Geographic variations of seasonality and coexistence in communities: The role of diversity and climate

ANDRÉS CANAVERO,[1,3]* MATÍAS ARIM[2,3] AND ALEJANDRO BRAZEIRO[1]

[1]*Sección Ecología Terrestre, Facultad de Ciencias, Universidad de la República, Uruguay, Iguá 4225 Piso 8 Sur, (Email: acanavero@fcien.edu.uy), and* [2]*Sección Zoología Vertebrados, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; and* [3]*Center for Advanced Studies in Ecology & Biodiversity (CASEB) and Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile*

Abstract One of the most conspicuous and widely analyzed patterns in ecology is the latitudinal gradient in species richness. Over the 200 years since its recognition, several hypotheses have accumulated in order to account for spatial variations in diversity. Geographic variations in seasonality have been repeatedly proposed as a determinant of community richness. However, the geographic structure of community seasonality has not yet been analyzed. In the present work we evaluated three hypotheses that account for variations in the temporal structuring of communities: first, environmental seasonality determines community seasonality; second, community richness determines its degree of structuring; and third, the presence of an increase in species segregation with latitude, reflected in a pattern of species negative co-occurrence. The hypotheses were evaluated using path analysis on 29 amphibian communities from South America, connecting latitude, environmental conditions, diversity, seasonality, and coexistence structure – nestedness and negative co-occurrence – within communities. Latitude positively affects community seasonality through an increase in temperature seasonality, but a weak negative direct effect suggests that other variables not considered in the model – such as the strength of biotic interactions – could also be involved. Both latitude and diversity (directly and indirectly) determine an increase in negative co-occurrence and nestedness. This suggests that groups of species that are mutually nested in time are internally segregated. Further, the strength of this structure is determined by community diversity and latitude. Temporal structuring of a community is associated with latitude and diversity, pointing to the existence of a systematic change in community organization far beyond, but probably interrelated, with the recognized latitudinal trend in richness. The available information and analysis supported the three hypotheses evaluated.

Key words: co-ocurrence, latitudinal trends, nestedness, temporal dimension.

INTRODUCTION

A main objective in ecology has been to understand diversity and coexistence patterns and to elucidate the mechanisms involved in their generation (Weiher & Keddy 1999). Particular attention has been devoted to latitudinal trends in species richness, ecology's longest recognized pattern, and several hypotheses have been presented to account for this trend (Rohde 1992; Willig *et al.* 2003). Among them, changes in environmental conditions and variations in community seasonality were identified as putative determinants of latitudinal trends in diversity (Rohde 1992; Hurlbert & Haskell 2003; Willig *et al.* 2003). However, no study has analyzed the assumed positive trend in latitudinal community seasonality. Furthermore, temporal variation in community composition represents a major

component of its structure (Pianka 1973; Schoener 1974; Morin 1999; Sandvik *et al.* 2002) but geographic patterns have been poorly explored in theoretical or empirical grounds (Kronfeld-Schor & Dayan 2003; Shurin *et al.* 2007). Phenology is the most conspicuous temporal pattern in the species richness and coexistence of communities which has been associated with seasonal trends in environmental variables (DeCoursey 2004; Nelson 2005; Bradshaw & Holzapfel 2007).

Nestedness and negative co-occurrence are two extended ways to measure community structure. Nestedness is the tendency for occurrences in less rich communities to be a subsample of the richest communities (Atmar & Patterson, 1993), possibly originating from differential dispersal, passive sampling, differential habitat quality, or nesting of habitats. Negative co-occurrence takes place when species tend to stay away from the same places, resulting in checkerboard patterns (Diamond 1975). This could arise from the

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operation of antagonistic interactions, alternative niche constraints, or historical processes (reviewed in Ulrich & Gotelli 2007a). Significant deviations from null expectations have been reported several times for both metrics, suggesting that they represent wide-spread components of community structure (Wright *et al.* 1998; Gotelli & McCabe 2002). It has been stated that negative co-occurrence and nestedness represent alternative patterns of community organization. However, a positive association between both attributes of community structure could originate from the nestedness of groups of species that are mutually segregated (Lewinsohn *et al.* 2006; Ulrich & Gotelli 2007a). Coexistence structures have been analyzed in the space domain, but little attention has been devoted to temporal coexistence (Kronfeld-Schor & Dayan 2003). Furthermore, the connection between temporal coexistence and system diversity or environmental conditions has not been considered.

A main constraint in order to analyze geographical trends in community seasonality and coexistence structure is the limited amount of information available for most taxa. Amphibians represent a notable exception, where several studies have reported the seasonal patterns of community composition from male calling behaviour (Duellman 1978). Boquimpani-Freitas *et al.* (2007) proposed two contrasting scenarios for seasonality of amphibian communities. The former scenario refers to aseasonal environments at equatorial zones where amphibians reproduce throughout the year and may temporally segregate activity to avoid antagonisms (Maiorana 1976; Donnelly & Guyer 1994). In the second scenario, regarding tropical zones, temperature is favourable throughout the year while seasonal precipitation in turn determines amphibian behavioural seasonality. At higher latitudes, however, the low and seasonal temperatures imply an annual harsh period, constraining amphibian activity to suitable temperature conditions, which combined with precipitation to determine its activity (Maiorana 1976; Duellman 1978; Donnelly & Guyer 1994). In this vein, the negative latitudinal trend in the temporal length of the suitable conditions to reproduce, constrain the potential for temporal segregation in species activity (Maiorana 1976; Duellman 1978; Donnelly & Guyer 1994; Bradshaw & Holzapfel 2007). In addition, it has been shown that the strength of competition could increase with latitude leading to more frequent exclusion of the subordinate competitor (Barnes 2002). This could produce a latitudinal trend in the patterns of species coexistence within communities. Latitudinal variations in species richness could also affect community structure. A connection between community diversity and its organization has been repeatedly proposed to exist in ecology, claiming that the richest communities should present a large degree of structuring (e.g. MacArthur & Levins 1967;

May 1972; Winemiller *et al.* 2001). Consequently, temporal community structure is expected to vary systematically with community diversity and latitude (e.g. nestedness and species co-occurrence).

In the current work we present the first geographical analysis of temporal community structures. We analyzed latitudinal trends in activity seasonality, temporal co-occurrence, and nestedness, drawing from 29 amphibian communities in South America. We then identify and discuss a putative causal connection between latitude, environmental conditions, and community structure.

METHODS

Data

Amphibian male breeding vocalizations are typically used as indicators of reproductive activity (Boquimpani-Freitas *et al.* 2007) and have been widely used to monitor seasonal activity in anuran communities (Bertoluci 1998; Prado *et al.* 2005). We carried out a survey of available literature and contacted regional researchers in order to compile 29 annual series of amphibian richness data with respect to geographic position (i.e. latitude). All focal communites are neotropical: 28 from Brazil, and one from Uruguay (Fig. 1 and Table 1). These data series were generated using similar methodologies and scales: monthly samplings from one to five nights long where the presence of the species was recorded by calling males. Temporal series covered from 10 to 22 months (Table 1). For each community we obtained environmental variables

Fig. 1. Geographical locations of the 29 neotropical time series used in this study.

Table 1. Bibliographic references of the data, their geographic locations, and the length of the data series

Reference	Study area	Months	S	R^2	S_{mean}	S_{amp}	P_{CV}	T_{sd}	Z-CS	Z-BR
Afonso and Eterovick (2007)	20°05′S; 43°29′W	15	12	0.42**	5.35**	1.71*	87.0	195.3	1.95	−0.28
Arzabe (1999)	7°17′S; 37°21′W	12	11	0.73**	3.33**	4.38**	101.3	147.2	−1.61	1.47
Arzabe (1999)	7°11′S; 37°19′W	12	16	0.53**	2.75*	4.01*	122.2	131.5	0.77	−2.52*
Arzabe et al. (1998)	11°20′S; 37°25′W	13	17	0.56**	7.72**	2.63*	56.0	143.2	1.32	−0.97
Ávila and Ferreira (2004)	18°58′S; 57°39′W	12	15	0.66*	2.67*	4.21*	60.1	223.7	1.21	−0.37
Bernarde (2007)	11°35′S; 60°41′W	12	33	0.98**	16.83**	11.33**	73.4	51.5	16.10*	−1.70
Bernarde and dos Anjos (1999)	23°27′S; 51°15′W	12	18	0.93**	9.42**	5.53**	36.4	252.8	10.61*	−2.42*
Bernarde and Kokubum (1999)	21°16′S; 50°37′W	12	19	0.93**	11.08**	8.22**	68.8	256.6	0.62	−0.05
Bernarde and Machado (2000)	25°27′S; 53°07′W	12	20	0.85**	10.08**	6.52**	26.4	338.5	4.40*	−0.56
Bertoluci (1998)	24°15′S; 48°24′W	12	26	0.94**	13.42**	10.91**	47.6	304.7	9.45*	−2.39*
Bertoluci and Rodrigues (2002)	23°38′S; 45°52′W	13	28	0.96**	16.67**	8.77**	45.0	237.4	8.06*	−0.38
Blamires et al. (1997)	16°39′S; 48°36′W	12	13	0.80**	4.75**	2.01**	78.5	128.2	2.36*	−0.63
Canavero et al. (2008)	34°47′S; 55°22′W	20	10	0.85**	3.47**	3.20**	8.1	425.9	1.37	−2.39*
Canelas and Bertoluci (2007)	20°05′S; 43°28′W	12	38	0.89**	16.42**	9.52**	86.4	207.7	10.48*	−1.61
Cardoso and Haddad (1992)	21°48′S; 46°35′W	12	19	0.87**	8.00**	7.87**	74.8	235.2	2.44*	−1.68
Cardoso and Souza (1990)	10°8′S; 67°35′W	12	31	0.83**	11.83**	11.26**	59.0	77.7	−0.35	1.25
Conte and Machado (2005)	25°57′S; 49°13′W	13	21	0.89**	8.84**	8.81**	27.5	303.3	8.19*	−1.06
Conte and Rossa-Feres (2006)	25°41′S; 49°03′W	17	31	0.85**	14.41**	10.13**	30.7	294.0	9.28*	−1.76
Heyer et al. (1990)	23°38′S; 45°52′W	12	35	0.72**	13.59**	11.17*	45.0	237.4	1.94	0.26
Kopp and Eterovick (2006)	20°06′S; 43°29′W	16	21	0.60**	5.28**	4.38**	87.0	195.3	4.20*	−1.35
Moreira et al. (2007)	29°42′S; 50°59′W	12	15	0.50*	3.74*	4.28*	8.9	347.8	0.54	−0.53
Papp (1997)	22°52′S; 46°02′W	22	13	0.91**	5.78**	4.50**	67.9	237.9	5.56*	0.11
Pombal (1997)	24°13′S; 48°46′W	12	19	0.84**	7.08**	5.70**	45.1	306.1	6.35*	−2.19*
Pombal and Gordo (2004)	24°25′S; 47°15′W	10	23	0.81**	11.97**	6.92*	47.5	258.6	3.78*	−0.67
Prado and Pombal (2005)	20°16′S; 40°28′W	12	17	0.81**	8.50**	3.49**	51.7	175.7	2.53*	−0.34
Prado et al. (2005)	19°34′S; 57°00′W	12	23	0.83**	10.08**	8.15**	60.3	234.9	10.47*	−0.98
Rossa-Feres and Jim (1994)	22°59′S; 48°25′W	13	25	0.77**	9.99**	5.78**	64.5	238.4	6.10*	0.70
Santos et al. (2007)	20°11′S; 50°53′W	12	16	0.85**	5.92**	6.64**	69.6	229.4	4.83*	−3.31*
Toledo et al. (2003)	22°25′S; 47°33′W	12	21	0.78**	4.92**	5.44**	75.0	240.1	2.76*	−2.26*

*$P < 0.05$; **$P < 0.001$. P_{CV}, coefficient of variation in annual precipitation; R^2, percentage of variance explained in the equations: $S_a = S_{mean} + S_{amp} \sin [2 \Pi (M + c)/12]$; S, total number of species that call at least once in the study period; S_{amp}, amplitude of the function; S_{mean}, mean value of S_a; T_{sd}, standard deviation of the mean monthly temperature in one year × 100; Z-BR, Z-transformed score of nestedness; Z-CS, Z-transformed score of C-score.

from the global database WORLDCLIM (Hijmans *et al.* 2005) with 18-km^2 spatial resolution. These environmental variables are: temperature seasonality (standard deviation of temperature; T_{sd}); and precipitation seasonality (coefficient of variation in annual precipitation; P_{CV}).

Sinusoidal models

A circannual rhythm of activity or phenology is characterized by its period and amplitude (Nelson 2005; Bradshaw & Holzapfel 2007). In order to compare different phenological patterns, sinusoidal models represent a valuable tool to quantify the circannual rhythms (Canavero *et al.* 2008). For each community, we adjusted a sinusoidal model ($S_a = S_{mean} + S_{amp} \sin [2 \Pi (M + c) / 12]$); where S_a is the number of species that call in a given month M, S_{mean}, is the mean number of species calling along the time series, S_{amp} is the maximum deviation from S_{mean} (amplitude of the function, community seasonality), and c is a correction factor that synchronizes the sinusoidal function with anuran calling data (see Canavero *et al.* 2008). Model parameters were estimated by an iteration procedure minimizing the sum of squares (Hilborn & Mangel 1997). Note that a significant estimation of the sinusoidal parameter S_{amp} indicates a community with seasonal calling activity (second scenario proposed by Duellman 1978).

## Nestedness – co-occurrence

A presence (1) – absence (0) matrix was constructed for each community with months in columns and species in rows (Gotelli 2000). We calculated C-score (Stone & Roberts 1990) to measure species co-occurrence. The C-score CS_{ij} for species pair ij is defined as: $CS_{ij} = (R_i - S)(R_j - S)$, where R_i is the row total for species i, R_j is the row total for species j, and S is the number of months that contain both species. The C-score (hereafter CS) is calculated for all unique species pairs in the matrix and averaged (Stone & Roberts 1990). A large CS indicates that more species pairs are segregated in their occurrences. We quantified the pattern of nestedness with the discrepancy index BR (Brualdi & Sanderson 1999), which is a count of the number of discrepancies (absences or presences) that must be erased to produce a perfectly nested matrix. The smaller the BR score, the stronger the pattern of nestedness. The proper null model algorithm to contrast observed indices with null expectations has been debated (Gotelli 2000; Gotelli & McCabe 2002; Ulrich & Gotelli 2007a,b). We used the fixed row–fixed column null model algorithm (FF) (sequential swap) to obtain significance levels for

co-occurrence and nestedness indices; this algorithm minimized type I and II error rates (Ulrich & Gotelli 2007a,b). The (FF) algorithm preserves both the row and column totals in the original matrix (Gotelli 2000) but randomizes the pattern of species co-occurrence. We calculated a standardized effect size (SES) (Ulrich & Gotelli 2007a) to quantify the direction and degree of deviation from the null model. SES is a Z-transformed score, $Z = (x - \mu)/\sigma$; where $x =$ observed index value, $\mu =$ arithmetic mean, and $\sigma =$ the standard deviation of the 100 index values from the simulated matrices. SES values below -2 or above 2 indicate statistical significance at the 5% error level (two-tailed test). The null models and co-occurrence and nestedness indices were calculated with the software applications Nestedness (Ulrich 2006), and Cooc (Ulrich 2007).

Structural equation modeling

We carried out a path analysis to understand the potential causal structure connecting latitudinal variations, environmental conditions and community organization. Structural equation modeling (SEM) was used to test the overall path diagram as a likely cause of observed data. This analysis allows the evaluation of potential causal connections among variables and the significance of each single path connecting couples of variables. Path analysis was used using maximum likelihood methods, working with the standardized coefficient and estimating explained variance for each endogenous variable as one minus the path coefficient between its associated error variable (Shipley 2000). Significance of the overall path model was assessed using the χ^2 statistic computed from the departure between the observed and expected covariance matrix from the proposed path model (Shipley 2000). In this analysis, a significant χ^2 ($P < 0.05$) indicates that the data do not support the model. SEM has two basic assumptions: multivariate normality and linearity among variables. No transformation was necessary to satisfy these assumptions.

As a rule of thumb, path analysis requires a minimum of five observations for each independent path estimated in the model (Shipley 2000). Because we had 29 observations, we restricted our contrast of putative causal structures to models with no more than six causal links. In this vein, we developed three SEM evaluating different hypotheses connecting latitude, environmental conditions, diversity, and community patterns. The first SEM translates the Duellman's hypothesis to a causal structure. We analyzed the relationship between latitude, seasonality in environmental conditions and seasonality in community richness. For this analysis, we included a potential connection
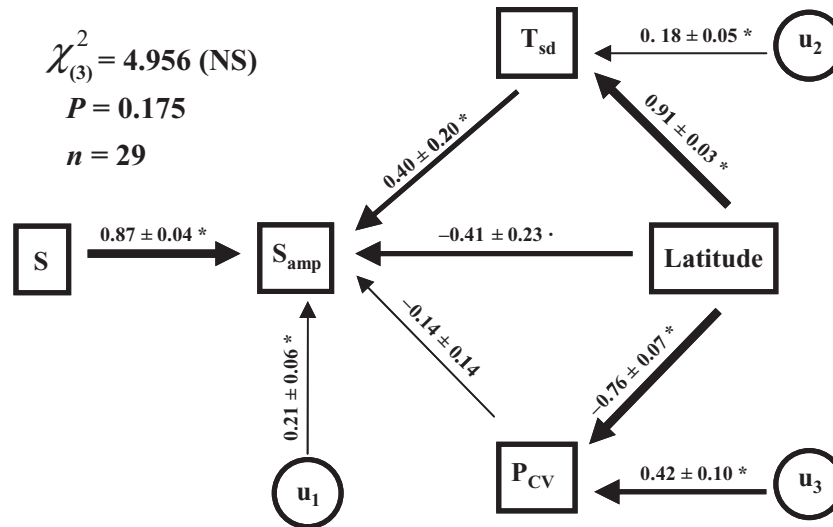
Fig. 2.   Evaluation of the Duellman hypothesis: environmental seasonality determines community seasonality. The model as a whole is consistent with observed data as indicated by its non-significant probability. Paths values are standardized effects ± 1 SE. Asterisks (⋆) denote significant coefficients ($P < 0.05$) and points (·) denote marginal significance ($P < 0.1$). Arrow width represents the strength of the causal link. P_{CV}, coefficient of variation in precipitation among months; S, richness; S_{amp}, community seasonality; these parameters were estimated from fitting a sinusoidal model to the time series; T_{sd}, standard deviation of temperature among months.
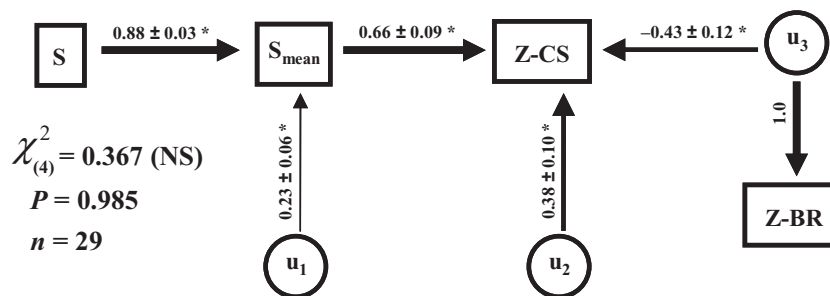

Fig. 3.   Diversity hypothesis: richest communities are more structured. Causal connection between community diversity and coexistence structure. Asterisks (⋆) denote significant coefficients ($P < 0.05$). Arrow width represents the strength of the causal link. S, richness; S_{mean}, mean richness; Z-BR, Z-transformed score of nestedness; Z-CS, Z-transformed score of C-score.

between latitude and seasonality in environmental variables (T_{sd} and P_{CV}) and a direct or indirect effect of latitude on community seasonality, S_{amp} (Fig. 2). The second SEM focused on the diversity hypothesis, where richest communities should present a large degree of internal structuring – e.g. species coexistence. This analysis considered the two parameters of the sinusoidal model (S_{amp} and S_{mean}) and the total richness, as the variables representing community diversity and its seasonality. Coexistence structure was measured by the standardized indices of nestedness and co-occurrence (ZBR and ZCS). Alternative models attempted to identify those variables that better captured the relationship between both components of community structure, diversity and coexistence (Fig. 3). The hypothesis evaluated in the third SEM states that at higher latitudes species activity

is restricted to times with suitable environmental conditions (Duellman 1978), producing a general nested pattern in occurrence. Simultaneously, the increase in competition with latitude produces an increase in species temporal segregation reflected in a rise in negative co-occurrences when species are active (Barnes 2002) (Fig. 4).

RESULTS AND DISCUSSION

The sinusoidal models describe the seasonal trends of anuran community activity, showing large values of R^2 in all of the adjustments (Table 1). All sinusoidal regressions and estimated parameters were statistically significant. Of all analyzed series, no community lacked seasonality (S_{amp} was always significant and of
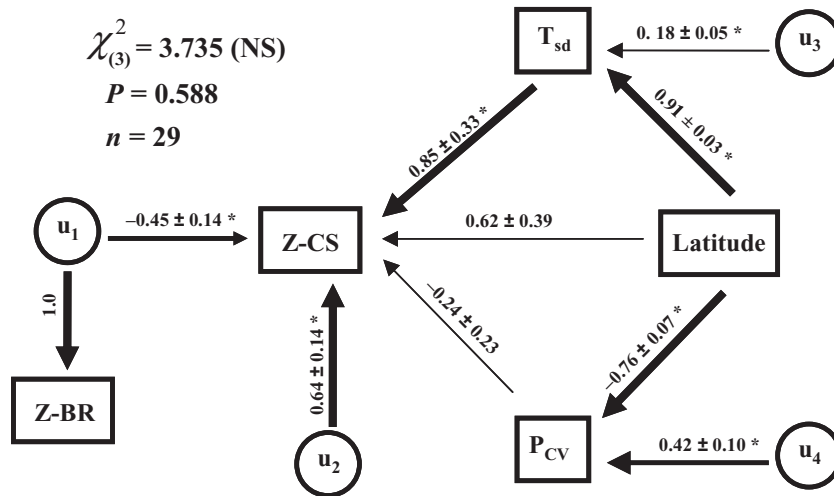
Fig. 4. Geographical trends in coexistence hypothesis: increase in the frequencies of species segregation with latitude. Asterisks (*) denote significant coefficients ($P < 0.05$). Arrow width represents the strength of the causal link. P_{CV}, coefficient of variation in precipitation among months; T_{sd}, standard deviation of temperature among months; Z-BR, Z-transformed score of nestedness; Z-CS, Z-transformed score of C-score.

large magnitude). This was inconsistent with the first scenario proposed by Duellman (1978) (aseasonal environments at equatorial zones where amphibians reproduce year round). Our results do support the second scenario, predicting a connection between activity and environmental conditions in seasonal environments. As seasonal fluctuations in temperature increase among systems, the diversity cycle amplitude increases (Fig. 2). This path model identified a causal link between latitude and community seasonality. Latitude was strongly associated with annual environmental variability. However, while variation in precipitation decreases, temperature markedly increases its seasonality at higher latitudes. Through this effect on temperature variation, latitude determines the magnitude of the community seasonality. A direct, negative effect of latitude on the amplitude of the richness seasonal cycle was also detected, but this was only marginally significant. This causal model accounted for 79% of the variation in amplitude for seasonal trend in richness. No alternative model was consistent with our data.

Our database does not allow us to simultaneously resolve the causal connection among latitude, diversity, and coexistence structure. We therefore gave priority to model estimations that represented key theoretical issues but retained an adequate balance between the number of observations and estimated parameters (Shipley 2000). This method allowed us to find, for the first time, a positive association among those three variables; mainly mediated by temperature seasonality (Figs 2–4). Of the 29 communities, 14 presented indices of co-occurrence (Z-CS) that positively and significantly deviated from null expectations, two

presented a significant degree of nestedness (Z-BR), and five presented evidence of both a significant nestedness and negative co-occurrence (Table 1). However, as presented below, communities with a significant degree of coexistence structuring lie on a large continuum with significant deviations from null models at the extremes.

The second structural model indicated a positive association between diversity and coexistence structure (Fig. 3). The selected variables related to diversity were total and mean richness, the former directly determining the value of the latter. Indices of co-existence representing nestedness (ZBR) and co-occurrence (ZCS) were negatively associated. Because large values of ZBR imply reduced community nestedness and negative values of ZCS imply low community negative co-occurrence, the observed association indicates that communities with larger degree of nestedness also tend to present more negative co-occurrence. This result agrees with previous evidence suggesting that these attributes are not necessarily inversely related (Gotelli & McCabe 2002; Ulrich & Gotelli 2007a). The association between coexistence metrics was summarized in a common error with a negative effect on ZCS and fixed to unit effect on ZBR, implying a negative correlation between indices. The selected model suggests that the effects of diversity on coexistence involve a link between mean richness and ZCS. This means that communities with more species that coexist during a given month have a larger degree of temporal segregation, evidenced by larger degrees of nestedness and negative co-occurrences. This model accounted for 62% of the variation in co-occurrence; no alternative model was

consistent with observations nor did they account for a significantly greater amount of variation.

In agreement with the two previous models, the third causal structure suggested a connection between latitude and coexistence patterns (Fig. 4). This model replicates the detected association between coexistence measures and between latitude and environmental variability. In this case, however, analysis demonstrates a strong indirect effect of latitude on coexistence structure – mediated by temperature seasonality. This model explains 36% of the variation in co-occurrence, and no alternative model improved the congruence with observations.

A connection between community diversity and structure has been theoretically predicted (e.g. MacArthur & Levins 1967; May 1972), but empirical evidence is limited (Winemiller et al. 2001). Similarly, the putative role of environmental variables in determining community diversity has been highlighted elsewhere (e.g. Hawkins et al. 2003, 2007). Herein, we present the first empirical evidence for a systematic increase in the temporal structuring of communities with richness and latitude (Figs 3,4). At higher latitudes, communities tend to present more nestedness (reduction in Z-BR) but at the same time, an increase in negative co-occurrences (increase in Z-CS). While this pattern seems counterintuitive, it simply indicates that nested groups of species may be internally segregated (Ulrich & Gotelli 2007a). Nevertheless, the negative co-occurrence within the nested pattern permits temporal isolation (Kronfeld-Schor & Dayan 2003).

Latitudinal trends in community structure could originate due to trends in biological interactions. The strength of predation and the diversity of parasites and diseases are reduced towards the poles, while competition increases, potentially affecting community diversity and interaction patterns (Barnes 2002; Buckley et al. 2003; Guernier et al. 2004; Krasnov et al. 2008). In addition, the seasonal nature of the higher latitudes potentially allows different species to find suitable conditions at alternate times, reducing interactions (Begon et al. 2006). These trends in biotic interactions, likely affected by abiotic conditions, are the putative determinants of coexistence patterns in latitudinal gradients (Barnes 2002). Therefore, our results are consistent with a variation on structural constraints (e.g. coexistence) as a determinant of latitudinal trends in community richness.

Latitude represents a human construction that in and of itself cannot affect biotic variables (Hawkins & Diniz-Filho 2004). The co-variations in abiotic and biotic variables with latitude are the roots of the potential mechanism leading to the geographic diversity patterns (Rohde 1992). To unravel the mechanism beyond the diversity trends with latitude has been challenging (Rohde 1992; Willig et al. 2003). Some

authors have proposed that those climatic variables related to latitude should be used in lieu of latitude in geographical studies (see Hawkins & Diniz-Filho 2004). However, these and other authors continue using latitude as a meaningful variable (see Hawkins et al. 2006; Diniz-Filho et al. 2007). The use of latitude is supported by several arguments: latitude better represents climatic conditions than any other single variable (Lovegrove 2003; Rezende et al. 2004), several biotic variables are related to latitude, for example, competition (Barnes 2002), predation (Tkadlec & Stenseth 2001), number of available habitats (Pagel et al. 1991), and finally, several historical processes in evolutionary and ecological times present latitudinal patterns (Brown 1995; Naya et al. 2008).

Explanations for species coexistence have typically focused on spatial patterns in order to consider the mechanisms involved in the temporal coexistence or segregation of species. Interspecific competition and alternative niche constraint could produce negative co-occurrence both in space (Diamond 1975) and time (Duellman 1978). However, since all species are present in the study area, those mechanisms that invoke colonization limitation are difficult to consider in the temporal domain. On the other hand, temporal nestedness in a seasonal environment could be driven by differential tolerance to the harshness period. This could be particularly important for amphibians that limit their activity to the warm-humid season (e.g. Heyer et al. 1990; Pombal 1997; Bertoluci 1998). If species have different environmental tolerances and activity is limited to time periods when conditions are favourable, a nested gradient of species richness is expected. Passive sampling, where a large number of records are taken in the richest conditions, could reinforce this pattern because of the positive association between community richness and rare species detection (Fischer & Lindenmayer 2002).

Several authors claim that there is a combined effect of temperature and precipitation on the strength of seasonality within amphibian communities (e.g. Heyer et al. 1990; Rossa-Feres & Jim 1994; Pombal 1997). We only detected a significant effect of temperature seasonality. Furthermore, the connection between latitude and coexistence structure or community seasonality are also mediated by this variable (Figs 2,4). Several interrelated hypotheses could be invoked to account for this pattern. The climate variables used in the present analysis are mean values representing data over 50 years (Hijmans et al. 2005). As a consequence, the seasonal nature of temperature variation could represent the environmental seasonality better than precipitation. Most organisms adjust their activity to suitable environmental conditions following circannual rhythms and photoperiods (Bradshaw & Holzapfel 2007). It is therefore possible that variation in temperature is strongly connected with the diversity

cycle because it best represents seasonality and not necessarily because amphibians directly track temperature (Shipley 2000). In addition, the scale of amphibian response to precipitation could also affect the connection between climate and seasonality. Studies that reported a significant effect of precipitation on the intra-annual variation are based on small temporal scales (e.g. days Donnelly & Guyer 1994; Oseen & Wassersug 2002; Saenz *et al.* 2006). While at small temporal scales amphibians respond to precipitation, at larger scales the internal activity cycle determines amphibian activity, and consequently, community dynamics (Canavero *et al.* 2008).

Our results reinforce the idea that biological latitudinal gradients emerge via a multifactor mechanism (Willig *et al.* 2003). Variation in community structure has typically been analyzed among different communities in space (Wright *et al.* 1998; Gotelli & McCabe 2002). In spite of the early recognition of temporal dynamics as an important component of community structure (Pianka 1973; Schoener 1974), the temporal dimension has accumulated comparatively few theoretical and empirical studies (Kronfeld-Schor & Dayan 2003; Bradshaw & Holzapfel 2007). Based on the strong patterns of temporal structuring in communities and their dependence on latitude and diversity found here, we call for a more thoughtful consideration of the temporal structuring of communities and the potential connection between temporal community dynamics and other ecological patterns.

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REFERENCES

Afonso L. G. & Eterovick P. C. (2007) Spatial and temporal distribution of breeding anurans in streams in southeastern Brazil. *J. Nat. Hist.* **41,** 949–63.

Arzabe C. (1999) Reproductive activity patterns of anurans in two different altitudinal sites within the Brazilian Caatinga. *Rev. Bras. Zool.* **16,** 851–64.

Arzabe C., De Carvalho C. X. & Goes Costa M. A. (1998) Anuran assemblages in Crasto Forest ponds (Sergipe State, Brazil): comparative structure and calling activity patterns. *Herpetol. J.* **8,** 111–13.

Atmar W. & Patterson B. D. (1993) The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* **96,** 373–82.

Ávila R. W. & Ferreira V. L. (2004) Riqueza e densidade de vocalizações de anuros (Amphibia) em uma área urbana de Corumbá, Mato Grosso do Sul, Brasil. *Rev. Bras. Zool.* **21,** 887–92.

Barnes D. K. A. (2002) Polarization of competition increases with latitude. *Proc. R. Soc. Lond.* **269,** 2061–9.

Begon M., Townsend C. & Harper M. (2006) *Ecology. From Individuals to Ecosystems*. Blackwell Publishing, Oxford.

Bernarde P. S. (2007) Ambientes e temporada de vocalização da anurofauna no Município de Espigão do Oeste, Rondônia, Sudoeste da Amazônia – Brasil (Amphibia: Anura). *Biota. Neotrop.* **7,** 87–92.

Bernarde P. S. & dos Anjos L. (1999) Distribução espacial e temporal da anurofauna no Parque Estadual Mata dos Godoy, Londrina, Paraná, Brasil (Amphibia: Anura). *Comun. Mus. Ciênc. Tecnol. PUCRS, Sér. Zool.* **12,** 127–40.

Bernarde P. S. & Kokubum M. N. C. (1999) Anurofauna do Municipio de Guararapes, Estado de São Paulo, Brasil (Amphibia: Anura). *Acta Biol. Leopoldensia* **21,** 89–97.

Bernarde P. S. & Machado R. A. (2000) Riqueza de espécies, ambientes de reprodução e temporada de vocalização da anurofauna em Três Barras do Paraná, Brasil (Amphibia: Anura). *Cuad. Herpetol.* **14,** 93–104.

Bertoluci J. (1998) Annual patterns of breeding activity in Atlantic rainforest anurans. *J. Herpetol.* **32,** 607–11.

Bertoluci J. & Rodrigues M. T. (2002) Seasonal patterns of breeding activity of Atlantic Rainforest anurans at Boracéia, southeastern Brazil. *Amphib-reptil.* **23,** 161–7.

Blamires D., Motta J. A. O., Sousa K. G. & Bastos R. P. (1997) Padroes de distribucao e analise de canto em uma comunidade de anuros no Brasil central. Contribuacao ao Conhecimento Ecológico do Cerrado. *Trabalhos Selecionados do 3° Congresso de Ecología do Brasil. Universidade de Brasilia*, 185–90.

Boquimpani-Freitas L., Ventura Marra R., Van Sluys M. & Duarte Rocha C. F. (2007) Temporal niche of acoustic activity in anurans: interspecific and seasonal variation in a neotropical assemblage from south-eastern Brazil. *Amphib-reptil.* **28,** 269–76.

Bradshaw W. E. & Holzapfel C. M. (2007) Evolution of animal photoperiodism. *Annu. Rev. Ecol. Evol. Syst.* **38,** 1–25.

Brown J. H. (1995) *Macroecology*. The University of Chicago Press, Chicago & London.

Brualdi R. A. & Sanderson J. G. (1999) Nested species subsets, gaps, and discrepancy. *Oecologia* **119,** 256–64.

Buckley H. L., Miller T. E., Ellison A. M. & Gotelli N. J. (2003) Reverse latitudinal trends in species richness of pitcher-plant food webs. *Ecol. Lett.* **6,** 825–9.

Canavero A., Arim M., Naya D. E., Camargo A., da Rosa I. & Maneyro R. (2008) Calling activity patterns in an anuran assemblage: the role of seasonal trends and weather determinants. *North-West. J. Zool.* **4,** 29–41.

Canelas M. A. S. & Bertoluci J. (2007) Anurans of the Serra do Caraça, southeastern Brazil: species composition and

phenological patterns of calling activity. *Iheringia, Série Zool.* **97,** 21–6.

Cardoso A. J. & Haddad C. F. B. (1992) Diversidade e turno de vocalizações de anuros em comunidade neotropical. *Acta Zool. Lilloana* **41,** 93–105.

Cardoso A. J. & Souza M. B. (1990) Distribucao temporal e espacial de anfibios anuros no Seringal Catuaba, Estado do Acre, Brasil. In: *Herpetología Neotropical. Acta II Congreso Latinoamericano de Herpetología. Univ. De los Andes, Mérida* (ed. J. E. Pefaur) pp. 271–91. Universidad de los Andes, Mérida.

Conte C. E. & Machado R. A. (2005) Riqueza de espécies e distribução espacial e temporal em comunidade de anuros (Amphibia, Anura) em uma oocalidade de Tijucas do Sul, Paraná, Brasil. *Rev. Bras. Zool.* **22,** 940–8.

Conte C. E. & Rossa-Feres D. C. (2006) Diversidade e ocorrência temporal da anurofoauna (Amphibia, Anura) em São José dos Pinhais, Paraná, Brasil. *Rev. Bras. Zool.* **23,** 162–75.

DeCoursey P. J. (2004) The behavioral ecology and evolution of biological timing systems. In: *Chronobiology, Biological Timekeeping* (eds J. C. Dunlap, J. J. Loros & P. J. DeCoursey) pp. 27–65. Sinauer Associates, Inc., Sunderland.

Diamond M. (1975) Assembly of species communities. In: *Ecology and Evolution of Communities* (eds M. L. Cody & J. M. Diamond) pp. 342–444. Belknap Press, Cambridge.

Diniz-Filho J. A. F., Bini L. M., Rangel T. F. L. V. B. & Hawkins B. A. (2007) Macroevolutionary dynamics in environmental space and the latitudinal diversity gradients in New World birds. *Proc. R. Soc. B Biol. Sci.* **274,** 43–52.

Donnelly M. A. & Guyer C. (1994) Patterns of reproduction and habitat use in an assemblage of neotropical hylid frogs. *Oecologia* **98,** 291–302.

Duellman W. E. (1978) The biology of an equatorial herpetofauna in Amazonian Ecuador. *Miscell. Publ. Mus. Nat. Hist. Univ. Kans.* **65,** 1–352.

Fischer J. & Lindenmayer D. B. (2002) Treating the nestedness temperature calculator as a 'black box' can lead to false conclusions. *Oikos* **99,** 193–9.

Gotelli N. J. (2000) Null model analysis of species cooccurrence patterns. *Ecology* **81,** 2606–21.

Gotelli N. J. & McCabe D. J. (2002) Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. *Ecology* **83,** 2091–6.

Guernier V., Hochberg M. E. & Guégan J. (2004) Ecology drives the worldwide distribution of human diseases. *PLoS Biol.* **2,** 740–6.

Hawkins B. A. & Diniz-Filho J. A. F. (2004) 'Latitude' and geographic patterns in species richness. *Ecography* **27,** 268–72.

Hawkins B. A., Diniz-Filho J. A. F., Jaramillo C. A. & Soeller S. A. (2006) Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *J. Biogeogr.* **33,** 770–80.

Hawkins B. A., Diniz-Filho J. A. F., Jaramillo C. A. & Soeller S. A. (2007) Climate, niche conservatism, and the global bird diversity gradient. *Am. Nat.* **170,** S16–S27.

Hawkins B. A., Field R., Cornell H. V. *et al.* (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84,** 3105–17.

Heyer R., Rand A., Cruz C., Peixoto L. & Nelson C. (1990) Frogs of Boracéia. *Arq. Zool.* **31,** 231–410.

Hijmans R. J., Cameron S. E., Parra J. L., Jones P. G. & Jarvis A. (2005) Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25,** 1965–78.

Hilborn R. & Mangel M. (1997) *The Ecological Detective: Confronting Models with Data. Monographs in Population Biology.* Princeton University Press, Princeton.

Hurlbert A. H. & Haskell J. P. (2003) The effect of energy and seasonality on avian species richness and community composition. *Am. Nat.* **161,** 83–97.

Kopp K. & Eterovick P. C. (2006) Factors influencing spatial and temporal structure of frog assemblages at ponds in southeastern Brazil. *J. Nat. Hist.* **40,** 1813–30.

Krasnov B. R., Shenbrot G. I., Khokhlova I. S., Mouillot D. & Poulin R. (2008) Latitudinal gradients in niche breadth: empirical evidence from haematophagous ectoparasites. *J. Biogeogr.* **35,** 592–601.

Kronfeld-Schor N. & Dayan T. (2003) Partitioning of time as an ecological resource. *Annu. Rev. Ecol. Evol. Syst.* **34,** 153–81.

Lewinsohn T. M., Prado P. I., Jordano P., Bascompte J. & Olesen J. M. (2006) Structure in plant-animal interaction assemblages. *Oikos* **113,** 174–84.

Lovegrove B. G. (2003) The influence of climate on the basal metabolic rate of small mammals: a slow-fast metabolic continuum. *J. Comp. Physiol. B* **173,** 87–112.

MacArthur R. H. & Levins R. (1967) The limiting similarity, convergence and divergence of coexisting species. *Am. Nat.* **101,** 377–85.

Maiorana V. C. (1976) Predation, submergent behavior, and tropical diversity. *Evol. Theory* **1,** 157–77.

May R. M. (1972) Will a large complex system be stable? *Nature* **238,** 413–14.

Moreira L. F. B., Machado I. F., Moraes Lace A. R. G. & Maltchik L. (2007) Calling perido and reproductive modes in an anuran community of a temporary pond in southern Brazil. *South Am. J. Herpetol.* **2,** 129–35.

Morin P. J. (1999) *Community Ecology.* Blackwell Science, Inc, Malden.

Naya D. E., Bozinovic F. & Karasov W. (2008) Latitudinal trends in physiological flexibility: testing the climatic variability hypothesis with data on the intestinal length of rodents. *Am. Nat.* **172,** E122–34.

Nelson R. J. (2005) *An Introduction to Behavioral Endocrinology*, 3rd edn Sinauer Associates, Inc, Sunderland.

Oseen K. L. & Wassersug R. J. (2002) Environmental factors influencing calling in sympatric anurans. *Oecologia* **133,** 616–25.

Pagel M. D., May R. M. & Collie A. R. (1991) Ecological aspects of the geographical distribution and diversity of mammalian species. *American Naturalist* **137,** 791–815.

Papp M. G. (1997) Reproducção de anuros (Amphibia) em duas lagoas de altitude na Serra da Mantiqueira. p. 62. Universidad Estadual de Campinas. UNICAMP.

Pianka E. (1973) The structure of lizard communities. *Annu. Rev. Ecol. Syst.* **4,** 53–74.

Pombal J. J. P. & Gordo M. (2004) Anfibios anuros da Juréia. In: *Estação Ecológica Juréia-Itatins. Ambioente Físico, Flora e Fauna* (eds O. V. Marques & D. Wânia) pp. 243–56. Holos, Ribeirão Preto.

Pombal J. P Jr. (1997) Distribução espacial e temporal de anuros (Amphibia) em uma poça permanente na Serra de Paranapiacaba, sudeste do Brasil. *Rev. Bras. Biol.* **57,** 583–94.

Prado C. P. A., Uetanabaro M. & Haddad C. F. B. (2005) Breeding activity patterns, reproductive modes, and habitat use by anurans (Amphibia) in a seasonal environment in the Pantanal, Brazil. *Amphib-reptil.* **26,** 211–21.

Prado G. M. & Pombal J. J. P. (2005) Distribução espacial e temporla dos anuros em um brejo da reserva biológica de

Duas Bocas, sudeste do Brasil. *Arq. Mus. Nac.* **63,** 685–705.

Rezende E. L., Bozinovic F. & Garland Jr. T. (2004) Climatic adaptation and the evolution of basal and maximum rates of metabolism in rodents. *Evolution* **58,** 1361–74.

Rohde K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65,** 514–27.

Rossa-Feres D. & Jim J. (1994) Distrubução sazonal em comunidades de anfíbios anuros na região de Botucatu, São Paulo. *Rev. Bras. Biol.* **54,** 323–34.

Saenz D., Fitzgerald L. A., Baum K. A. & Conner R. N. (2006) Abiotic correlates of anuran calling phenology: the importance of rain, temperature, and season. *Herpetological Monographs* **20,** 64–82.

Sandvik G., Seip K. L. & Pleym H. (2002) An anatomy of interactions among species in a seasonal world. *Oikos* **99,** 260–71.

Santos T. G., Rossa-Feres D. C. & Casatti L. (2007) Diversidade e distribuição espaço-temporal de anuros em região com pronunciada estação seca no sudeste do Brasil. *Iheringia Série Zool.* **97,** 37–49.

Schoener T. W. (1974) Resource partitioning in ecological communities. *Science* **185,** 27–39.

Shipley B. (2000) *Cause and Correlation in Biology. A User's Guide to Path Analysis Structural Equation and Causal Inference*. Cambridge University Press, Cambridge.

Shurin J. B., Arnott S. E., Hillebrand H. *et al.* (2007) Diversity – stability relationship varies with latitude in zooplankton. *Ecol. Lett.* **10,** 127–34.

Stone L. & Roberts A. (1990) The checkerboard score and species distributions. *Oecologia* **85,** 74–9.

Tkadlec E. & Stenseth N. C. (2001) A new geographical gradient in vole population dynamics. *Proc. R. Soc. B, Biol. Sci.* **268,** 1547–52.

Toledo L. F., Zina J. & Haddad C. F. B. (2003) Distribução espacial e temporal de uma comunidade de anfíbios anuros do Municipio de Rio Claro, São Paulo, Brasil. *Holos Environ.* **3,** 136–49.

Ulrich W. (2006) Nestedness – a Fortran program for measuring order and disorder in ecological communities. [Cited 9 March 2008.] Available from URL: http://www.uni.torun. pl/~ulrichw.

Ulrich W. (2007) Cooc – a Fortran program for species cooccurrence analysis. [Cited 9 March 2008.] Available from URL: http://www.uni.torun.pl/~ulrichw.

Ulrich W. & Gotelli N. J. (2007a) Disentangling community patterns of nestedness and species co-occurrence. *Oikos* **116,** 2053–61.

Ulrich W. & Gotelli N. J. (2007b) Null model analysis of species nestedness patterns. *Ecology* **88,** 1824–31.

Weiher E. & Keddy P. A. (1999) *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge University Press, Cambridge.

Willig M. R., Kaufman D. M. & Stevens R. D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* **34,** 273–309.

Winemiller K. O., Pianka R. E., Vitt L. J. & Joern A. (2001) Food web laws or niche theory? six independent empirical tests. *Am. Nat.* **158,** 193–9.

Wright D. H., Patterson B. D., Mikkelson G. M., Cutler A. & Atmar W. (1998) A comparative analysis of nested subset patterns of species composition. *Oecologia* **113,** 1–20.