

Journal of Tropical Ecology

<http://journals.cambridge.org/TRO>

Additional services for *Journal of Tropical Ecology*:

Email alerts: [Click here](#)

Subscriptions: [Click here](#)

Commercial reprints: [Click here](#)

Terms of use : [Click here](#)



Climatic variables and altitude as predictors of anuran species richness and number of reproductive modes in Brazil

Tiago da Silveira Vasconcelos, Tiago Gomes dos Santos, Célio Fernando Baptista Haddad and Denise de Cerqueira Rossa-Feres

Journal of Tropical Ecology / Volume 26 / Issue 04 / July 2010, pp 423 - 432
DOI: 10.1017/S0266467410000167, Published online: 28 May 2010

Link to this article: http://journals.cambridge.org/abstract_S0266467410000167

How to cite this article:

Tiago da Silveira Vasconcelos, Tiago Gomes dos Santos, Célio Fernando Baptista Haddad and Denise de Cerqueira Rossa-Feres (2010). Climatic variables and altitude as predictors of anuran species richness and number of reproductive modes in Brazil. *Journal of Tropical Ecology*, 26, pp 423-432 doi:10.1017/S0266467410000167

Request Permissions : [Click here](#)

Climatic variables and altitude as predictors of anuran species richness and number of reproductive modes in Brazil

Tiago da Silveira Vasconcelos^{*,1}, Tiago Gomes dos Santos^{*}, Célio Fernando Baptista Haddad[†] and Denise de Cerqueira Rossa-Feres[‡]

^{*} Programa de Pós Graduação em Zoologia, Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista (UNESP), Caixa Postal 199, 13506-900 Rio Claro, SP, Brazil

[†] Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista (UNESP), Caixa Postal 199, 13506-900 Rio Claro, SP, Brazil

[‡] Departamento de Zoologia e Botânica, Universidade Estadual Paulista (UNESP), 15054-000 São José do Rio Preto, São Paulo, Brazil
(Accepted 25 March 2010)

Abstract: Because anuran species are highly dependent on environmental variables, we hypothesized that anuran species richness and the number of reproductive modes from different Brazilian localities vary according to climatic and altitudinal variables. Published data were compiled from 36 Brazilian localities and climatic and altitudinal data were extracted from an available database. A partial redundancy analysis (pRDA) showed that 23.5% of the data set's variation was explained by climatic and altitudinal data, while the remaining 76.5% remained unexplained. This analysis suggests that other factors not analysed herein may also be important for predicting anuran species richness and the number of reproductive modes in Brazil. Altitude and total annual rainfall were positively correlated with anuran species richness and the number of reproductive modes, and total annual rainfall was strongly associated with these two biotic variables in the triplot of pRDA. The positive association of total annual rainfall and the negative association of the concentration of annual rainfall were already expected based on physiological and reproductive requirements of anurans. On the other hand, temperature was not associated with richness or the number of reproductive modes.

Key Words: Amphibia, Brazilian biomes, climatic effects, herpetology, meta-analysis, redundancy analysis

INTRODUCTION

Although water is probably the most important physical factor affecting the ecology of terrestrial organisms (Krebs 2001), animal groups can respond differently to a given environmental variable. For example, bird species richness in South America is primarily affected by topography, latitude and precipitation (Rahbek & Graves 2001), and reptile species richness in China is most influenced by temperature (Qian *et al.* 2007).

Particularly for amphibians, whose life cycle is strongly influenced by the distribution and abundance of water, usually in the form of rain (McDiarmid 1994), the influence of abiotic variables has long been recognized as an important factor for structuring frog assemblages

(Duellman & Trueb 1994). Few tetrapod vertebrates are as dependent on environmental moisture as amphibians, due to their permeable skin (where cutaneous gas exchange occurs), as well as their dependence on aquatic and terrestrial habitats during their life cycles (Duellman & Trueb 1994). Even species with terrestrial reproductive modes (*sensu* Duellman & Trueb 1994, Haddad & Prado 2005) are more frequent in environments with continuously highly atmospheric moisture (Duellman & Trueb 1994). Therefore, the species richness of amphibians is higher in areas with high moisture levels and moderate to warm temperatures (Duellman & Trueb 1994). This dependence on climatic variables has shown that, in some areas, abiotic factors are more important for the structuring of frog assemblages than biotic factors are (Parris 2004, Werner *et al.* 2007), but other studies have shown that spatial effects and stochasticity can also influence amphibian community composition (Ernst & Rödel 2005, 2008).

¹ Corresponding author. Email: zoologia@ig.com.br

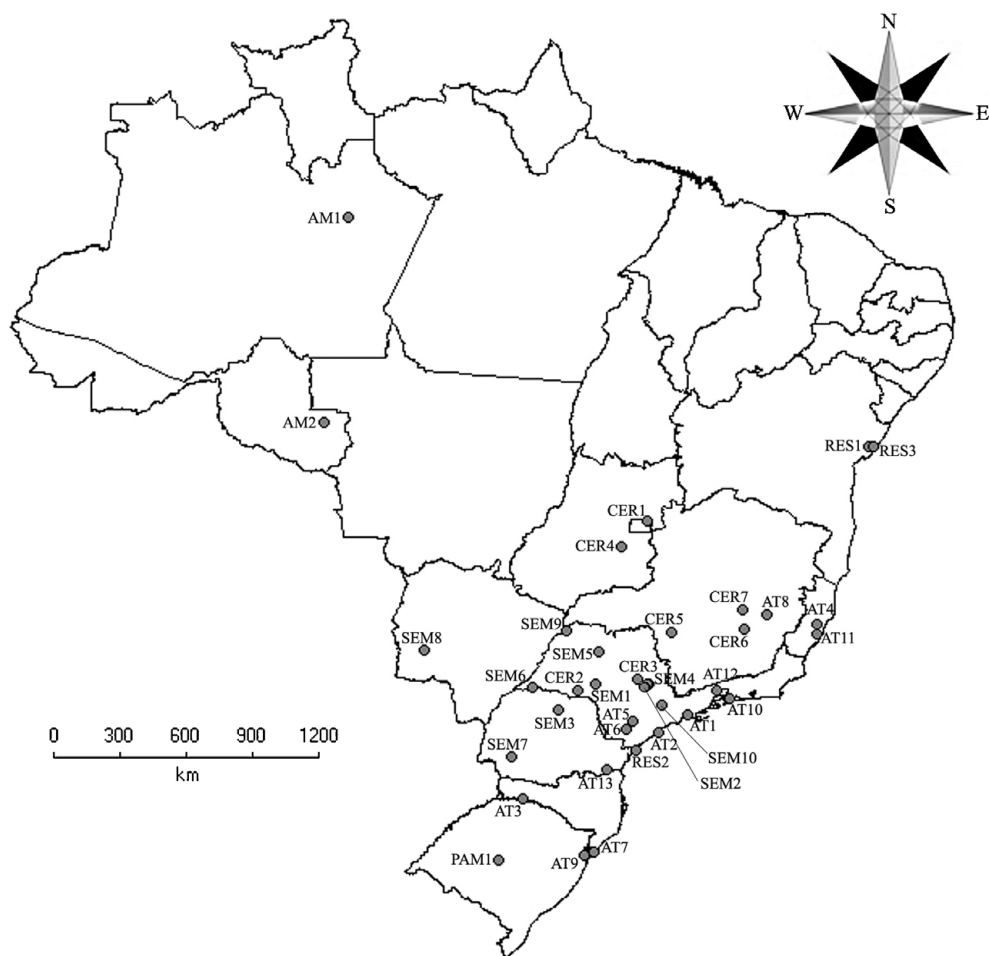


Figure 1. Geographic localization of the 36 Brazilian localities selected for the present study (abbreviations of each locality as in Appendix 1).

Studies that verify the influence of the climatic variables on patterns of species richness distribution have been performed for amphibians in different regions of the world (Qian *et al.* 2007, Rodríguez *et al.* 2005, Williams & Hero 2001), and also for different animal groups in Brazil (Diniz-Filho *et al.* 2008, Terribile & Diniz-Filho 2009), but this kind of study is still scarce for South American amphibians. The only study that verifies how spatial distribution of amphibian species richness responds to environmental variables was performed in the Brazilian cerrado biome, but results are inconclusive mainly because of the lack of a more extensive database on species occurrence at the analysed scale (Diniz-Filho *et al.* 2008). Herein we assess the influence of climatic variables and altitude on anuran species richness of Brazilian localities from different biomes. Because anuran species are highly dependent on environmental variables, we hypothesized that anuran species richness from different Brazilian localities would vary according to climatic (temperature, annual rainfall volume and a measure of the concentration of annual rainfall) and altitudinal variables. Then, we examined not only the total species

richness, but also the reproductive diversity (by means of number of reproductive modes in each locality) according to climatic and altitudinal variables.

METHODS

Selection of localities and collection of climatic data variables

Among the available published studies, we selected only those in which there were sequential samplings during the hot and wet months of the year (the suitable period for reproduction and, consequently, the most effective one for recording the majority of anuran species; Bertoluci & Rodrigues 2002, Duellman & Trueb 1994). In this way, we were able to obtain a general list of anuran species from 36 Brazilian localities (Figure 1, Appendix 1). The reproductive modes (*sensu* Haddad & Prado 2005, updated from Duellman & Trueb 1994) of anuran species from each locality were determined using the information presented by the authors of the lists (when

this information was available), and were also determined using information available on the natural history of each species in the literature (Duellman 2005, Haddad & Prado 2005, Haddad *et al.* 2008). *Lithobates catesbeianus* (Shaw, 1802), an exotic species from North America, was excluded from the analysis, as were those species for which information about their reproductive mode was not available, such as *Megaelasia goeldii* (Baumann, 1912), or species whose reproductive mode is uncertain in a given locality (i.e. species that, according to literature, can exhibit more than one reproductive mode, and for whom there is not sufficient information to determine the reproductive mode for a given locality).

The studied localities selected (Appendix 1) come from six Brazilian phytogeographies (Ab'Sáber 1977, IBGE available at http://www2.ibge.gov.br/download/mapas_murais/biomas_pdf.zip): (1) The Amazonian rain forest: characterized by the predominance of moist forest and a hot and wet climate, where rainfall is well distributed through the year, and located in northern Brazil; (2) Atlantic forest *sensu stricto*: also characterized by moist forest formation and a hot and wet climate, located from the north-eastern to the southern Brazilian coast; (3) cerrado: characterized by a savanna-like vegetation with riparian forest along streams, and two well-defined seasons in the year, a hot and wet season, and a dry and cold season, and located mainly in central Brazil; (4) pampa: characterized by grassland physiognomy in southern Brazil, well-distributed rains through the year, and sub-zero temperatures during the cold period; (5) mesophytic semideciduous forest: classified as a sub-domain of Atlantic forest, mainly characterized by the partial loss of leaves, as a consequence of low rainfall during the cold period of the year, and located mainly in south and south-eastern Brazil; and (6) restinga: also part of the Atlantic forest domain, comprised of coastal sand dune habitats covered with herbaceous and shrubby vegetation, which is common along the Brazilian coast.

The climate data (mean average, mean minimum and mean maximum annual temperature, and mean total annual rainfall) and altitude in each locality, part of a historical record between 1950 and 2000, were obtained from global land area interpolation of climate point data at a spatial resolution of 2.5 arc-min (~5 km *sensu* Hijmans *et al.* 2005, available at <http://www.worldclim.org>). Although selected climate stations were not randomly distributed within the Brazilian territory, the specific localities selected for the present study are within the areas covered by the stations (see Figure 1 in Hijmans *et al.* 2005 to verify the locations of weather stations from which data were used in the interpolation). When necessary, climate stations used in the worldclim data base were removed or corrected when errors were detected (e.g. the wrong coordinates or the use of different units).

According to Hijmans *et al.* (2005), Latin American rainfall data were collected from 18 895 stations, while minimum and maximum temperature was collected from 5321 stations, and mean temperature was collected from 13 842 stations. These data were extracted using DIVA-GIS software (Hijmans *et al.* 2002).

The selected studies vary in relation to the time when the anuran faunas were surveyed. Some studies detected species disappearance or a reduction in population size during the years studied as a possible consequence of human impact (e.g. *Crossodactylus dispar* Lutz, 1925 at Boracéia, south-eastern Brazil: Heyer *et al.* 1990), but this topic is still open to interpretation, as amphibian populations are known to fluctuate greatly over time, with cycles up to 12 y long (Beebe 1996). Therefore, some possible declines may actually represent natural fluctuations (Beebe 1996, Vitt & Caldwell 2009). On the other hand, some studies were performed after the period for which climate data were available (1950–2000). However, we are assuming that changes in climate data after 2000 are not so extensive to result in significant changes (local extinction or addition of species) to the selected anuran communities studied after 2000.

Statistical analysis

The influence of rainfall was assessed in two ways: total annual rainfall and a measure of the concentration of annual rainfall. Total annual rainfall was obtained by adding up the rainfall values of each month of the year, while the measure of the concentration of annual rainfall was determined by a circular statistical analysis (Zar 1999), using the software Oriana for Windows 2.02 (developed by Kovach Computer Services, available at <http://www.kovcomp.com>). Months were converted into angles (at intervals of 30°) and the volume of rainfall of each month was measured as the frequency of each angle (month) observed (Both *et al.* 2008). We estimated the length of the mean vector (*r*), representing a measure of data concentration around the circle (year), ranging from 0 (scattered data = homogeneous rainfall through the year) to 1 (concentrated data = concentrated rainfall in any season of the year).

In this study, we considered only data on the average minimum temperature of each locality, because this variable was the one that had the largest coefficient of variation (CV = 19.5%) when compared with the average maximum temperature (CV = 10.9%) and the average annual temperature (CV = 13.5%) (Ayres *et al.* 2003).

In order to evaluate the effects of climate variables (total annual rainfall, measure of concentration of annual rainfall and minimum temperature) and altitude on

anuran species richness and the number of reproductive modes of selected localities, we used a partial constrained linear ordination method (partial redundancy analysis: pRDA), which is analogous to a multiple regression analysis (Legendre & Legendre 1998). Because locality area was not held constant among the selected localities, we first regressed species richness and number of reproductive modes, separately, on locality size area in order to statistically remove the effect of locality area before we conduct pRDA (Qian *et al.* 2007). Then, we used the residual values as biotic variables for pRDA, because they contain the true information on species richness and reproductive modes. Species richness, the number of reproductive modes, and locality area were \log_{10} -transformed in order to remove the heterogeneity of variance of the original data (correction of the heteroscedasticity of the data, *sensu* Zar 1999). Next, we constructed three matrices for pRDA: (1) a biotic matrix containing the residual values of species richness and the number of reproductive modes; (2) an environmental variable matrix containing the explanatory variables (total annual rainfall, measure of concentration of annual rainfall, average minimum temperature, and altitude); and (3) a covariable matrix, containing geographic coordinates of each locality (latitude and longitude expressed in decimal degree). This last matrix was used to evaluate the variation in terms of spatial-autocorrelation, because our data set was not randomly distributed in Brazil (Figure 1). Before running pRDA, all environmental variables were normalized using standard deviation and the significance of each explanatory variable was manually tested through forward selection (analogous to forward stepwise regression), using 999 Monte Carlo permutations. In this way, we retained only variables that explained a statistically significant proportion of the variation in the species matrix in the model, and used alpha set at 0.05. The Variance Inflation Factor (VIF) was also calculated for each explanatory variable, and was related to the (partial) multiple correlation between two environmental variables. A high VIF of a variable (>20) indicates multicollinearity with the other variables and therefore has no unique contribution to the regression equation, which renders its regression coefficient unstable, and does not require interpretation (ter Braak 1986). Significance of the first canonical axis was tested using 999 Monte Carlo permutations, which were constrained by the covariable matrix. We also performed a variation partitioning analysis (Borcard *et al.* 1992, Both *et al.* 2009) in order to verify (1) the contribution of environmental variables alone (without spatial effect, i.e. geographic position); (2) the contribution of geographic position alone; and (3) the contribution of spatially structured environmental variables (i.e. indistinguishable effect of environment and space). We were then able to calculate an environmental

RDA, a spatial RDA, a pRDA using environmental variables and geographic coordinates (with this last variable being covariable data), and a pRDA using geographic coordinates and environmental variables (this last one as covariable data). The total variation (total inertia) equals the sum of all eigenvalues of a Redundancy Analysis of biotic data. The sum of all canonical eigenvalues represents the part of total inertia explained by RDA. To transform these measurements into percentages of the total variation of biotic data, one divides the sum of all the canonical eigenvalues by the total inertia (Borcard *et al.* 1992, Both *et al.* 2009). All permutation tests and pRDA were performed using CANOCO 4.5 for Windows software (ter Braak & Smilauer 2002).

RESULTS

Among the 36 selected localities, species richness varied from 16 to 65 and the number of reproductive modes varied from four to 17 in each locality (Appendix 1). After forward selection analysis, pRDA retained all environmental variables ($P < 0.05$ for all explanatory variables). These variables are not collinear, since the VIF values varied from 1.21 (total annual rainfall) to 11.5 (temperature). The first pRDA axis relating species richness and number of reproductive modes to environmental variables was significant ($F = 5.77$, $P = 0.001$). The first two axes explained 23.5% of the variation, but interpretation on the second axis becomes unfeasible because the first axis alone explained 22.5% of the total inertia (Figure 2). The first axis was positively correlated with total annual rainfall ($r = 0.25$) and altitude ($r = 0.15$), and negatively correlated with the concentration of annual rainfall ($r = -0.29$) and temperature ($r = -0.23$). In the triplot, anuran species richness and the number of reproductive modes were directly associated with total annual rainfall and altitude vectors, and indirectly associated with the concentration of annual rainfall vector and temperature (Figure 2). In general, Atlantic forest localities were widely scattered in the triplot, but seven out of 13 localities (AT1, AT2, AT5, AT7, AT9, AT10 and AT11) were more closely associated with the total annual rainfall vector (Figure 2). On the other hand, most mesophytic semideciduous forest (SEM1, SEM2, SEM4, SEM5 and SEM9) and cerrado localities (CER1, CER2, CER3 and CER4) were most closely associated to the concentration of annual rainfall (Figure 2). As altitude and temperature vectors are more closely associated with the second axis, no conclusive association could be determined between these environmental variables and selected localities. The few other localities from the Amazonian rain

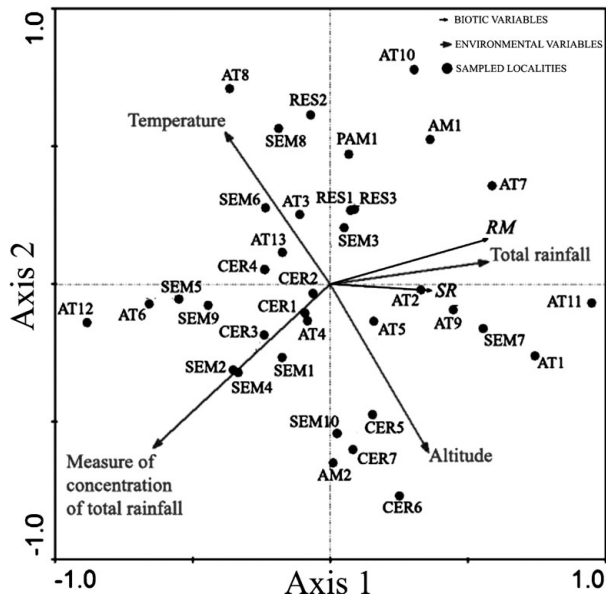


Figure 2. Ordination triplot showing the two axis of the partial RDA, considering the biotic variables (SR = total anuran species richness; RM = number of reproductive modes), environmental variables, and sampled localities whose anuran species richness and reproductive modes were considered in the current study (abbreviation of each locality means the predominant phytophysiognomy, as in Appendix 1). Eigenvalues: axis 1 = 0.194; axis 2 = 0.008. Percentage variance of species data: axis 1 = 22.5%; axis 2 = 1%.

forest, pampa and restinga did not show a common pattern.

The variation partitioning showed that 15.5% of the variation was explained solely by the environmental matrix, 6.6% was explained by geographic position (i.e. due to spatial autocorrelation), and 1.43% was explained by the indistinguishable effect of environment and space. The remaining 76.5% of the variation was unexplained.

DISCUSSION

In the present study, much of the variance remained unexplained by explanatory variables (76.5%), which may be made up of other variables not tested. Among the few studies that analysed patterns of amphibian species richness distribution, habitat heterogeneity (e.g. rain-forest area and shape, and diversity of structural vegetation types), altitudinal diversity, and latitude are important for determining patterns of frog species richness in Australia (Williams & Hero 2001, Williams & Pearson 1997). Other variables considered important for amphibians are those concerning environmental productivity, such as net primary productivity explaining part of distribution of amphibian species richness in China

(Qian *et al.* 2007) and the amount of plant biomass as one of the main predictors of amphibian species richness in Europe (Rodríguez *et al.* 2005). However, these variables are not considered the most important predictors of amphibian species richness in their respective localities, instead, rainfall has been pointed out as the main factor for determining species richness (Australia: Williams & Hero 2001; China: Qian *et al.* 2007). Although Rodríguez *et al.* (2005) did not find a direct relationship between rainfall and amphibian species richness in Europe, water availability and energy (primary productivity) were the main factors related to species richness there. On the other hand, recent studies have shown that a large number of stochastic events can lead to variation in community composition (Ernst & Rödel 2005). In addition, some studies have found that anuran species diversity of some guilds is also associated with historical biogeography (especially extinctions and subsequent recolonizations) of a given area (Williams & Hero 2001).

Among the explanatory variables studied herein (which explained 23.5% of the variance), the present study found that rainfall was the main variable related to species richness of anuran amphibians in Brazil, as it was in the previous studies performed in Australia (Williams & Hero 2001) and China (Qian *et al.* 2007). The association of amphibians with humid areas is expected based on their physiological requirements (moist environments prevent desiccation of the animal, and allow cutaneous gas exchange) and also based on their reproductive requirements (anamniotic eggs that depend on water bodies or moist environments for an adequate development), which are unique characteristics of this animal group (Duellman & Trueb 1994). This becomes evident in the current study because of the higher species richness in localities with higher values of total annual rainfall (e.g. Boracéia – AT1 and Manaus – AM1, with 65 and 50 species respectively; Heyer *et al.* 1990 and Lima *et al.* 2006, respectively). The same result occurs in the case of the relationship between rainfall and the number of reproductive modes. Even though species richness is considered moderate in a humid locality, the number of reproductive modes tends to be high, because humidity can provide a suitable microhabitat for terrestrial reproductive modes (Hödl 1990). For example, the Estação Ecológica Juréia-Itatins (AT2; Pombal & Gordo 2004) shelters 30 anuran species (lower species richness than most of the localities in the Atlantic forest *sensu stricto*), but there are 14 known reproductive modes in this area, six of them with terrestrial or arboreal eggs (modes 19, 23, 24, 25, 32 and 36, *sensu* Haddad & Prado 2005). The importance of total annual rainfall is more evident for Atlantic forest *sensu stricto* localities, where the rainfall is continuous throughout the year (Haddad *et al.* 2008). Thus, one possible explanation for the high diversity of reproductive modes in Atlantic forest frogs is

their successful adaptations to reproduce in the different available humid microhabitats found in the moist forest (Haddad & Prado 2005).

On the other hand, the measure of the concentration of annual rainfall was negatively correlated with species richness and the number of reproductive modes. According to Duellman (1988) and Hödl (1990), areas with little seasonal variation (that is, with continuous high humidity) favour semi-terrestrial and terrestrial reproductive modes, which are generally absent or rarely represented in anuran assemblages from seasonally dry areas. In the present study, localities with less seasonal variation tend to shelter moderate-to-high species richness and numbers of reproductive modes, as is seen in Mangaratiba, Rio de Janeiro State (with 54 species and 17 different reproductive modes: Carvalho-e-Silva *et al.* 2008, Silva *et al.* 2008), and São José do Barreiro, São Paulo State (with 35 species and 13 different reproductive modes: Serafim *et al.* 2008), which are localities where rainfall is continuous through the year. On the other hand, anuran species richness and number of reproductive modes of seasonal localities (most cerrado and mesophytic semideciduous forest localities) were most closely associated with the concentration of annual rainfall in the triplot; that is to say, anuran assemblages in seasonal areas of Brazil are more affected by climatic seasonality of rainfall than they are by other climatic variables analysed. In fact, the high overlap between cerrado and mesophytic semideciduous forest localities recorded herein was expected due to the high climatic seasonality of these two phytophysiognomies, which makes the occurrence of most typical anuran species from Atlantic forest *sensu stricto* impossible (Santos *et al.* 2009).

In the present study, species richness and the number of reproductive modes were not associated with temperature. Although temperature is often correlated with breeding activities of anuran species throughout the year in the Neotropical region (Canavero *et al.* 2008, Duellman & Trueb 1994, Vasconcelos & Rossa-Feres 2005), it is believed that this variable plays a secondary role in the regulation of reproductive activity of anurans (Heyer 1973), because it is probably correlated with rainfall occurrence, mainly in regions with climatic seasonality (Santos *et al.* 2007, Toledo *et al.* 2003, Vasconcelos & Rossa-Feres 2005). Despite this probable secondary importance of temperature, a stronger influence of this variable on anuran assemblages might be recorded in future studies with the inclusion of more localities in the southernmost Brazilian region, because while variation in precipitation decreases, temperature markedly increases its seasonality at higher latitudes, which in turn influences anuran activities at these locations (Canavero *et al.* 2009).

We identified here that altitude was positively correlated with species richness and the number of reproductive modes. Neither Rodríguez *et al.* (2005) in Europe nor Qian *et al.* (2007) in China found any correlation between altitudinal variables (topographic relief, minimum and maximum elevation) and amphibian species richness in those regions. Although Williams & Hero (2001) found a positive correlation between altitudinal diversity and amphibian species richness in Australia, altitudinal importance should be considered carefully in this case, since differences in elevation may also be associated with differences in climate at finer scales (Rodríguez *et al.* 2005), and increasing elevation results in decreasing temperature (Qian *et al.* 2007, Williams & Hero 2001). No association between elevation and temperature was found in the present study, maybe because we did not include high-altitude sites. Altitude can be important for providing habitat diversity in a given locality, which can differ substantially if elevation range starts at a different base elevation (Qian *et al.* 2007). Although it had not been possible to measure the true values of geographic isolation of selected localities in order to assess topographic diversity, mountainous areas are known to contain many different habitats, producing more geographic isolation of populations, and may therefore promote speciation (Krebs 2001). In the same way, the rough topography of Atlantic forest in the Brazilian coastal area is one of the explanations for the high diversity of anurans in this biome, because it breaks the biome up into many small microhabitats, and could lead to high rates of endemism and geographic isolation among populations (Haddad & Prado 2005). Thus, in order to generalize such a hypothesis for Brazilian anurans, we recommend more surveys in high-altitude sites in different Brazilian areas, particularly in those not studied, such as the North Amazonian upland region.

In conclusion, total annual rainfall was the main climatic variable predicting anuran species richness and the number of reproductive modes in the Brazilian localities studied. However, only 23.5% of the total variance of the data was explained by the climatic variables, altitudinal variables and the geographic position of studied localities, whereas only 15.5% was explained solely by climatic and altitudinal variables. These findings suggest that other factors not analysed herein (e.g. habitat heterogeneity, primary productivity, phylogenetic constraints and even stochastic events) may also be important for predicting anuran species richness and the number of reproductive modes throughout the Brazilian territory. In addition to the inclusion of more environmental variables, we strongly recommend the inclusion of new localities in future studies, particularly those located in Brazilian biomes that were insufficiently

represented or not included herein, such as the seasonally flooded area of Brazil (the Pantanal) and the north-eastern Brazilian semi-arid region (caatinga).

ACKNOWLEDGEMENTS

The authors are grateful to João Gabriel R. Giovanelli, for support with the software DIVA-GIS, and an anonymous reviewer for comments and suggestions in the first version of the manuscript. This study was supported by FAPESP (Biota/Fapesp proc. 01/13341-3, 02/13602-4, 08/50928-1, and 09/17195-3), CNPq and Capes.

LITERATURE CITED

- AB'SABER, A. N. 1977. Os domínios morfoclimáticos na América do Sul. *Geomorfologia* 52:1–159.
- AFONSO, L. G. & ETEROVICK, P. C. 2007. Spatial and temporal distribution of breeding anurans in streams in southeastern Brazil. *Journal of Natural History* 41:949–963.
- AYRES, M., AYRES, M., AYRES, D. L. & SANTOS, A. S. 2003. *BioEstat 3.0. Aplicações estatísticas nas áreas das ciências biológicas e médicas*. Sociedade Civil de Mamirauá, Belém. 291 pp.
- BASTAZINI, C. V., MUNDURUCA, J. F. V., ROCHA, P. L. & NAPOLI, M. F. 2007. Which environmental variables better explain changes in anuran community composition? A case study in the restinga of Mata de São João, Bahia, Brazil. *Herpetologica* 63:459–471.
- BASTOS, R. P., MOTTA, J. A. O., LIMA, L. P. & GUIMARÃES, L. D. 2003. *Anfíbios da Floresta Nacional de Silvânia, estado de Goiás*. Stylo Gráfica e Editora, Goiânia. 82 pp.
- BEEBEE, T. J. C. 1996. *Ecology and conservation of amphibians*. Chapman & Hall, London. 214 pp.
- 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 Neotropica* 7: <http://www.biotaneotropica.org.br/v7n2/pt/abstract?article+bn015070-22007>.
- BERNARDE, P. S. & MACHADO, R. A. 2001. Riqueza de espécies, ambientes de reprodução e temporada de vocalização da anurofauna em Três Barras do Paraná, Brasil (Amphibia: Anura). *Cuadernos de Herpetologia* 14:93–104.
- BERTOLUCI, J. & RODRIGUES, M. T. 2002. Utilização de habitats e micro-habitats de vocalização em uma taxocenose de anuros (Amphibia) da Mata Atlântica do sudeste do Brasil. *Papéis Avulsos de Zoologia* 42:287–397.
- BERTOLUCI, J., BRASSALOTI, R. A., JÚNIOR, J. W. R., VILELA, V. M. F. N. & SAWAKUCHI, H. O. 2007. Species composition and similarities among anuran assemblages of forests in southeastern Brazil. *Scientia Agricola* 64:364–374.
- BORCARD, D., LEGENDRE, P. & DRAPEAU, P. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055.
- BOTH, C., KAEFER, I. L., SANTOS, T. G. & CECHEIN, S. T. Z. 2008. An austral anuran assemblage in the Neotropics: seasonal occurrence correlated with photoperiod. *Journal of Natural History* 42:205–222.
- BOTH, C., SOLÉ, M., SANTOS, T. G. & CECHEIN, S. Z. 2009. The role of spatial and temporal descriptors for Neotropical tadpole communities in southern Brazil. *Hydrobiologia* 624:125–138.
- BRANDÃO, R. A. & ARAUJO, A. F. B. 1998. A herpetofauna da Estação Ecológica de Águas Emendadas. Pp. 9–21 in Marinho-Filho, J., Rodrigues, F. & Guimarães, M. (eds.). *Vertebrados da Estação Ecológica de Águas Emendadas. História natural e ecologia em um fragmento de cerrado do Brasil Central*. SEMATEC/IEMA, Brasília. 92 pp.
- BRASILEIRO, C. A., SAWAYA, R. J., KIEFER, M. C. & MARTINS, M. 2005. Amphibians of an open cerrado fragment in southeastern Brazil. *Biota Neotropica* 5: <http://www.biotaneotropica.org.br/v5n2/pt/abstract?article+BN00405022005>.
- CANAVERO, A., ARIM, M., NAYA, D. E., CAMARGO, A., ROSA, I. & MANEYRO, R. 2008. Calling activity patterns in an anuran assemblage: the role of seasonal trends and weather determinants. *North-Western Journal of Zoology* 4:29–41.
- CANAVERO, A., ARIM, M. & BRAZEIRO, A. 2009. Geographic variations of seasonality and coexistence in communities: the role of diversity and climate. *Austral Ecology* 34:741–750.
- 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 Zoologia* 97:21–26.
- CARVALHO-E-SILVA, A. M. T., SILVA, G. R. & CARVALHO-E-SILVA, S. P. 2008. Anuros da Reserva Rio das Pedras, Mangaratiba, RJ, Brasil. *Biota Neotropica* 8: <http://www.biotaneotropica.org.br/v8n1/en/abstract?inventory+bn02608012008>.
- COLOMBO, P., KINDEL, A., VINCIPROVA, G. & KRAUSE, L. 2008. Composição e ameaças à conservação dos anfíbios anuros do Parque Estadual de Itapeva, município de Torres, Rio Grande do Sul, Brasil. *Biota Neotropica* 8: <http://www.biotaneotropica.org.br/v8n3/pt/abstract?inventory+bn01208032008>.
- CONTE, C. E. & MACHADO, R. A. 2005. Riqueza de espécies e distribuição espacial em comunidade de anuros (Amphibia, Anura) em uma localidade de Tijucas do Sul, Paraná, Brasil. *Revista Brasileira de Zoologia* 22:940–948.
- DINIZ-FILHO, J. A. F., BINI, L. M., VIEIRA, C. M., BLAMIRE, D., TERRIBILE, L. C., BASTOS, R. P., OLIVEIRA, G. & BARRETO, B. S. 2008. Spatial patterns of terrestrial vertebrate species richness in the Brazilian Cerrado. *Zoological Studies* 47:146–157.
- DUELLMAN, W. E. 1988. Pattern of species diversity in anuran amphibians in the American tropics. *Annals of the Missouri Botanical Garden* 75:79–104.
- DUELLMAN, W. E. 2005. *Cusco Amazônico: the lives of amphibians and reptiles in an Amazonian Rainforest*. Cornell University Press, Ithaca. 433 pp.
- DUELLMAN, W. E. & TRUEB, L. 1994. *Biology of amphibians*. McGraw-Hill, Baltimore. 670 pp.
- ERNST, R. & RÖDEL, M.-O. 2005. Anthropogenically induced changes of predictability in tropical anuran assemblages. *Ecology* 86:3111–3118.

- ERNST, R. & RÖDEL, M.-O. 2008. Patterns of community composition in two tropical tree frog assemblages: separating spatial structure and environmental effects in disturbed and undisturbed forests. *Journal of Tropical Ecology* 24:111–120.
- ETEROVICK, P. C. & SAZIMA, I. 2004. *Anfíbios da Serra do Cipó – Minas Gerais – Brasil*. Editora PUCMinas, Belo Horizonte. 152 pp.
- FEIO, R. N., BRAGA, U. M. L., WIEDERHECKER, H. & SANTOS, P. S. 1998. *Anfíbios do Parque Estadual do Rio Doce (Minas Gerais)*. Universidade Federal de Viçosa, Instituto Estadual de Florestas, Viçosa. 32 pp.
- HADDAD, C. F. B. & PRADO, C. P. A. 2005. Reproductive modes in frogs and their unexpected diversity in the Atlantic Forest of Brazil. *BioScience* 55:207–217.
- HADDAD, C. F. B. & SAZIMA, I. 1992. Anfíbios anuros da Serra do Japi. Pp. 188–211 in Morellato, L. P. C. (ed.). *História Natural da Serra do Japi: Ecologia e Preservação de uma Área Florestal no Sudeste do Brasil*. Editora UNICAMP/FAPESP, Campinas.
- HADDAD, C. F. B., ANDRADE, G. V. & CARDOSO, A. J. 1988. Anfíbios anuros no Parque Nacional da Serra da Canastra, Estado de Minas Gerais. *Brasil Florestal* 64:9–20.
- HADDAD, C. F. B., TOLEDO, L. F. & PRADO, C. P. A. 2008. *Anfíbios da Mata Atlântica: Guia dos anfíbios anuros da Mata Atlântica*. Editora Neotropica, São Paulo. 244 pp.
- HEYER, W. R. 1973. Ecological interactions of frog larvae at seasonal tropical location in Thailand. *Journal of Herpetology* 7:337–361.
- HEYER, W. R., RAND, A. S., CRUZ, C. A. G., PEIXOTO, O. L. & NELSON, C. E. 1990. Frogs of Boracéia. *Arquivos de Zoologia* 31:231–410.
- HIJMAN, R. J., GUARINO, L. & ROJAS, E. 2002. *DIVA-GIS. A geographic information system for the analysis of biodiversity data*. Manual – International Potato Center, Lima. 73 pp.
- HIJMAN, R. J., CAMERON, S. E., PARRA, J. L., JONES, P. G. & JARVIS, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965–1978.
- HÖDL, W. 1990. Reproductive diversity in Amazonian lowland frogs. *Fortschritte der Zoologie* 38:41–60.
- JUNCA, F. A. 2006. Diversidade e uso de habitat por anfíbios anuros em duas localidades de Mata Atlântica, no norte do estado da Bahia. *Biota Neotropica* 6: <http://www.biotaneotropica.org.br/v6n2/pt/abstract?article+bn03006022006>.
- KOPP, K. & ETEROVICK, P. C. 2006. Factors influencing spatial and temporal structure of frog assemblages at ponds in southeastern Brazil. *Journal of Natural History* 40:1813–1830.
- KREBS, C. J. 2001. *Ecology: the experimental analysis of distribution and abundance*. Benjamin Cummings, San Francisco. 695 pp.
- KWET, A. & DI-BERNARDO, M. 1999. *Anfíbios – Amphibien – Amphibians*. EDIPUCRS, Porto Alegre. 107 pp.
- LEGENDRE, P. & LEGENDRE, L. 1998. *Numerical ecology*. Elsevier Scientific Publishing Company, Amsterdam. 870 pp.
- LIMA, A. P., MAGNUSSON, W. E., MENIN, M., ERDTMANN, L. K., RODRIGUES, D. J., KELLER, C. & HÖDL, W. 2006. *Guide to the frogs of Reserva Adolpho Ducke – Central Amazonia*. Attema, Design Editorial, Manaus. 168 pp.
- LUCAS, E. M. & FORTES, V. B. 2008. Frog diversity in the Floresta Nacional de Chapécó, Atlantic Forest of southern Brazil. *Biota Neotropica* 8: <http://www.biotaneotropica.org.br/v8n3/pt/abstract?article+bn00508032008>.
- MACHADO, R. A., BERNARDE, P. S., MORATO, S. A. A. & ANJOS, L. 1999. Análise comparada da riqueza de anuros entre duas áreas com diferentes estados de conservação no município de Londrina, Paraná, Brasil (Amphibia, Anura). *Revista Brasileira de Zoologia* 16:997–1004.
- McDIARMID, R. W. 1994. Amphibian diversity and natural history: an overview. Pp. 5–15 in Heyer, W. R., Donnelly, M. A., McDiarmid, R. W., Hayek, L. A. C. & Foster, M. S. (eds). *Measuring and monitoring biological diversity: standard methods for amphibians*. Smithsonian Institution Press, Washington. 388 pp.
- MORAES, R. A., SAWAYA, R. J. & BARRELLA, W. 2007. Composição e diversidade de anfíbios anuros em dois ambientes de Mata Atlântica no Parque Estadual Carlos Botelho, São Paulo, sudeste do Brasil. *Biota Neotropica* 7: <http://www.biotaneotropica.org.br/v7n2/pt/abstract?article+bn00307022007>.
- PARRIS, K. M. 2004. Environmental and spatial variables influence the composition of frog assemblages in sub-tropical eastern Australia. *Ecography* 27:392–400.
- POMBAL, J. P. & GORDO, M. 2004. Anfíbios anuros da Juréia. Pp. 243–256 in Marques, O. A. V. & Duleba, W. (eds). *Estação ecológica Juréia-Itatins. Ambiente físico, flora e fauna*. Holos Editora, Ribeirão Preto.
- PRADO, G. M. & POMBAL, J. P. 2005. Distribuição espacial e temporal dos anuros em um brejo da Reserva Biológica de Duas Bocas, sudeste do Brasil. *Arquivos do Museu Nacional* 63:685–705.
- QIAN, H., WANG, X., WANG, S. & LI, Y. 2007. Environmental determinants of amphibian and reptile species richness in China. *Ecography* 30:471–482.
- RAHBEK, C. & GRAVES, G. R. 2001. Multiscale assessment of patterns of avian species richness. *Proceeding of the National Academy of Sciences USA* 98:4534–4539.
- RAMOS, A. D. & GASPARINI, J. L. 2004. *Anfíbios do Goiapaba-Açu, Fundão, Estado do Espírito Santo*. Gráfica Santo Antônio, Vitória. 75 pp.
- RIBEIRO, R. S., EGITO, G. T. B. T. & HADDAD, C. F. B. 2005. Chave de identificação: anfíbios anuros da vertente de Jundiá da Serra do Japi, estado de São Paulo. *Biota Neotropica* 5: <http://www.biotaneotropica.org.br/v5n2/pt/abstract?identification-key+bn03005022005>.
- RODRÍGUEZ, M. Á., BELMONTES, J. A. & HAWKINS, B. A. 2005. Energy, water and large-scale patterns of reptile and amphibian species richness in Europe. *Acta Oecologica* 28:65–70.
- SANTOS, T. G., CASATTI, L. & ROSSA-FERES, D. C. 2007. Diversidade e distribuição espaço-temporal de anuros em região com pronunciada estação seca no sudeste do Brasil. *Iheringia, série Zoologia* 97:37–49.
- SANTOS, T. G., KOPP, K., SPIES, M. R., TREVISAN, R. & CECHEIN, S. Z. 2008. Distribuição temporal e espacial de anuros em área de Pampa, Santa Maria, RS. *Iheringia, Série Zoologia* 98:244–253.
- SANTOS, T. G., VASCONCELOS, T. S., ROSSA-FERES, D. C. & HADDAD, C. F. B. 2009. Anurans of a seasonally dry tropical forest: Morro do Diabo State Park, São Paulo state, Brazil. *Journal of Natural History* 43:973–993.
- SERAFIM, H., IENNE, S., CICCHI, P. J. P. & JIM, J. 2008. Anurofauna de remanescentes de floresta Atlântica do município de São José do

- Barreiro, estado de São Paulo, Brasil. *Biota Neotropica* 8: <http://www.biotaneotropica.org.br/v8n2/pt/abstract?article+bn01008022008>.
- SILVA, H. R., CARVALHO, A. L. G. & BITTENCOURT-SILVA, G. B. 2008. Frogs of Marambaia: a naturally isolated Restinga and Atlantic Forest remnant of southeastern Brazil. *Biota Neotropica* 8: <http://www.biotaneotropica.org.br/v8n4/pt/abstract?inventory+bn01808042008>.
- TER BRAAK, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179.
- TER BRAAK, C. J. F. & SMILAUER, P. 2002. *CANOCO Reference manual and Canodraw for Windows User's guide: Software for Canonical Community Ordination (version 4.5)*. Microcomputer Power, Ithaca. 500 pp.
- TERRIBILE, L. C. & DINIZ-FILHO, J. A. F. 2009. Spatial patterns of species richness in New World coral snakes and the metabolic theory of ecology. *Acta Oecologica* 35:163–173.
- TOLEDO, L. F., ZINA, J. & HADDAD, C. F. B. 2003. Distribuição espacial e temporal de uma comunidade de anfíbios anuros do município de Rio Claro, São Paulo, Brasil. *Holos Environment* 3:136–149.
- UETANABARO, M., SOUZA, F. L., FILHO, P. L., BEDA, A. F. & BRANDÃO, R. A. 2007. Anfíbios e répteis do Parque Nacional da Serra da Bodoquena, Mato Grosso do Sul, Brasil. *Biota Neotropica* 7: <http://www.biotaneotropica.org.br/v7n3/pt/abstract?article+bn01207032007>.
- VASCONCELOS, T. S. & ROSSA-FERES, D. C. 2005. Diversidade, distribuição espacial e temporal de anfíbios anuros (Amphibia, Anura) na região noroeste do estado de São Paulo, Brasil. *Biota Neotropica* 5: <http://www.biotaneotropica.org.br/v5n2/pt/abstract?article+BN01705022005>.
- VITT, L. J. & CALDWELL, J. P. 2009. *Herpetology: an introductory biology of amphibians and reptiles*. Academic Press, Burlington. 697 pp.
- WERNER, E. E., SKELLY, D. K., RELYEA, R. A. & YUREWICZ, K. L. 2007. Amphibian species richness across environmental gradients. *Oikos* 116:1697–1712.
- WILLIAMS, S. E. & HERO, J.-M. 2001. Multiple determinants of Australian tropical frog biodiversity. *Biological Conservation* 98:1–10.
- WILLIAMS, S. E. & PEARSON, R. G. 1997. Historical rainforest contractions, localized extinctions and patterns of vertebrate endemism in the rainforests of Australia's Wet Tropics. *Proceedings of the Royal Society of London B* 264:709–716.
- ZAR, J. H. 1999. *Biostatistical analysis*. Prentice Hall, New Jersey. 663 pp.
- ZINA, J., ENNSER, J., PINHEIRO, S. C. P., HADDAD, C. F. B. & TOLEDO, L. F. 2007. Taxocenose de anuros de uma mata semidecídua do interior do Estado de São Paulo e comparações com outras taxocenoses do Estado, sudeste do Brasil. *Biota Neotropica* 7: <http://www.biotaneotropica.org.br/v7n2/pt/abstract?article+bn00607022007>.

Appendix 1. Predominant phytophysognomy of the Brazilian localities whose species richness and reproductive modes were considered in the current study (cited references and abbreviations follow after the name of their respective localities). RICH = species richness of each locality; RM = number of reproductive modes in each locality; AREA = total sampled area; ALT = altitude; RAIN = total annual rainfall; TEMP = mean minimum temperature; RAIN2 = measure of concentration of annual rainfall.

Localities and abbreviation of states: abbreviation codes	RICH	RM	AREA (km ²)	ALT (m)	RAIN (mm)	TEMP (°C)	RAIN2
Amazonian forest							
Reserva Ducke, AM (Lima <i>et al.</i> 2006): AM1	50	14	100	92	2185	23	0.29
Espigão d'Oeste, RO (Bernarde 2007): AM2	47	10	10	258	1956	17	0.502
Atlantic forest <i>sensu stricto</i>							
Estação Ecológica da Boracéia, SP (Heyer <i>et al.</i> 1990): AT1	65	16	164	908	2416	11.8	0.238
Estação Ecológica Juréia-Itatins, SP (Pombal & Gordo 2004): AT2	30	14	800	614	2320	13.8	0.294
Floresta Nacional de Chapecó, SC (Lucas & Fortes 2008): AT3	28	7	16.1	574	1954	13.9	0.379
Goiapaba-Açú, ES (Ramos & Gasparini 2004): AT4	41	13	37.4	584	1264	16.7	0.338
Parque Estadual Carlos Botelho, SP (Bertoluci <i>et al.</i> 2007, Moraes <i>et al.</i> 2007): AT5	37	13	376	665	1209	13.4	0.321
Parque Estadual Intervales, SP (Bertoluci & Rodrigues 2002): AT6	47	15	380	893	1399	12.3	0.292
Parque Estadual de Itapeva, RS (Colombo <i>et al.</i> 2008): AT7	28	6	10	23	1420	15.2	0.499
Parque Estadual do Rio Doce, MG (Feio <i>et al.</i> 1998): AT8	38	10	360	256	1138	17.9	0.53
Pró-Mata, RS (Both <i>et al.</i> 2009, Kwet & Di-Bernardo 1999): AT9	35	9	45	701	1871	11.5	0.006
Mangaratiba, RJ (Carvalho-e-Silva <i>et al.</i> 2008, Silva <i>et al.</i> 2008): AT10	54	17	42.1	297	1463	16.6	0.009
Reserva Biológica Duas Bocas, ES (Prado & Pombal 2005): AT11	34	11	0.51	248	1181	19.2	0.295
São José do Barreiro, SP (Serafim <i>et al.</i> 2008): AT12	35	13	40.5	1059	1587	11	0.033
Tijucas do Sul, PR (Conte & Machado 2005): AT13	23	8	1.79	926	1469	11	0.157
Cerrado							
Estação Ecológica de Águas Emendadas, GO (Brandão & Araujo 1998): CER1	26	8	105	1106	1431	15.7	0.552
Estação Ecológica de Assis, SP (Bertoluci <i>et al.</i> 2007): CER2	19	6	13.1	569	1346	14.3	0.31
Estação Ecológica de Itirapina, SP (Brasileiro <i>et al.</i> 2005): CER3	28	6	23	745	1373	14.3	0.462
Floresta Nacional de Silvânia, GO (Bastos <i>et al.</i> 2003): CER4	29	11	4.67	902	1371	16.5	0.525
Parque Nacional da Serra da Canastra, MG (Haddad <i>et al.</i> 1988): CER5	29	10	715	1347	1611	12.1	0.526
Santuário do Caraça, MG (Afonso & Eterovick 2007, Canelas & Bertoluci 2007, Kopp & Eterovick 2006): CER6	45	11	102	1424	1630	11.1	0.553
Serra do Cipó, MG (Eterovick & Sazima 2004): CER7	43	12	258	1226	1582	12.7	0.562
Pampa							
Santa Maria, RS (Santos <i>et al.</i> 2008): PAM1	25	4	6	129	1674	14	0.05
Mesophytic semideciduous forest							
Estação Ecológica de Caetetus, SP (Bertoluci <i>et al.</i> 2007): SEM1	24	8	21.8	628	1296	13.9	0.4
Floresta Estadual Edmundo Navarro de Andrade, SP (Toledo <i>et al.</i> 2003): SEM2	21	5	22.2	627	1306	14.4	0.491
Londrina, PR (Machado <i>et al.</i> 1999): SEM3	27	11	6.7	606	1502	14.4	0.249
Mata São José, SP (Zina <i>et al.</i> 2007): SEM4	24	5	2.43	653	1322	14.3	0.493
Nova Itapirema, SP (Vasconcelos & Rossa-Feres 2005): SEM5	27	4	1.87	470	1173	16.2	0.496
Parque Estadual do Morro do Diabo, SP (Santos <i>et al.</i> 2009): SEM6	28	7	338	386	1188	15.8	0.273
Parque Estadual do Rio Guarani, PR (Bernarde & Machado 2001): SEM7	22	10	22.3	551	1834	11.7	0.095
Parque Nacional da Serra da Bodoquena, MS (Uetanabaro <i>et al.</i> 2007): SEM8	37	8	370	642	1349	16.3	0.3
Santa Fé do Sul, SP (Santos <i>et al.</i> 2007): SEM9	20	4	1.02	411	1250	16.3	0.46
Serra do Japi, SP (Haddad & Sazima 1992, Ribeiro <i>et al.</i> 2005): SEM10	31	8	192	1006	1369	11.7	0.442
Restinga							
Mata de São João, BA (Bastazini <i>et al.</i> 2007): RES1	30	10	5	51	1631	20.6	0.294
Parque Estadual Ilha do Cardoso, SP (Bertoluci <i>et al.</i> 2007): RES2	16	9	225	167	2390	17.4	0.284
Sapiranga, BA (Juncá 2006): RES3	25	8	6	62	1765	20.7	0.312