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Padrões espaciais de ocorrência de tiranídeos (Aves: Tyrannidae) nas florestas com *Araucaria*: aspectos filogenéticos e funcionais

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“Eu não sou uma pessoa convencional. Sempre fui fascinado pela variedade dos seres vivos.”
James Brown (1995)

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RESUMO

Os gradientes de riqueza e diversidade foram extensivamente explorados por ecólogos, estudando as interações dos organismos com o meio em escalas locais, e biogeógrafos, que buscam entender como os organismos se distribuem atualmente e no passado na superfície da terra em relação a dinâmicas de extinção, especiação e dispersão. Mas tão fundamental quanto saber o que determina o número de espécies em um determinado local, é saber o que determina quem são as espécies que ocorrem ali, ou seja, a composição de espécies. Nas últimas décadas, os ecólogos têm reconhecido que a organização das comunidades não é determinada apenas pelo ambiente atual e por interações biológicas, mas também pela história evolutiva dos clados que compõem as comunidades e pelo histórico biogeográfico da região. Os caminhos evolutivos de cada linhagem que compõe o *pool* de espécies se tornam as peças chave na explicação dos padrões de riqueza e diversidade atuais. Eu avaliei fatores ambientais e espaciais que influenciaram a organização dos clados de tiranídeos em sítios distribuídos ao longo da área de ocorrência da floresta com *Araucaria*, e como os gradientes de estrutura filogenética, juntamente com variáveis espaciais, ambientais e de disponibilidade de recurso, afetam a distribuição dos tiranídeos frugívoros naquele bioma. Os resultados mostraram que fatores históricos são os principais determinantes da organização dos clados e da variação espacial da frugivoria por Tyrannidae ao longo do gradiente de distribuição da floresta com *Araucaria*. Os resultados indicam que os processos ecológicos de organização das diferentes comunidades localizadas nesse tipo florestal são, de maneira geral, determinados pela dinâmica histórica de retração e expansão da floresta com *Araucaria* como um todo. A utilização de gradientes filogenéticos ajudou a elucidar alguns mecanismos históricos, como dinâmicas passadas de dispersão e especiação dos grupos, por trás de padrões de variação na frugivoria, que indicam uma possível conservação filogenética de nicho.

PALAVRAS-CHAVE: Floresta com *Araucaria*, Tyrannidae, fatores históricos, conservação filogenética de nicho.

ABSTRACT

Gradients of richness and diversity were extensively addressed by ecologists studying the interactions between organisms and the environment in local scales, and by biogeographers seeking to understand the current and past distribution of organisms in relation to extinction, speciation and dispersal dynamics. Besides untangling the drivers of species richness in a certain site, it is also important to understand what species occur in that site, i.e. species composition. Recently, ecologists have recognized that community assembly is not only influenced by current environment and biological interactions, but also by the evolutionary history of clades in the community and by the biogeographical history of the region. The evolutionary path of each lineage within the species pool is now considered important to explain the current richness and diversity patterns. I evaluated how environmental and spatial factors drive Tyrannidae phylogenetic assembly in sites distributed along *Araucaria* forest range and how phylogenetic gradients, together with resource availability, spatial and environmental variables, affect the frugivorous Tyrannidae in that biome. The results showed that historical factors are the main determinants of phylogenetic assembly and of spatial variation in frugivory by Tyrannidae in the distribution range of the *Araucaria* forests. The results indicated that ecological processes that structure community assemblies in the *Araucaria* forests are, in a general way, determined by the historical dynamic of expansion and contraction of *Araucaria* forest as a hole. The use of phylogenetic information helped us to elucidate some historical mechanisms behind the variation pattern of frugivory, which indicated possible phylogenetic niche conservatism.

KEYWORDS: *Araucaria* forest, Tyrannidae, historical factors, phylogenetic niche conservatism.

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INTRODUÇÃO GERAL

Os pesquisadores da área das ciências da vida sempre foram fascinados pela grande diversidade de espécies existente e pela busca dos fatores que determinam seus padrões de distribuição espacial. O padrão mais antigo e mais fundamental no estudo dos seres vivos é o aumento da diversidade biológica dos pólos em direção ao equador (Willig *et al.* 2003). Os gradientes de riqueza e diversidade foram extensivamente explorados por ecólogos, estudando as interações dos organismos com o meio em escalas locais, e biogeógrafos, que buscam entender como os organismos se distribuem atualmente e no passado na superfície da terra em relação a dinâmicas de extinção, especiação e dispersão (Brown 1995). Nesse contexto, Brown e Maurer (1989) propuseram a criação de uma nova disciplina, a macroecologia, que surge como um esforço para integrar as perspectivas históricas e geográficas em estudos ecológicos, para entender mais completamente a abundância local, distribuição e diversidade de espécies e para gerar *insights* sobre a história e a composição das biotas regionais e continentais (Brown 1995).

Mas tão fundamental quanto saber o que determina o número de espécies em um determinado local, é saber o que determina quem são as espécies que ocorrem ali, ou seja, a composição de espécies. A ecologia de comunidades se ocupa disso, investigando a natureza das interações biológicas, as suas origens e as suas conseqüências ecológicas e evolutivas (Cavender-Bares *et al.* 2009). Nas últimas décadas, os ecólogos têm reconhecido que a organização das comunidades não é determinada apenas pelo ambiente atual e por interações biológicas, mas também pela história evolutiva dos clados que compõem as comunidades e pelo histórico biogeográfico da região (Kissling *et al.* 2009). As espécies que ocorrem em um determinado local constituem um subconjunto do *pool* regional de espécies. Isso levanta algumas questões, como por exemplo, a pergunta levantada por Brown e Lomolino (2006): Quais fatores históricos e ecológicos limitam a composição de biotas a um número restrito de espécies e linhagens filogenéticas? Os caminhos evolutivos de cada linhagem que compõe o *pool* de espécies se tornam as peças chave na explicação dos padrões atuais (Brown e Lomolino 2006).

As florestas com *Araucaria* ocorrem nas cotas mais altas do planalto sul – brasileiro (Hueck, 1972, Fig 1) e a sua fisionomia é dominada pela presença de uma conífera emergente, a *Araucaria angustifolia*. Essa formação florestal é considerada um tipo de floresta Atlântica por Oliveira-Filho & Fontes (2000). No sudeste do sudeste brasileiro, as florestas com *Araucaria* ocorrem em manchas, restringindo-se a sítios úmidos em altitudes elevadas (Safford, 1999). Na região sul, encontra-se formando um mosaico com campos de altitude (Behling 2002). A distribuição geográfica da floresta com *Araucaria* parece refletir sua dinâmica dos últimos milênios (Behling, 2002; Behling & Pillar, 2007). Análises de registros paleopolínicos indicaram que em torno de 14.000 a 10.000 anos atrás o clima no sul e sudeste do Brasil era frio e seco, fazendo com que prevalecessem os campos nas áreas de planalto e fazendo com que a floresta com *Araucaria* ficasse reclusa a encostas e vales no sudeste e quase ausentes na região sul (Behling, 2002). Desde 10.000 até 3.000 anos atrás, o clima começou a ficar mais quente, o que favoreceu a expansão florestal sobre os campos sendo que, mais ao sul, essa expansão foi acelerada a cerca de 1.500 anos atrás até atingir seu limite austral atual (Behling & Pillar, 2007).

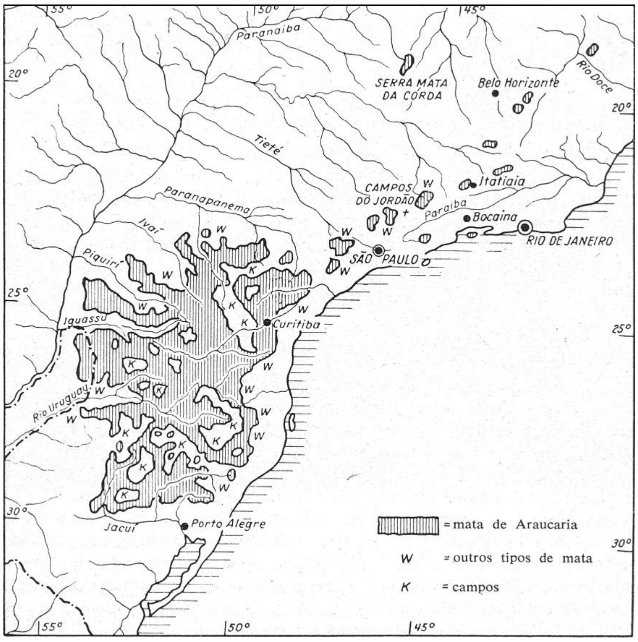

Figura 1: Mapa da área de distribuição da floresta com *Araucaria*, obtido em Hueck (1972).

Tyrannidae é uma das maiores e mais diversas famílias de ave do mundo (*c.* 400 espécies e *c.* 100 gêneros, Fitzpatrick 1980). Segundo Sick (1997), os cantos das espécies da família Tyrannidae são os mais ouvidos em amostragens nas florestas do Brasil. A sua espécie mais conhecida é o bem-te-vi (*Pitangus sulphuratus*, Fig. 2). Pertencentes a ordem Passeriforme, tem a sua distribuição restrita às Américas (Sick 1997). A linhagem que deu origem à família imigrou para a América do Sul por volta de 40 milhões de anos atrás (Ericson *et al.* 2003) e os tiranídeos surgiram dentro das florestas tropicais da América do Sul (Ohlson *et al.* 2008). Alguns grupos conservaram o hábito florestal enquanto outras linhagens sofreram uma intensa radiação adaptativa (Ohlson *et al.* 2008). Hoje em dia ocupam uma grande variedade de nichos continentais e dentro das florestas ocupam todos os estratos da estrutura vertical (Sick 1997). São excepcionalmente diversificados em forma e alimentam-se de invertebrados e frutos (Ridgely e Tudor, 1994). A sua grande diversidade e abundância na região nos neotrópicos faz com que esse grupo seja ideal para estudos sobre radiação adaptativa em aves continentais (Fitzpatrick 1980).

Figura 2: Espécime de Bem-te-vi (*Pitangus sulphuratus*).

No presente estudo eu tive dois objetivos gerais: (1) avaliar como a distribuição dos clados da família de passeriformes Tyrannidae encontrados em comunidades ao longo da distribuição da floresta com *Araucaria* é determinada por variáveis ambientais atuais e pela distribuição espacial dos pontos e (2) avaliar quem são as variáveis que influenciam a distribuição espacial de espécies de Tyrannidae frugívoras. Os objetivos mencionados acima foram tratados nos artigos 1 e 2, respectivamente.

CAPÍTULO 1[1]

Article type: Original article

Spatial and environmental factors determining the phylogenetic assembly of Tyrannidae birds in the Brazilian *Araucaria* forest biome

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[1] Este artigo será submetido ao periódico *Ecography* e já se encontra formatado de acordo com as normas da revista.

ABSTRACT

In this study we evaluate the drivers of phylogenetic assembly of Tyrannidae birds distributed along the *Araucaria* forest biome, accessing the roles of environment, historical factors and neutral dynamics in phylogenetic structure. *Araucaria* forest biome is northern limit in latitude 20°S, and the southern limit is on latitude 29°S, though some areas are also found south of latitude 31°S. We used range maps to obtain Tyrannidae species composition at 33 sites distributed along the *Araucaria* forest distribution and we compiled the phylogenetic distances between species from an available phylogeny. We computed PCPS using phylogenetic fuzzy-weighting and described the site using PCNM as spatial filters and environmental variables. We evaluated the proportion of the variation in phylogenetic gradients that was explained by environmental and spatial filters through variation partitioning using distance-based Redundancy Analysis (db-RDA). Variation partitioning showed that space and temperature seasonality explained together 59% of the variation in phylogenetic structure. Space was the major factor explaining data variation, followed by environment. Tyrannidae clades are not homogeneously distributed along *Araucaria* forest, most likely due to differences in speciation and dispersal rates between them. The past dynamics of *Araucaria* forest might have influenced the distribution of Tyrannidae clades among site too. Temperature seasonality along the year may influence the availability of insects and fruits, which are the major component of Tyrannidae diet. Furthermore, the analysis of additional niche dimensions, such as food availability, could be useful to explain Tyrannidae phylogenetic assembly, as well as past environmental conditions.

Keywords: phylogenetic assembly, Tyrannidae, *Araucaria* forest, phylogenetic habitat filtering, PCPS, PCNM, db-RDA.

INTRODUCTION

The major goal of community ecology relies in determining the rules that drive species assembly process in order to predict the composition of local communities from regional species pools (Webb *et al.*, 2002, Cavender-Bares et al 2009). Besides the well known environmental influence on species assembly (Hawkins *et al.*, 2003a, Melo *et al.*, 2009), we have to consider the geographical space where these species are scattered (Bell, 2001, Hubbell, 2001). Species are usually assembled by environmental factors related to their niches (Keddy and Weiher, 1999) and by neutral processes, such as dispersal limitation (Hubbell, 2001). However, species pools result to some extent from historical patterns of speciation, extinction and biogeographical dispersal (Pennington *et al.*, 2006, Cavender-Bares et al 2009). The historical perspective and the phylogenetic approach in macroecological studies help to elucidate ecological and evolutionary questions underlying species assembly (Cavender-Bares *et al* 2009).

Since species share different degrees of evolutionary relatedness between them, closely-related species are likely to show higher trait similarity in relation to each other than distant-related species (Felsenstein, 1985). As a consequence, it is expected a tendency of closely related species to retain similar ecological niches over time scale (phylogenetic niche conservatism; Wiens and Graham, 2005). Consequently, the species assembly could be driven to some extent not by local adaptations, but by the filling of available niches to which species, or clades, are pre-adapted (Donoghue, 2008). Thus, it is expected that closely-related species would be assembled by environmental filtering (phylogenetic habitat filtering; Duarte 2010). Some studies have addressed the role of environmental gradients in phylogenetic community assembly (Kembel and Hubbell, 2006, Graham *et al.*, 2009, Willis *et al.*, 2010; Duarte *et al.* submitted). Nonetheless, phylogenetic assembly at broader geographical scales is likely to result to some extent from historical factors related to biogeographical and evolutionary processes (Webb *et al.*, 2002, Cavender-Bares *et al* 2009). Therefore, in order to assess which are the drivers of phylogenetic assembly in a given array of sites it is necessary to discriminate environmental effects from other processes related to the spatial distribution of the sites, such as historical factors and neutral dynamics (Cavender-Bares et al 2009).

Tyrannidae (tyrants flycatchers) is the one of the largest and most diverse of all bird families (*c*. 400 species in *c*. 100 genera, Fitzpatrick, 1980), being restricted to the New World (Sick, 1997). Their diversity and abundance in the Neotropics makes Tyrannidae well-suited for a variety of studies regarding adaptive radiation in a continental avian group (Fitzpatrick, 1980). This family belongs to New World suboscines group and has its origin inside South American tropical rainforests around 25 Mya BP (Ohlson *et al.*, 2008). Species from Tyrannidae are adapted to a great array of ecological niches, as they occupy all different vertical strata inside complex tropical forest (Sick, 1997). This great ecological diversification has been favored by the absence of oscine birds in South America, which inhabited the northern hemisphere before the rise of the Panama isthmus and the Great American Biotic Interchange (Sick, 1997, Ericson *et al.*, 2003).

Most studies on phylogenetic community structure uses plants as model organisms (Emerson and Gillespie, 2008). To our knowledge, there is only one study about phylogenetic structure focusing on bird communities, more specifically on hummingbirds (Trochilidae) (see Graham *et al.*, 2009). In that study, Graham *et al.* (2009) found that hummingbird communities located at higher elevations were phylogenetic clustered, probably due to environmental filtering in these habitats. In this study we aimed to evaluate the influence of environmental and spatial factors on the phylogenetic assembly of Tyrannidae birds distributed along *Araucaria* forest biome. We employed Principal Coordinates of Phylogenetic Structure (PCPS) analysis and variation partitioning (using distance-based Redundancy Analysis, hereafter called db-RDA) to assess the role of environmental and spatial filters in phylogenetic assembly and how Tyrannidae clades respond to both gradients.

METHODS

Study Site

We analyzed phylogenetic assembly in Tyrannidae birds occurring along the geographical range of Brazilian *Araucaria* forest biome. The *Araucaria* forest is a vegetation type typically found on the highland plateau in southern Brazil, at elevation around 500 m a.s.l. (Hueck, 1972), physiognomically characterized by an emergent conifer tree, *Araucaria angustifolia*. Its northern limit is the Serra da Mantiqueira (latitude 20°S), and the southern limit is on latitude 29˚(Hueck, 1972), though some patches are also found down to latitude 31° in the Serra do Sudeste granitic plateau (Reitz *et al.*, 1983). The mean annual rainfall and temperature range from 1400 and 2200 and 12 to 18 ˚C, respectively (Behling, 2002).

Tyrannidae species composition

The occurrence of Tyrannidae birds was obtained for *Araucaria* forest sites that were previously compiled by Duarte *et al.* (submitted) in relation to shrub/tree species composition. We coincided bird and vegetation plots in order to enable us to use plot vegetation composition as an environmental factor in the analysis. We defined 33 cells, using a 15’ × 15’grid (Fig. 1) based on floristic plots mentioned above (some cells contained more than one point). Each cell was taken as a bird plot. We obtained the Tyrannidae composition of each grid cell using the bird distribution range database (Ridgely *et al.*, 2005) available at <http://www.natureserve.com>. The database was processed using ESRI ArcView GIS 3.2, to record species’ presence in each cell. Only forest Tyrannidae species were considered in this study. The Tyrannidae composition of each cell was arranged in a presence/absence matrix (**W**) of sites by bird species. We followed IOC World Bird Names v2.6 (Gill and Donsker, 2010) to circumscribe the Tyrannidae clade and to standardize taxonomic nomenclature.

Spatial and environmental factors

We generated spatial models using principal coordinates of neighbor matrices analysis (PCNM, Borcard and Legendre, 2002). For this we used the geographical coordinates (latitude, longitude) of the central point of each cell, To calculate PCNM variables, geographic distances between sites were truncated at the maximum distance connecting all sites (268.8 km), based on a minimum spanning tree criterion (Rangel *et al.*, 2006). PCNM analysis was performed using SAM 4.0 software (Rangel *et al.*, 2010).

To characterize environmental conditions in each plot, we used six environmental variables: altitude, annual mean temperature, temperature seasonality (standard deviation of temperature along the year x 100), annual mean rainfall, rainfall seasonality (rainfall's coefficient of variation) and floristic structure. The first five variables were compiled from WorldClim 1.4 database (Hijmans *et al.*, 2005), and the last one consists of the first axis of a principal coordinate analysis performed on the floristic composition of each cell. The first ordination axis contained only 15.3% of the total variation; nonetheless, bootstrap autoresampling analysis (Pillar 1999) indicated that it was statistically stable (P=0.01).

Phylogenetic structure

We built a phylogenetic tree for the Tyrannidae species pool occurring in *Araucaria* forests using the phylogenetic hypothesis published by Ohlson *et al.* (2008), which takes into account clade age estimates. We computed a phylogenetic pairwise distance matrix ($\mathbf{D}_F$) for the species pool using the PhyDist module of Phylocom 4.1 (Webb *et al.*, 2008).

In order to obtain the phylogenetic structure of each cell, we employed the phylogenetic fuzzy-weighting method, a new analytical tool recently developed by Pillar and Duarte (2010) and implemented in the software R (R Development Core Team, 2009. R-script for phylogenetic fuzzy weighting is available at http://www.ufrgs.br/leff/resources_english.html). First, we transformed the phylogenetic pairwise distance matrix ($\mathbf{D}_F$) into a phylogenetic similarity matrix ($\mathbf{S}_F$) by taking the one complement. Then, bird species composition in matrix **W** was weighted by the phylogenetic similarities in $\mathbf{S}_F$ using a fuzzy set algorithm (Pillar and Duarte 2010). This procedure generated a matrix **P** containing bird species composition weighted by phylogeny.

Further, we performed a Principal Coordinates Analysis on matrix **P**, based on Bray-Curtis dissimilarities between plots followed by Lingoes correction for negative eigenvalues (Legendre and Anderson, 1999), which generated principal coordinates of phylogenetic structure (PCPS, Duarte 2010) for the plots. Each eigenvector of PCPS represents an orthogonal phylogenetic gradient for the array of cells, but using all eigenvectors to assess environmental and spatial drivers of phylogenetic assembly of Tyrannidae birds would introduce some noise in the analysis. Therefore, we selected a subset of orthogonal PCPS expressing the maximum association between phylogenetic variation and all environmental variables, by performing a set of distance-based Redundancy Analysis (db-RDA, Legendre & Anderson, 1999), in a similar way as proposed by Anderson & Willis (2003).

The selection procedure consists of: (1) performing db-RDA using increasing numbers of PCPS, starting from that containing the largest proportion of total variation in **P**; (2) at each db-RDA, adding one PCPS and perform a permutation test to obtain a *F* statistics (Legendre & Anderson, 1999) and (3) selecting the subset of PCPS that maximizes *F* value, which is a measure of overall db-RDA fit. In the end, this subset contains the fraction of the phylogenetic composition gradient scaled-up to the site level that is maximally related to the environmental gradient of interest. PCPS and db-RDA analysis were performed using CANOCO 4.5 (Ter Braak & Smilauer 2002).

Before assessing environmental and spatial drivers of phylogenetic assembly, we performed a forward selection procedure to select environmental and spatial variables to be used as explanatory variables in db-RDA variation partitioning. We employed the forward selection procedure implemented in CANOCO 4.5 (Ter Braak & Smilauer 2002), separately for each set of explanatory variables (space or environment). To reduce the type I error generated by forward selection analysis, we followed the double selection criteria proposed by Blanchet *et al.* (2008), which consists in (1) performing a global test including all explanatory variables correcting the $R^2_{(\mathbf{Y|X})}$ according to Ezekiel´s correction (Peres-Neto *et al.*, 2006). The $R^2_{(\mathbf{Y|X})\mathrm{adj}}$ of the global test is then used as a second criterion besides the alpha-value of 0.05 to select which explanatory variables will be kept; (2) performing the forward routine, which starts by selecting the available explanatory variable that maximizes model fitting and computing a *F*-ratio for the analysis. Then, a *P*-value for the analysis is generated by permutation of residuals (full model approach, see Legendre &Legendre, 1998); (3) computing a $R^2_{(\mathbf{Y|X})\mathrm{adj}}$ for the forward db-RDA whenever a *P*-value ≤ 0.05 is obtained. If the $R^2_{(\mathbf{Y|X})\mathrm{adj}}$ of the forward db-RDA is lower than that of the global test, a new variable is added to the analysis and the permutation test is performed again; otherwise, the procedure is terminated. Only the explanatory previously selected will remain for further analyses.

Variation Partitioning

We performed variation partitioning using db-RDA (Legendre & Anderson, 1999) to discriminate the contribution of environmental and spatial factors on phylogenetic bird assembly (Borcard et al. 1992). A set of three db-RDA were performed: (i) A partial db-RDA of the selected set of PCPS on the selected environment variables ($R^2_{(\mathbf{Y|X})\mathrm{adj}}$ (E)): the fraction of variation that can be explained by the environmental variables independently of spatial structure; (ii) A partial db-RDA of the selected set of PCPS on the selected PCNM variables ($R^2_{(\mathbf{Y|X})\mathrm{adj}}$ (S)): the fraction of variation that can be explained by the spatial distribution of the communities independently of environmental structure; (iii) A db-RDA of the selected set of PCPS and the selected environment and PCNM variables together ($R^2_{(\mathbf{Y|X})\mathrm{adj}}$ (S + S∩E + E)). $R^2_{(\mathbf{Y|X})\mathrm{adj}}$ of each db-RDA was adjusted according the number of explanatory variables using the Ezekiel’s correction (Peres-Neto *et al.*, 2006). The fraction corresponding spatially-structured environmental effect (S∩E) on selected PCPS was defined as:

$$R^2_{(\mathbf{Y}|\mathbf{X})\mathrm{adj}}(S \cap E) = R^2_{(\mathbf{Y}|\mathbf{X})\mathrm{adj}}(S + S \cap E + E) - R^2_{(\mathbf{Y}|\mathbf{X})\mathrm{adj}}(S) - R^2_{(\mathbf{Y}|\mathbf{X})\mathrm{adj}}(E)$$

All db-RDA were perfomed using CANOCO 4.5 (Ter Braak & Smilauer 2002).

In order to assess the association between Tyrannidae phylogenetic clades and predictors (environmental and/or PCNM variables) we calculated the correlation between either sets of variables and db-RDA scores. Then, multivariate associations between Tyrannidae phylogenetic clades and explanatory variables were plotted in a correlation scatter plot.

RESULTS

Tyrannidae species pool in *Araucaria* forests contained 46 birds species distributed in four major clades (Fig 2): Pipromorphines, Elaeniines, Fluvicolines, Myiarchines and Tyrannines; *Attila phoenicurus*, *Piprites chloris* and *Piprites pileata* not belong to any major clade.

Principal Coordinates Analysis on matrix **P** generated 31 PCPS with eigenvalues higher than zero. Our forward selection procedure using db-RDA showed that the maximum association between the PCPS and the six environmental variables were obtained using the three first PCPS ($F = 3.951$, $P = 0.002$). Other combinations of numbers of PCPS used in the analysis decreased F-values, increasing the residual error of db-RDA. Those three PCPS contained ≅ 47 % of total information of matrix **P** and were used in the further analyses.

The global db-RDA using the three first PCPS as response variables and the seven spatial filters as predictors was performed ($R^2_{(\mathbf{Y}|\mathbf{X})\mathrm{adj}} = 0.551$). The forward procedure selected four spatial filters, in decreasing order of importance: PCNM 1, PCNM 2, PCNM 6 and PCNM 5 ($R^2_{(\mathbf{Y}|\mathbf{X})\mathrm{adj}} = 0.566$, $P = 0.003$). Since the $R^2_{(\mathbf{Y}|\mathbf{X})\mathrm{adj}}$ obtained for four variables was higher than that of the global test, we eliminated the fourth variable added to the model (PCNM 5), which decreased the $R^2_{(\mathbf{Y}|\mathbf{X})\mathrm{adj}} = 0.437$ ($P = 0.004$). The same procedure was employed to select the six environmental variables. The forward procedure selected only temperature seasonality ($R^2_{(\mathbf{Y|X})\mathrm{adj}} = 0.195$, $P = 0.0006$), but this time the $R^2_{(\mathbf{Y|X})\mathrm{adj}}$ obtained was lower than that of the global test ($R^2_{(\mathbf{Y|X})\mathrm{adj}} = 0.365$, $P = 0.001$), not being necessary watch out the selected variables. Thus, forward selection procedure shows that temperature seasonality and PCNM 1, 2 and 6 as important variables explained phylogenetic assembly of Tyrannidae birds (Fig 3).

Variation partitioning based on db-RDA showed that space (PCNM 1, 2 and 6) and temperature seasonality explained together 59% of the total variation in phylogenetic community assembly of Tyrannidae birds (Table 1). Space was the major factor explaining data variation (35.8%, $P < 0.001$), followed by environment (12.7%, $P < 0.001$). Spatially-structured environmental variables, i.e. temperature seasonality spatially structured according to selected spatial filters (PCNM 1, PCNM 2 and PCNM 6) explained 10.5% of total variation in phylogenetic assembly.

Temperature seasonality and PCNM 1 and 6 were positively correlated with first db-RDA axis, and PCNM 2 showed a low and negative correlation with this axis (Fig. 4). In the second db-RDA axis, PCNM 1 and 6 had their scores positively correlated, while PCNM 2 and temperature seasonality scores were negatively correlated (Fig. 4). Variation in temperature seasonality was strongly associated with PCNM 2 spatial filter (Fig. 4). Elaeniines clade and *Piprites* were associated with higher values of temperature seasonality and PCNM 2, both variables presenting higher values southwards (Fig. 3). On the opposite side of the same environmental and spatial gradient, pipromorphines clade was associated with lower values of temperature seasonality and PCNM 2. Myiarchines, tyrannines, fluvicolines clades and *Atilla* were strongly and positively related with PCNM 1 and 6 that presented higher values in higher latitudes and longitudes (Fig. 3).

DISCUSSION

Most variation of phylogenetic structure in Tyrannidae birds along the *Araucaria* forest distribution was explained by spatial gradients, which might be related to dispersal limitation of some clades due neutral dynamics and historical factors (Cavender-Bares *et al.*, 2009). At broader spatial scales, species distributions are determined largely by biogeographical processes that involve speciation, extinction and dispersal (Cavender-Bares et al 2009). Tyrannidae clades are not homogeneously distributed along *Araucaria* forest, probably due differences in diversification and dispersal rates among them. Differences in the geographical starting point of dispersal and the amount of time since the origin of the clade, during which niche evolution and dispersal could occur, might also determine geographical distribution of a given clade (Wiens & Donoghue, 2004). Thus, some Tyrannidae clades could be more dispersal-limited than others, generating an association pattern among clades and some regions determined by neutral dynamics. The importance of spatial gradients could be due different environmental variables, spatially-structured, that were not considered in our study and could have influence in the phylogenetic assembly of Tyrannidae birds.

The Tyrannidae family has its origin in South American tropical forests and pipromorphines clade is strikingly conservative in ecology and behavior, being tied to humid forest interior with few exceptions (Ohlson et al 2008). Pipromorphine clade was negatively selected by the seasonal variation of temperature, while elaeniines and *Piprites* had an association with more seasonal sites. Pipromorphines are apparently submitted to phylogenetic habitat filtering (Duarte 2010) in a large spatial scale, reaching only habitats with more forested areas. The occurence of pipromorphines in the north, where the *Araucaria* forest is highly patchy, may be due to the originally extensive surrounding area of continuous Atlantic and seasonal forests (Safford 1999, Behling 2002). Moreover, we found an association between *Atilla*, Myiarchines, tyrannines, fluvicolines clades and higher latitudes and longitudes. The diversification in elaeniines, myiarchines, tyrannines and fluvicolines clades were temporally correlated with the expansion of open habitats during the late Neogene climate cooling and aridification (Ohlson et al 2008). In addition, the past dynamics of *Araucaria* forest might have influenced the association of those clades and southernmost points. During the late glacial (14,000 - 10,000 yr BP) *Araucaria* forest were scarce in Southern Brazilian highlands and probably only found as scattered patches in places with sufficient moisture in the Southeast Brazil, as deep and protected valleys (Behling 2002). The climate at that time was cold and dry, and grasslands dominated the landscape (Behling and Pillar 2007), that extended from glacial to early Holocene and was replaced by *Araucaria* forests only during the late Holocene (Behling 2002). Considering that elaeniines, myiarchines, tyrannines and fluvicolines clades had their diversification in open habitats and that during a long time open vegetation dominated the southern and southeast region of *Araucaria* forest distribution, we could expect a major association between clades related to open areas and places that historically were dominated by grassland vegetation. Nowadays, the southernmost portion of *Araucaria* forest distribution is merged with highland grasslands. The substantial diversification of open-habitat lineages that these clades had suffered (Ohlson et al 2008) maybe allow them to inhabit transitional landscapes as ecotones between forest and grasslands, what also could explain why elaeniines, myiarchines, tyrannines and fluvicolines clades were strongly associated with southernmost sites.

Broad-scale richness patterns are generally determined by climate- and productivity-related variables (Hawkins *et al.*, 2003a, Field *et al.*, 2009). For terrestrial birds, Hawkins *et al.* (2003b) found that measures of energy availability (as potential evapotranspiration and mean annual temperature) were the main factors determining the diversity gradient in the northern hemisphere, while in southern hemisphere water-related variables best predicts bird diversity variation. Although Tyrannidae communities analyzed here were located in southern hemisphere, temperature seasonality, an energy-related variable, was important to explain the phylogenetic assembly of these birds. Temperature seasonality along the year may influence the availability of resources as insects and fruits, which are the major component of Tyrannidae diet (Sick, 1997). Water- and energy-related factors usually are better predictors of plant diversity patterns than of animals (Hawkins *et al.*, 2003a). It is known that climatic factors might exert an indirect effect on animal diversity patterns by means of trophic relationships. Accordingly, animal richness could be determined by abundance, distribution and diversity of food resources (Kissling *et al.*, 2007). Some studies already showed the dependence of frugivorous bird species richness in relation to plant richness in a broad spatial scale (Marquez *et al.*, 2004, Kissling *et al.*, 2007, Kissling *et al.*, 2008). Therefore, niche dimensions related to food availability could be useful to explain Tyrannidae phylogenetic assembly, as well as past environmental conditions. By doing so, we could achieve a more complete portrait on the influence of historical processes (Ricklefs 1987) on current assembly patterns.

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Table 1 Variation partitioning of phylogeny-weighted species composition of Tyrannidae birds occurring in *Araucaria* forest on spatial filters and environmental variables using distance-based Redundancy Analysis (db-RDA).

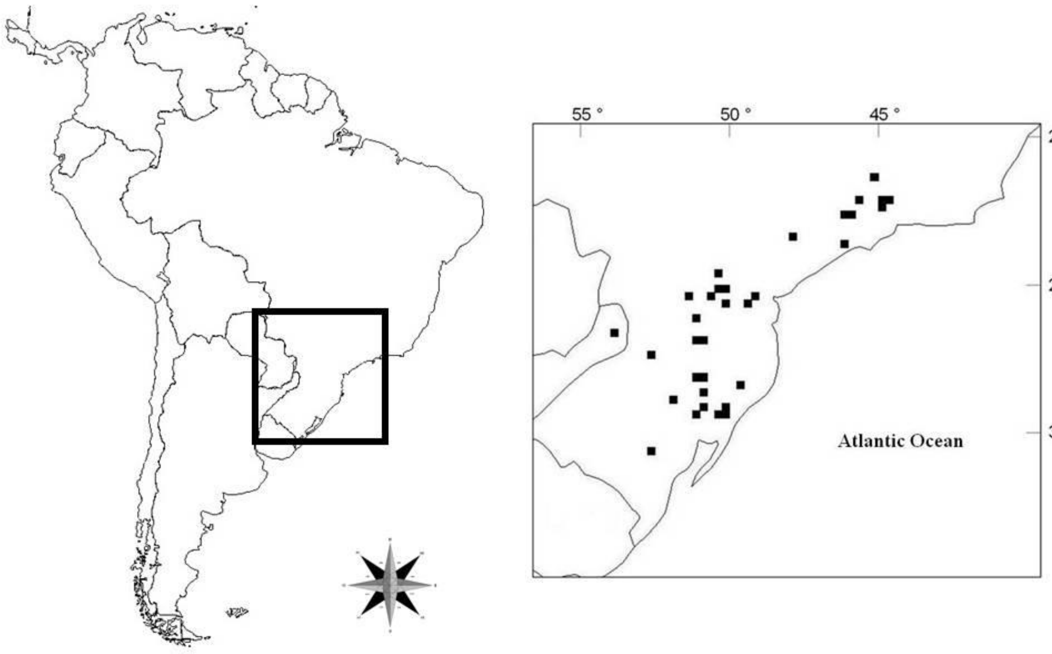
Source of variation	$R^2_{(Y\|X)adj}$	Pseudo-F	*P*-value
[S] Space + [S∩E] Spatially-structured environment + [E] Environment	0.590	12.483	< 0.001
[S] Space	0.358	10.866	< 0.001
[S∩E] Spatially-structured environment	0.105		
[E] Environment	0.127	12.000	< 0.001
[U] Unexplained	0.410		
[S] + [S∩E] + [E] +[U]	1		

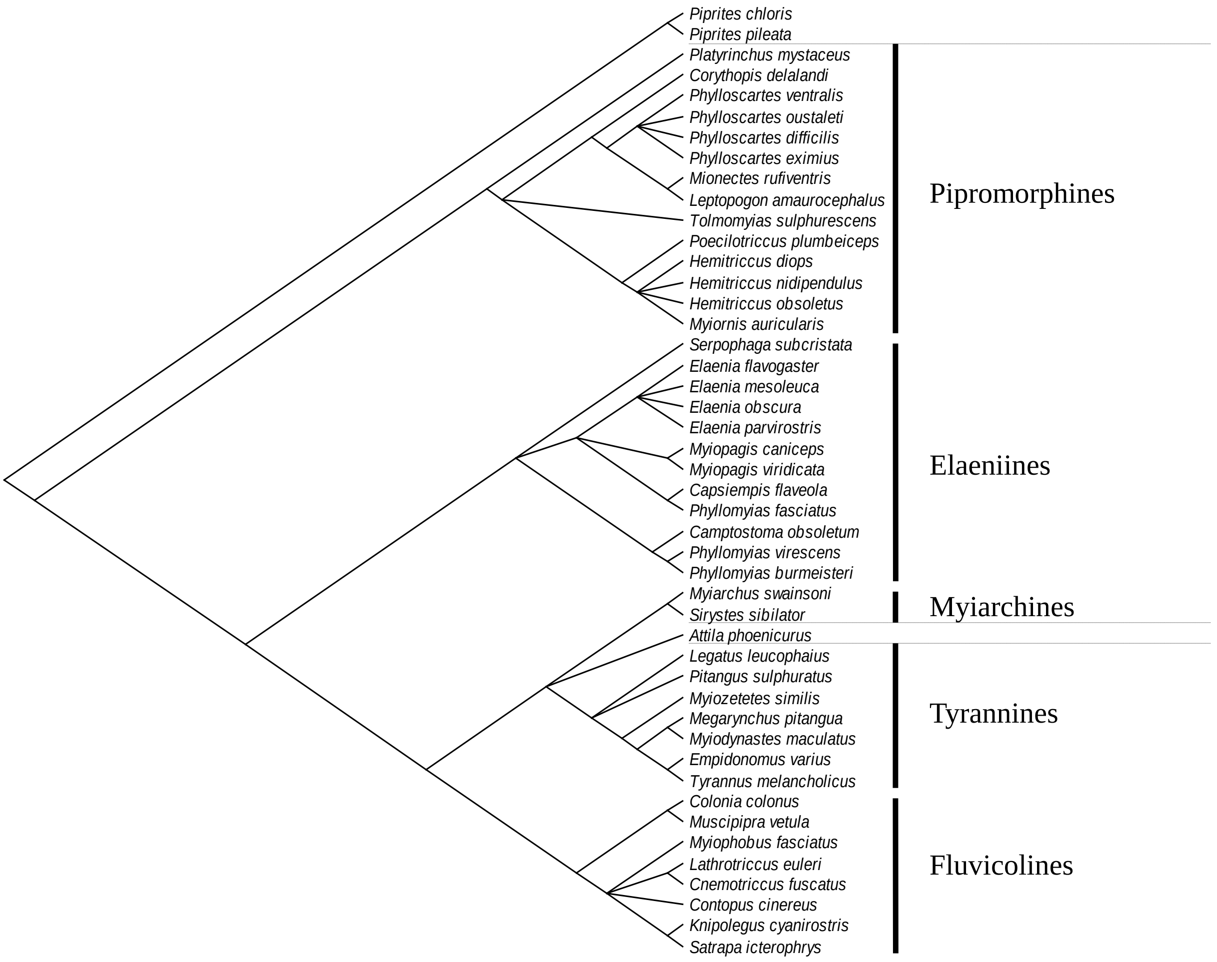
Figure 1 Location of Tyrannidae communities distributed along south and south-eastern Brazil and Argentina.

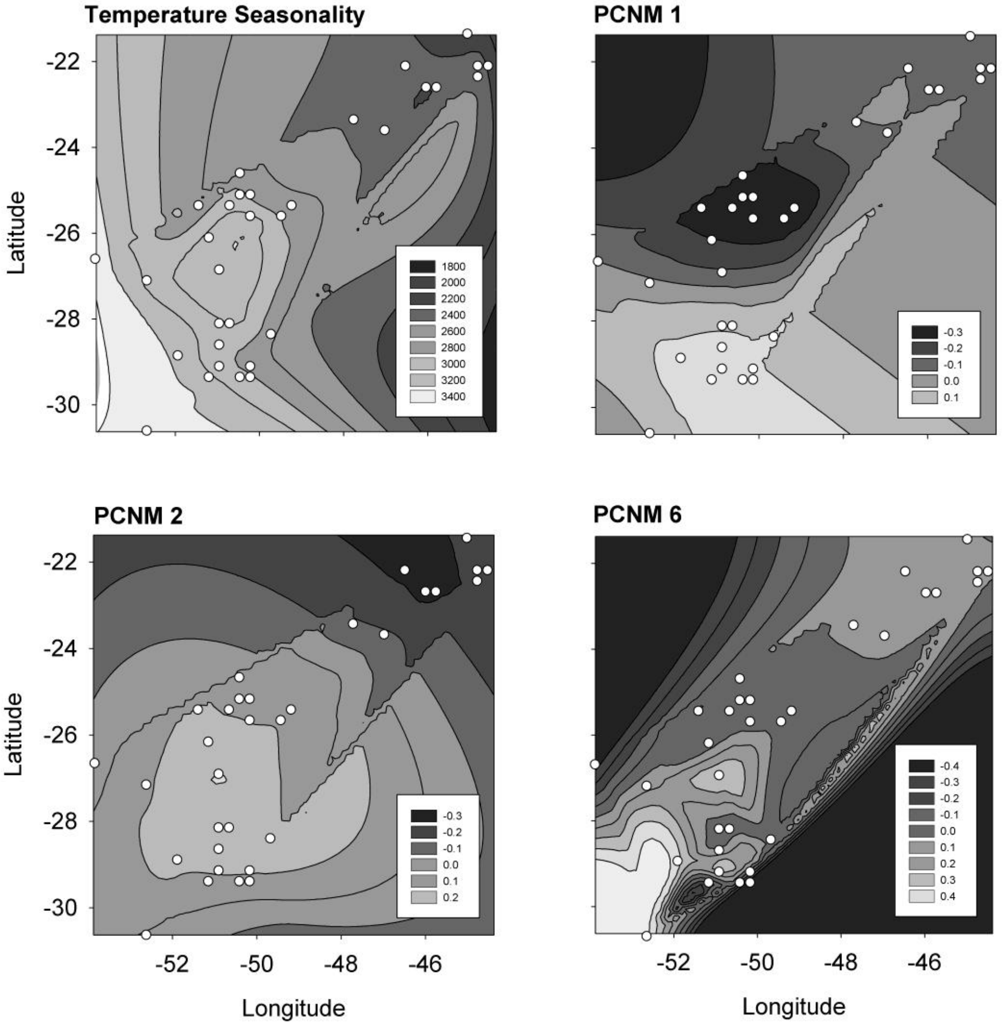
Figure 2 Phylogenetic tree for Tyrannidae birds occurring in sites distributed along *Araucaria* forest distribution. Clade names in bold are used throughout the text and figures. Ornithological nomenclature follows IOC World Bird Names v2.6 (Gill & Donsker 2010).

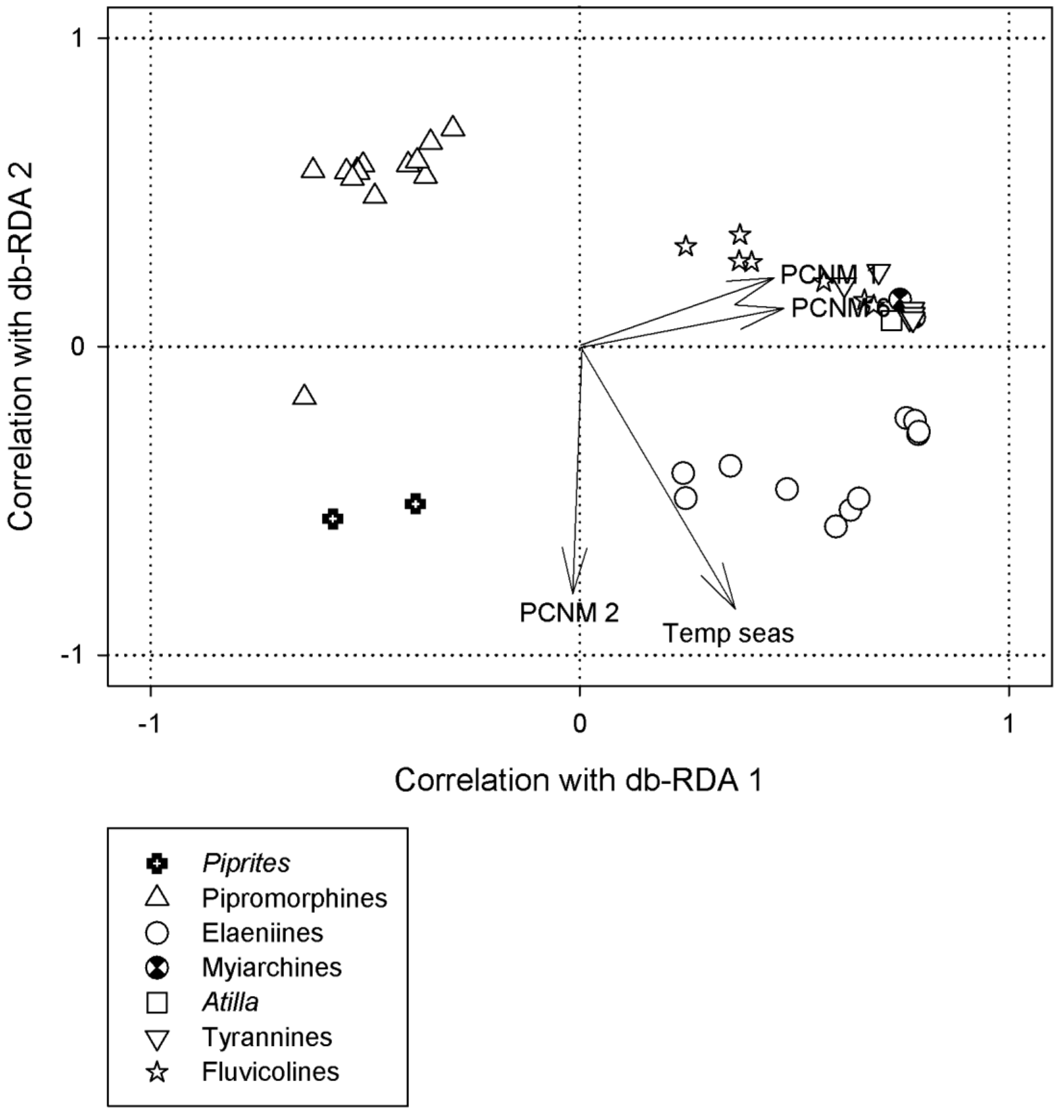
Figure 3 Contour plots for temperature seasonality and three principal coordinates of neighborhood matrices (PCNM 1, 2 and 6) selected by forward variable selection in relation to three first PCPS of Tyrannidae communities. White squares indicate the locations of 33 sites. Temperature seasonality data provided by WorldClim 1.4 (Hijmans *et al.*, 2005), with spatial resolution $\cong$ 1 km^2. Distance of truncation site used in PCNM analysis = 268.8 km.

Figure 4 Correlation scatter plot for Tyrannidae phylogenetic clades and explanatory variables (temperature seasonality and PCNM 1, 2 and 6) showing correlation values with distance-based Redundancy Analysis (db-RDA) axes.


55 °
50 °
45 °
20 °
25 °
30 °
Atlantic Ocean


Piprites chloris
Piprites pileata
Platyrinchus mystaceus
Corythopis delalandi
Phylloscartes ventralis
Phylloscartes oustaleti
Phylloscartes difficilis
Phylloscartes eximius
Mionectes rufiventris
Leptopogon amaurocephalus
Tolmomyias sulphurescens
Poecilotriccus plumbeiceps
Hemitriccus diops
Hemitriccus nidipendulus
Hemitriccus obsoletus
Myiornis auricularis
Serpophaga subcristata
Elaenia flavogaster
Elaenia mesoleuca
Elaenia obscura
Elaenia parvirostris
Myiopagis caniceps
Myiopagis viridicata
Capsiempis flaveola
Phyllomyias fasciatus
Camptostoma obsoletum
Phyllomyias virescens
Phyllomyias burmeisteri
Myiarchus swainsoni
Sirystes sibilator
Attila phoenicurus
Legatus leucophaius
Pitangus sulphuratus
Myiozetetes similis
Megarynchus pitangua
Myiodynastes maculatus
Empidonomus varius
Tyrannus melancholicus
Colonia colonus
Muscipipra vetula
Myiophobus fasciatus
Lathrotriccus euleri
Cnemotriccus fuscatus
Contopus cinereus
Knipolegus cyanirostris
Satrapa icterophrys
Pipromorphines
Elaeniines
Myiarchines
Tyrannines
Fluvicolines


Temperature Seasonality
PCNM 1
PCNM 2
PCNM 6
Latitude
Longitude
-22
-24
-26
-28
-30
-52
-50
-48
-46
1800
2000
2200
2400
2600
2800
3000
3200
3400
-0.4
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4


1
0
-1
-1
0
1
Correlation with db-RDA 2
Correlation with db-RDA 1
PCNM 1
PCNM 6
PCNM 2
Temp seas
Piprites
Pipromorphines
Elaeniines
Myiarchines
Atilla
Tyrannines
Fluvicolines

CAPÍTULO 2[2]

Article type: Original article

Does zoochory determine the frequency of frugivory in Tyrannidae birds in Brazilian *Araucaria* forests?

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Running title: Zoochory and historical factors driving frugivory

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[2] Este artigo será submetido ao periódico Global Ecology and Biogeography e já se encontra formatado de acordo com as normas da revista.

ABSTRACT

Aim: To verify if frugivory in Tyrannidae birds (tyrants flycatchers) is influenced by the availability of fleshy fruits along the *Araucaria* forest biome in southern Brazil.

Location: *Araucaria* forests in southern and southeastern Brazil and northeastern Argentina, from 30ºS to 20ºS and elevations mostly above 500 m a.s.l..

Methods: We used range maps to obtain Tyrannidae species composition of 33 cell distributed along the *Araucaria* forest distribution. We compiled the feeding habits of each species from literature to calculate the proportion of frugivorous Tyrannidae species at each cell. After that, we used environmental, spatial (PCNM), phylogenetic (PCPS) and resource availability (proportion of zoochorous species) variables to explain the variation in the proportion of frugivorous birds. We evaluated causal connections between the variables using linear regressions and path analysis.

Results: Our best path model showed that phylogenetic and spatial gradients were the main factors determining the variation in frugivory along *Araucaria* forest sites. Environment and zoochory had no direct effect on frugivory, but the environmental variable (rainfall seasonality) presented an indirect effect via phylogenetic structure and the causal connection between zoochory and frugivory increased the path model fitting.

Main conclusions: Our results showed that the influence of environment on frugivory by Tyrannidae birds was indirect via zoochory and that phylogenetic niche conservatism exerts a role in structuring frugivory in Tyrannidae bird.

Keywords: *Araucaria* forest, Tyrannidae, PCNM, PCPS, zoochory, frugivory, historical process, path analysis.

INTRODUCTION

Ecologists are usually interested in assessing how species abundance, distribution and diversity are affected by interactions with other taxa and abiotic variables (Brown, 1995). Nowadays, broad geographical patterns of species distribution have received a lot of attention by ecologists (Kissling *et al.*, 2009). Several hypotheses have been tested in order to explain broad scale patterns in species richness and diversity. Climatic variables (e.g. temperature, rainfall and/or evapotranspiration) are recognized as major factors determining geographical patterns of species richness (Hawkins *et al.*, 2003a). Other factors, such as habitat heterogeneity and evolutionary history, also have been found as determinants of spatial variation in species richness (Jetz & Rahbek, 2002, Kissling *et al.*, 2007).

Water- and energy-related factors are usually better predictors of plant diversity patterns than of other taxa, like birds (Hawkins *et al.*, 2003a). However, climatic factors may exert indirect effects on animal diversity patterns via trophic relationships; for instance, animal richness could be mostly determined by abundance, distribution and diversity of food resources, rather than by climate itself (Kissling *et al.*, 2007). Unfortunately, studies examining such relationships are still scarce, although recent research has advanced in this direction (Hawkins & Pausas, 2004, Marquez *et al.*, 2004, Kissling *et al.*, 2007, Kissling *et al.*, 2008).

Frugivorous birds constitute a functional group composed of species that use fruits as food resource (Fleming *et al.*, 1987), and are ecologically important for seed dispersal dynamics (Howe & Smallwood, 1982). Frugivorous birds constitute a good model to assess the role of historical, environmental and biotic factors on species diversification and spatial distribution (Kissling *et al.*, 2009). Some authors found that the global pattern of frugivorous bird richness has been strongly associated with actual evapotranspiration (AET) (Kissling *et al.*, 2009), which is an estimate of primary productivity (Hawkins *et al.*, 2003b). Indeed, zoochorous plants are more abundant in regions with high rainfall levels (Tabarelli *et al.*, 2003), although historical factors related to botanical composition of local sites has been demonstrated to be more important than climatic factors as determinants of zoochory levels in Brazilian *Araucaria* forests (Duarte *et al.* 2009). Moreover, some studies showed the influence of richness of fleshy-fruit plants on the richness of frugivorous birds when compared to climate, which exerted only a minor effect (Márquez *et al*., 2004, Kissling *et al.*, 2007, Kissling *et al.*, 2008). For instance, Kissling *et al.* (2007) found that the richness of *Ficus* species was the best predictor variable explaining frugivorous bird richness in sub-Saharan Africa.

The influence of historical and evolutionary events in broad-scale diversity patterns has been addressed by many studies (Hawkins *et al.*, 2003a, Hawkins *et al.*, 2003b, Diniz-Filho *et al.*, 2004, Hawkins *et al.*, 2005). Some authors have highlighted a strong historical signal in global patterns of avian frugivory (Kissling *et al.*, 2009) and in the intracontinental patterns of species richness of Australian birds (Hawkins *et al*, 2005). In this sense, phylogenetic data provide a historical framework to quantify evolutionary and ecological patterns and to infer evolutionary and ecological processes (Emerson & Gillespie, 2008).

This study aimed to verify if the proportion of frugivory in Tyrannidae birds (tyrants flycatchers) is influenced by the availability of fleshy fruits along the *Araucaria* forest biome in southern Brazil. We assessed the effects of space, environmental conditions, phylogenetic structure and food availability on the proportion of Tyrannidae bird species that consume fleshy fruits in Brazilian *Araucaria* forests. Causal relationships between those different factors were analyzed by means of path analysis. Based on the evidence from other studies (Marquez *et al.*, 2004, Kissling *et al.*, 2007, Kissling *et al.*, 2008), we hypothesize that resource availability is the main factor determining the proportion of frugivorous Tyrannidae birds in Brazilian *Araucaria* forests.

MATERIAL AND METHODS

Study Area

We analyzed the variation in the proportion of frugivorous Tyrannidae birds occurring along the geographical range of Brazilian *Araucaria* forest biome. The *Araucaria* forest is a vegetation type typically found on the highland plateau in southern Brazil, at elevation around 500 m a.s.l. (Hueck, 1972), physiognomically characterized by an emergent conifer tree, *Araucaria angustifolia*. Its northern limit is the Serra da Mantiqueira (latitude 20°S), and the southern limit is on latitude 29˚(Hueck, 1972), though some patches are also found down to latitude 31° in the Serra do Sudeste granitic hills (Reitz *et al.*, 1983). The mean annual rainfall and temperature range from 1400 and 2200 and 12 to 18 ˚C, respectively (Behling, 2002). Tyrannidae is the one of the largest and most diverse of all bird families (*c*. 400 species in *c*. 100 genera, Fitzpatrick, 1980), being restricted to the New World (Sick, 1997). According to Kissling *et al.* (2009), there is 124 frugivorous bird species within Tyrannidae family.

Tyrannidae composition and feeding habit

The occurrence of Tyrannidae birds was characterized in *Araucaria* forest sites that were previously compiled by Duarte *et al.* (submitted) for floristic composition of tree and shrub species. We defined 33 map cells, using a 15’ × 15’grid (Fig. 1) based on floristic sites mentioned above. We coincided bird cells and vegetation plots in order to enable using the proportion of zoochorous plants as a proxy of food availability in our analysis. We obtained the Tyrannidae composition of each grid cell using the bird distribution range database (Ridgely *et al.*, 2007) available at <http://www.natureserve.com>. The database was processed using ESRI ArcView GIS 3.2 to record species’ presence in each cell. Only forest Tyrannidae species were considered in this study, since we aim to verify if fleshy fruits availability in the forest influences the frugivorous species distribution. The Tyrannidae composition of each cell was arranged in a presence/absence matrix (**W**) of bird species by sites. We followed IOC World Bird Names v2.6 (Gill and Donsker, 2010) to circumscribe the Tyrannidae clade and to standardize taxonomic nomenclature. After that, we classified

Tyrannidae species according to their feeding habits, based on available literature and information provided by ornithologists (Glayson Bencke pers. comm.). Tyrannidae birds generally feed on fruits and invertebrates (Sick, 1997). Thus, we separated Tyrannidae species in two categories: frugivorous and non-frugivorous. In this study we considered all species that exclusively feed on fleshy fruits and species that feed on fleshy fruits and invertebrates as fruit consumers and these species will be hereafter regarded just as frugivorous. Then, using the feeding habit classification and the composition matrix **W**, we calculated the proportion of frugivorous Tyrannidae species occurring in each cell.

Spatial filters and environmental conditions

We generated spatial models using principal coordinates of neighbor matrices analysis (PCNM, Borcard & Legendre, 2002). For this, we used the geographical coordinates (latitude, longitude) of the centroid of each cell. To calculate PCNM variables, geographic distances between sites were truncated at the maximum distance connecting all sites (268.8 km), based on a minimum spanning tree criterion (Rangel *et al.*, 2006). PCNM analysis generated seven orthogonal spatial filters and was performed using SAM 4.0 software (Rangel *et al.*, 2010).

To characterize environmental conditions in each cell, we used five environmental variables: altitude, annual mean temperature, temperature seasonality (standard deviation of temperature along the year x 100), annual mean rainfall and rainfall seasonality (rainfall’s coefficient of variation). All five variables were compiled from WorldClim 1.4 database (Hijmans *et al.*, 2005).

Fruit availability

As we mentioned above, we chose the study cells following the tree and shrub species composition plots compiled by Duarte *et al.* (submitted). Consequently, we had data on the floristic composition of *Araucaria* forest occurring in each cell. Then we classified shrub/tree species according to seed dispersal strategy into two categories, following the same criteria used by Duarte *et al.* (2009): zoochorous (dispersed by animals through endo- or syn-zoochory) and abiotically-dispersed (other dispersal mechanisms). After that, we obtained the proportion of woody species producing fleshy fruits (food resource for frugivorous birds) in each study cell.

Phylogenetic structure

We built a phylogenetic tree for the Tyrannidae species pool occurring in *Araucaria* forests using the phylogenetic hypothesis published by Ohlson *et al.* (2008), which takes into account clade age estimates. The phylogenetic tree of these Tyrannidae species that occur in *Araucaria* forest biome and their feeding habits may be visualized in Fig. 2. We computed a phylogenetic pairwise distance matrix ($\mathbf{D}_F$) for the species pool using the PhyDist module of Phylocom 4.1 (Webb *et al.*, 2008).

In order to obtain the phylogenetic structure of the Tyrannidae assembly at each cell, we employed the phylogenetic fuzzy-weighting method (Pillar & Duarte, 2010) and implemented in the software R (R Development Core Team, 2009. R-script for phylogenetic fuzzy weighting is available at http://www.ufrgs.br/leff/resources_english.html). First, we transformed the phylogenetic pairwise distance matrix ($\mathbf{D}_F$) into a phylogenetic similarity matrix ($\mathbf{S}_F$) by taking the one complement. Then, bird species composition in matrix **W** was weighted by the phylogenetic similarities in $\mathbf{S}_F$ using a fuzzy set algorithm (Pillar &Duarte 2010). This procedure generated a matrix **P** containing bird species composition weighted by phylogeny.

Further, we performed a principal coordinate analysis on matrix **P** using the software Multiv 2.4 (Pillar, 2006), based on Euclidean distances between bird cells which generated principal coordinates of phylogenetic structure (PCPS; Duarte, 2011). Each PCPS describes an orthogonal phylogenetic gradient in the array of sites, and indicates which clades are mostly associated with it (Duarte, 2011).

Path analysis

Before performing path analysis, we evaluated the influence of the environmental, spatial and phylogenetic variables on the frugivory level in the sites using forward stepwise multiple regression (separately for each group of variables), in order to select variables to be used as explanatory variables in further analysis. Then, we evaluated causal connections between the selected variables (PCNM1, PCNM3, PCPS2, PCPS3 and rainfall seasonality, Table 1), zoochory and frugivory using path analysis (Sokal & Rohlf, 1994; Legendre & Legendre, 1998). The goal of this analytical approach is to evaluate the strength of causal relationships between more than two variables by decomposing the covariation between variable pairs. Firstly, we evaluated covariation patterns between the variables using Pearson correlation. Then we built path models, describing causal relationships between variables. We used the significance of the correlations (Table 2) as the starting point to build the models. A hierarchical causal order among variables was assumed; spatial variables (PCNM) had the highest causal order, i.e. they were variables that were not determined by any other known variable (Shipley, 2000). The environmental variable selected, rainfall seasonality, also has the highest causal order, since it does not have significant correlation with spatial variables and no other variable could determine it. Frugivory was the variable with the lowest causal order. After that we linked each pair of variables showing significant correlation with an arrow (causal relationship) (Fig 3a). In order to evaluate if zoochory and environment had a direct or an indirect effect on frugivory, we built alternative models (Fig 3b-d) removing or adding causal relationships.

We used d-separation procedure (Shipley, 2000) to validate/reject the models by evaluating the independence relationships between the variables in each path model. Depending on the model that is being tested, there are a certain number of independence relationships that must be observed to make this model valid, which is called basis set (Shipley, 2000). The first step to obtain the basis set is to list all pairs of variables lacking an arrow between them. The number of pairs of variables that do not have an arrow between them, i.e. independence relationships (*k*) in the basis set, is always equal to

$$k = \frac{p!}{2(p-2)!} - a$$

where *p* is the number of variables in the model and *a* is the number of causal links (arrows) between them (Shipley, 2000). For each independence test in the basis set, we evaluated the independence relationships by using partial correlation to control for the effects of all variables with direct ascendancy on both variables included in the independence relationship. In order to validate the entire path model we employed Fisher's test for composite probabilities (Sokal & Rohlf, 1994), called the *C* statistics by Shipley (2000), which is

$$C = -2\sum_{i=1}^{k} \ln P_i$$

where *k* is the number of independence relationships, P_i is the probability resulting from the partial multiple regression test for the independence relationship *i*. The *C* statistics follows a chi-square distribution with *2k* degrees of freedom and the corresponding *P* value was used to validate/reject the path model (Shipley, 2000). The null hypothesis was that the independence relationships postulated in the model are valid, i.e. a *P* value below determined threshold would indicate that the independence assumptions of the basis set are false, and thus the model must be rejected. We considered valid all the path models that obtained *P* values higher than 0.1 and, among the valid models, we selected the one with the highest *P* values. We obtained path coefficients for the model selected by linear multiple/simple regressions, being β regression coefficient equivalent to the path coefficient. We also computed the non-determination coefficient U_i, which indicates the amount of variation in the response variable *i* that unexplained by the model, subtracting the R^2 value from 1 (Sokal & Rohlf, 1994).

Stepwise multiple regressions, partial multiple regressions and linear regressions were performed using the software STATISTICA 7 (StatSoft Inc.2004).

RESULTS

Along the 33 *Araucaria* forest sites we found 46 Tyrannidae species. From these, 46% were classified as frugivorous (see Fig 2). Elaeniines and tyrannines clades were the two clades with the highest number of frugivorous species, each one with seven.

The forward stepwise regression showed that rainfall seasonality was the only environmental variable that explained significantly the variation in the proportion of frugivorous species along the *Araucaria* forest biome (Table 1). In relation to spatial variables, the stepwise procedure selected PCNM 1 and PCNM 3 as important spatial variables influencing Tyrannidae frugivorous species (Table 1).

Principal coordinates analysis for phylogeny-weighted species composition on matrix **P** generated 15 PCPS. The first three PCPS contained, respectively, 68%, 20% and 8% of the total variation of matrix **P**. Only the first three PCPS were submitted to forward stepwise regression, since most variation in phylogeny-weighted species composition (≅ 96%) was concentrated in these three orthogonal axes. Forward stepwise regression selected PCPS 2 and PCPS 3 as significant explanatory variables (Table 1) of frugivory, despite the great amount of the total variation contained in PCPS 1. The correlation of Tyrannidae phylogenetic clades and explanatory variables with PCPS 2 and PCPS 3 are represented by a correlation scatter plot in Fig. 4.

PCNM 1 showed a low and positive correlation with PCPS 2, and rainfall seasonality and PCNM 3 were negatively correlated with this axis (Fig. 4). In relation to PCPS 3, rainfall seasonality was positively correlated, while PCNM 1 and 3 scores were negatively correlated (Fig. 4). Pipromorphines clade was associated with higher values of rainfall seasonality, which presents higher values southwards. In the opposite, elaeniines, myiarchines, *Atilla* and Tyrannines were more associated to lower values of rainfall seasonality. Only pripromorphines clade was negatively correlated with PCPS 2, all other clades were positively correlated with the second phylogenetic gradient (Fig. 4).

From the four proposed path models involving the seven explanatory variables (rainfall seasonality, PCNM 1 and PCNM 3, PCPS 2 and PCPS 3, zoochory and frugivory), the model *c* (Fig. 3c) had the highest *P*-value (0.84, Table 3). According to this model (Fig. 5), zoochory was strongly determined by rainfall seasonality and by PCNM 3. PCPS 2 was determined only by rainfall seasonality, while PCPS 3 was determined by both rainfall seasonality and PCNM 1. The variation in the proportion of frugivorous Tyrannidae birds was determined by two gradients of phylogenetic structure (PCPS 2 and 3), by two spatial models (PCNM 1 and 3) and by the proportion of zoochorous plant species (this path coefficient was not statistically significant). Almost all the variation in the proportion of frugivorous Tyrannidae species was explained by the variables presented in the model *c* ($U = 0.06$).

DISCUSSION

There is no consensus about the influence of resource availability on consumer diversity at broad geographical scales. According to Burns (2004), fruit-frugivore interactions are highly variable in relation to the correlation between bird abundance and fruit diversity, suggesting some degree of neutrality in plant-frugivore networks. Nonetheless, the relationship between plant diversity and animal consumers has been demonstrated to vary with geographic location (Márquez *et al.,* 2004; Kissling *et al.*, 2007, Kissling *et al.*, 2008), evolutionary history (Fleming *et al.*,1987), spatio-temporal scale of analysis (Burns, 2004), and the metabolic ecology of animal consumers (Currie *et al.*, 2004). Our model showed that the environmental variable, rainfall seasonality, exerted indirect effect on the variation of frugivory along the *Araucaria* forest biome, via phylogenetic structure and zoochory, although climate and productivity variables appear to have strong effects on the global frugivorous diversity (Kissling *et al.*, 2009). The recent evidences of indirect effect of environment on frugivorous bird richness via plant diversity had been assigned to vegetation structural complexity (habitat heterogeneity, Kissling *et al.*, 2008) and to resource-consumer interaction (food resource, Kissling *et al.*, 2007). Despite the non-significance of the path coefficient linking zoochory and frugivory, the direct relation between the proportion of zoochorous species and frugivorous species seems to be important to some extent, because the removal of the arrow connecting zoochory and frugivory considerably decreased the fitting of the model c, and, consequently, the associated *P*-value. Maybe our proxy of resource availability (the proportion of zoochorous plant species) was not the best resource descriptor. This variable does not take into account the species abundance and fruit production at each cell, which might characterize better the availability of fleshy fruits to frugivorous birds. But, considering the scale of this study, we hardly find reliable data on plant abundance and fruit production.

Our analyses indicated that spatial and phylogenetic gradients were the main determinants of the variation in the proportion of frugivorous Tyrannidae birds in Brazilian *Araucaria* forests. The influence of spatial variables might be reflecting regional and evolutionary historical dynamics (Cavender-Bares *et al*., 2009). Species distributions at broadest spatial scales are, in some extent, determined by biogeographical processes that involve speciation, extinction and dispersal (Cavender-Bares *et al*., 2009). The majority of frugivorous species belong to few clades, as elaeniines, fluvicolines and tyrannines. Our results indicated that the frugivore habit, or some trait that could be related to fruit consumption, showed strong phylogenetic signal at the metacommunity level (*sensu* Pillar & Duarte 2010), because the effect of the environment and the phylogenetic structure on the proportion of frugivorous birds are not independent from each other, i.e. the influence of the environment on frugivory is mediated by the phylogenetic composition of the communities.

Furthermore, the second phylogenetic gradient (PCPS 2) was strongly determined by rainfall seasonality and Tyrannidae clades were distributed separately in this phylogenetic gradient. There is a tendency of closely-related species to retain similar ecological niches over time scale (phylogenetic niche conservatism, Wiens & Graham, 2005), which will influence species distribution along a given environmental gradient. Thus, it is expected that closely-related species would be assembled by a set of environmental conditions (phylogenetic habitat filtering; Duarte 2011). Considering the high correlation between the phylogenetic gradient and rainfall seasonality, it seems that Tyrannidae clades were subject of phylogenetic habitat filtering (Duarte, 2011), inhabiting the available niches to which clades are pre-adapted.

In conclusion, our results showed that phylogenetic niche conservatism plays a role in structuring frugivory levels in Tyrannidae birds occurring in the Brazilian *Araucaria* forest biome, through the indirect influence of the environment via phylogenetic structure, and that the relationship between zoochory and frugivory seems not to be direct as postulated by some authors (Márquez *et al.*, 2004; Kissling *et al.*, 2007, Kissling *et al.*, 2008). By incorporating the evolutionary perspective into the assessment of ecological drivers of diversity and niche assembly patterns in broad geographical scales we should likely advance in the solution of this macroecological puzzle. Our study points out to the need of assessing in higher detail which are the traits underlying bird frugivory patterns across macroecological gradients, and evaluating to what extent such traits are phylogenetically conserved.

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BIOSKETCHES

Fernanda Thiesen Brum is a graduate student. Her master thesis aimed to answer which are the main macroecological factors determining phylogenetic and functional structure of tyrant flycatchers (Tyrannidae) birds communities in *Araucaria* forests biome.

Andreas Kindel is a conservation biologist interested on the comprehension of the processes that generate and transform biodiversity and the development of approaches and tools for their conservation.

Sandra Maria Hartz is a community ecologist interested in processes of nucleation and fragmentation in the Atlantic Forest Biome.

Leandro Da Silva Duarte is a community ecologist. His research aims to investigate the ways the phylogenetic structure of communities interacts with environmental and spatial factors, as well as with ecological traits of species assembled in communities.

Table 1 Forward stepwise regression of the proportion of frugivorous Tyrannidae bird species in 33 sites distributed along the Brazilian *Araucaria* forest biome on (1) seven principal coordinates of neighbor matrices (PCNM), (2) 15 principal coordinates of phylogenetic structure (PCPS) and (3) five environmental variables (altitude, annual mean temperature, temperature seasonality, annual mean rainfall and rainfall seasonality). Analysis in (1), (2) and (3) were separated. Only selected variables are showed.

	Cumulative R^2	*F*	d.f.	*P*
(1) *Principal coordinates of neighbor matrices*				
PCNM 1	0.66	60.61	1,31	≤0.001
PCNM 3	0.82	27.31	2,30	≤0.001
(2) *Principal coordinates of phylogenetic structure*				
PCPS 3	0.40	20.73	1,31	≤0.001
PCPS 2	0.70	30.03	2,30	≤0.001
(3) *Environmental variables*				
Rainfall seasonality	0.22	8.85	1.31	0.005

Table 2 Pearson correlation coefficients between principal coordinates of neighbor matrices (PCNM) 1 and 3, rainfall seasonality, principal coordinates of phylogenetic structure (PCPS) 2 and 3, the proportion of zoochorous plant species (Zoochory) and the proportion of frugivorous Tyrannidae bird species (Frugivory) of 33 sites distributed along *Araucaria* forest biome.

	PCNM 1	PCNM 3	Rainfall seasonality	PCPS 2	PCPS 3	Zoochory
PCNM 3	0.00					
Rainfall seasonality	-0.22	0.01				
PCPS 2	0.12	-0.23	-0.60***			
PCPS 3	-0.76***	-0.11	0.34**	0.00		
Zoochory	0.01	-0.30*	-0.39**	0.28	-0.05	
Frugivory	0.75***	-0.43**	-0.47**	0.55***	-0.63***	0.32*

***P≤0.001; ** P≤0.05; *P≤0.09

Table 3 *C*- values for four models explaining the causal relationships between principal coordinates of neighbor matrices (PCNM) 1 and 3, rainfall seasonality, principal coordinates of phylogenetic structure (PCPS) 2 and 3, the proportion of zoochorous plant species (Zoochory) and the proportion of frugivorous Tyrannidae bird species (Frugivory) in 33 sites distributed along *Araucaria* forest biome (see Fig. 3 for model details).

Model	*C* statistics*	d.f. †	*P*
a	15.38	20	0.754
b	19.54	22	0.612
c	15.44	22	0.843
d	20.25	24	0.682

* *C*- statistics follows the chi-square distribution.

†d.f., degrees of freedom.

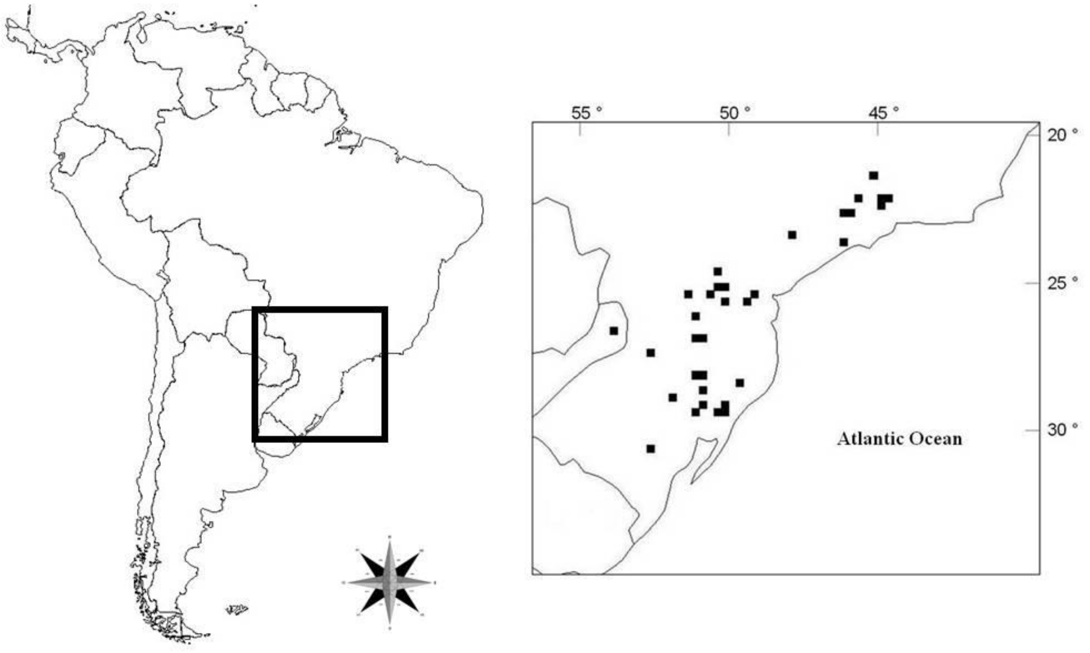
Figure 1 Location of Tyrannidae communities distributed along south and south-eastern Brazil and Argentina.

Figure 2 Phylogenetic tree for Tyrannidae birds occurring in Brazilian *Araucaria* forests. Clade names in bold are used throughout the text and figures. The point aside the species name indicates frugivorous habit.

Figure 3 Path models explaining the relationships between principal coordinates of neighbor matrices (PCNM) 1 and 3, rainfall seasonality, principal coordinates of phylogenetic structure (PCPS) 2 and 3, the proportion of zoochorous plant species (Zoochory) and the proportion of frugivorous Tyrannidae bird species (Frugivory) in Brazilian *Araucaria* forests.

Figure 4 Correlation scatter plot for Tyrannidae phylogenetic clades and explanatory variables (Rainfall seasonality and PCNM1 and 3) showing correlation values with two Principal Coordinates of Phylogenetic Structure (PCPS 2 and PCPS3) axes.

Figure 5 Causal relationships between variable as predicted by path model *c*. *Ui* is the non-determination coefficient of the *i*th variable. ** $P \leq 0.001$, * $P \leq 0.06$.


55 °
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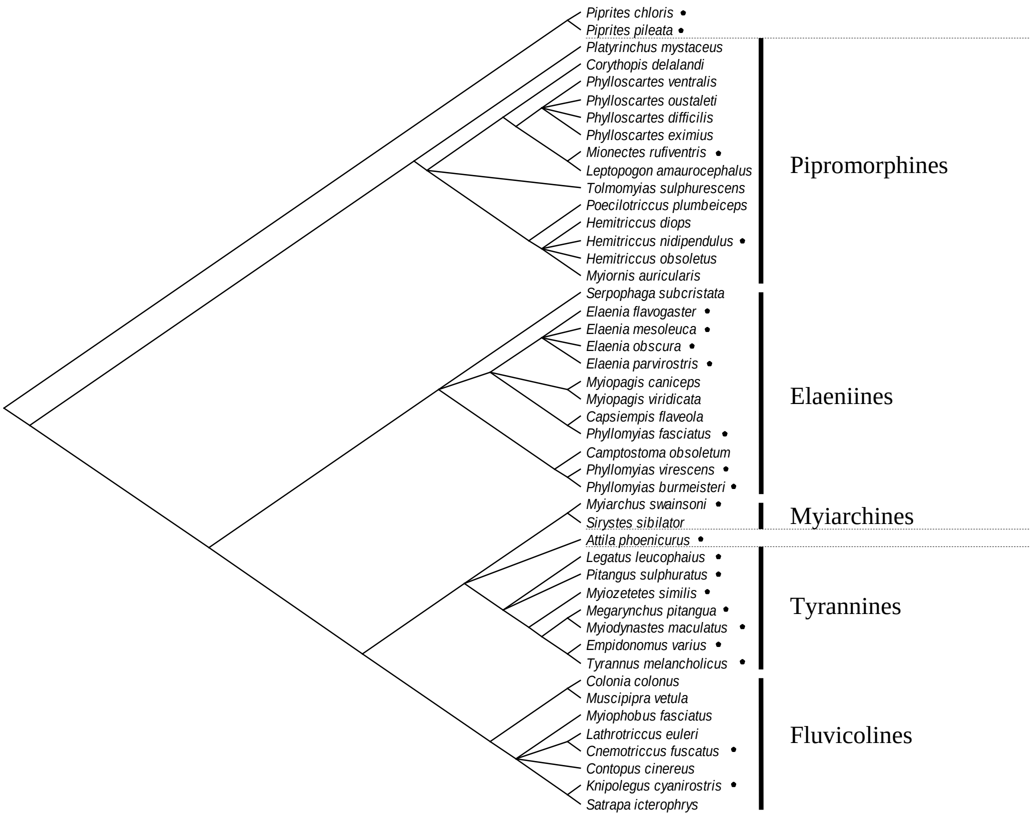
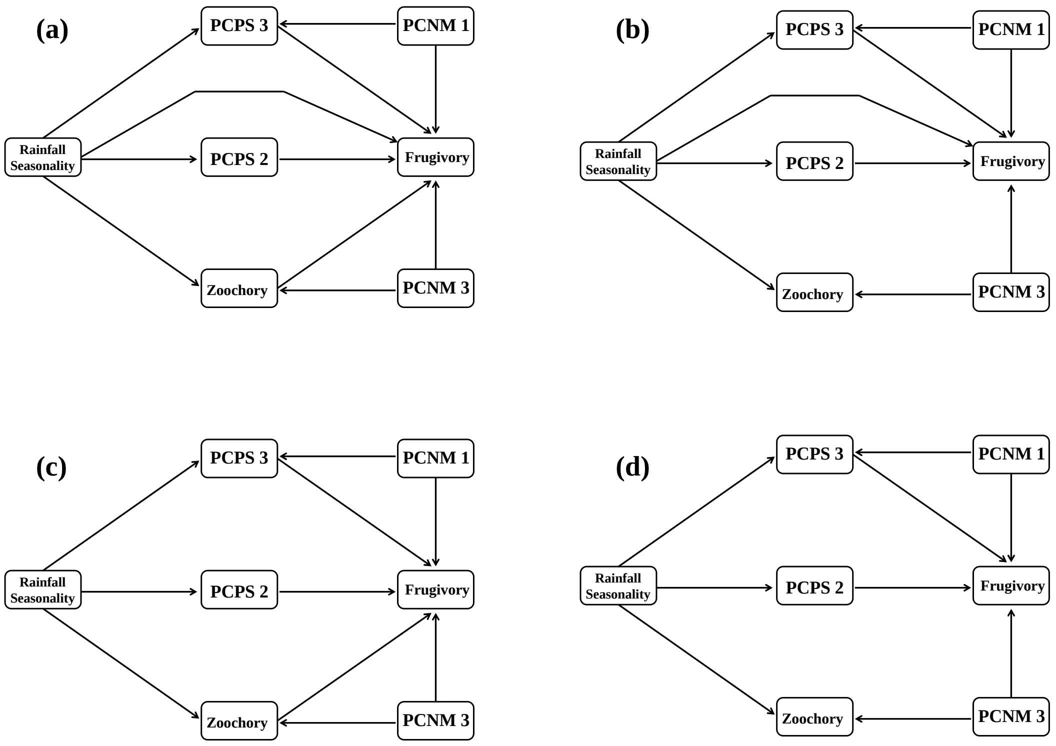
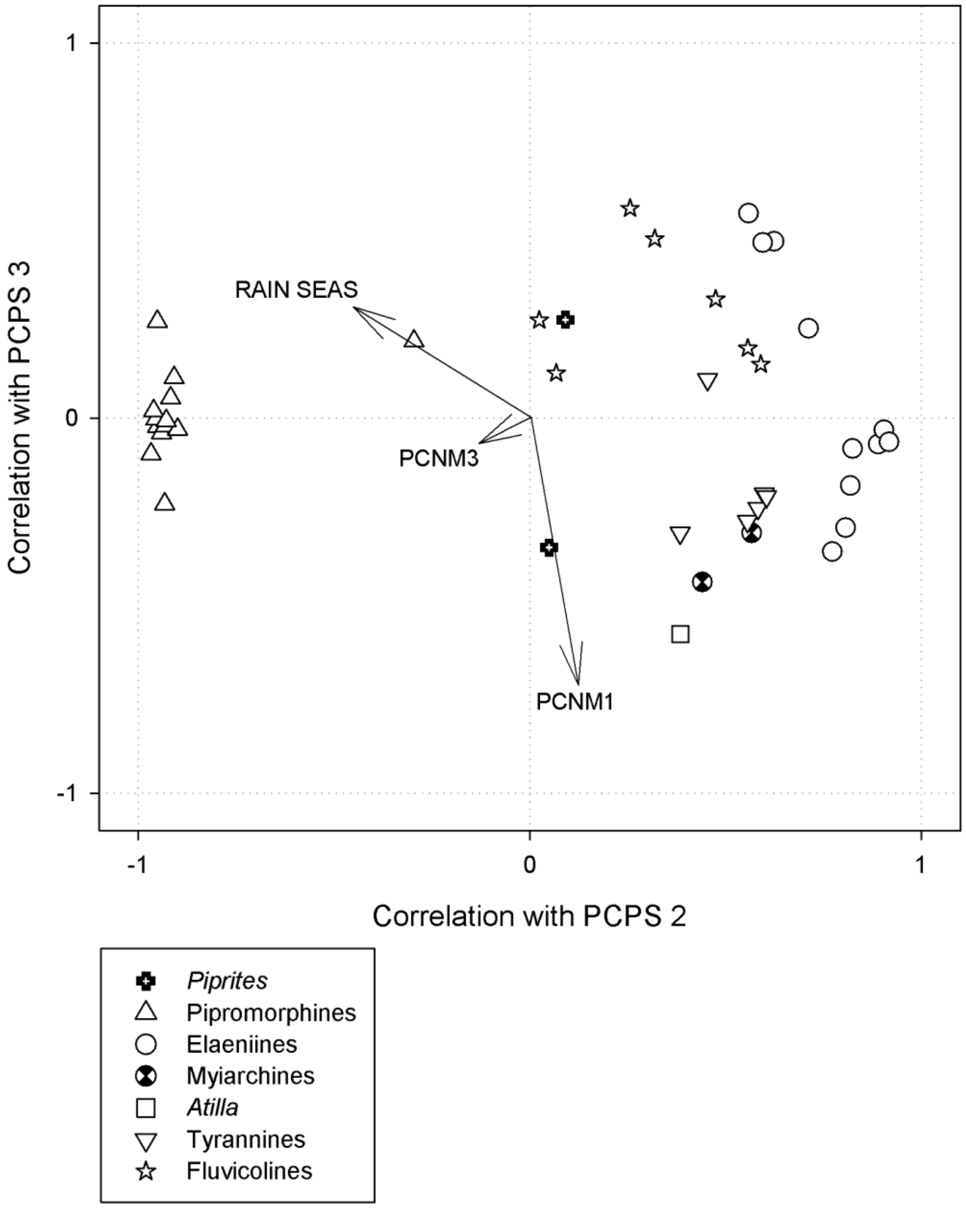
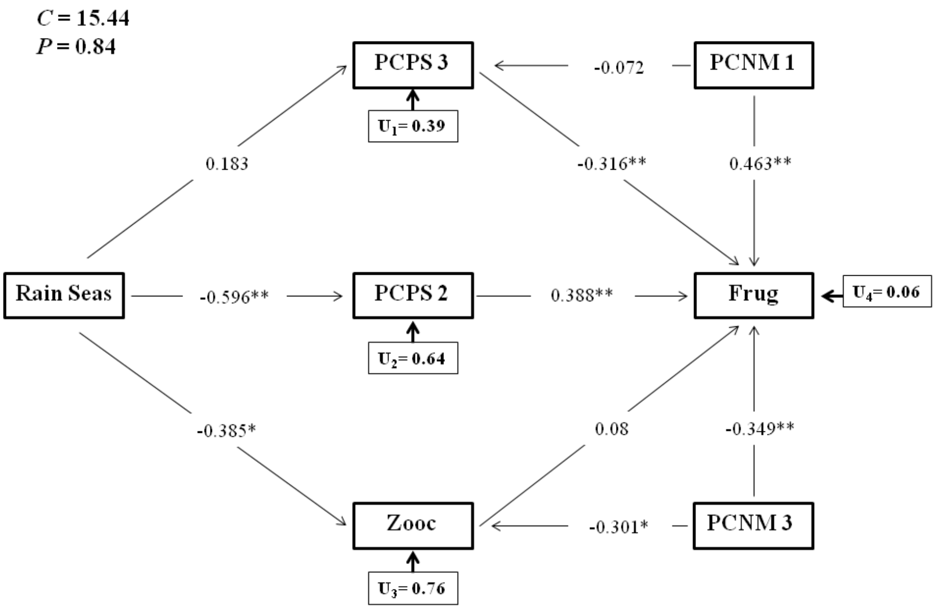
Atlantic Ocean


Piprites chloris •
Piprites pileata •
Platyrinchus mystaceus
Corythopis delalandi
Phylloscartes ventralis
Phylloscartes oustaleti
Phylloscartes difficilis
Phylloscartes eximius
Mionectes rufiventris •
Leptopogon amaurocephalus
Tolmomyias sulphurescens
Poecilotriccus plumbeiceps
Hemitriccus diops
Hemitriccus nidipendulus •
Hemitriccus obsoletus
Myiornis auricularis
Serpophaga subcristata
Elaenia flavogaster •
Elaenia mesoleuca •
Elaenia obscura •
Elaenia parvirostris •
Myiopagis caniceps
Myiopagis viridicata
Capsiempis flaveola
Phyllomyias fasciatus •
Camptostoma obsoletum
Phyllomyias virescens •
Phyllomyias burmeisteri •
Myiarchus swainsoni •
Sirystes sibilator
Attila phoenicurus •
Legatus leucophaius •
Pitangus sulphuratus •
Myiozetetes similis •
Megarynchus pitangua •
Myiodynastes maculatus •
Empidonomus varius •
Tyrannus melancholicus •
Colonia colonus
Muscipipra vetula
Myiophobus fasciatus
Lathrotriccus euleri
Cnemotriccus fuscatus •
Contopus cinereus
Knipolegus cyanirostris •
Satrapa icterophrys
Pipromorphines
Elaeniines
Myiarchines
Tyrannines
Fluvicolines


(a)
PCPS 3
PCNM 1
Rainfall Seasonality
PCPS 2
Frugivory
Zoochory
PCNM 3
(b)
PCPS 3
PCNM 1
Rainfall Seasonality
PCPS 2
Frugivory
Zoochory
PCNM 3
(c)
PCPS 3
PCNM 1
Rainfall Seasonality
PCPS 2
Frugivory
Zoochory
PCNM 3
(d)
PCPS 3
PCNM 1
Rainfall Seasonality
PCPS 2
Frugivory
Zoochory
PCNM 3


Correlation with PCPS 3
1
0
-1
-1
0
1
Correlation with PCPS 2
RAIN SEAS
PCNM3
PCNM1
Piprites
Pipromorphines
Elaeniines
Myiarchines
Atilla
Tyrannines
Fluvicolines


C = 15.44
P = 0.84
PCPS 3
PCNM 1
-0.072
U1= 0.39
0.183
-0.316**
0.463**
Rain Seas
-0.596**
PCPS 2
0.388**
Frug
U4= 0.06
U2= 0.64
-0.385*
0.08
-0.349**
Zooc
-0.301*
PCNM 3
U3= 0.76

CONSIDERAÇÕES FINAIS

Os resultados mostraram que fatores históricos são os principais determinantes da organização dos clados e da variação espacial da frugivoria por Tyrannidae, ambos ao longo do gradiente de distribuição da floresta com *Araucaria*. Em estudo anterior realizado no âmbito do gradiente latitudinal da floresta com *Araucaria*, Duarte *et al.* (2009) também encontraram que padrões históricos associados a essa vegetação explicaram mais a proporção de espécies de árvores e arbustos que produzem frutos zoocóricos do que fatores ambientais. O que os meus resultados, juntamente com o encontrado por Duarte *et al.* (2009), indicam é que os processos ecológicos de estruturação e organização das diferentes comunidades localizadas nesse tipo florestal são, de maneira geral, determinados pela dinâmica histórica de retração e expansão da floresta com *Araucaria* como um todo.

Ao contrário do que usualmente se encontra em estudos que exploram gradientes de diversidade em frugívoros, o ambiente não teve uma influência direta na frugivoria por Tyrannidae, mas apresentou influencia indireta via gradientes filogenéticos. No caso do presente estudo, a utilização de gradientes filogenéticos ajudou a elucidar alguns mecanismos históricos por trás de padrões de variação na frugivoria, que indicaram uma possível conservação filogenética de nicho. Seria interessante, como um próximo passo, avaliar se existe algum atributo funcional mais correlacionado com o hábito frugívoro como, por exemplo, largura de bico, estrato de forrageamento e tamanho corpóreo. Se houver, esses atributos muito provavelmente são conservados filogeneticamente. Avaliar o comportamento de atributos funcionais em relação à filogenia (sinal filogenético) e quais são os fatores de influenciam a distribuição geográfica dos clados pode ajudar no esclarecimento de alguns padrões funcionais atuais.

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