 = \mathbf{D}$			Samp	NDVI	PEI
1) Abrumbaga at al [92]	22050'S. 42027'W	10	2 210*	N 0.574	F	1 622	2 175	82.002
1) Adjumiosa $et ut. [62]$ 2) Afonso & Eterovick [83]	22 30 3, 42 27 W	19	0.623*	0.374	0.003	4.033	2.175	79.910
3) Arzabe [84]	07°17'S· 37°21'W	11	3 524*	0.324	0.027	4 378	4 700	103 820
4) Arzabe [84]	07°11'S: 37°19'W	16	3 257	0.323	0.021	4.014	4 700	103.820
5) Arzabe <i>et al</i> [55]	11°20'S· 37°25'W	17	-1 033*	0.525	0.007	2 632	2 241	115 073
$\begin{array}{c} \text{6} \text{Ávila & Ferreira [85]} \end{array}$	18°58'S: 57°39'W	15	2 562*	0.619	0.007	4 215	2.241	126 480
7) Bernarde & dos Anios [86]	23°27'S: 51°15'W	18	0.754*	0.335	0.049	5 532	1 970	81 373
8) Bernarde & Kokubum [87]	21°16'S: 50°37'W	19	1 735*	0.449	0.017	8 220	3 000	98 930
9) Bernarde & Machado [88]	25°27'S: 53°07'W	20	0.997*	0.513	0.009	6 515	1 860	69 233
10) Bernarde [89]	11°35'S: 60°41'W	33	0 354	0.002	0.890	11 332	1 100	87 138
11) Bertoluci & Rodrigues [90]	23°38'S: 45°52'W	28	0.951*	0.414	0.018	6.275	2.327	77.917
12) Bertoluci [91]	24°15'S: 48°24'W	26	0.978*	0.362	0.038	10.911	1.450	73.162
13) Blamires <i>et al.</i> [92]	16°39'S: 48°36'W	13	1.476*	0.661	0.001	2.009	4.080	85.403
14) Borges <i>et al.</i> [93]	17°87'S: 49°23'W	25	2.318*	0.727	< 0.001	7.342	3.920	97.730
15) Both <i>et al.</i> [37]	29°32'S: 53°47'W	18	0.859*	0.359	0.039	5.676	2.060	77.418
16) Canavero <i>et al.</i> [39]	34°47'S: 55°22'W	10	0.674*	0.303	0.018	3.203	2.809	68.460
17) Candeira [94]	20°20'S: 49°11'W	24	3.181*	0.874	< 0.001	9.500	3.620	95.515
18) Canelas & Bertoluci [95]	20°05'S; 43°28'W	32	1.606*	0.778	< 0.001	7.956	3.100	79.910
19) Cardoso & Haddad [96]	21°48'S; 46°35'W	19	1.657*	0.525	0.008	7.871	2.860	74.593
20) Cardoso & Souza [97]	10°08'S; 67°35'W	31	2.598	0.103	0.309	11.261	1.000	119.998
21) Conte & Machado [98]	25°57'S; 49°13'W	21	1.682*	0.370	0.027	8.813	2.350	66.385
22) Conte & Rosa-Feres [99]	25°41'S; 49°03'W	31	0.847*	0.275	0.037	10.134	2.350	66.385
23) Conte & Rosa-Feres [100]	25°39'S; 49°16'W	29	1.550*	0.437	0.007	9.732	2.350	66.385
24) Filho [101]	20°05'S; 56°36'W	15	2.156*	0.539	0.007	4.960	2.020	108.575
25) Forti [102]	24°02'S; 47°53'W	20	0.482	0.178	0.081	3.832	2.790	76.278
26) Grandinetti & Jacobi [103]	20°07'S; 43°52'W	11	0.167	0.085	0.335	1.401	3.100	79.910
27) Heyer et al. [104]	23°38'S; 45°52'W	35	2.972*	0.463	0.021	11.169	2.327	77.917
28) Kopp & Eterovick [105]	20°06'S; 43°29'W	20	1.612*	0.431	0.006	4.382	3.100	79.910
29) Kopp et al. [106]	17°49'S; 52°39'W	25	2.589*	0.448	0.005	8.180	4.000	94.135
30) Maffei [107]	22°48'S; 48°55'W	39	1.345*	0.416	< 0.001	11.634	3.000	83.813
31) Moreira et al. [108]	29°42'S; 50°59'W	15	-0.721	0.104	0.334	4.278	2.400	72.685
32) Narvaes et al. [109]	24°31'S; 47°16'W	11	0.248	0.083	0.390	1.450	1.717	86.390
33) Nascimento et al. [110]	20°00'S; 43°50'W	9	-0.455	0.080	0.271	0.177	3.100	79.910
34) Nomura [111]	23°10'S; 46°31'W	29	0.452	0.130	0.108	4.558	3.562	70.257
35) Nomura [111]	20°21'S; 49°16'W	23	1.898*	0.805	< 0.001	5.837	3.620	95.515
36) Nomura [111]	20°12'S; 50°29'W	23	2.033*	0.827	< 0.001	6.493	3.410	94.618
37) Oda et al. [112]	14°09'S; 48°20'W	21	4.958	0.378	0.105	8.728	4.000	90.233
38) Papp [113]	22°52'S; 46°02'W	13	1.211*	0.474	< 0.001	4.503	2.180	74.198
39) Pombal & Gordo [114]	24°25'S; 47°15'W	23	0.920	0.425	0.057	6.920	1.717	86.390
40) Pombal [115]	24°13'S; 48°46'W	19	1.020	0.310	0.060	5.699	1.450	73.162
41) Prado <i>et al.</i> [116]	19°34'S; 57°00'W	23	1.574*	0.689	< 0.001	8.149	3.330	125.963
42) Prado & Pombal [117]	20°16'S; 40°28'W	17	0.604	0.166	0.189	3.494	3.000	93.137
43) Rossa-Feres & Jim [118]	22°59'S; 48°25'W	25	0.481	0.125	0.237	5.785	3.000	83.813
44) Santos [119]	08°43′S; 35°50′W	28	-0.221	0.074	0.346	3.122	3.065	93.912
45) Santos <i>et al.</i> [120]	20°11'S; 50°53'W	13	2.956*	0.843	< 0.001	6.562	3.410	94.618
46) Santos <i>et al.</i> [121]	29°42′S. 53°42′W	24	0.535	0.321	0.055	4.332	2.060	77.418
4/) Sao Pedro & Feio [122]	20°31′S. 43°41′W	28	0.676	0.115	0.281	6.706	3.100	79.910
48) Silva [123]	20°20'S. 49°11'W	18	2.43/*	0.727	< 0.001	6.481	3.620	95.515
49) Teixeira [124]	22°59′S; 48°30′W	15	1.094*	0.586	0.004	3.133	3.000	83.813
50) 101edo <i>et al.</i> [125]	22°25'8;4/°33'W	19	1.825*	0.449	0.017	5.440	5.000	80.825
51) Vieira <i>et al.</i> [126]	0/°25′8; 36°30′W	15	5.184*	0.271	0.009	4.849	5.490	95.245
52) Zina <i>et al.</i> $[127]$	22°22′S; 47°28′W	22	2.172*	0.816	< 0.001	7.200	3.000	80.825

FIGURE LEGENDS

Figure 1. Geographic locations of the 52 Neotropical data series.

Figure 2. Fitted random intercept and slope model with the reciprocal temperature in Kelvin multiplied by Boltzmann's constant (k) as independent variable, and as dependent variables the natural logarithm of the number of species that call per month. The black line represents the fitted values for all communities, and the grey lines represent the local communities fitted curves. Dots represent the number of species that call in a particular month of a particular community.

Figure 3. Activation energy histogram. *E*, activation energy calculated with the metabolic model presented by Allen *et al.* (2002): $\ln(S)=(-E/1000k)(1000/T)+C$; S, number of species with calling behavior per month; T, mean month temperature in Kelvin degrees; k=Boltzmann constant=8.62*10⁻⁵ eV K⁻¹; calculated with the 34 of 52 data series with a significant fit.

Figure 4. Evaluation of the putative role of the environment and community richness on the activation energy of anuran calling activity. S_{loc} , total number of species that call at least once in the study period; NDVI, normalized difference vegetation index; PET, potential evapotranspiration; S_{amp} is a parameter of the sinusoidal function: $S=S_{mean}+S_{amp} \sin [2*Pi (month + c)/12]$; S, number of species that call in a particular month; S_{amp} , amplitude of the sinusoidal function; S_{mean} , mean value of S estimated from the sinusoidal function. Paths values are standardized effects. Arrow width represents the strength of the causal link. In the figure was included the result of correlations of latitude as independent variable with T_{amean} , T_{CV} , T_{min} , Rain and T_{CV} ; external arrows represent variances unexplained by the model, and the explained variance for endogenous variables is represented by one minus the path coefficient between its associated error variable. SRMS, Standardized Root Mean Square Residual.

Figure 5. A) Summary of partial and simple Mantel tests (10,000 permutations) between the environmental (NDVI, PET, and latitude), phylogenetic (MPD distance), and activation energy distance matrices. B) Summary of simple Mantel tests (10,000 permutations) between the phylogenetic (MPD distance) and activation energy distance matrices. Arrow width represents the strength of the link. **P<0.01; ***P<0.001.



Figure 1.



Figure 2.



Figure 3.



Figure 4.



Figure 5.

SUPPORTING INFORMATION

A metabolic view of amphibian local community structure: the role of activation energy

Andrés Canavero, Matías Arim, Fernanda Pérez, Fabián M. Jaksic & Pablo A. Marquet

SI MATERIALS AND METHODS

Structural equation modeling

In order to evaluate the putative connection between environment local species richness (S_{loc} , total number of species that call at least once in the study period), community seasonality (S_{amp} , amplitude of the sinusoidal function), and the activation energy of the calling activity (*E*), we performed four Structural Equation Models (SEM) [1]. In all of them we constructed a latent variable, ENVIRONMENT, with three components: NDVI (normalized difference vegetation index), PET (*potential evapotranspiration*) and Latitude. We performed alternative path models including a central role of local species richness (S_{loc}) connecting the environment with *E* (Fig. S1 and S2), an external role of S_{loc} on *E* which is also connected with the environment (Fig. S3), and the last SEM includes *E*, S_{loc} and S_{amp} affected by the environment with only a connection between the last two variables (Fig. S4).

Phylogenetic tree reconstruction

To reconstruct the phylogeny of the 361 species of Neotropical anurans found in our community datasets we began by finding the species in common with the molecular matrix of Pyron & Wiens [2]. Because some species were not represented in the molecular matrix, we used "surrogate" species of the same genus: *Dendrophryniscus* sp. was represented by *Dendrophryniscus minutus*; *Eleutherodactylus* sp. by *Eleutherodactylus abbotti*; *Chiasmocleis albopunctata* by *Chiasmocleis hudsoni*; *Flectonotus ohausi* by *Flectonotus fitzingeri*; *Megaelosia boticariana* by *Megaelosia goeldi*; *Pleurodema fuscomaculatum* by *P. diplolister* together with *Pleurodema bibroni*. In addition, Pyron & Wiens [2] did not sample *Stereocyclops incrassatus*, which we added to the root of the family Microhylidae following Frost et al. [3]; *Centrolenella* sp. registered by [4] in our ecological matrix was considered a sister group of *Vitreorana* because it belongs to the family Centrolenidae. Finally, "Gen. sp." registered by Bernarde [5] was included to the root of Centrolenidae (Bernarde com. pers.).

With all of these sequences we estimated a new tree of 164 species; including *Homo sapiens* as outgroup, with the program RAXML using the same concatenated sequences and models of Pyron & Wiens [2]. To this tree of 164 species we added the remaining taxa of the ecological matrix that did not have genetic information using a taxonomic criterion. The added species were collapsed to the ancestral node of the genus in order to avoid any assumptions about their affinity with other species in their respective genera. Those species that were assigned by authors to other species (i.e. "affinis" and conferred), we collapsed to them. This method did not modify the known relationships between other species already in the tree. In order to estimate the node ages of the 164 species tree, we used eight nodes shared with the tree dated by Wiens [6] (Fig. 2) and the software r8s 1.8 [7]. These eight fixed nodes were those

which clustered *Homo sapiens* with *Pipa carvalhoi* (400 My), *Pipa carvalhoi* with *Lithobates catesbeianus* (250 My), *Lithobates catesbeianus* with *Leptodactylus fuscus* (200 My), *Leptodactylus fuscus* with *Dendrophryniscus minutus* (159.8 My), *Thoropa miliaris* with *Scinax ruber* (152.5 My), *Flectonotus fitzingeri* with *Oreobates quixensis* (133.6 My), *Phyllomedusa tomopterna* with *Scinax.nasicus* (125.4 My), *Flectonotus fitzingeri* with *Gastrotheca fissipes* (114.7 My), *Pseudis paradoxa* with *Scinax fuscovarius* (107.4 My), *Leptodactylus fuscus* with *Leptodactylus mystacinus* (54.1 My), *Dendrophryniscus minutus* with *Rhinella marina* (39.3 My), *Trachycephalus venulosus* with *Osteocephalus taurinus* (39.3 My). Using the BLADJ module of PHYLOCOM software [8], we estimated the branch lengths of the tree of 361 anuran species (Fig. S5). The anuran taxonomy used in this article follows Frost [9].



Figure SI1:

Evaluation of the putative role of the environment and local community richness (S_{loc}) on the activation energy of anuran calling activity through local species richness. S_{loc} , total number of species that call at least once in the study period; NDVI, normalized difference vegetation index; PET, *potential evapotranspiration*; S_{amp} is a parameter of the sinusoidal function: $S=S_{mean}+S_{amp} \sin [2*Pi (month + c)/12]$; S, number of species that call in a particular month; S_{amp} , amplitude of the sinusoidal function; S_{mean} , mean value of S estimated from the sinusoidal function. Path values are standardized effects ± 1 SE. Arrow width represents the strength of the causal link. u1 to u6 represent variances unexplained by the model, and the explained variance for endogenous variables is represented by one minus the path coefficient between its associated error variable. RMS, root mean square error.



Figure SI2:

Evaluation of the putative role of the environment and local community richness on the activation energy of anuran calling activity through local species richness. For figure references see Figure SI1.



Figure SI3:

Evaluation of the putative role of the environment and local community richness on the activation energy of anuran calling activity with independent and direct effects of environment and local species richness. For figure references see Figure SI1.



Figure SI4:

Evaluation of the putative role of the environment on the activation energy of anuran calling activity. For figure references see Figure SI1.



Figure S5:

Phylogenetic tree reconstruction. To reconstruct the phylogeny of 361 species of Neotropical anurans found in our community datasets.

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CHAPTER II: Unraveling the thermal dependence of calling amphibians: a place for phylogenetic structure, external resources, and the modular organization of biodiversity

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ABSTRACT

Understanding the effect of global warming on the architecture and functioning of biodiversity is a challenge for sustainability, because it may reveal the potential of communities to absorb or withstand disturbances. Time at different scales has received an early recognition as a main dimension of community organization. Species' phenology is the coupling of vital activities to specific times of the year. The metabolic dependence on temperature determines a causal connection from individual behavior to community structure, which jointly with the evolutionary history of species determines the type and strength of biological interactions in the phenological dimension. Phylogenetic signal in the breeding period could determine that related species in similar environmental conditions conform phylogenetically aggregated phenological modules, which may play a role in community functioning and stability. Amphibians are a good model for analyzing the phenological connection between environmental conditions, individual behavior, and community structure, because they are ectotherms, with permeable skin and aquatic reproduction. Here, we report the phenological structure in 52 communities of Neotropical anurans: phylogenetic diversity, phenological modularity, and phenological temperature dependence. To explore the putative effects of global warming we analyzed the connections between community structure and environmental variables of 34 communities that present thermal dependence. For each community we recorded data of latitude, potential evapotranspiration, total number of species that call at least once in the study period, an index of normalized modularity, and a distance phylogenetic index. We describe the thermal dependence of amphibian activity with the apparent activation energy of calling. Of the 34 phenological data with thermal dependence, 22 were modular, 15

showed phylogenetic attraction, and three repulsion. The structural model with better support involves a latent variable positively connected with latitude and phylogenetic relatedness, and negatively with activation energy and potential evapotranspiration. The effects on modularity were negative from activation energy, and positive from potential evapotranspiration and local species richness. This model accounted for 27% of the variation in phylogenetic relatedness, 42% of the modularity variance, and 68% of the variation in thermal dependence. The present study expands the scope of amphibian phenological studies, exploring the thermal dependence in an explicit metabolic framework, and its interplay with phylogenetic community structure and modularity. The observed phylogenetic structure of phylogenetic attraction is congruent with a role of species filtering, a pattern reinforced with latitude that could be related to harsher environments. The identification of modularity as a prevalent feature of phenologies is a novel contribution for understanding the temporal structuring of species activities. The apparent activation energy of calling allows us to explore the interdependence between temperature, productivity, latitude, and main features of communities such as richness, modularity, and phylogenetic structure. Analyzing the geographical gradients of thermo-dependent communities, we found an interconected complex system of phylogenetic attraction associated to environmental filtering, and an increase of modularity in less energetic and variable environments. Better recognition of complexity is needed to understand the extent and magnitude of global warming impacts on biodiversity structure and functioning.

INTRODUCTION

Global warming is predicted to have strong impacts upon ecosystems and the services they provide to humanity as well as at the levels of communities, populations and individuals (Parmesan 2006, Visser 2008, Naeem et al. 2009, Naeem et al. 2012, Bozinovic et al. 2014, IPCC 2014). Ecophysiological analyses have typically assessed the impact of warming at the level of individuals with a focus on thermal tolerance and performance (Bozinovic et al. 2011, Bozinovic and Portner 2015), generating predictions for ectotherm species tolerance along latitudinal gradients (Deutsch et al. 2008, Gaston et al. 2009). Some authors emphasize that beyond understanding the effects of a particular warming level (e.g. environmental tolerances), we need to understand how climate and global change affects the architecture and functioning of biodiversity, because this is a challenge for sustainability (McCann 2007, Naeem et al. 2012, Rohr et al. 2014). It is not only important understand changes in the strength of interactions between species within an interactions network, but also how the network structure is affected (e.g., modular, nested) by an environmental forcing (Saavedra et al. 2013, Dakos and Bascompte 2014). The entire network and its structure will determine the existence of possible thresholds and critical transitions of the system (Scheffer et al. 2012, Lever et al. 2014). It also highlights the importance of knowing and incorporating the evolutionary history of the species components of the network (e.g., central or matching species) in order to understand the potential of communities to absorb or withstand disturbances (Rezende et al. 2007, Naisbit et al. 2012, Bascompte 2013, Rohr and Bascompte 2014).

Congruently with its relevance for the understanding of ecosystem functioning, time in general and phenology in particular, have received an early and

persistent recognition as a main dimension of community organization (Pianka 1973, Schoener 1974, Chesson 2000, Kronfeld-Schor and Dayan 2003, Bradshaw and Holzapfel 2007). Species' phenology typically involves reproductive (Davies et al. 2012) and migratory behaviors (Cotton 2003) and large changes in organisms physiology (Gillooly and Dodson 2000, Yamahira 2004, Pearce-Higgins et al. 2005), coupling vital activities to specific times of the year (Bradshaw and Holzapfel 2007, Emerson et al. 2008, Canavero and Arim 2009, Visser et al. 2010). The reported quantitative and qualitative impact of global change on species phenology, places the environment-phenologies connections as one of the 100 fundamental ecological questions (Sutherland et al. 2013). Specifically, the ability to predict the magnitude and direction of changes in phenologies along environmental gradients is a pressing issue in order to forecast future ecosystem composition and functioning (Walther 2010, Pau et al. 2011).

The congruence between species life cycles and environmental conditions demands changes in individual behavior in response to present or future environments (Canavero and Arim 2009). These responses impact the whole community structure (i.e. richness, composition), which typically shows strong association with seasonal trends in environmental conditions—precipitation, productivity, temperature (Oseen and Wassersug 2002, Saenz et al. 2006, Both et al. 2008, Canavero et al. 2008, Steen et al. 2013, Protázio et al. 2015). Further, the temperature dependence of metabolic rate (Gillooly et al. 2001) is manifested first as changes at the individual level behavior (Dell et al. 2011a, Dell et al. 2014), which could scale up to trends in community structure with temperature (e.g. Allen et al. 2001, Storch 2012). This trend resembles the dependence of chemical reactions on temperature and the slope of the relationship is considered as a measure of the "apparent activation energy" of

communities (Craine et al. 2010, Sinsabaugh and Follstad Shah 2010, Yvon-Durocher et al. 2012). This activation energy describes the dependence of community structure on environmental temperature (Segura et al. 2015).

Phenologies are shaped by cycles of environmental variables but also by the idiosyncratic species composition (i.e. phylogenetic structure) of communities and its interactions (e.g. Aizen and Rovere 2010, Brito et al. 2014). The phylogenetic structure of communities could affect the type and strength of biological interactions, at the same time that resemble the ecological and evolutionary processes shaping local communities (Rezende et al. 2009, Schleuning et al. 2014). Several communities show phylogenetic attraction or repulsion, suggesting that the diversification history of species is a prominent component of communities' organization (e.g. Kamilar and Guidi 2010, Maherali and Klironomos 2012). Niche conservatism and phylogenetic signal in the breeding period could determine that related species are active at similar conditions conforming phylogenetically aggregated modules of species reproducing during the same months (Losos 2008, Wiens et al. 2010). This modular structure of species co-occurrence and interactions is expected to have a large role on communities functioning and stability (Olesen et al. 2007, Thébault and Fontaine 2010, Clune et al. 2013, Borthagaray et al. 2014a, Borthagaray et al. 2014b, Takemoto et al. 2014, Trøjelsgaard et al. 2015).

Amphibians are a classical model for analyzing the connection between environmental conditions, individual behavior, and community structure (Blair 1961, Crump 1974, Canavero et al. 2009). As ectotherms their metabolic rate is directly related to environmental temperature (Angilletta and Sears 2011). In addition, they depend on water availability for reproduction and to preserve homeostasis with a highly permeable skin (Zug et al. 2001). Indeed, many studies have reported strong

associations between the number of amphibian species engaged in a particular activity (e.g. reproducing) and environmental conditions (e.g. Oseen and Wassersug 2002, Saenz et al. 2006, Both et al. 2008, Canavero et al. 2008, Steen et al. 2013, Protázio et al. 2015). The temporal patterns of reproduction (i.e. breeding period) in anurans can be assigned between two ends of a continuum, from explosive to prolonged breeders (sensu Wells 1977, 2007). It has been proposed that these temporal strategies are associated to habitat quality and parental investment (Wells 1977, 2007). For instance, explosive breeding tends to occur in ephemeral ponds, usually involving similar numbers of males and females, without fish predators, and among species with very active tadpoles (Wellborn et al. 1996). In contrast, prolonged breeders tend to reproduce in permanent ponds or streams, with very structured males choruses, and females arriving asynchronously to breeding sites (Wells 1977, Oseen and Wassersug 2002, Saenz et al. 2006, Steen et al. 2013). This temporal pattern of reproduction determines that related species could be active at similar conditions conforming phylogenetically aggregated modules of amphibians reproducing simultaneously (Canavero et al. 2009). Species active at similar times would then be phylogenetically close, determining modules of related species-e.g. phylogenetic attraction (Webb et al. 2002).

In this work, we report the phenological structure in 52 communities of Neotropical anurans. We focus on three central components of community structure: phylogenetic diversity, modularity (i.e. species coexistence in time), and the temperature dependence of species richness. In order to explore the putative effects of global warming, we explore the latitudinal trend in community structure and its connection with environmental variables of 34 communities that show significant thermal dependence.

MATERIAL AND METHODS

We compiled 52 published databases of phenological activity patterns of Neotropical anuran communities (see chapter 1). For each community we recorded data on latitude, potential evapotranspiration (PET) (Hijmans et al. 2005, Rangel et al. 2006), total number of species that call at least once in the study period (S_{LOC}), an index of normalized modularity (ZMOD) (Newman and Girvan 2004, Guimera and Amaral 2005, Reichardt and Bornholdt 2006), and a phylogenetic distance index (net relatedness index, NRI) (Webb et al. 2008). In addition, we describe the thermal dependence of amphibian activity (species richness of calling males) with the community "apparent activation energy" (Allen et al. 2001). This parameter is the slope of the relationship between natural logarithm of species richness and the inverse value of temperature in degrees Kelvin multiplied by the Boltzmann constant (1/KT) (Brown and Silby 2012).

Indices estimation

Modularity was estimated using the spinglass community function in the R-Package igraph (Csardi and Nepusz 2006). Standardized deviations from null expectation in modularity (ZMOD) were estimated with a null model that randomized presence, but retained total number of species in months and the total number of months in which species were observed. Null expectations in modularity and standard deviation were estimated from 10,000 simulations. In order to measure the phylogenetic distances among communities we constructed a phylogenetic tree of the 361 species of Neotropical anurans found in our community datasets (see chapter 1, Supporting Information). Following Webb et al. (2002), the phylogenetic structure of

local communities (e.g. phylogentic attraction or repulsion) was estimated with the Net Relatedness Index (NRI)

$$NRI_{sample} = -1 \times \frac{MPD_{sample} - MPD_{rndsample}}{sd (MPD_{rndsample})}$$

where MPD_{sample} (mean pairwise distance) is the average phylogentic distance between each taxon in a sample (i.e. local community) to all other taxa from the same sample. Random communities were constructed with a null model that shuffles species labels across the phylogeny, randomizing phylogenetic relationships among species. A positive NRI value indicates that the MPD is lower than expected, suggesting phylogenetic attraction, and a negative NRI means phylogenetic repulsion. This analysis was performed with the program Phylocom (Webb et al. 2008).

Structural equation modeling

The putative causal connection between temperature dependence of amphibians' activity and the environment and community structure was studied with path analysis (Shipley 2000). Toward this aim we focused on the 34 communities that showed significant relationship between richness and temperature (e.g. with significant apparent calling activation energy, *E*). We first estimated a latent variable (unobserved variable that is correlated with observed ones) related with a subjacent gradient of environmental conditions (see Shipley 2000; Canavero and Arim 2009). This latent variable was associated with latitude, Potential evapotranspiration (PET), phylogenetic species relationship (NRI), local community richness (S_{LOC}), modularity (ZMOD), and calling activation energy (*E*). We used maximum likelihood methods and standardized coefficients in our path analysis. The overall path diagram and the significance of each single connection between couples of variables were tested using
the Structural Equation Modeling (SEM). To assess the significance of the overall path model, we used a χ^2 statistic computed from the departure between the observed and expected covariance matrix from the proposed path model (Shipley 2000). A significant χ^2 (P < 0.05) indicates that the model is not supported by the data. The explained variance for each endogenous variable is estimated as one minus the path coefficient between its associated error variable (Shipley 2000). Because our data matrix does not present multivariate normality based on kurtosis (using the mvnorm.kur.test function of the ICS R-Package, W = 27.4605, w1 = 0.48, df1 =35.00, w2 = 0.80, df2 = 1.00, p-value < 0.05) we used the Satorra–Bentler robust estimation of the Chi-squared statistic and standard error (Rosseel 2012). This method corrects excessive kurtosis, problems in which the errors are not independent of their causal non-descendants and is important for models with latent variables (Shipley 2000). In order to identify plausible causal models, we considered 15 models covering the potential range of connections that could be expected in the study system (see Supporting Figure 1). All SEM models were fitted using the R-Package lavaan (Rosseel 2012) and compared by the Akaike's Information Criterion corrected for small samples (AIC_C); the lowest AIC_C values were selected (see the Supporting Information). Analyses were performed using R version 3.03 (R Core Team 2014).

RESULTS

Of the 34 time series considered, 25 yielded ZMOD index significantly deviated from null expectations (P<0.05), 22 positively and three negatively (Table

1). Eleven communities presented significant deviations (P<0.05) from null expectations of NRI and seven presented marginal deviations (P<0.1). Of the eighteen communities that presented marginal and significant deviations, fifteen showed phylogenetic attraction and three repulsion (Table 1). Along the 15 models of path analysis considered (see Supporting Figure 1), one of them presented a significantly better performance and no discrepancy with observed covariation matrix (w_i AIC_C=0.571) (Fig. 2). This model considered a latent variable directly related with a positive connection with latitude (r=0.81) and NRI (r=0.52), and a negative connection with *E* (r=-0.82) and PET (r=-0.70) (Fig. 2). Further, the path model also indicated an effect over ZMOD from *E* (r=-0.60), PET (r=0.56), and S_{LOC} (r=0.36). This model accounted for 27% of the variation in phylogenetic relatedness (NRI), 42% of the ZMOD variance, and 68% of the variation in thermal dependence of the activity in amphibian communities (Fig. 2).

DISCUSSION

Phenology is a key pattern of community structure, determining the intensity and nature of biotic interactions, community structure, and ecosystem functioning (Forrest and Miller-Rushing 2010). In a scenario of global change in climatic conditions and species diversity, understanding the interplay between enviornmental temperature, phenology, species richness, and community structure has became a pressing issue (Root et al. 2003, Parmesan 2006, Thackeray et al. 2010, Jenouvrier and Visser 2011, Pau et al. 2011, Sutherland et al. 2013). Amphibian phenologies present a number of advantages to approach these aims (Forrest and Miller-Rushing

2010, Steen et al. 2013). First, herpetologists have reported annual trends in activity for several locations, covering a wide geographic range in the Neotropics, with significant climatic and biodiversity variability. Second, the evolutionary history of amphibians in this region is relatively well known (e.g. Wiens et al. 2006) allowing to quantify and compare the phylogenetic community structure (Pyron and Wiens 2011, Wiens 2011). The present study expands the scope of amphibian phenological studies, exploring the thermal dependence in an explicit metabolic framework, and its interplay with phylogenetic community structure and modularity.

Environmental filtering is probably a main mechanisms shaping phenologies and their geographic trends among local communities (Cornell and Harrison 2014, Mittelbach and Schemske 2015). Since the origins of modern ecology, researchers have tried to integrate ecological and evolutionary processes in order to understand the structure of biological communities (Darwin 1859, Hutchinson 1965). Community phylogenetics recently highlighted the prevalence of eco-evolutionary mechanisms structuring communities, and emphasized the connection between phylogeny and species traits, which determines organisms' interactions and environmental requirements (Webb et al. 2002, Cavender-Bares et al. 2009, Cavender-Bares et al. 2012, Mouquet et al. 2012). The amphibian phenologies herein analyzed show phylogenetic structure indicating that processes such as niche conservatism and phylogenetic signal are involved (Losos 2010, Wiens et al. 2010). The detection of both, phylogenetic attraction and repulsion, suggest two important patterns in amphibian phenologies: First, relevant traits for the temporal structuring of amphibian communities are well captured in their phylogeny (Wiens et al. 2006), and secondly, a trait-mediated assembly of community structure (Shipley 2010). The observed phylogenetic structure is congruent with a role of species filtering and also of

antagonistic interactions. Without trait convergence phylogenetic attraction is the result of environmental filtering; however, the opposite is true when trait convergence has occurred (Webb et al. 2002).

The identification of a modular structure in species activity through time implies that species tend to call together along the year for most of the Neotropical communities (Kronfeld-Schor and Dayan 2003). The identification of modularity as a prevalent feature of phenologies is a novel contribution for the understanding of the temporal structuring of species activities (Canavero et al. 2009). Indeed, this result is congruent with the recent identification of a modular organization of species interactions as a main feature of communities, closely related with their phylogenetic structure (Olesen et al. 2007, Rezende et al. 2009) and stability (Fonseca and Ganade 2001, Cadotte et al. 2011, Naeem et al. 2012). Further, modularity has been associated to network stability (Thébault and Fontaine 2010, Borthagaray et al. 2014a), landscape perception (Borthagaray et al. 2014b), and geographic structure (Trøjelsgaard and Olesen 2013, Borthagaray et al. 2014b, Takemoto et al. 2014).

Using a phenological perspective, in chapter 1 we reported a thermal dependency of the number of anuran species that present calling activity in a given month (Allen et al. 2002). The thermal dependence of amphibian community activity as captured in the apparent activation energy of calling—E—was reported elsewhere as an emerging parameter in thermal biology, potentially connecting patterns at different level of organization with temperature (Craine et al. 2010, Sinsabaugh and Follstad Shah 2010, Yvon-Durocher et al. 2012, Segura et al. 2015). The community activity with temperature (chapter 1). But it should be considered that the interpretation of this parameter is not necessarily restricted to a mechanistic connection between

temperature, metabolism and species coexistence (Craine et al. 2010, Sinsabaugh and Follstad Shah 2010, Yvon-Durocher et al. 2012). Indeed, it represents a useful index, which in the present study allows us exploring the interdependence between temperature, productivity, latitude and main features of communities such as richness, modularity, and phylogenetic structure. Understanding the interplay among the functional energetics of organisms, their dependence on temperature, and their consequences at higher levels of organization is a pressing issue for ecology in a global warming scenario (Dell et al. 2011b, Amarasekarek and Coutinho 2014, Dell et al. 2014).

The description of latitudinal diversity patterns and the understanding of the underlying mechanisms has been a main concern of ecology and biogeography for more than two centuries (Willig et al. 2003, Hawkins and Diniz-Filho 2004, Hillebrand 2004, Araújo and Costa-Pereira 2013). Here we show the interdependence among phylogenic structure, modular structure, thermal dependence, and environmental energy supply (i.e. potential evapotranspiration). Several insights emerge from the path analysis (Fig. 2), from which a gradient involving latitude, activation energy, potential evapotranspiration and phylogenetic structure is detected, as well as a dependence of the degree of community modularity on the available energy (PET), local richness, and activation energy. It should be first highlighted that phylogenetic attraction becomes more important at higher latitudes, which is congruent with an increasing role of species filtering; probably related to the harsher environmental conditions for amphibians (Cornell and Harrison 2014, Mittelbach and Schemske 2015). Supporting this view is the detection of a phylogenetic signal in climatic niches of amphibians (Hof et al. 2010, Olalla-Tárraga et al. 2011, Fritz and Rahbek 2012), with a strong niche conservatism for cold tolerance (Olalla-Tárraga et

al. 2011), and in that temperature seasonality is one of the factors limiting geographic expansion of Hylid frogs (Wiens et al. 2006). A second point to highlight is that thermal dependence, as is captured in the apparent activation energy, decreases with latitude but increases with available energy. These trends are congruent with ectotherm biology. Higher latitude environments with lower temperatures provide lower thermic resources for ectotherm activity (Allen et al. 2002). The negative association between activation energy and latitude (i.e. opposite correlations with the latent variable, see Fig. 2) is congruent with a larger use of environmental temperature to fuel activities when temperature is high, and a tendency to thermal independence, to activate the metabolism of ectotherms, in those communities placed in environments with lower temperatures (see also Dell et al. 2011a, Dell et al. 2014).

Finally, it is important to discuss the connection of environmental energy supply (PET), activation energy (community thermal dependence), and species richness, as determinants of the modular organization of amphibian phenologies. The increase in modularity with richness is a long-standing prediction in ecology (May 1972) rarely evaluated on empirical grounds (but see Thébault and Fontaine 2010). It has been suggested that modularity could be favored in changing environments (e.g. Clune et al. 2013, Friedlander et al. 2013), which is in agreement with the lower thermal dependence at higher latitudes, since latitude is typically associated with the strength of environmental variation (e.g., temperature, precipitation, productivity, day length). If anything, our results reinforce the idea that the connection between modularity and environmental conditions is a "key area for active investigation" (Takemoto et al. 2014).

In synthesis we found significant patterns of three main components of community structure: phylogenetic structure, phenological modularity, and

phenological thermal dependence (Morin 2010). Analyzing the geographical gradients of thermo-dependent communities, we found an interconected complex system. To embrace this complexity and to look for its underlining basis, is an urgent task to understand the extent and magnitude of the impacts of global change on biodiversity structure and functioning (McCann 2007, Naeem et al. 2012, Rohr et al. 2014).

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Table 1.

Reference of the Neotropical anuran data and their geographic locations. S_{LOC} , total number of species that call at least once in the study period. Included is the fit of the metabolic parameter *E*, apparent calling activation energy (for statistical details of the metabolic model see Canavero et al. chapter 1); ZMOD, modularity index; NRI, net relatedness index; and PET, potential evapotranspiration. Dark and light grey cells indicate significant Z values at P < 0.05 and marginal Z values at P < 0.1, respectively.

1.Abrunhosa et al. (2006) $22^{\circ}50'S; 42^{\circ}27'W$ 19 2.319 1.64 0.481 82.002 2.Afonso & Eterovick (2007) $20^{\circ}05'S; 43^{\circ}29'W$ 12 0.623 $3.51'$ 0.6848 79.910 3.Arzabe (1999) $07^{\circ}11'S; 37^{\circ}11'W$ 16 3.257 -0.13 -1.660 103.820 5.Arzabe et al. (1998) $11^{\circ}20'S; 37^{\circ}21'W$ 17 -1.033 5.72 -0.512 115.073 6.Ávila & Ferreira (2004) $18^{\circ}58'S; 57^{\circ}39'W$ 15 2.562 -0.80 -0.823 126.480 7.Bernarde & do Anjos (1999) $21^{\circ}16'S; 50^{\circ}37'W$ 19 $1.735'$ 0.14 -0.186 98.930 9.Bernarde & Machado (2000) $25^{\circ}27'S; 51^{\circ}15'W$ 18 $0.754'$ $2.242'$ $77.917'$ 10.Bernarde (2007) $11^{\circ}35'S; 60^{\circ}41'W$ 31 $0.354'$ 6.63 $0.333'$ $87.138'$ 11.Bertoluci (1998) $24^{\circ}15'S; 48^{\circ}24'W$ 26 $0.978'$ $3.54'$ $1.974'$ $73.162'$ 12.Bertoluci (1997) $16^{\circ}39'S; 48^{\circ}36'W'$ 13 $1.476'$ $2.57'$ $0.443'$ $85.403'$ 13.Blamires et al. (2007) $17^{\circ}87'S; 49^{\circ}23'W'$ 25 $2.31'$ $4.14'$ $-1.032'$ $97.730'$ 15.Both et al. (2008) $29^{\circ}32'S; 53^{\circ}47'W'$ 18 $0.859'$ $-0.78'$ $-0.35'$ $77.418'$ 16.Canavero et al. (2007) $20^{\circ}95'S; 43^{\circ}28'W'$ 32 $1.666'$ $6.80'$ </th <th></th> <th>Reference</th> <th colspan="2">Locality S_{LOC} <i>E</i> ZMOD NR</th> <th>NRI</th> <th>PET</th>		Reference	Locality S_{LOC} <i>E</i> ZMOD NR		NRI	PET		
2.Afonso & Eterovick (2007) $20^{\circ}0^{\circ}5^{\circ}; 43^{\circ}29^{\circ}W$ 12 0.623 3.51 0.848 79.910 3.Arzabe (1999) $07^{\circ}17^{\circ}5; 37^{\circ}21^{\circ}W$ 11 3.524 -1.05 -0.687 103.820 5.Arzabe (1999) $07^{\circ}11^{\circ}5; 37^{\circ}25^{\circ}W$ 17 -1.033 5.72 -0.512 115.073 6.Ávila & Ferreira (2004) $18^{\circ}8^{\circ}8^{\circ}5; 51^{\circ}15^{\circ}W$ 18 0.754 2.24 0.457 81.373 7.Bernarde & Kokubum (1999) $21^{\circ}16^{\circ}5; 50^{\circ}37^{\circ}W$ 19 1.735 0.14 -0.186 89.30 9.Bernarde & Kodubum (1999) $21^{\circ}16^{\circ}5; 50^{\circ}37^{\circ}W$ 10 0.997 -1.57 -1.647 69.233 10.Bernarde & Rodrigues (2002) $23^{\circ}38^{\circ}5, 45^{\circ}52^{\circ}W$ 28 0.951 4.23 2.462 77.917 12.Bertoluci (1998) $24^{\circ}15^{\circ}5; 48^{\circ}24^{\circ}W$ 26 0.978 3.54 -1.032 97.330 13.Blamires et al. (1997) $16^{\circ}39^{\circ}5; 48^{\circ}36^{\circ}W$ 13 1.476 2.57 0.443 85.403 14.Borges et al. (2008) $29^{\circ}22^{\circ}5; 53^{\circ}47^{\circ}W$ 18 0.859 -0.78 -0.335 77.418 16.Canavero et al. (2008) $34^{\circ}47^{\circ}5; 52^{\circ}22^{\circ}W$ 10 0.674 2.31 -1.325 68.460 17.Candeira (2007) $20^{\circ}05^{\circ}5; 49^{\circ}11^{\circ}W$ 24 3.181 -2.81 -1.293 95.515 18.Canavero et al. (2008)<	1.	Abrunhosa et al. (2006)	22°50'S; 42°27'W	19	2.319	1.64	0.481	82.002
3.Arzabe (1999) $07^{\circ}17'S; 37^{\circ}21'W$ 113.524-1.05-0.687103.8204.Arzabe (1999) $07^{\circ}11'S; 37^{\circ}21'W$ 163.257-0.13-1.260103.8205.Arzabe et al. (1998) $11^{\circ}20'S; 37^{\circ}25'W$ 17-1.0335.72-0.512115.0736.Ávila & Ferreira (2004)18°58'S; 57'39'W152.562-0.80-0.823126.4807.Bernarde & Machado (2000)25°27'S; 51°15'W180.7542.240.45781.3738.Bernarde & Machado (2000)25°27'S; 53°07'W200.997-1.57-1.64769.23310.Bernarde (2007)11°35'S; 60°41'W330.3546.630.03387.13811.Bertoluci (1998)24°15'S; 48°24'W260.9783.541.97473.16212.Bertoluci (1997)16°39'S; 48°36'W131.4762.570.44385.40314.Borges et al. (2007)17°87'S; 49°23'W252.3184.14-1.03297.3015.Both et al. (2008)29°32'S; 53°47'W180.859-0.78-0.33577.41816.Canavero et al. (2007)20°02'S; 49°11'W243.181-2.81-1.29395.1515.Cancleas & Berloluci (2007)20°07'S; 43°28'W321.6666.801.32179.91019.Cardoso & Suza (1996)10°08'S; 67°35'W312.598-0.721.848119.99821. <t< td=""><td>2.</td><td>Afonso & Eterovick (2007)</td><td>20°05'S; 43°29'W</td><td>12</td><td>0.623</td><td>3.51</td><td>0.848</td><td>79.910</td></t<>	2.	Afonso & Eterovick (2007)	20°05'S; 43°29'W	12	0.623	3.51	0.848	79.910
4.Arzabe (1999) $07^{\circ}11'S; 37^{\circ}19'W$ 16 3.257 -0.13 -1.260 103.820 5.Árzabe et al. (1998) $11^{\circ}20'S; 37^{\circ}25'W$ 17 -1.033 5.72 -0.512 115.073 6.Ávila & Ferreira (2004) $18'58'S; 57'35'W$ 15 2.562 -0.80 -0.823 126.480 7.Bernarde & dos Anjos (1999) $23'27'S; 51^{\circ}15'W$ 18 0.754 2.24 0.457 81.373 8.Bernarde & Machado (2000) $25'27'S; 53'07'W$ 20 0.997 -1.57 -1.647 69.233 10.Bernarde (2007) $11'35'S; 60'41'W$ 30.354 6.63 0.033 87.138 11.Bertoluci & Rodrigues (2002) $23'3'8'S; 45'52'W$ 28 0.951 4.23 2.462 77.917 12.Bertoluci (1998) $24'15'S; 48'24'W$ 26 0.978 3.54 1.974 73.162 13.Blamires et al. (2007) $1'6'39'S; 48'36'W$ 13 1.476 2.57 0.443 85.403 14.Borges et al. (2007) $29'22'S; 53'47'W$ 18 0.859 -0.78 -0.335 77.418 16.Canavero et al. (2008) $34'47'S; 55'22'W$ 10 0.674 2.31 -1.325 68.460 17.Candeira (2007) $20''20'S; 49'91'W$ 24 3.181 -2.81 -1.293 95.515 18.Canelas & Bertoluci (2007) $20''20'S; 45'^35'W$ 11 1.657 -0.76 -0.650 74.593	3.	Arzabe (1999)	07°17'S; 37°21'W	11	3.524	-1.05	-0.687	103.820
5.Arzabe et al. (1998) $11^{\circ}20^{\circ}S; 37^{\circ}25^{\circ}W$ 17 -1.033 5.72 -0.512 115.073 6.Ávila & Ferreira (2004) $18^{\circ}58^{\circ}S; 57^{\circ}39^{\circ}W$ 15 2.562 -0.80 -0.823 126.480 7.Bernarde & dos Anjos (1999) $23^{\circ}27^{\circ}S; 51^{\circ}15^{\circ}W$ 18 0.754 2.24 0.457 81.373 9.Bernarde & Machado (2000) $25^{\circ}27^{\circ}S; 53^{\circ}07^{\circ}W$ 20 0.997 -1.57 -1.647 69.233 10.Bernarde (2007) $11^{\circ}35^{\circ}S; 60^{\circ}41^{\circ}W$ 33 0.354 6.63 0.033 87.138 11.Bertoluci (198) $24^{\circ}15^{\circ}S; 48^{\circ}24^{\circ}W$ 26 0.978 3.54 1.977 73.162 12.Bertoluci (1998) $24^{\circ}15^{\circ}S; 48^{\circ}24^{\circ}W$ 26 0.978 3.54 1.977 73.162 13.Blamires et al. (1997) $16^{\circ}39^{\circ}S; 48^{\circ}36^{\circ}W$ 13 1.476 2.57 0.443 85.403 14.Borges et al. (2007) $17^{\circ}87^{\circ}S; 55^{\circ}22^{\circ}W$ 10 0.674 2.31 -1.325 68.400 15.Both et al. (2008) $34^{\circ}47^{\circ}S; 55^{\circ}22^{\circ}W$ 10 0.674 2.31 -1.325 68.460 17.Candeira (2007) $20^{\circ}05^{\circ}S; 43^{\circ}28^{\circ}W$ 32 1.666 6.80 1.321 79.910 19.Candeira (2007) $20^{\circ}05^{\circ}S; 43^{\circ}28^{\circ}W$ 31 0.674 2.31 -1.253 75.15 18.Candeira (2007) $20^{\circ}05^{\circ}S; 43^{\circ}28^{\circ}$	4.	Arzabe (1999)	07°11'S; 37°19'W	16	3.257	-0.13	-1.260	103.820
6.Ávila & Ferreira (2004) $18^{\circ}58^{\circ}S; 57^{\circ}39^{\circ}W$ 15 2.562 -0.80 -0.823 126.480 7.Bernarde & Kokubum (1999) $21^{\circ}27^{\circ}S; 51^{\circ}15^{\circ}W$ 18 0.754 2.24 0.457 81.373 8.Bernarde & Kokubum (1999) $21^{\circ}16^{\circ}S; 50^{\circ}37^{\circ}W$ 10 0.14 -0.186 98.930 9.Bernarde & Machado (2000) $25^{\circ}27^{\circ}S; 53^{\circ}07^{\circ}W$ 20 0.997 -1.57 -1.647 69.233 10.Bernarde (2007) $11^{\circ}35^{\circ}S; 60^{\circ}41^{\circ}W$ 33 0.354 6.63 0.033 87.138 11.Bertoluci (1998) $24^{\circ}15^{\circ}S; 48^{\circ}24^{\circ}W$ 26 0.978 3.54 1.974 73.162 13.Blamires et al. (2007) $17^{\circ}87; 49^{\circ}23^{\circ}W$ 25 2.318 4.14 -1.032 97.730 15.Both et al. (2008) $29^{\circ}32^{\circ}S; 33^{\circ}47^{\circ}W$ 18 0.859 -0.78 -0.335 77.418 16.Canavero et al. (2007) $20^{\circ}05^{\circ}S; 43^{\circ}22^{\circ}W$ 22 1.666 6.80 1.321 79.910 19.Cardoso & Haddad (1992) $21^{\circ}48^{\circ}36^{\circ}55^{\circ}W$ 19 1.657 -0.76 -0.650 74.593 20.Cardoso & Souza (1996) $10^{\circ}08^{\circ}S; 67^{\circ}55^{\circ}W$ 31 2.598 -0.72 1.848 119.998 21.Conte & Machado (2005) $25^{\circ}57^{\circ}S; 49^{\circ}13^{\circ}W$ 21 1.682 0.50 1.833 66.385 22.Conte & Machado (2005)	5.	Arzabe et al. (1998)	11°20'S; 37°25'W	17	-1.033	5.72	-0.512	115.073
7.Bernarde & dos Anjos (1999) $23^{\circ}27$ 'S; $51^{\circ}15$ 'W18 0.754 2.24 0.457 81.373 8.Bernarde & Kokubum (1999) $21^{\circ}16$ 'S; $50^{\circ}37$ 'W19 1.735 0.14 -0.186 98.930 9.Bernarde & Machado (2000) $25^{\circ}27$ 'S; $53^{\circ}07$ 'W20 0.997 -1.57 -1.647 69.233 10.Bernarde (2007) $11^{\circ}35$ 'S; $46^{\circ}24$ 'W20 0.978 3.54 6.63 0.033 87.138 11.Bertoluci (1998) $24^{\circ}15$ 'S; $48^{\circ}24$ 'W26 0.978 3.54 1.974 73.162 13.Blamires et al. (1997) $16^{\circ}39$ 'S; $48^{\circ}36'$ W13 1.476 2.57 0.443 85.403 14.Borges et al. (2007) $17^{\circ}87$ 'S; $49^{\circ}23'$ W25 2.318 4.14 -1.032 97.730 15.Both et al. (2008) $29^{\circ}32$ 'S; $55^{\circ}24'$ W10 0.674 2.31 -1.325 68.460 17.Candeira (2007) $20^{\circ}20$ 'S; $49^{\circ}11'$ W24 3.181 -2.81 -1.293 95.515 18.Candoso & Haddad (1992) $21^{\circ}48'$ S; $46^{\circ}35'$ W19 1.657 -0.76 -0.660 74.593 20.Cardoso & Kasa-Feres (2006) $25^{\circ}71'$ S; $49^{\circ}03'$ W31 0.847 2.51 0.836 66.385 22.Conte & Machado (2005) $25^{\circ}57'$ S; $49^{\circ}03'$ W31 0.847 2.51 0.836 66.385 23.Conte & Machado (2005) $25^{\circ}57'$ S; $49^{\circ}03'$ W <td>6.</td> <td>Ávila & Ferreira (2004)</td> <td>18°58'S; 57°39'W</td> <td>15</td> <td>2.562</td> <td>-0.80</td> <td>-0.823</td> <td>126.480</td>	6.	Ávila & Ferreira (2004)	18°58'S; 57°39'W	15	2.562	-0.80	-0.823	126.480
8.Bernarde & Kokubum (1999) $21^{\circ}16'S; 50^{\circ}37'W$ 19 1.735 0.14 -0.186 98.930 9.Bernarde & Machado (2000) $25^{\circ}27'S; 53^{\circ}07'W$ 20 0.997 -1.57 -1.647 69.233 10.Bernarde (2007) $11^{\circ}35'S; 60^{\circ}41'W$ 33 0.351 6.63 0.033 87.138 11.Bertoluci (1998) $24^{\circ}15'S; 48^{\circ}24'W$ 26 0.978 3.54 1.974 73.162 13.Blamires et al. (1997) $16^{\circ}39'S; 48^{\circ}36'W$ 13 1.476 2.57 0.443 85.403 14.Borges et al. (2007) $17^{\circ}87'S; 49^{\circ}23'W$ 25 2.318 4.14 -1.032 97.730 15.Both et al. (2008) $29^{\circ}22'S; 53^{\circ}47'W$ 18 0.859 -0.78 -0.335 77.418 16.Canavero et al. (2008) $34^{\circ}47'S; 55^{\circ}22'W$ 10 0.674 2.31 -1.233 95.515 18.Canelas & Bertoluci (2007) $20^{\circ}05'S; 43^{\circ}28'W$ 32 1.606 6.80 1.321 79.910 19.Cardoso & Souza (1996) $10^{\circ}08'S; 67^{\circ}35'W$ 31 2.598 -0.72 1.848 119.998 21.Conte & Machado (2005) $25^{\circ}57'S; 49^{\circ}13'W$ 24 0.847 2.51 0.836 66.385 22.Conte & Machado (2005) $25^{\circ}57'S; 56^{\circ}3'W$ 31 0.847 2.51 0.836 66.385 23.Conte & Rosa-Feres (2006) $25^{\circ}41^{\circ}S, 45^{\circ}2'W$ 20 0	7.	Bernarde & dos Anjos (1999)	23°27'S; 51°15'W	18	0.754	2.24	0.457	81.373
9.Bernarde & Machado (2000) $25^{\circ}27$ 'S; $53^{\circ}07$ 'W20 0.997 -1.57 -1.647 69.233 10.Bernarde (2007) $11^{\circ}35$ 'S; $60^{\circ}41$ 'W33 0.354 6.63 0.033 87.138 11.Bertoluci & Rodrigues (2002) $23^{\circ}38$ 'S; $45^{\circ}52$ 'W28 0.951 4.23 2.462 77.917 12.Bertoluci (1998) $24^{\circ}15$ 'S; $48^{\circ}24$ 'W26 0.978 3.54 1.974 73.162 13.Blamires et al. (2007) $17^{\circ}87'S$; $49^{\circ}23'W$ 25 2.318 4.14 -1.032 97.730 15.Both et al. (2008) $29^{\circ}32'S$; $53^{\circ}47'W$ 18 0.859 -0.78 -0.335 77.418 16.Canavero et al. (2008) $34^{\circ}47$ 'S; $55^{\circ}22'W$ 10 0.674 2.31 -1.252 68.460 17.Candeira (2007) $20^{\circ}20'S$; $49^{\circ}11'W$ 24 3.181 -2.81 -1.293 95.515 18.Canelas & Bertoluci (2007) $20^{\circ}05'S$; $43^{\circ}28'W$ 32 1.666 6.80 1.321 79.910 19.Cardoso & Souza (1996) $10^{\circ}08'S$; $67^{\circ}35'W$ 31 2.598 -0.72 1.848 119.998 21.Conte & Rosa-Feres (2006) $25^{\circ}41'S$; $49^{\circ}03'W$ 31 0.847 2.51 0.836 66.385 23.Conte & Rosa-Feres (2007) $25^{\circ}95'S$; $49^{\circ}13'W$ 21 1.682 0.50 1.833 66.385 24.Filho (209) $24^{\circ}02'S$; $47^{\circ}53'W$ 20 $0.$	8.	Bernarde & Kokubum (1999)	21°16'S; 50°37'W	19	1.735	0.14	-0.186	98.930
10.Bernarde (2007) $11^{\circ}35^{\circ}S; 60^{\circ}41^{\circ}W$ 33 0.354 6.63 0.033 87.138 11.Bertoluci & Rodrigues (2002) $23^{\circ}38^{\circ}S; 45^{\circ}52^{\circ}W$ 28 0.951 4.23 2.462 77.917 12.Bertoluci (1998) $24^{\circ}15^{\circ}S; 48^{\circ}24^{\circ}W$ 26 0.978 3.54 1.974 73.162 13.Blamires et al. (1997) $17^{\circ}87^{\circ}S; 49^{\circ}23^{\circ}W$ 25 2.318 4.14 -1.032 97.730 15.Both et al. (2008) $29^{\circ}32^{\circ}S; 53^{\circ}47^{\circ}W$ 18 0.859 -0.78 -0.335 77.418 16.Canavero et al. (2008) $34^{\circ}47^{\circ}S; 55^{\circ}22^{\circ}W$ 10 0.674 2.31 -1.325 68.460 17.Candeira (2007) $20^{\circ}20^{\circ}S; 43^{\circ}28^{\circ}W$ 32 1.666 6.80 1.321 79.910 19.Cardoso & Haddad (1992) $21^{\circ}48^{\circ}S; 46^{\circ}35^{\circ}W$ 11 1.657 -0.76 -0.650 74.593 20.Cardoso & Souza (1996) $10^{\circ}08^{\circ}S; 67^{\circ}35^{\circ}W$ 31 2.598 -0.72 1.888 163.85 22.Conte & Rosa-Feres (2006) $25^{\circ}41^{\circ}S; 49^{\circ}03^{\circ}W$ 31 0.847 2.51 0.836 66.385 23.Conte & Rosa-Feres (2007) $25^{\circ}39^{\circ}S; 47^{\circ}53^{\circ}W$ 20 0.482 0.87 1.330 76.278 24.Filho (2009) $20^{\circ}5^{\circ}S; 56^{\circ}6^{\circ}W$ 15 2.156 4.32 -0.20 $18.85^{\circ}52^{\circ}W$ 25.Forti (2009) $24^{\circ}05^$	9.	Bernarde & Machado (2000)	25°27'S; 53°07'W	20	0.997	-1.57	-1.647	69.233
11.Bertoluci & Rodrigues (2002) $23^{\circ}38'S; 45^{\circ}52'W$ 28 0.951 4.23 2.462 77.917 12.Bertoluci (1998) $24^{\circ}15'S; 48^{\circ}24'W$ 26 0.978 3.54 1.974 73.162 13.Blamires <i>et al.</i> (1997) $16^{\circ}39'S; 48^{\circ}36'W$ 13 1.476 2.57 0.443 85.403 14.Borges <i>et al.</i> (2007) $17^{\circ}87'S; 49^{\circ}23'W$ 25 2.318 4.14 -1.032 97.730 15.Both <i>et al.</i> (2008) $29^{\circ}32'S; 53^{\circ}47'W$ 18 0.859 -0.78 -0.335 77.418 16.Canavero <i>et al.</i> (2007) $20^{\circ}05'S; 49^{\circ}11'W$ 24 3.181 -2.81 -1.293 95.515 18.Canclas & Bertoluci (2007) $20^{\circ}05'S; 43^{\circ}28'W$ 32 1.606 6.80 1.321 79.910 19.Cardoso & Haddad (1992) $21^{\circ}48'S; 46^{\circ}35'W$ 19 1.657 -0.76 -0.650 74.593 20.Cardoso & Souza (1996) $10^{\circ}08'S; 67^{\circ}35'W$ 31 2.598 -0.72 1.848 119.998 21.Conte & Rosa-Feres (2006) $25^{\circ}41'S; 49^{\circ}03'W$ 31 0.847 2.51 0.836 66.385 23.Conte & Rosa-Feres (2007) $20^{\circ}05'S; 56^{\circ}36'W$ 15 2.156 4.32 -0.220 108.575 25.Forti (2009) $24^{\circ}02'S; 47^{\circ}53'W$ 20 0.482 0.87 1.330 76.278 26.Grandinetti & Jacobi (2005) $20^{\circ}07'S; 43^{\circ}52'W$ 35 $2.$	10.	Bernarde (2007)	11°35'S; 60°41'W	33	0.354	6.63	0.033	87.138
12.Bertoluci (1998) $24^{\circ}15'S; 48^{\circ}24'W$ 26 0.978 3.54 1.974 73.162 13.Blamires et al. (1997) $16^{\circ}39'S; 48^{\circ}36'W$ 13 1.476 2.57 0.443 85.403 14.Borges et al. (2007) $17^{\circ}87'S; 49^{\circ}23'W$ 25 2.318 4.14 -1.032 97.730 15.Both et al. (2008) $29^{\circ}32'S; 53^{\circ}47'W$ 18 0.859 -0.78 -0.335 77.418 16.Canavero et al. (2007) $20^{\circ}20'S; 49^{\circ}11'W$ 24 3.181 -2.81 -1.293 95.515 18.Canclas & Bertoluci (2007) $20^{\circ}05'S; 43^{\circ}28'W$ 32 1.606 6.80 1.321 79.910 19.Cardoso & Haddad (1992) $21^{\circ}48'S; 66^{\circ}35'W$ 19 1.657 -0.76 -0.650 74.593 20.Cardoso & Souza (1996) $10^{\circ}08'S; 67^{\circ}35'W$ 31 2.598 -0.72 1.848 119.998 21.Conte & Rosa-Feres (2006) $25^{\circ}1'S; 49^{\circ}13'W$ 21 1.682 0.50 1.883 66.385 23.Conte & Rosa-Feres (2007) $25^{\circ}39'S; 49^{\circ}16'W$ 29 1.550 -1.58 0.690 66.385 25.Forti (2009) $24^{\circ}02'S; 47^{\circ}53'W$ 20 0.482 0.87 1.330 79.910 27.Heyer et al. (1990) $23^{\circ}38'S; 45^{\circ}52'W$ 35 2.972 0.76 1.343 79.910 28.Kopp & Eterovick (2006) $20^{\circ}06'S; 43^{\circ}29'W$ 20 1.612 2.08 <td>11.</td> <td>Bertoluci & Rodrigues (2002)</td> <td>23°38'S; 45°52'W</td> <td>28</td> <td>0.951</td> <td>4.23</td> <td>2.462</td> <td>77.917</td>	11.	Bertoluci & Rodrigues (2002)	23°38'S; 45°52'W	28	0.951	4.23	2.462	77.917
13. Blamires et al. (1997) $16^{\circ}39^{\circ}S; 48^{\circ}36^{\circ}W$ 13 1.476 2.57 0.443 85.403 14. Borges et al. (2007) $17^{\circ}87^{\circ}S; 49^{\circ}23^{\circ}W$ 25 2.318 4.14 -1.032 97.730 15. Both et al. (2008) $29^{\circ}32^{\circ}S; 53^{\circ}47^{\circ}W$ 18 0.859 -0.78 -0.335 77.418 16. Canavero et al. (2008) $34^{\circ}47^{\circ}S; 55^{\circ}22^{\circ}W$ 10 0.674 2.31 -1.325 68.460 17. Candeira (2007) $20^{\circ}05^{\circ}S; 43^{\circ}28^{\circ}W$ 32 1.606 6.80 1.321 79.910 19. Cardoso & Haddad (1992) $21^{\circ}48^{\circ}S; 46^{\circ}35^{\circ}W$ 31 2.598 -0.72 1.848 119.998 20. Cardoso & Souza (1996) $10^{\circ}08^{\circ}S; 67^{\circ}35^{\circ}W$ 31 2.598 -0.72 1.848 119.998 21. Conte & Machado (2005) $25^{\circ}57^{\circ}S; 49^{\circ}13^{\circ}W$ 21 1.682 0.50 1.883 66.385 22. Conte & Rosa-Feres (2006) $25^{\circ}41^{\circ}S; 49^{\circ}03^{\circ}W$ 31 0.847 2.51 0.836 66.385 23. Conte & Rosa-Feres (2007) $25^{\circ}39^{\circ}S; 56^{\circ}36^{\circ}W$ 15 2.156 4.32 -0.220 108.575 25. Forti (2009) $24^{\circ}02^{\circ}S; 43^{\circ}23^{\circ}W$ 20 0.482 0.87 1.330 76.278 26. Grandinetti & Jacobi (2005) $20^{\circ}07^{\circ}S; 43^{\circ}23^{\circ}W$ 20 0.482 0.87 1.330 76.278 26. Grandinetti & Jacobi (2005) $20^{\circ}07^{\circ}S; 43^{\circ}23^{\circ}W$ 20 1.612 2.0	12.	Bertoluci (1998)	24°15'S; 48°24'W	26	0.978	3.54	1.974	73.162
14. Borges et al. (2007) $17^{\circ}87^{\circ}S; 49^{\circ}23^{\circ}W$ 25 2.318 4.14 -1.032 97.730 15. Both et al. (2008) $29^{\circ}32^{\circ}S; 53^{\circ}47^{\circ}W$ 18 0.859 -0.78 -0.335 77.418 16. Canavero et al. (2008) $34^{\circ}47^{\circ}S; 55^{\circ}22^{\circ}W$ 10 0.674 2.31 -1.325 68.460 17. Candeira (2007) $20^{\circ}20^{\circ}S; 49^{\circ}11^{\circ}W$ 24 3.181 -2.81 -1.293 95.515 18. Canelas & Bertoluci (2007) $20^{\circ}05^{\circ}S; 43^{\circ}28^{\circ}W$ 32 1.666 6.80 1.321 79.910 19. Cardoso & Haddad (1992) $21^{\circ}48^{\circ}S; 46^{\circ}35^{\circ}W$ 31 2.598 -0.72 1.848 119.998 20. Cardoso & Souza (1996) $10^{\circ}08^{\circ}S; 67^{\circ}35^{\circ}W$ 31 2.598 -0.72 1.848 119.998 21. Conte & Rosa-Feres (2006) $25^{\circ}41^{\circ}S; 49^{\circ}03^{\circ}W$ 31 0.847 2.51 0.836 66.385 23. Conte & Rosa-Feres (2007) $25^{\circ}37^{\circ}S; 49^{\circ}13^{\circ}W$ 20 0.482 0.87 1.330 76.278 24. Filho (2009) $24^{\circ}02^{\circ}S; 56^{\circ}36^{\circ}W$ 15 2.156 4.32 -0.220 108.575 25. Forti (2009) $24^{\circ}02^{\circ}S; 43^{\circ}52^{\circ}W$ 35 2.972 0.76 1.343 77.910 27. Heyer et al. (1990) $23^{\circ}38^{\circ}S; 45^{\circ}52^{\circ}W$ 35 2.972 0.76 1.343 77.917 28. Kopp & Eterovick (2006) $20^{\circ}06^{\circ}S; 43^{\circ}29^{\circ}W$ 20 1.612 2.08 0.896 79.910	13.	Blamires et al. (1997)	16°39'S; 48°36'W	13	1.476	2.57	0.443	85.403
15.Both et al. (2008) $29^{\circ}32^{\circ}S; 53^{\circ}47^{\circ}W$ 18 0.859 -0.78 -0.335 77.418 16.Canavero et al. (2008) $34^{\circ}47^{\circ}S; 55^{\circ}22^{\circ}W$ 10 0.674 2.31 -1.325 68.460 17.Candeira (2007) $20^{\circ}20^{\circ}S; 49^{\circ}11^{\circ}W$ 24 3.181 -2.81 -1.293 95.515 18.Canelas & Bertoluci (2007) $20^{\circ}20^{\circ}S; 43^{\circ}28^{\circ}W$ 32 1.606 6.80 1.321 79.910 19.Cardoso & Souza (1996) $10^{\circ}08^{\circ}S; 67^{\circ}35^{\circ}W$ 31 2.598 -0.72 1.848 119.998 20.Cardoso & Souza (1996) $10^{\circ}08^{\circ}S; 67^{\circ}35^{\circ}W$ 31 2.598 -0.72 1.848 119.998 21.Conte & Machado (2005) $25^{\circ}57^{\circ}S; 49^{\circ}13^{\circ}W$ 21 1.682 0.50 1.883 66.385 22.Conte & Rosa-Feres (2006) $25^{\circ}41^{\circ}S; 49^{\circ}03^{\circ}W$ 31 0.847 2.51 0.836 66.385 23.Conte & Rosa-Feres (2007) $25^{\circ}37^{\circ}S; 49^{\circ}13^{\circ}W$ 20 0.482 0.87 1.330 76.278 24.Filho (2009) $24^{\circ}02^{\circ}S; 47^{\circ}53^{\circ}W$ 20 0.482 0.87 1.330 76.278 24.Grandinetti & Jacobi (2005) $20^{\circ}06^{\circ}S; 43^{\circ}22^{\circ}W$ 35 2.972 0.76 1.343 77.917 28.Kopp et al. (2010) $17^{\circ}49^{\circ}S; 52^{\circ}39^{\circ}W$ 25 2.589 -1.93 -0.694 94.135 30.Maffei	14.	Borges <i>et al.</i> (2007)	17°87'S; 49°23'W	25	2.318	4.14	-1.032	97.730
16. Canavero et al. (2008) $34^{\circ}47^{\circ}S$; $55^{\circ}22^{\circ}W$ 10 0.674 2.31 -1.325 68.460 17. Candeira (2007) $20^{\circ}20^{\circ}S$; $49^{\circ}11^{\circ}W$ 24 3.181 -2.81 -1.293 95.515 18. Canelas & Bertoluci (2007) $20^{\circ}05^{\circ}S$; $43^{\circ}28^{\circ}W$ 32 1.606 6.80 1.321 79.910 19. Cardoso & Souza (1996) $10^{\circ}08^{\circ}S$; $67^{\circ}35^{\circ}W$ 31 2.598 -0.72 1.848 119.998 21. Conte & Machado (2005) $25^{\circ}57^{\circ}S$; $49^{\circ}13^{\circ}W$ 21 1.682 0.50 1.883 66.385 22. Conte & Rosa-Feres (2006) $25^{\circ}41^{\circ}S$; $49^{\circ}03^{\circ}W$ 31 0.847 2.51 0.836 66.385 23. Conte & Rosa-Feres (2007) $25^{\circ}39^{\circ}S$; $49^{\circ}16^{\circ}W$ 29 1.550 -1.58 0.690 66.385 24. Filho (2009) $24^{\circ}02^{\circ}S$; $56^{\circ}36^{\circ}W$ 15 2.156 4.32 -0.220 108.575 25. Forti (2009) $24^{\circ}02^{\circ}S$; $43^{\circ}52^{\circ}W$ 10 0.167 1.331 1.300 79.910 27. Heyer et al. (1990) $23^{\circ}38^{\circ}S$; $48^{\circ}52^{\circ}W$ 35 2.972 0.76 1.343 77.917 28. Kopp & Eterovick (2006) $20^{\circ}6^{\circ}S$; $43^{\circ}29^{\circ}W$ 20 1.612 2.08 0.896 79.910 29. Narvaes et al. (2010) $17^{\circ}49^{\circ}S$; $52^{\circ}39^{\circ}W$ 25 2.589 -1.93 -0.694 94.135 30. Maffei (2010) $22^{\circ}48^{\circ}S$; $48^{\circ}55^{\circ}W$ 39 1.345 $7.$	15.	Both <i>et al.</i> (2008)	29°32'S; 53°47'W	18	0.859	-0.78	-0.335	77.418
17. Candeira (2007) $20^{\circ}20^{\circ}S; 49^{\circ}11^{\circ}W$ 24 3.181 -2.81 -1.293 95.515 18. Canelas & Bertoluci (2007) $20^{\circ}05^{\circ}S; 43^{\circ}28^{\circ}W$ 32 1.606 6.80 1.321 79.910 19. Cardoso & Haddad (1992) $21^{\circ}48^{\circ}S; 46^{\circ}35^{\circ}W$ 19 1.657 -0.76 -0.650 74.593 20. Cardoso & Souza (1996) $10^{\circ}08^{\circ}S; 67^{\circ}35^{\circ}W$ 31 2.598 -0.72 1.848 119.998 21. Conte & Machado (2005) $25^{\circ}57^{\circ}S; 49^{\circ}13^{\circ}W$ 21 1.682 0.50 1.883 66.385 22. Conte & Rosa-Feres (2006) $25^{\circ}41^{\circ}S; 49^{\circ}03^{\circ}W$ 31 0.847 2.51 0.836 66.385 23. Conte & Rosa-Feres (2007) $25^{\circ}39^{\circ}S; 49^{\circ}16^{\circ}W$ 29 1.550 -1.58 0.690 66.385 24. Filho (2009) $20^{\circ}05^{\circ}S; 56^{\circ}36^{\circ}W$ 15 2.156 4.32 -0.220 108.575 25. Forti (2009) $24^{\circ}02^{\circ}S; 47^{\circ}53^{\circ}W$ 20 0.482 0.87 1.330 76.278 26. Grandinetti & Jacobi (2005) $20^{\circ}07^{\circ}S; 43^{\circ}52^{\circ}W$ 35 2.972 0.76 1.343 77.917 28. Kopp & Eterovick (2006) $20^{\circ}06^{\circ}S; 43^{\circ}29^{\circ}W$ 20 1.612 2.08 0.896 79.910 29. Kopp <i>et al.</i> (2010) $17^{\circ}49^{\circ}S; 52^{\circ}39^{\circ}W$ 25 2.589 -1.93 -0.694 94.135 30. Maffei (2010) $22^{\circ}48^{\circ}S; 48^{\circ}55^{\circ}W$ 39 -3.45 7.74 $0.$	16.	Canavero et al. (2008)	34°47'S; 55°22'W	10	0.674	2.31	-1.325	68.460
18. Canelas & Bertoluci (2007) $20^{\circ}05'S; 43^{\circ}28'W$ 32 1.606 6.80 1.321 79.910 19. Cardoso & Haddad (1992) $21^{\circ}48'S; 46^{\circ}35'W$ 19 1.657 -0.76 -0.650 74.593 20. Cardoso & Souza (1996) $10^{\circ}08'S; 67^{\circ}35'W$ 31 2.598 -0.72 1.848 119.998 21. Conte & Machado (2005) $25^{\circ}57'S; 49^{\circ}13'W$ 21 1.682 0.50 1.883 66.385 22. Conte & Rosa-Feres (2006) $25^{\circ}41'S; 49^{\circ}03'W$ 31 0.847 2.51 0.836 66.385 23. Conte & Rosa-Feres (2007) $25^{\circ}39'S; 49^{\circ}16'W$ 29 1.550 -1.58 0.690 66.385 24. Filho (2009) $20^{\circ}05'S; 56^{\circ}36'W$ 15 2.156 4.32 -0.220 108.575 25. Forti (2009) $24^{\circ}02'S; 47^{\circ}53'W$ 20 0.482 0.87 1.330 76.278 26. Grandinetti & Jacobi (2005) $20^{\circ}07'S; 43^{\circ}52'W$ 35 2.972 0.76 1.343 77.917 28. Kopp & Eterovick (2006) $20^{\circ}06'S; 43^{\circ}29'W$ 20 1.612 2.08 0.896 79.910 29. Kopp <i>et al.</i> (2010) $17^{\circ}49'S; 52^{\circ}39'W$ 25 2.589 -1.93 -0.694 94.135 30. Maffei (2010) $22^{\circ}48'S; 46^{\circ}5'W$ 39 1.345 7.74 0.188 83.813 31. Moreira <i>et al.</i> (2007) $29^{\circ}42'S; 50^{\circ}59'W$ 15 -0.721 4.13 -0.737 72.685 32. Narxeas <i>et al.</i> (2009) $24^{\circ}31'S; 47^{\circ$	17.	Candeira (2007)	20°20'S; 49°11'W	24	3.181	-2.81	-1.293	95.515
19. Cardoso & Haddad (1992) $21^{\circ}48^{\circ}S; 46^{\circ}35^{\circ}W$ 19 1.657 -0.76 -0.650 74.593 20. Cardoso & Souza (1996) $10^{\circ}08^{\circ}S; 67^{\circ}35^{\circ}W$ 31 2.598 -0.72 1.848 119.998 21. Conte & Machado (2005) $25^{\circ}57^{\circ}S; 49^{\circ}13^{\circ}W$ 21 1.682 0.50 1.883 66.385 22. Conte & Rosa-Feres (2006) $25^{\circ}41^{\circ}S; 49^{\circ}03^{\circ}W$ 31 0.847 2.51 0.836 66.385 23. Conte & Rosa-Feres (2007) $25^{\circ}39^{\circ}S; 49^{\circ}16^{\circ}W$ 29 1.550 -1.58 0.690 66.385 24. Filho (2009) $20^{\circ}05^{\circ}S; 56^{\circ}36^{\circ}W$ 15 2.156 4.32 -0.220 108.575 25. Forti (2009) $24^{\circ}02^{\circ}S; 47^{\circ}53^{\circ}W$ 20 0.482 0.87 1.330 76.278 26. Grandinetti & Jacobi (2005) $20^{\circ}07^{\circ}S; 43^{\circ}52^{\circ}W$ 35 2.972 0.76 1.343 77.917 28. Kopp & Eterovick (2006) $20^{\circ}06^{\circ}S; 43^{\circ}29^{\circ}W$ 20 1.612 2.08 0.896 79.910 29. Kopp <i>et al.</i> (2010) $17^{\circ}49^{\circ}S; 52^{\circ}39^{\circ}W$ 25 2.589 -1.93 -0.694 94.135 30. Maffei (2010) $22^{\circ}48^{\circ}S; 48^{\circ}55^{\circ}W$ 39 1.345 7.74 0.188 83.813 31. Moreira <i>et al.</i> (2007) $29^{\circ}42^{\circ}S; 50^{\circ}59^{\circ}W$ 15 -0.721 -4.13 -0.737 72.685 32. Narxaes <i>et al.</i> (2009) $24^{\circ}31^{\circ}S; 46^{\circ}31^{\circ}W$ 9 0.452 1.09 2.073 70.25	18.	Canelas & Bertoluci (2007)	20°05'S; 43°28'W	32	1.606	6.80	1.321	79.910
20. Cardoso & Souza (1996) $10^{\circ}08'S; 67^{\circ}35'W$ 31 2.598 -0.72 1.848 119.998 21. Conte & Machado (2005) $25^{\circ}57'S; 49^{\circ}13'W$ 21 1.682 0.50 1.883 66.385 22. Conte & Rosa-Feres (2006) $25^{\circ}41'S; 49^{\circ}03'W$ 31 0.847 2.51 0.836 66.385 23. Conte & Rosa-Feres (2007) $25^{\circ}39'S; 49^{\circ}16'W$ 29 1.550 -1.58 0.690 66.385 24. Filho (2009) $20^{\circ}05'S; 56^{\circ}36'W$ 15 2.156 4.32 -0.220 108.575 25. Forti (2009) $24^{\circ}02'S; 47^{\circ}53'W$ 20 0.482 0.87 1.330 76.278 26. Grandinetti & Jacobi (2005) $20^{\circ}07'S; 43^{\circ}52'W$ 11 0.167 1.33 1.300 79.910 27. Heyer <i>et al.</i> (1990) $23^{\circ}38'S; 45^{\circ}52'W$ 35 2.972 0.76 1.343 77.917 28. Kopp & Eterovick (2006) $20^{\circ}06'S; 43^{\circ}29'W$ 20 1.612 2.08 0.896 79.910 29. Kopp <i>et al.</i> (2010) $17^{\circ}49'S; 52^{\circ}39'W$ 25 2.589 -1.93 -0.694 94.135 30. Maffei (2010) $22^{\circ}48'S; 48^{\circ}55'W$ 39 1.345 7.74 0.188 83.813 31. Moreira <i>et al.</i> (2007) $29^{\circ}42'S; 50^{\circ}59'W$ 15 -0.721 -4.13 -0.737 72.685 32. Narvaes <i>et al.</i> (2008) $23^{\circ}10'S; 46^{\circ}31'W$ 29 0.452 1.09 2.073 70.257 35. Nomura (2008) $23^{\circ}10'S; 46^{\circ}31'W$ 29	19.	Cardoso & Haddad (1992)	21°48'S; 46°35'W	19	1.657	-0.76	-0.650	74.593
21. Conte & Machado (2005) $25^{\circ}57^{\circ}S; 49^{\circ}13^{\circ}W$ 21 1.682 0.50 1.883 66.385 22. Conte & Rosa-Feres (2006) $25^{\circ}41^{\circ}S; 49^{\circ}03^{\circ}W$ 31 0.847 2.51 0.836 66.385 23. Conte & Rosa-Feres (2007) $25^{\circ}39^{\circ}S; 49^{\circ}16^{\circ}W$ 29 1.550 -1.58 0.690 66.385 24. Filho (2009) $20^{\circ}05^{\circ}S; 56^{\circ}36^{\circ}W$ 15 2.156 4.32 -0.220 108.575 25. Forti (2009) $24^{\circ}02^{\circ}S; 47^{\circ}53^{\circ}W$ 20 0.482 0.87 1.330 76.278 26. Grandinetti & Jacobi (2005) $20^{\circ}07^{\circ}S; 43^{\circ}52^{\circ}W$ 11 0.167 1.33 1.300 79.910 27. Heyer <i>et al.</i> (1990) $23^{\circ}38^{\circ}S; 45^{\circ}52^{\circ}W$ 35 2.972 0.76 1.343 77.917 28. Kopp & Eterovick (2006) $20^{\circ}06^{\circ}S; 43^{\circ}29^{\circ}W$ 20 1.612 2.08 0.896 79.910 29. Kopp <i>et al.</i> (2010) $17^{\circ}49^{\circ}S; 52^{\circ}39^{\circ}W$ 25 2.589 -1.93 -0.694 94.135 30. Maffei (2010) $22^{\circ}48^{\circ}S; 48^{\circ}55^{\circ}W$ 39 1.345 7.74 0.188 83.813 31. Moreira <i>et al.</i> (2007) $29^{\circ}42^{\circ}S; 50^{\circ}59^{\circ}W$ 15 -0.721 -4.13 -0.737 72.685 32. Narvaes <i>et al.</i> (2009) $24^{\circ}31^{\circ}S; 46^{\circ}31^{\circ}W$ 29 0.455 2.72 0.147 79.910 34. Nomura (2008) $23^{\circ}10^{\circ}S; 46^{\circ}31^{\circ}W$ 23 1.898 4.57 -0.745 <td>20.</td> <td>Cardoso & Souza (1996)</td> <td>10°08'S; 67°35'W</td> <td>31</td> <td>2.598</td> <td>-0.72</td> <td>1.848</td> <td>119.998</td>	20.	Cardoso & Souza (1996)	10°08'S; 67°35'W	31	2.598	-0.72	1.848	119.998
22. Conte & Rosa-Feres (2006) $25^{\circ}41^{\circ}S; 49^{\circ}03^{\circ}W$ 31 0.847 2.51 0.836 66.385 23. Conte & Rosa-Feres (2007) $25^{\circ}39^{\circ}S; 49^{\circ}16^{\circ}W$ 29 1.550 -1.58 0.690 66.385 24. Filho (2009) $20^{\circ}05^{\circ}S; 56^{\circ}36^{\circ}W$ 15 2.156 4.32 -0.220 108.575 25. Forti (2009) $24^{\circ}02^{\circ}S; 47^{\circ}53^{\circ}W$ 20 0.482 0.87 1.330 76.278 26. Grandinetti & Jacobi (2005) $20^{\circ}07^{\circ}S; 43^{\circ}52^{\circ}W$ 11 0.167 1.33 1.300 79.910 27. Heyer <i>et al.</i> (1990) $23^{\circ}38^{\circ}S; 45^{\circ}52^{\circ}W$ 35 2.972 0.76 1.343 77.917 28. Kopp & Eterovick (2006) $20^{\circ}06^{\circ}S; 43^{\circ}29^{\circ}W$ 20 1.612 2.08 0.896 79.910 29. Kopp <i>et al.</i> (2010) $17^{\circ}49^{\circ}S; 52^{\circ}39^{\circ}W$ 25 2.589 -1.93 -0.694 94.135 30. Maffei (2010) $22^{\circ}48^{\circ}S; 48^{\circ}55^{\circ}W$ 39 1.345 7.74 0.188 83.813 31. Moreira <i>et al.</i> (2007) $29^{\circ}42^{\circ}S; 50^{\circ}59^{\circ}W$ 15 -0.721 -4.13 -0.737 72.685 32. Narvaes <i>et al.</i> (2009) $24^{\circ}31^{\circ}S; 46^{\circ}31^{\circ}W$ 29 0.452 1.09 2.073 70.257 35. Nomura (2008) $20^{\circ}21^{\circ}S; 50^{\circ}2W$ 23 1.898 4.57 -0.745 95.515 36. Nomura (2008) $20^{\circ}21^{\circ}S; 50^{\circ}2W$ 23 2.033 1.03 -0.816 94.618	21.	Conte & Machado (2005)	25°57'S: 49°13'W	21	1.682	0.50	1.883	66.385
23. Conte & Rosa-Feres (2007) $25^{\circ}39^{\circ}S; 49^{\circ}16^{\circ}W$ 29 1.550 -1.58 0.690 66.385 24. Filho (2009) $20^{\circ}05^{\circ}S; 56^{\circ}36^{\circ}W$ 15 2.156 4.32 -0.220 108.575 25. Forti (2009) $24^{\circ}02^{\circ}S; 47^{\circ}53^{\circ}W$ 20 0.482 0.87 1.330 76.278 26. Grandinetti & Jacobi (2005) $20^{\circ}07^{\circ}S; 43^{\circ}52^{\circ}W$ 11 0.167 1.33 1.300 79.910 27. Heyer <i>et al.</i> (1990) $23^{\circ}38^{\circ}S; 45^{\circ}52^{\circ}W$ 35 2.972 0.76 1.343 77.917 28. Kopp & Eterovick (2006) $20^{\circ}06^{\circ}S; 43^{\circ}29^{\circ}W$ 20 1.612 2.08 0.896 79.910 29. Kopp <i>et al.</i> (2010) $17^{\circ}49^{\circ}S; 52^{\circ}39^{\circ}W$ 25 2.589 -1.93 -0.694 94.135 30. Maffei (2010) $22^{\circ}48^{\circ}S; 48^{\circ}55^{\circ}W$ 39 1.345 7.74 0.188 83.813 31. Moreira <i>et al.</i> (2007) $29^{\circ}42^{\circ}S; 50^{\circ}59^{\circ}W$ 15 -0.721 -4.13 -0.737 72.685 32. Narvaes <i>et al.</i> (2009) $24^{\circ}31^{\circ}S; 47^{\circ}16^{\circ}W$ 11 0.248 -0.51 3.023 86.390 33. Nascimento <i>et al.</i> (1994) $20^{\circ}00^{\circ}S; 43^{\circ}50^{\circ}W$ 9 -0.455 2.72 0.147 79.910 34. Nomura (2008) $23^{\circ}10^{\circ}S; 46^{\circ}31^{\circ}W$ 29 4.57 -0.745 95.515 36. Nomura (2008) $20^{\circ}12^{\circ}S; 50^{\circ}29^{\circ}W$ 23 2.033 1.03 -0.816 94.618 </td <td>22.</td> <td>Conte & Rosa-Feres (2006)</td> <td>25°41'S: 49°03'W</td> <td>31</td> <td>0.847</td> <td>2.51</td> <td>0.836</td> <td>66.385</td>	22.	Conte & Rosa-Feres (2006)	25°41'S: 49°03'W	31	0.847	2.51	0.836	66.385
24. Filho (2009) $20^{\circ}05^{\circ}S; 56^{\circ}36^{\circ}W$ 15 2.156 4.32 -0.220 108.575 25. Forti (2009) $24^{\circ}02^{\circ}S; 47^{\circ}53^{\circ}W$ 20 0.482 0.87 1.330 76.278 26. Grandinetti & Jacobi (2005) $20^{\circ}07^{\circ}S; 43^{\circ}52^{\circ}W$ 11 0.167 1.33 1.300 79.910 27. Heyer <i>et al.</i> (1990) $23^{\circ}38^{\circ}S; 45^{\circ}52^{\circ}W$ 35 2.972 0.76 1.343 77.917 28. Kopp & Eterovick (2006) $20^{\circ}06^{\circ}S; 43^{\circ}29^{\circ}W$ 20 1.612 2.08 0.896 79.910 29. Kopp <i>et al.</i> (2010) $17^{\circ}49^{\circ}S; 52^{\circ}39^{\circ}W$ 25 2.589 -1.93 -0.694 94.135 30. Maffei (2010) $22^{\circ}48^{\circ}S; 48^{\circ}55^{\circ}W$ 39 1.345 7.74 0.188 83.813 31. Moreira <i>et al.</i> (2007) $29^{\circ}42^{\circ}S; 50^{\circ}59^{\circ}W$ 15 -0.721 -4.13 -0.737 72.685 32. Narvaes <i>et al.</i> (2009) $24^{\circ}31^{\circ}S; 46^{\circ}31^{\circ}W$ 9 -0.455 2.72 0.147 79.910 34. Nomura (2008) $20^{\circ}01^{\circ}S; 46^{\circ}31^{\circ}W$ 29 0.452 1.09 2.073 70.257 35. Nomura (2008) $20^{\circ}21^{\circ}S; 50^{\circ}29^{\circ}W$ 23 1.898 4.57 -0.745 95.515 36. Nomura (2008) $20^{\circ}12^{\circ}S; 48^{\circ}20^{\circ}W$ 23 2.033 1.03 -0.816 94.618 37. Ode at al (2000) $20^{\circ}12^{\circ}S; 48^{\circ}20^{\circ}W$ 23 2.033 1.03 -0.618 90.628	23.	Conte & Rosa-Feres (2007)	25°39'S: 49°16'W	29	1.550	-1.58	0.690	66.385
25. Forti (2009) $24^{\circ}02^{\circ}S; 47^{\circ}53^{\circ}W$ 20 0.482 0.87 1.330 76.278 26. Grandinetti & Jacobi (2005) $20^{\circ}07^{\circ}S; 43^{\circ}52^{\circ}W$ 11 0.167 1.33 1.300 79.910 27. Heyer <i>et al.</i> (1990) $23^{\circ}38^{\circ}S; 45^{\circ}52^{\circ}W$ 35 2.972 0.76 1.343 77.917 28. Kopp & Eterovick (2006) $20^{\circ}06^{\circ}S; 43^{\circ}29^{\circ}W$ 20 1.612 2.08 0.896 79.910 29. Kopp <i>et al.</i> (2010) $17^{\circ}49^{\circ}S; 52^{\circ}39^{\circ}W$ 25 2.589 -1.93 -0.694 94.135 30. Maffei (2010) $22^{\circ}48^{\circ}S; 48^{\circ}55^{\circ}W$ 39 1.345 7.74 0.188 83.813 31. Moreira <i>et al.</i> (2007) $29^{\circ}42^{\circ}S; 50^{\circ}59^{\circ}W$ 15 -0.721 -4.13 -0.737 72.685 32. Narvaes <i>et al.</i> (2009) $24^{\circ}31^{\circ}S; 47^{\circ}16^{\circ}W$ 11 0.248 -0.51 3.023 86.390 33. Nascimento <i>et al.</i> (1994) $20^{\circ}00^{\circ}S; 43^{\circ}50^{\circ}W$ 9 -0.455 2.72 0.147 79.910 34. Nomura (2008) $23^{\circ}10^{\circ}S; 46^{\circ}31^{\circ}W$ 23 1.898 4.57 -0.745 95.515 36. Nomura (2008) $20^{\circ}12^{\circ}S; 50^{\circ}29^{\circ}W$ 23 2.033 1.03 -0.816 94.618 37. Ode <i>s.et al.</i> (2000) $20^{\circ}12^{\circ}S; 48^{\circ}20^{\circ}W$ 23 2.033 1.03 -0.816 94.618	24.	Filho (2009)	20°05'S; 56°36'W	15	2.156	4.32	-0.220	108.575
26. Grandinetti & Jacobi (2005) $20^{\circ}07^{\circ}S; 43^{\circ}52^{\circ}W$ 11 0.167 1.33 1.300 79.910 27. Heyer <i>et al.</i> (1990) $23^{\circ}38^{\circ}S; 45^{\circ}52^{\circ}W$ 35 2.972 0.76 1.343 77.917 28. Kopp & Eterovick (2006) $20^{\circ}06^{\circ}S; 43^{\circ}29^{\circ}W$ 20 1.612 2.08 0.896 79.910 29. Kopp <i>et al.</i> (2010) $17^{\circ}49^{\circ}S; 52^{\circ}39^{\circ}W$ 25 2.589 -1.93 -0.694 94.135 30. Maffei (2010) $22^{\circ}48^{\circ}S; 48^{\circ}55^{\circ}W$ 39 1.345 7.74 0.188 83.813 31. Moreira <i>et al.</i> (2007) $29^{\circ}42^{\circ}S; 50^{\circ}59^{\circ}W$ 15 -0.721 -4.13 -0.737 72.685 32. Narvaes <i>et al.</i> (2009) $24^{\circ}31^{\circ}S; 47^{\circ}16^{\circ}W$ 11 0.248 -0.51 3.023 86.390 33. Nascimento <i>et al.</i> (1994) $20^{\circ}00^{\circ}S; 43^{\circ}50^{\circ}W$ 9 -0.455 2.72 0.147 79.910 34. Nomura (2008) $23^{\circ}10^{\circ}S; 46^{\circ}31^{\circ}W$ 23 1.898 4.57 -0.745 95.515 36. Nomura (2008) $20^{\circ}12^{\circ}S; 50^{\circ}29^{\circ}W$ 23 2.033 1.03 -0.816 94.618 37. Ode <i>s.t.et</i> (2000) $24^{\circ}25; 50^{\circ}29^{\circ}W$ 23 2.033 1.03 -0.816 94.618	25.	Forti (2009)	24°02'S; 47°53'W	20	0.482	0.87	1.330	76.278
27. Heyer et al. (1990) $23^{\circ}38^{\circ}S; 45^{\circ}52^{\circ}W$ 35 2.972 0.76 1.343 77.917 28. Kopp & Eterovick (2006) $20^{\circ}06^{\circ}S; 43^{\circ}29^{\circ}W$ 20 1.612 2.08 0.896 79.910 29. Kopp et al. (2010) $17^{\circ}49^{\circ}S; 52^{\circ}39^{\circ}W$ 25 2.589 -1.93 -0.694 94.135 30. Maffei (2010) $22^{\circ}48^{\circ}S; 48^{\circ}55^{\circ}W$ 39 1.345 7.74 0.188 83.813 31. Moreira et al. (2007) $29^{\circ}42^{\circ}S; 50^{\circ}59^{\circ}W$ 15 -0.721 -4.13 -0.737 72.685 32. Narvaes et al. (2009) $24^{\circ}31^{\circ}S; 47^{\circ}16^{\circ}W$ 11 0.248 -0.51 3.023 86.390 33. Nascimento et al. (1994) $20^{\circ}00^{\circ}S; 43^{\circ}50^{\circ}W$ 9 -0.455 2.72 0.147 79.910 34. Nomura (2008) $23^{\circ}10^{\circ}S; 46^{\circ}31^{\circ}W$ 23 1.898 4.57 -0.745 95.515 36. Nomura (2008) $20^{\circ}12^{\circ}S; 50^{\circ}29^{\circ}W$ 23 2.033 1.03 -0.816 94.618 37. Ode at al (2000) $44^{\circ}200^{\circ}S; 48^{\circ}20^{\circ}W$ 23 2.033 1.03 -0.628 0.628	26.	Grandinetti & Jacobi (2005)	20°07'S: 43°52'W	11	0.167	1.33	1.300	79.910
28. Kopp & Eterovick (2006) $20^{\circ}06^{\circ}S; 43^{\circ}29^{\circ}W$ 20 1.612 2.08 0.896 79.910 29. Kopp et al. (2010) $17^{\circ}49^{\circ}S; 52^{\circ}39^{\circ}W$ 25 2.589 -1.93 -0.694 94.135 30. Maffei (2010) $22^{\circ}48^{\circ}S; 48^{\circ}55^{\circ}W$ 39 1.345 7.74 0.188 83.813 31. Moreira et al. (2007) $29^{\circ}42^{\circ}S; 50^{\circ}59^{\circ}W$ 15 -0.721 -4.13 -0.737 72.685 32. Narvaes et al. (2009) $24^{\circ}31^{\circ}S; 47^{\circ}16^{\circ}W$ 11 0.248 -0.51 3.023 86.390 33. Nascimento et al. (1994) $20^{\circ}00^{\circ}S; 43^{\circ}50^{\circ}W$ 9 -0.455 2.72 0.147 79.910 34. Nomura (2008) $23^{\circ}10^{\circ}S; 46^{\circ}31^{\circ}W$ 23 1.898 4.57 -0.745 95.515 36. Nomura (2008) $20^{\circ}12^{\circ}S; 50^{\circ}29^{\circ}W$ 23 2.033 1.03 -0.816 94.618 37. Ode at al (2000) $44200^{\circ}S; 48^{\circ}20^{\circ}W$ 23 4.058 5.077 0.628 0.628	27.	Hever <i>et al.</i> (1990)	23°38'S: 45°52'W	35	2.972	0.76	1.343	77.917
29. Kopp et al. (2010) $17^{\circ}49'S; 52^{\circ}39'W$ 25 2.589 -1.93 -0.694 94.135 30. Maffei (2010) $22^{\circ}48'S; 48^{\circ}55'W$ 39 1.345 7.74 0.188 83.813 31. Moreira et al. (2007) $29^{\circ}42'S; 50^{\circ}59'W$ 15 -0.721 -4.13 -0.737 72.685 32. Narvaes et al. (2009) $24^{\circ}31'S; 47^{\circ}16'W$ 11 0.248 -0.51 3.023 86.390 33. Nascimento et al. (1994) $20^{\circ}00'S; 43^{\circ}50'W$ 9 -0.455 2.72 0.147 79.910 34. Nomura (2008) $23^{\circ}10'S; 46^{\circ}31'W$ 29 0.452 1.09 2.073 70.257 35. Nomura (2008) $20^{\circ}12'S; 50^{\circ}29'W$ 23 1.898 4.57 -0.745 95.515 36. Nomura (2008) $20^{\circ}12'S; 50^{\circ}29'W$ 23 2.033 1.03 -0.816 94.618 27. Ode at al. (2000) $40^{\circ}24'S; 48^{\circ}20'W$ 21 $40^{\circ}58$ 5.077 0.628 0.228	28.	Kopp & Eterovick (2006)	20°06'S; 43°29'W	20	1.612	2.08	0.896	79.910
30. Maffei (2010) $22^{\circ}48^{\circ}S; 48^{\circ}55^{\circ}W$ 39 1.345 7.74 0.188 83.813 31. Moreira <i>et al.</i> (2007) $29^{\circ}42^{\circ}S; 50^{\circ}59^{\circ}W$ 15 -0.721 -4.13 -0.737 72.685 32. Narvaes <i>et al.</i> (2009) $24^{\circ}31^{\circ}S; 47^{\circ}16^{\circ}W$ 11 0.248 -0.51 3.023 86.390 33. Nascimento <i>et al.</i> (1994) $20^{\circ}00^{\circ}S; 43^{\circ}50^{\circ}W$ 9 -0.455 2.72 0.147 79.910 34. Nomura (2008) $23^{\circ}10^{\circ}S; 46^{\circ}31^{\circ}W$ 29 0.452 1.09 2.073 70.257 35. Nomura (2008) $20^{\circ}12^{\circ}S; 50^{\circ}29^{\circ}W$ 23 1.898 4.57 -0.745 95.515 36. Nomura (2008) $20^{\circ}12^{\circ}S; 48^{\circ}20^{\circ}W$ 23 2.033 1.03 -0.816 94.618	29.	Kopp <i>et al.</i> (2010)	17°49'S: 52°39'W	25	2.589	-1.93	-0.694	94.135
31. Moreira et al. (2007) $29^{\circ}42^{\circ}S; 50^{\circ}59^{\circ}W$ 15 -0.721 -4.13 -0.737 72.685 32. Narvaes et al. (2009) $24^{\circ}31^{\circ}S; 47^{\circ}16^{\circ}W$ 11 0.248 -0.51 3.023 86.390 33. Nascimento et al. (1994) $20^{\circ}00^{\circ}S; 43^{\circ}50^{\circ}W$ 9 -0.455 2.72 0.147 79.910 34. Nomura (2008) $23^{\circ}10^{\circ}S; 46^{\circ}31^{\circ}W$ 29 0.452 1.09 2.073 70.257 35. Nomura (2008) $20^{\circ}12^{\circ}S; 50^{\circ}29^{\circ}W$ 23 1.898 4.57 -0.745 95.515 36. Nomura (2008) $20^{\circ}12^{\circ}S; 48^{\circ}20^{\circ}W$ 23 2.033 1.03 -0.816 94.618 27. Ode et al. (2000) $14^{\circ}200^{\circ}S: 48^{\circ}20^{\circ}W$ 21 4.058 5.077 0.628 0.223	30.	Maffei (2010)	22°48'S: 48°55'W	39	1.345	7.74	0.188	83.813
32. Narvaes et al. (2009) $24^{\circ}31'S; 47^{\circ}16'W$ 11 0.248 -0.51 3.023 86.390 33. Nascimento et al. (1994) $20^{\circ}00'S; 43^{\circ}50'W$ 9 -0.455 2.72 0.147 79.910 34. Nomura (2008) $23^{\circ}10'S; 46^{\circ}31'W$ 29 0.452 1.09 2.073 70.257 35. Nomura (2008) $20^{\circ}21'S; 49^{\circ}16'W$ 23 1.898 4.57 -0.745 95.515 36. Nomura (2008) $20^{\circ}12'S; 50^{\circ}29'W$ 23 2.033 1.03 -0.816 94.618 37. Ode et al. (2000) $14^{\circ}20^{\circ}S: 48^{\circ}20'W$ 21 4.058 5.077 0.628 0.223	31.	Moreira <i>et al.</i> (2007)	29°42'S: 50°59'W	15	-0.721	-4.13	-0.737	72.685
33. Nascimento <i>et al.</i> (1994) $20^{\circ}00^{\circ}S; 43^{\circ}50^{\circ}W$ 9 -0.455 2.72 0.147 79.910 34. Nomura (2008) $23^{\circ}10^{\circ}S; 46^{\circ}31^{\circ}W$ 29 0.452 1.09 2.073 70.257 35. Nomura (2008) $20^{\circ}21^{\circ}S; 49^{\circ}16^{\circ}W$ 23 1.898 4.57 -0.745 95.515 36. Nomura (2008) $20^{\circ}12^{\circ}S; 50^{\circ}29^{\circ}W$ 23 2.033 1.03 -0.816 94.618 27. Ode et al. (2000) $14^{\circ}20^{\circ}S: 48^{\circ}20^{\circ}W$ 21 4.058 5.077 0.628 00.223	32	Narvaes $et al.$ (2009)	24°31'S: 47°16'W	11	0.248	-0.51	3.023	86.390
34. Nomura (2008) $23^{\circ}10^{\circ}S; 46^{\circ}31^{\circ}W$ 29 0.452 1.09 2.073 70.257 35. Nomura (2008) $20^{\circ}21^{\circ}S; 49^{\circ}16^{\circ}W$ 23 1.898 4.57 -0.745 95.515 36. Nomura (2008) $20^{\circ}12^{\circ}S; 50^{\circ}29^{\circ}W$ 23 2.033 1.03 -0.816 94.618 27. Oda at at (2000) $14800^{\circ}S; 48820^{\circ}W$ 21 4.058 5.077 0.628 00.222	33	Nascimento <i>et al.</i> (1994)	20°00'S·43°50'W	9	-0.455	2.72	0.147	79 910
35. Nomura (2008) $20^{\circ}21^{\circ}S; 49^{\circ}16^{\circ}W$ 23 1.898 4.57 -0.745 95.515 36. Nomura (2008) $20^{\circ}21^{\circ}S; 50^{\circ}29^{\circ}W$ 23 2.033 1.03 -0.816 94.618 37. Oda at at (2000) $40^{\circ}28; 50^{\circ}29^{\circ}W$ 23 2.033 1.03 -0.816 94.618	34	Nomura (2008)	23°10'S: 46°31'W	29	0.452	1.09	2.073	70 257
36. Nomura (2008) $20^{\circ}12^{\circ}S; 50^{\circ}29^{\circ}W$ 23 2.033 1.03 -0.816 94.618 37. Oda at at (2000) $10^{\circ}29^{\circ}S; 50^{\circ}29^{\circ}W$ 23 2.033 1.03 -0.816 94.618	35	Nomura (2008)	20°21'S: 49°16'W	23	1 898	4 57	-0.745	95 515
$27 \text{ Ode at at } (2000)$ $14200^2 \text{ S} \cdot 4220^2 \text{ W}$ $21 \text{ A} 052 \text{ S} 07 \text{ O} 632 \text{ O} 0222 \text{ O} 2320^2 \text{ W}$	36	Nomura (2008)	20°12'S: 50°29'W	23	2.033	1.03	-0.816	94,618
-3/. (Jula et al. (2009) $-14093.4620 w + 214936 -30/1 - 20/2 + 90/233$	37	Oda <i>et al.</i> (2009)	14°09'S: 48°20'W	21	4.958	-5.07	-0.628	90.233
38. Papp (1997) 22°52'S; 46°02'W 13 1.211 4.13 1.883 74.198	38.	Papp (1997)	22°52'S; 46°02'W	13	1.211	4.13	1.883	74.198

39.	Pombal & Gordo (2004)	24°25'S; 47°15'W	23	0.92	-0.12	1.752	86.390
40.	Pombal (1997)	24°13'S; 48°46'W	19	1.02	3.40	0.783	73.162
41.	Prado et al. (2005)	19°34'S; 57°00'W	23	1.574	10.00	-0.372	125.963
42.	Prado & Pombal (2005)	20°16'S; 40°28'W	17	0.604	0.66	2.730	93.137
43.	Rossa-Feres & Jim (1994)	22°59'S; 48°25'W	25	0.481	4.09	-0.342	83.813
44.	Santos (2009)	08°43'S; 35°50'W	28	-0.221	0.86	2.377	93.912
45.	Santos et al. (2007)	20°11'S; 50°53'W	13	2.956	0.73	-0.419	94.618
46.	Santos et al. (2008)	29°42'S. 53°42'W	24	0.535	4.70	-0.977	77.418
47.	São Pedro & Feio (2010)	20°31'S. 43°41'W	28	0.676	0.70	0.789	79.910
48.	Silva (2007)	20°20'S. 49°11'W	18	2.437	-0.53	-0.914	95.515
49.	Teixeira (2009)	22°59'S; 48°30'W	15	1.094	-0.48	1.572	83.813
50.	Toledo et al. (2003)	22°25'S; 47°33'W	19	1.825	-0.35	-0.716	80.825
51.	Vieira et al. (2007)	07°25'S; 36°30'W	15	3.184	2.25	-2.938	95.245
52.	Zina et al. (2007)	22°22'S; 47°28'W	22	2.172	0.08	-0.166	80.825

FIGURE LEGENDS

Figure 1. Geographic locations of the 52 Neotropical anuran data series.

Figure 2. Construction of a latent variable representing the covariation of environmental variables and the putative connection with community modularity. *E*, calling activation energy; Latent, latent variable; NRI, net relatedness index; PET, potential evapotranspiration; ZMOD, modularity index. Exogenous arrows represent variances unexplained by the model; the explained variance for endogenous variables is calculated as one minus the path coefficient between its associated error variable. Paths values are standardized effects. Arrow width represents the strength of the causal link. (•) = P < 0.1, (*) = P < 0.05, and (**) P < 0.01. Shaded graphs (*E*, I and M) highlight those models that were not rejected by the Chi2 test and that minimize the AIC_C.



Figure 1.



Figure 2.

SUPPORTING INFORMATION

Unraveling the thermal dependence of calling amphibians: a place for phylogenetic structure, external resources, and the modular organization of biodiversity

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SI MATERIALS AND METHODS

Structural equation modeling

In order to improve understanding of the potential causal connection between environment and community structure we performed a path analysis that reconstructs a latent variable incorporating all the covariation. We start the reconstruction of the latent variable (model A) with environmental variables (Latitude, PET), phylogenetic species relationship (NRI), apparent activation energy of calling (*E*), local community richness (S_{LOC}) and modularity (ZMOD). The second model (model B) was constructed after removing those variables with non-significant connection in model A. The third step was to describe ZMOD, looking for connection with the exogenous variables (model C to Q). Path analysis was used with maximum likelihood methods and standardized coefficient. The overall path diagram and the significance of each single connection between couples of variables were tested using the Structural Equation Modeling (SEM). To assess the significance of the overall path model, we used a χ^2 statistic computed from the departure between the observed and expected covariance matrix from the proposed path model. A significant χ^2 (*P* < 0.05) indicates that the data do not support the model. The explained variance for each endogenous variable is estimated as one minus the path coefficient between its associated error variable (Shipley 2000). Because our data matrix does not present multivariate normality based on kurtosis (using the 'mvnorm.kur.test' function of the ICS R-Package, W = 27.4605, w1 = 0.48, df1 = 35.00, w2 = 0.80, df2 = 1.00, p-value < 0.05) we develop the Satorra–Bentler robust estimations of the Chi-squared statistic and standard errors. It corrects excessive kurtosis, problems in which the errors are not independent of their causal non-descendants, and is important for models with latent variables. Akaike's Information Criterion corrected for small samples (AIC_C) was calculated for each fitted model in order to compare it; the lowest AIC_C values were selected. The w_i (AIC_C) were calculated using the 'Weights' function of the 'MuMIn' R-Package version 1.13.4. All SEM models were fitted using the R-Package lavaan (Rosseel 2012).

SI RESULTS

Of the 52 time series of anuran communities, 25 yielded ZMOD index significantly deviated from null expectations, 22 positively, and three negatively (Table 1). Eleven communities presented significant deviations (P<0.05) from null expectations of NRI and seven presented marginal deviations (P<0.1) (Table 1). In relation with the path analysis and the construction of a latent variable that incorporated environmental geographical variation, model A was rejected (p<0.05, Table 1) but the latent variable presented correlation with latitude, NRI, E and PET, but no significant connection

was observed with S_{LOC} or ZMOD (Fig. 2a). Model B was not rejected by the Chi² test (P>0.05) and represents the reconstruction of the latent variable by the covariation of community and environmental variables (Table 2, Fig. 2a). The latent variable was reconstructed by two environmental variables: Latitude and PET, and two community variables: *E* and NRI, and reporting a positive connection with Latitude (r=0.81) and NRI (r=0.52), and a negative one with *E* (r=-0.82) and PET (r=-0.70) (Fig. 2a B). Of the 14 models (model C to Q) evaluated to explore a putative role of exogenous variables on ZMOD, five were not rejected by the Chi² test (C, D, G, I and L, Table 2, Fig. 2), and model L minimized the AIC_C (AIC_C=1078.36). Model L represents the latent variable constructed as in model B and a putative role over ZMOD of three exogenous variables: *E* (r=-0.60), PET (r=0.56), and S_{LOC} (r=0.36). This model accounted for 42% of the ZMOD variance (1-0.58) (Fig. 2b L).

Table SI1.

Chi² represents the robust Satorra–Bentler Chi-squared statistic; df, degrees of freedom; P-value, P value of the Chi test; AIC_C, Akaike's information criterion corrected for small samples; Δ_i (AIC_C) = [AIC_C - min AIC_C]; w_i (AIC_C) = the rounded Akaike's weights; SRMR, Standardized Root Mean Square Residual.

Path model	Chi ²	df	P-value	AIC _C	$\Delta_i (AIC_C)$	$w_i(AIC_C)$	SRMR
А	22.896	9	0.006	1102.73	24.37	2.91E-6	0.104
В	2.700	2	0.259				0.031
С	7.054	6	0.316	1093.63	15.27	2.76E-4	0.088
D	7.867	7	0.344	1084.07	5.71	3.28E-2	0.100
E	15.633	8	0.048	1103.10	24.74	2.42E-6	0.106
F	23.915	8	0.002	1090.31	11.95	1.45E-3	0.133
G	12.300	8	0.138	1082.11	3.75	8.75E-2	0.104
Н	27.232	9	0.001	1103.28	24.92	2.21E-6	0.134
Ι	16.622	9	0.055	1096.61	18.25	6.21E-5	0.116
J	21.725	9	0.010	1084.01	5.65	3.38E-2	0.125

Κ	24.389	10	0.007	1095.12	16.76	1.31E-4	0.131
L	11.932	8	0.154	1078.36	0	5.71E-1	0.097
М	18.478	9	0.030	1094.26	15.9	2.01E-4	0.108
Ν	24.233	9	0.004	1082.24	3.88	8.20E-2	0.140
0	27.751	10	0.002	1094.21	15.85	2.06E-4	0.141
Р	18.933	9	0.026	1080.56	2.2	1.90E-1	0.116
Q	21.405	10	0.018	1091.25	12.89	9.06E-4	0.129
Figure SI1.

Construction of a latent variable representing the covariation of environmental variables and the putative connection with community modularity. *E*, apparent activation energy of calling; Latent, latent variable; NRI, net relatedness index; PET, potential evapotranspiration; ZMOD, modularity index. Exogenous arrows represent variances unexplained by the model; the explained variance for endogenous variables is calculated as one minus the path coefficient between its associated error variable. Paths values are standardized effects. Arrow width represents the strength of the causal link. (·) = P < 0.1, (*) = P < 0.05, and (**) P < 0.01. Shaded graphs (E, I and M) highlight those models that were not rejected by the Chi2 test and that minimize the AIC_{*C*}.



Figure SI1a.



Figure SI1b.

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CHAPTER III: Structure of phenological modules and seasonality as a species trait

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ABSTRACT

Understanding the structure and functioning of biological communities and the underlying eco-evolutionary mechanisms is a central aim for ecology. The phenological dimension of communities is an ecological space where ecological mechanisms affecting the maintenance of links in biological networks operate. The network framework provides metrics to detect interacting groups of speciesmodules-which along with the phylogenetic history of species allows untangling the species functional roles in the assembly of communities. We use phenological data on 22 Neotropical anuran communities to explore the temporal module structure (i.e., seasonality and phylogenetic relatedness) and its connection to community species richness. We tested for the degree of seasonality of each module assigning them to two categories: seasonal and aseasonal. In order to understand the rules associated to the addition of species as community richness increases, we performed regression analysis between the total community richness with: (a) module richness, (b) seasonal module richness, (c) aseasonal module richness, and (d) coefficient of variation of module richness of each community. The phylogenetic structure of modules was explored through the net relatedness index (NRI). We reconstructed the evolution of the seasonality trait by maximum likelihood and Bayesian methods, and tested for phylogenetic signal of categorical traits. Our results show that 46 modules were seasonal, three marginally seasonal, and 25 showed an aseasonal pattern of calling activity. We found significant and positive associations between community richness with module richness, seasonal module richness, and aseasonal module richness. No correlation was found between the number of modules per community and coefficient of variation of module richness of each community. Module seasonality was

associated positively with module species richness, and negative with module phylogenetic distance. We estimated the seasonal state as ancestral at the root of the phylogenetic tree. The families Leptodactylidae and Microhylidae presented the seasonal state, species within the family Bufonidae genus *Rhinella* presented the derived state, aseasonal. Family Hylidae presented a gradient from the genus Phyllomedusa with the seasonal state, to the clade of genera Hypsiboas and Aplastodiscus with the aseasonal state. Here we report a saturation pattern of module-functional-diversity; species are assigned to a small number of key temporal groups. Seasonal modules have higher redundancy, which could generate ecosystem stability. We detect a pattern of phylogenetic signal on seasonality trait with the seasonal state as ancestral. This may reflect the temperate origin of amphibians by a mechanism of temporal niche conservatism. In relation with historical assemblage of Neotropical anuran communities, the aseasonal species may have advantages in tropical communities by using the entire temporal window, which seasonal species may not; but in temperate regions the latter may find the appropriate moments for being active out of the peak of seasonal species.

INTRODUCTION

A central question in ecology lies in understanding the structure and functioning of biological communities detecting the eco-evolutionary mechanisms involved in its assembly (Morin 2011, Cavender-Bares et al. 2012). During the past decade, the network framework has been providing theory and metrics to understand the structure of communities and their underlying assembly mechanisms (Gotelli and McCabe 2002, Lewinsohn et al. 2006, Ulrich and Gotelli 2007). Recently, a new metric was incorporated to improve the detection of groups of species-modulesthat is, a group of species that tend to interact or co-use resources (Marquitti et al. 2013), a pattern reported in very different systems (e.g., Olesen et al. 2007, Rezende et al. 2009, Borthagaray et al. 2014). Further, the incorporation of the phylogenetic history of species allows untangling evolutionary mechanisms determining the species role in the network and within modules (Krasnov et al. 2012, Schleuning et al. 2014). Some authors have found phylogenetic structure associated to food web and hostparasite modules (Rezende et al. 2009, Krasnov et al. 2012). But this is not always the case, because Donatti et al. (2011) reported a limited phylogenetic effect on the modules of a seed-dispersal network. The identification of species modules with the footprint of evolutionary history can be used as a tool to explore possible functional roles of modules at the community level (Hooper et al. 2002, Cadotte et al. 2009, Cavender-Bares et al. 2012).

The study of functional groups is becoming a conservation priority mainly because of the human need for ecosystem services and the risk of losing them because of species extinction (Hooper et al. 2002, Naeem et al. 2009, Cadotte et al. 2011, Naeem et al. 2012). The main goal of this research program focuses on the

relationship between functional diversity, species richness, and community stability. Analyzing the connection between richness and functional groups, it has been frequently reported a pattern of saturation in the functional diversity (Hooper et al. 2002, Halpern and Floeter 2008, Petchey et al. 2009, Cadotte et al. 2011). Therefore, species are allocated to a small group of key functional groups rather than new groups (Halpern and Floeter 2008). This pattern implies functional redundancy of species (i.e., species displaying similar roles) that generates stability in ecosystem functioning (Fonseca and Ganade 2001, Pillar et al. 2013, Mouillot et al. 2014).

The phenological dimension of communities is an emerging area of analysis because it has proven important for the maintenance of links in biological networks (Forrest and Miller-Rushing 2010, Gilman et al. 2010, Sutherland et al. 2013). Time can also be interpreted as an ecological resource where biological mechanisms operate (e.g., competition, facilitation), capable of structuring communities (Schoener 1974, but see also Jaksic 1982, Kronfeld-Schor and Dayan 2003). Previous studies have analyzed the community phenology as a bipartite network of species using time, where structuring was found and phenological modules predicted (Canavero et al. 2009). Finding phenological modules and relating them with phylogenetic structure allows a better understanding of the functioning of biological communities and sheds light on the assembly processes (Rezende et al. 2009, Krasnov et al. 2012, Schleuning et al. 2014).

In this contribution we analyze phenological data in Neotropical anuran communities, which have proved to be an interesting group for a number of reasons: they exhibit a strong seasonality in patterns of activity (Canavero et al. 2009), are strongly dependent on environmental variables (Saenz et al. 2006, Canavero and Arim 2009, Steen et al. 2013), and display high diversity in life histories and reproductive

strategies (Wells 1977, Haddad and Prado 2005, Gomez-Mestre et al. 2012, Crump 2015). Furthermore, Neotropical anuran communities show a large variability in richness (Buckley and Jetz 2007, Wiens 2007, Gouveia et al. 2013), and have well known phylogenetic affinities (Pyron and Wiens 2011). In this work, we describe seasonality and phylogenetic structure of phenological modules of 22 Neotropical anuran communities. Modules were classified in seasonal and aseasonal types based on circular statistics. We explored the relation between modules number, richness, and phylogenetic relatedness among species with community phylogeny and richness. The ancestral character estimation for the evolution of species seasonality was performed by maximun likelihood and Bayesian methods. We also estimated the phylogenetic signal of the seasonality character and discussed the possible relevance of species seasonality in the assembly history of these communities.

MATERIAL AND METHODS

In Chapter 1 we presented 52 published databases of phenological activity patterns of Neotropical anuran communities (Fig. 1). We estimated an index of normalized modularity (ZMOD) using the spinglass.community function (Csardi & Nepusz 2006) in the R-Package igraph (Newman and Girvan 2004, Guimera and Amaral 2005, Reichardt and Bornholdt 2006). To test the degree of seasonality of each module and the entire set of modules, we transformed the linear axis of time into a circular axis using the circular function at the R-Package 'circular' version 0.4-7. With this transformation, each month corresponds to an angle of 30 degrees. We performed a circular histogram (rose.diag function at the R-Package 'circular' version

0.4-7.) with the angular frequencies of the number of species that present calling activity for each module, and estimated the angular mean of these frequencies (mean.circular function at the R-Package 'circular' version 0.4-7). Then we tested the degree of seasonality of the angular means of the entire set of modules applying the Rayleigh test of uniformity (Zar 1999), which assesses the significance of the mean resultant length. The alternative hypothesis is a unimodal distribution with unknown mean direction and unknown mean resultant length (rayleigh.test function at the R-Package 'circular' version 0.4-7). We also tested the degree of seasonality of each module, applying the Rayleigh test of uniformity. To understand how species are incorporated to modules as community richness as an independent variable with: (a) module richness, (b) seasonal module richness, (c) aseasonal module richness, and (d) coefficient of variation of module richness of each community.

In order to analyze the phylogenetic structure of modules in relation to phylogenetic community structure, we estimated an index of phylogenetic distance net relatedness index (NRI). This index describes the difference between average phylogenetic distances in observed as compared to null communities, standardized by the standard deviation of phylogenetic distances in the latter (Webb et al. 2008). This null model shuffles species labels across the entire phylogeny (i.e., local community phylogeny), randomizing phylogenetic relationships among species, with reshuffling being carried out 10,000 times for each community. Positive values of NRI indicate phylogenetic attraction (i.e., species in the module tend to be more phylogenetically related than expected by chance), and negative values imply phylogenetic repulsion (i.e., species in the module tend to be less phylogenetically related than expected by chance). We used multiple and simple logistic regressions to describe the seasonal or

aseasonal module characteristics with the phylogenetic relationships of species in modules and module richness. We plotted logistic regressions curves associated with the histogram of data (recommended by Smart et al. 2004) using the logi.hist.plot function at the R-Package 'popbio' version 2.4 (de la Cruz Rot 2005).

To explore the evolution of the seasonality trait, we performed the ancestral character estimation using the ace function of the R-Package 'ape' version 3.1-1 with the maximum likelihood (ML) criterion (Pagel 1994). We developed two models: an equal-rates model (one parameter for both transition rates), and an all-rates-different model (two parameters, one for each transition rate), for a trait called species seasonality with two states: seasonal (species found in seasonal modules) and aseasonal (species found in aseasonal modules). We performed a Likelihood ratio test to select the most parsimonious model. We also simulated and summarized the reconstructions of stochastic character maps on the phylogenetic tree by Bayesian methods using the functions make.simmap and densityMap at the R-Package 'phytools' (Revell 2012). In order to compare the probabilities of character transitions along the tree, we performed a correlation analysis between the probabilities of transitions estimated with both ML and Bayesian methods.

Finally, we tested for phylogenetic signal in discrete trait with two states (seasonal *vs.* aseasonal) employing a function designed *ad hoc* (function *phylo.signal.disc*; E. L. Rezende pers. comm). This function implements the "Fixed Tree, Character Randomly Reshuffled" model proposed in Maddison and Slatkin (1991), and estimates the minimum character changed from parsimony based on an assigned matrix of costs of character state transition (see Maddison and Maddison 2000).

RESULTS

The Rayleigh test of uniformity for the distribution of means of all modules, vielded a significant result (Test Statistic: 0.426, P < 0.001) with an angular mean of 337.9 degrees (corresponding to December) (Fig. 2). Of the 74 modules analyzed, 46 had a significant degree of seasonality, three were marginally seasonal, and 25 showed an aseasonal pattern of calling activity (Table 1). In Fig. 3 we show an example of aseasonal (A) and seasonal (B) modules applied to Rossa-Feres and Jim (1994) study. The regression analysis between total community richness as the independent variable with module richness (Fig. 4A, $S_{module} = 0.36 * S_{community} - 1.10$, p < 0.001, Adjusted R² = 0.48), seasonal module richness (Fig. 4B, S_{seasonal module} = 0.40 * $S_{community}$ - 0.90, p < 0.001, Adjusted $R^2 = 0.55$), and aseasonal module richness (Fig. 4C, $S_{aseasonal module} = 0.24 * S_{community} - 0.52$, p < 0.001, Adjusted R² = 0.54) found significant and positive associations. An increase in community richness was reflected in a growth of module richness with a tendency slightly biased toward seasonal modules. There is a lack of correlation between the total community richness and the number of modules per community (Fig. 4D, Number of modules = $-0.02 * S_{community}$ + 3.73, p = 0.289, Adjusted $R^2 = 0.01$) and with the coefficient of variation of module richness of each community (Fig. 4E, $CVS_{module} = 0.002 * S_{community} + 0.37$, p = 0.605, Adjusted $R^2 = -0.04$). Regarding module seasonality, we found significant associations with both variables (Module seasonality = exp (-1.05 + $0.34 * S_{module}$ -0.51 * NRI) / (1 + exp (-1.05 + 0.34 * S_{module} - 0.51 * NRI_{module}))): positive with module species richness (Table 2, Fig. 5A) and negative with module phylogenetic distance (Table 2, Fig. 5B). Aseasonal modules tended to be less rich (Table 2, Fig.

5A), and with phylogenetic attraction; while seasonal modules were the richest and showed phylogenetic repulsion (Table 2, Fig. 5B).

Only two species, Rhinella schneideri and Hypsiboas faber, were observed in both aseasonal and seasonal modules. These two species were removed to perform the ancestral character estimation and to test for phylogenetic signal. The comparison with the likelihood ratio test found no significant differences ($Chi^2 = 0.110$, df = 1, p > 0.05) between the equal-rates and all-rates-different models of the evolution of seasonality. Therefore, we used the equal-rates model with one parameter of transition for ancestral character estimation. The ancestral state seasonal was estimated at the tree root with a probability of 0.85, and the aseasonal pattern being the derived the state (Fig. 6). Among the most representative families of Neotropical amphibians, the Leptodactylidae and Microhylidae families displayed the ancestral seasonal state. On the other hand, species within the family Bufonidae, specifically the genus Rhinella presented the derived state, aseasonal; and within the family Hylidae, we found a gradient that went from genus *Phyllomedusa* presenting the seasonal state, to the clade of genera Hypsiboas and Aplastodiscus with the aseasonal state, and an intermediate group of species from genera Dendropsophus and Scinax, with species varying between both states of seasonality. The simulated stochastic character mapping revealed a similar pattern of transitions (Fig. 7), supported by the significant correlation between node probabilities estimated by the ML and Bayesian methods $(R^2 = 0.998, p < 0.0001)$. Finally, we detected a significant phylogenetic signal for seasonality (evolutionary transitions observed = 19, p < 0.0001, randomizations = 10,000, Fig. 8).

DISCUSSION

In this contribution we explored the seasonal patterns of activity of Neotropical anuran communities in a deconstructive way starting from exploring phenological module structure (Marquet et al. 2004). We found that species richness within modules grows as the richness of communities increases, but the number of modules and the variation of module richness remain constant. This result agrees with the saturation pattern of functional diversity, where as community richness increases, species are assigned to a small number of key temporal groups (Hooper et al. 2002, Halpern and Floeter 2008, Petchey et al. 2009, Cadotte et al. 2011). We also classified phenological modules between seasonal (i.e., species tend to be active in consecutive months of the year) and aseasonal (species tend to be active in any month of the year). We found that seasonal modules tend to be richer than aseasonal modules, which tend to have phylogenetically related species. Therefore, seasonal modules have higher functional redundancy in phenology, which could generate ecosystem stability (Fonseca and Ganade 2001, Pillar et al. 2013, Mouillot et al. 2014). However, the diversity differences between seasonal and aseasonal modules could reduce functional evenness and consequently, could also decrease system stability (Fonseca and Ganade 2001).

Exploring the evolution of anuran seasonality of activity, we found a pattern of phylogenetic signal with the seasonal state as ancestral for Neotropical anurans. This pattern may reflect the temperate origin of ancient amphibian linages by a mechanism of temporal niche conservatism (Wiens 2007, Wiens et al. 2010, Pyron and Wiens 2013). We found a representative genus and two families of the Neotropical fauna, basal in our phylogenetic tree (e.g., *Pipa*, Microhylidae spp.,

Leptodactylidae spp.) but with a tropical origin, displaying seasonal phenologies conforming the most diverse phenological modules. This could be the reason of the prevalence of seasonal over aseasonal phenological patterns at community level (Canavero et al. 2009). In the same vein, Schleuning et al. (2014) pointed out that seasonal environments with species able to adapt behaviorally to be active in benign periods, may promote the generation of species modules that overlap their phenologies. We consider that the incorporation of a historical view of phenological behavior represents a novel contribution to anuran phenological framework, which has been often centered in the analysis of current environmental conditions (Oseen and Wassersug 2002, Saenz et al. 2006, Both et al. 2008, Canavero et al. 2008, Steen et al. 2013).

The aseasonal state of the seasonality character represents a derived state, which may have represented an ecological opportunity to occupy an available temporal niche space left by seasonal species ('niche filling hypothesis', Rosenzweig 1975). If time is effectively an important ecological dimension as a limiting resource (Kronfeld-Schor and Dayan 2003), and an important portion of the faunas is restricted to the benign season, we could expect an acceleration of diversification of the aseasonal lineages since the acquisition of the aseasonal phenological pattern. On the contrary, the 'old' seasonal lineages could be more diverse because they have had more time for diversification (Mittelbach et al. 2007), but as the seasonal time space was already occupied by more species, we expect a decrease in speciation and an increase in extinction rates leading to a limited radiation (Wiens et al. 2011, Tanentzap et al. 2015).

Another important question that emerges from our results is how this evolutionary novelty—the aseasonal pattern of activity—could impact on the

latitudinal species gradient and the historical assembly of Neotropical anuran communities? There are three main causes of the latitudinal species gradient in anurans: high tropical speciation, low extinction in relation with temperate regions, and limited dispersal from tropical to temperate regions (Wiens et al. 2006, Pyron and Wiens 2013). In addition, we think that the evolution of seasonality could be a historical cause accounting at least partially for the latitudinal gradient of species richness. Aseasonal species could have advantages in tropical communities by using the entire temporal window, which seasonal species evade; but in temperate regions they could find the appropriate time for being active apart from the peak of seasonal species where negative interactions may be stronger. Aseasonal lineages may have found opportunities for increased tropical diversification and radiation towards higher latitudes. For instance, in our analysis we found two specious genera of Neotropical anurans that presents aseasonal activity: Hypsiboas (90 sp., Frost 2015) that reaches its southern range limit at 38.35°S (Wiens et al. 2006), and Rhinella (88 sp., Frost 2015) that reaches up to latitude 43°S (Kwet et al. 2004) and has a recent history of rapid diversification during the Miocene (Medeiros et al. 2010, Vallinoto et al. 2010). Based on our results, we conclude that there is a connection between the seasonal patterns of activity with two relevant aspects of the life history of anurans that should be further explored: the reproductive modes and the prolonged-explosive strategies of reproduction (Wells 1977, Haddad and Prado 2005, Gomez-Mestre et al. 2012, Crump 2015).

In this work, we explored the calling phenology of Neotropical anurans in a deconstructive way, from community structures to species characters and up again to the evolution of community assemblage (Marquet et al. 2004). We interpret phenological modules (i.e., emergent groups identified from the phenological

network) as temporal functional groups (Hooper et al. 2002). This functional diversity not only informs us about the functioning of ecosystems, but also helps us to identify conservation priorities (Cadotte et al. 2011, Naeem et al. 2012). We found that aseasonal modules have low redundancy and are composed of closely related species. These anuran species become an important focus for conservation, because they may play an important role in connecting food webs in periods where the species of seasonal modules are inactive. Finally, we suggest a putative role for the evolution of the aseasonal phenology in the historical assemblage of Neotropical amphibian communities.

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1 **Table 1.**

Modules reference of the Neotropical anuran data. S_{mod} , module richness; NRI, Net Relatedness Index; NTI, Nearest Taxon Index; Angular Mean, mean in degrees of the months (one month equals 30 degrees) that the species of a module were active, in degrees; Angular SD, standard deviation in degrees of the months that the species of a module were active. Dark and light grey cells indicate significant values at *P*<0.05 and marginal values at *P*<0.1, respectively (in the case of Angular Mean, the dark and light grey represents the result of the Rayleigh Test of Uniformity).

Reference	S _{comm}	Module	\mathbf{S}_{mod}	CVS _{mod}	NRI _{mod}	Angular mean	Angular SD
1. Afonso & Eterovick (2007)	12	1	4	0.205	1.597	346.29	41.60
		2	5		-0.108	150.00	121.00
		3	3		-1.173	309.90	68.94
2. Arzabe et al. (1998)	17	1	5	0.204	2.625	300.00	163.62
		2	7		0.118	229.53	52.71
		3	5		-1.052	160.67	59.34
3. Bernarde & dos Anjos (1999)	18	1	8	0.529	0.404	331.42	61.07
		2	3		-0.855	350.10	89.60
		3	3		-1.050	322.63	13.01
		4	4		0.066	204.90	110.42
4. Bernarde (2007)	33	1	18	0.568	-1.961	352.99	54.14
		2	9		2.484	248.79	127.90
		3	6		0.502	15.83	72.82
5. Bertoluci & Rodrigues (2002)	28	1	6	0.376	0.134	34.83	80.32
		2	9		0.628	259.46	123.28
		3	13		-0.604	343.71	63.83
6. Bertoluci (1998)	26	1	16	0.810	-0.780	346.72	48.58
		2	2		0.500	345.00	81.65
		3	8		0.970	284.47	119.19
7. Blamires et al. (1997)	13	1	5	0.462	-0.897	323.79	64.21
		2	2		3.811	345.00	82.62
		3	4		1.115	102.63	95.41
		4	2		-0.681	270.00	0.00
8. Borges et al. (2007)	25	1	5	0.500	0.050	25.89	65.80
		2	13		-1.374	346.55	49.76
		3	7		1.477	221.10	129.02
9. Canavero et al. (2008)	10	1	4	0.346	-0.911	15.00	31.64
		2	4		0.397	340.76	56.16
		3	2		1.622	353.79	96.32
10. Canelas & Bertoluci (2007)	32	1	12	0.390	-1.225	342.35	52.96
		2	14		0.482	16.52	62.62
		3	6		0.932	182.95	111.37
11. Conte & Rosa-Feres (2006)	29	1	9	0.148	-2.362	271.61	45.87
		2	10		1.845	214.53	75.97

		3	12		1.315	355.18	57.67
12. Filho (2009)	15	1	6	0.346	1.573	307.48	88.60
		2	6		-0.291	44.07	67.75
		3	3		0.901	5.60	60.83
13. Kopp & Eterovick (2006)	20	1	5	0.652	2.202	13.65	62.62
		2	3		0.926	178.53	85.66
		3	1			315.00	15.09
		4	2		1.345	8.79	96.88
		5	9		-0.656	347.31	34.11
14. Maffei (2010)	39	1	15	0.266	-1.471	92.89	52.19
		2	15		1.444	99.03	58.33
		3	9		1.781	150.00	164.61
15. Nascimento et al. (1994)	9	1	2	0.247	-0.517	309.90	14.20
		2	1			240.00	0.00
		3	2		-0.466	351.74	31.35
		4	3		2.957	157.09	88.28
16. Nomura (2008)	23	1	4	0.261	-0.149	302.37	126.49
		2	5		-1.183	344.58	40.04
		3	7		2.858	296.01	60.75
		4	7		1.827	23.71	65.28
17. Papp (1997)	13	1	2	0.480	2.703	352.05	143.48
		2	6		-0.731	0.53	55.33
		3	5		-0.312	315.00	49.51
18. Pombal (1997)	19	1	9	0.629	-1.534	330.86	39.33
		2	4		3.015	341.17	71.85
		3	2		-0.480	297.63	37.34
		4	4		1.649	105.00	153.86
19. Prado et al. (2005)	23	1	5	0.718	-0.290	221.93	119.77
		2	14		-1.319	11.96	38.17
		3	4		2.674	63.99	61.10
20. Rossa-Feres & Jim (1994)	25	1	6	0.201	0.781	205.03	95.40
		2	5		2.553	329.52	108.48
		3	8		1.669	335.43	39.50
		4	6		-1.459	355.11	59.20
21. Santos et al. (2008)	24	1	4	0.451	-0.333	306.64	66.40
		2	11		-1.106	358.46	71.19
		3	9		1.385	210.58	97.51
22. Vieira et al. (2007)	15	1	5	0.200	0.921	69.27	35.30
		2	6		1.049	45.00	15.09
		3	4		-1.884	108.29	53.34

Table 2.

Logistic regressions between S_{module} and NRI_{module} as independent variables and Module seasonality as dependent variable. Dark grey cells indicate significant values at *P*<0.05.

	Estimate	Std. Error	Z-value	p-value
(Intercept)	-1.048	0.670	-1.564	0.118
S _{module}	0.336	0.120	2.800	0.005
NRI _{module}	-0.506	0.223	-2.266	0.023
Illodule		0.220		

FIGURE LEGENDS

Figure 1. Geographic locations of the 22 Neotropical data series.

Figure 2. Circular histogram of mean values of activity of all modules of Neotropical anuran communities.

Figure 3. Two circular histograms to exemplify modules that present seasonal and aseasonal patterns of activity. (a) An aseasonal module (module number 2, S=5, data from Rossa-Feres and Jim 1994), and (b) a seasonal module (module number 3, S=8, in with an angular mean of activity=335.43°, data from Rossa-Feres and Jim 1994).

Figure 4. Correlations between total community richness and richness of each module (a), of seasonal modules (b), of aseasonal modules (c), and of the coefficient of variation of the module richness of each community (d).

Figure 5. Logistic regression model showing the association between module richness and the probability of being a seasonal module (a). Logistic regression model showing the association between module phylogenetic distance (NRI) and probability of being a seasonal module (b). In both figures we show the frequency histograms of seasonal and aseasonal modules for the dependent variable.

Figure 6. Maximum likelihood ancestral state reconstruction ('ace' function 'ape' package version 3.1-1). Red squares correspond to aseasonal species, and black ones to seasonal species. The colors of the cakes correspond to the same code, showing

probability of the ancestor to present the aseasonal or seasonal state of the seasonality character. Branch lengths are proportional to time.

Figure 7. Bayesian method for ancestral state reconstruction ('phytools' package version 0.4-45) along the Neotropical anuran tree branches and nodes (10,000 simulations). Branch lengths are proportional to time.

Figure 8. Histogram of the null model to estimate phylogenetic signal. Grey arrow indicates the evolutionary transitions observed = 19, number of randomizations = 10,000.



Figure 1.



Figure 2.



Figure 3.



Figure 4.


Figure 5.



Figure 6.







Figure 8.

PHENOLOGY, AS A COMPONENT AND DETERMINANT OF ANURAN COMMUNITY STRUCTURE

GENERAL CONCLUSIONS

In order to characterize the temperature dependent activity of Neotropical anuran communities, in Chapter 1 I estimated the "apparent activation energy of acoustic behavior" (E) and the performance of MTE predictions for 52 local communities. The activation energy values found were significantly higher than previously reported, and than those expected according to the MTE theory. This may be attributed to the energetically expensive nature of mating calls in anurans. The distribution of activation energies was contrasted with previous reports, and its variation among communities is apparently related to their phylogenetic structure, local environmental conditions, species richness, and phenology. We found that organisms couple what the environment offers with their own metabolic demands for calling, diminishing activation energy at high latitudes, where phenologies are more seasonal and environments less productive and less energetic. We also detected a main role of niche conservatism and community filtering in amphibian communities, but individual flexibility in activation energy could also account for the environmentactivation energy relationship. Our results consolidate the view of activation energy as a main parameter of biodiversity organization, which unravels the effects of important ecological and evolutionary processes on biodiversity structure and function

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In Chapter 2 I expand the scope of amphibian phenological studies by exploring the interplay between phylogenetic community structure and modularity. The observed phylogenetic structure, or more specifically phylogenetic attraction (i.e. species at local communities tend to be more phylogenetically related in relation with a random sample of the regional pool of species), is congruent with a mechanism of species filtering; a pattern that is reinforced with latitude and that could be related to environmental harshness for anurans. The identification of modularity as a prevalent feature of phenologies is a novel contribution for understanding the temporal structuring of species activities. The apparent activation energy of calling, allows us exploring the interdependence between temperature, productivity, latitude and some important features of communities such as richness, modularity, and phylogenetic composition. To recognize the complexity underlying the phenological structure of communities is urgently needed to anticipate and mitigate the impacts of global warming on biodiversity structure and functioning.

Finally, in Chapter 3 I analyzed modular structure and patterns of modular assembly along community richness gradients. We found a saturation pattern in module—functional—diversity; species are assigned to a small number of key temporal groups. Seasonal modules have higher redundancy, which could generate ecosystem stability. We detect a pattern of phylogenetic signal associated to seasonality, with the seasonal state being ancestral. This may reflect the temperate climate origin of amphibians by a mechanism of temporal niche conservatism. In relation to the historical assemblage of Neotropical anuran communities, we suggest that aseasonal species could have advantages in tropical communities by using the entire temporal window, which seasonal species could not; while in temperate regions

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they could find the appropriate moments for being active out of the peak of seasonal species.