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Dissertação de Mestrado

O gradiente latitudinal de riqueza de espécies
de Tiranídeos suporta a
hipótese da conservação de nicho tropical?

Alina van Dijk

Porto Alegre, Agosto de 2019.

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Mestre em Ecologia.

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Porto Alegre, Agosto de 2019.

In memoriam Tia Corie e Oma Didy

"I hope that you will find what I have done here interesting and useful. I also hope, however, that you will soon go well beyond where I have left off."

James Brown, Macroecology, pag 247,1995.

AGRADECIMENTOS

RESUMO

Duas hipóteses propostas para explicar o gradiente de diversidade latitudinal são a Conservação de Nicho Tropical (TNC) e a Fora dos trópicos (OTT). Elas diferem na importância da dispersão: rara para TNC (poucos clados que colonizam latitudes extratropicais) e frequente para OTT (expansões frequentes para latitudes extratropicais). Isso gera duas predições. Primeiro, na estrutura filogenética da assembleia: se algumas linhagens chegaram aos biomas temperados (TNC), as assembleias serão agrupadas filogeneticamente. Caso contrário, se muitas linhagens chegaram às assembleias temperadas (OTT), as assembleias serão dispersas filogeneticamente. Segundo, a idade da assembleia para a TNC será recente e, para a OTT, pode ser recente ou antiga. Para testar a primeira predição, quantificamos o agrupamento filogenético para assembleias de pássaros de Tyrannidae no continente americano e, para a segunda predição, desenvolvemos uma nova abordagem analítica que permite inferir quando o ancestral chegou ao local onde à espécie atual ocorre (bioma). Encontramos altos valores de agrupamento em assembleias temperadas e uma idade recente das assembleias em biomas temperados. Esses resultados corroboram as predições para a TNC: poucos e recentes eventos de dispersão em direção aos biomas temperados. Isto traz implicações na distribuição atual da biodiversidade, uma vez que se os trópicos são as origens das linhagens e que se os eventos dispersivos contribuíram para a riqueza encontrada nas zonas temperadas, perdas de biodiversidade, nos biomas tropicais, trará consequências evolutivas para todos os biomas.

Palavras-chave: Padrão global de riqueza, dispersão ancestral, aves.

ABSTRACT

Two hypotheses proposed to explain the latitudinal diversity gradient are the Tropical Niche Conservatism (TNC) and the Out of the Tropics (OTT). They differ in the importance of dispersal: it is rare for TNC (few clades colonizing extratropical latitudes) and frequent for OTT (frequent latitudinal range expansions. This generates two predictions. First, in the phylogenetic structure of the assemblage: if a few lineages arrive in temperate biomes (TNC) the assemblages will be in clustering. Otherwise, if many lineages arrive in temperate assemblages (OTT), the assemblages will be overdispersed. Second, the age of the assemblage for TNC will be recent and for OTT, could be recent or old. To test the first prediction, we quantified phylogenetic clustering for bird assemblages of Tyrannidae within the America continent and for the second prediction we developed a new analytical approach that allows inferring when the ancestor arrived where actual species occur (biome). We found high values of clustering in temperate assemblages and recent age of assemblage in temperate biome. These results support the predictions for TNC: few and recent events of dispersion to temperate assemblages. This has implications for the current distribution of biodiversity, since if the tropics are the origin of lineages and if dispersive events contributed to the richness found in temperate zones, biodiversity losses, in tropical biomes, will bring evolutionary consequences for all biomes.

Key words: Global pattern of richness, ancestral dispersal, birds.

SUMÁRIO

INTRODUÇÃO GERAL

Por que os trópicos possuem maior número de espécies em relação a zonas temperadas? Este padrão é conhecido desde os tempos de Humboldt (Hawkins 2001), Darwin e Wallace (Mittelbach *et al.* 2007), e é caracterizado pelo crescente aumento da riqueza de espécies dos polos para os trópicos (Rohde 1992; Gaston 2000; Willig *et al.* 2003; Pontarp *et al.* 2019), sendo conhecido por gradiente latitudinal de diversidade ou padrão global de riqueza.

O padrão de aumento da riqueza com a diminuição da latitude não difere entre os hemisférios norte e sul, nem entre grupos marinhos e terrestres, ectotérmicos ou endotérmicos, e, devido a isso, corrobora com a ideia de que este é o padrão estatístico mais consistente (Hillebrand 2004) e antigo da ecologia (Hawkins 2001). Mesmo sendo um padrão conspícuo ainda há pouco consenso sobre suas causas e o que determina esta distribuição (Gaston 2000; Hawkins *et al.* 2006). Existem mais de 120 hipóteses propostas para explicar a grande quantidade de espécies nos trópicos sendo que muitas são vagas, imprecisas, tautológicas, implausíveis e não suportadas pela evidência empírica (Rahbek & Graves 2001; Bini *et al.* 2004). Mesmo que a riqueza possa estar correlacionada com variações nas condições ambientais, como vários trabalhos já encontraram (Mittelbach *et al.* 2001; Hawkins *et al.* 2003; Willig *et al.* 2003; Rodríguez-Castañeda *et al.* 2017) ainda é necessário entender como o mecanismo desta variação interagem. Ou seja, é preciso compreender os mecanismos evolutivos e biogeográficos que atuam numa escala local e regional, que são: a especiação, a extinção e a dispersão (Wiens & Donoghue 2004; Duchêne & Cardillo 2015).

Algumas das hipóteses evolutivas mais discutidas para explicar o gradiente latitudinal de diversidade levam em consideração estes mecanismos evolutivos e biogeográficos (Mittelbach *et al.* 2007) que são: a Hipótese da Conservação de Nicho

Tropical (Wiens & Donoghue 2004; Wiens & Graham 2005) e a Fora dos Trópicos (Jablonski *et al.* 2006). A primeira defende que a maioria dos clados se originou nos trópicos e que as transições das linhagens dos trópicos para as zonas temperadas são raras. Isto seria causado porque o ancestral tropical teria um nicho fortemente conservado (Pontarp *et al.* 2019) e a riqueza encontrada em latitudes menores seria causada pelo acumulo de espécies (via diversificação *in situ* de um ou poucos dispersores) nestas regiões ao longo do tempo (Wiens & Donoghue 2004; Jansson *et al.* 2013). Já a Hipótese Fora dos Trópicos sugere que mesmo que a maioria dos clados tenham se originado nos trópicos a tendência é a expansão da sua distribuição. Desta maneira, a transição entre zonas tropicais para temperadas será mais frequente (Jablonski *et al.* 2006; Jansson *et al.* 2013).

Motivados pelo cenário exposto, nosso objetivo nesta dissertação foi analisar o gradiente latitudinal de riqueza de espécies tendo em vista estas duas hipóteses. Como já foi apontado, por existirem muitas hipóteses para o gradiente latitudinal, o progresso a ser feito nesta área depende da evidencia empírica que pode eliminar algumas das hipóteses propostas (Jablonski *et al.* 2006). Por este motivo, neste capítulo testamos especificamente a Hipótese da Conservação de Nicho Tropical e a Fora dos Trópicos. Para tanto, utilizamos uma família de aves da Subordem Suboscines como modelo de estudo, a família Tyrannidae (Kennedy *et al.* 2014). Esta família apresenta uma distribuição restrita ao novo mundo, com ampla diversidade de formas corporais, de papéis ecológicos e devido a estas características, torna-se ideal para estudos sobre radiação evolutiva em um grupo de aves continental (Fitzpatrick 1980).

CAPÍTULO 1

Does the latitudinal species richness gradient of Tyrannidae support tropical

conservatism hypothesis?

ABSTRACT [1]

Two hypotheses proposed to explain the latitudinal diversity gradient are the Tropical Niche Conservatism (TNC) and the Out of the Tropics (OTT). They differ in the importance of dispersal: it is rare for TNC (few clades colonizing extratropical latitudes) and frequent for OTT (frequent latitudinal range expansions). This generates two predictions. First, in the phylogenetic structure of the assemblage: if a few lineages arrive in temperate biomes (TNC) the assemblages will be in clustering. Otherwise, if many lineages arrive in temperate assemblages (OTT), the assemblages will be overdispersed. Second, the age of the assemblage for TNC will be recent and for OTT, could be recent or old. To test the first prediction, we quantified phylogenetic clustering for bird assemblages of Tyrannidae within the America continent and for the second prediction we developed a new analytical approach that allows inferring when the ancestor arrived where actual species occur (biome). We found high values of clustering in temperate assemblages and recent age of assemblage in temperate biome. These results support the predictions for TNC: few and recent events of dispersion to temperate assemblages. This has implications for the current distribution of biodiversity, since if the tropics are the origin of lineages and if dispersive events contributed to the richness found in temperate zones, biodiversity losses, in tropical biomes, will bring evolutionary consequences for all biomes.

Keywords: Global pattern of richness, ancestral dispersal, birds.

INTRODUCTION

The latitudinal diversity gradient is defined as an increase in species richness from poles to equator and it is the most striking pattern in ecology and biogeography (Hawkins 2001; Hillebrand 2004; Wiens & Graham 2005; Jablonski *et al.* 2006). Although many hypotheses were developed to explain this pattern, the majority are untestable, vague, tautological or unsatisfactory supported by empirical evidence (Rahbek & Graves 2001; Bini *et al.* 2004) and until now there is limited consensus about the mechanisms underlying this pattern (Duchêne & Cardillo 2015; Pontarp *et al.* 2019). While some explanations for the latitudinal diversity gradient have support, such as correlations between richness and climatic variables, productivity, and habitat diversity, generally these correlations do not mechanistically explain how these variables increase species richness (Wiens & Donoghue 2004; Wiens & Graham 2005).

In fact, the mechanisms affecting species richness must be based on evolutionary and biogeographic processes such as speciation, extinction and dispersal (Wiens & Graham 2005; Mittelbach *et al.* 2007; Duchêne & Cardillo 2015). Following their point of view, some of the most discussed evolutionary hypotheses that incorporate these processes (Table 1), are the Tropical Niche Conservatism (TNC) and the Out of the Tropics (OTT).

The TNC proposes that most clades originated in the tropics and then a subset of them spread to temperate biomes. In this situation, dispersal events are infrequent, since only few species could have adapted and evolved to invade and persist in freezing temperatures. Such perspective implies that niche conservatism helped to keep the difference in species richness in tropics and temperate regions over time (Pontarp *et al.* 2019).

The OTT also suggests that most clades originated in the tropics, but states that these clades tended to disperse and expand their distribution to temperate zones, more frequently. The pattern of species richness, in this situation, was sustained by two different processes: higher speciation in the tropics and frequent dispersal to temperate zones (Jablonski *et al.* 2006).

Therefore, TNC and OTT differ in the frequency of dispersal to temperate regions: lower/rare in TNC and higher/common in OTT. The different strength of dispersal would lead to different phylogenetic structures of the assemblages in temperate zones. While TNC predicts that the temperate biomes will have phylogenetically clustered assemblages (i.e temperate species are more closely related to each other than expected), OTT assumes that temperate biomes will have phylogenetically overdispersed assemblages (i.e temperate species are less closely related to one another than expected).

It is important to remind that the phylogenetic structure of the assemblage fails to distinguish when and where the dispersal event occurs. This is a major issue, when testing both hypotheses: TNC assumes that dispersal to temperate biomes is recent because during the Eocene-Oligocene Climate Transition (around 34 Ma) the average temperatures in high latitudes dropped by around 5º C (Liu *et al.* 2009) and, as a consequence, permitted the emergence of new large areas with temperate climate, which benefited the dispersal of tropical lineages throughout temperate biomes (Wiens & Donoghue 2004; Jansson *et al.* 2013; Duchêne & Cardillo 2015). On the other hand, OTT suggests a continuous dispersal of lineages into temperate biomes, and is less explicit about the timing of the dispersal events (Jablonski *et al.* 2006; Duchêne & Cardillo 2015). To sum up, for the TNC the age of the assemblage in temperate biomes

would be necessarily recent, while OTT, states that the age of the assemblage, could be either recent or much earlier (Figure 1).

In this study, we calculated the phylogenetic structure of the assemblage based in the value of net relatedness index (NRI), a standardized measure of the mean distance between species (Webb 2000; Webb *et al.* 2002). After that, in order to test the prediction of the age of the assemblage, we developed an analytical framework capable to estimate the arrival of the ancestor in the biome in which the species are found. Using this, we aimed to distinguish between the hypotheses. If the TNC is supported, the temperate assemblages will exhibit clustered assemblages because the dispersal event happened recently. As a consequence, temperate assemblages would be younger than tropical ones. However, if OTT receive better support, we expect that temperate assemblages will be overdispersed and the age of the assemblage could be recent or older (Figure 1).

To infer speciation and dispersal, we can use phylogenetic data, as these two processes affect the phylogenetic structure of the assemblage. If *in situ* speciation is predominant in the assemblage, the assemblage exhibits a clustered structure. Otherwise, if dispersal is more frequent, the assemblage will have a overdispersed structure (Webb 2000; Crouch *et al.* 2019). So, using phylogenetic data, we can infer historical process that contributed to generate that assemblage (Crouch *et al.* 2019). Moreover, it is essential to note that both processes do not receive equal attention: many studies investigated rates of speciation (Haffer 1969; Lovette & Bermingham 1999; Stephens & Wiens 2003; Cardillo *et al.* 2005; Allen *et al.* 2006; Weir & Schluter 2007; Rabosky & Matute 2013; Rabosky *et al.* 2013, 2015; Cutter & Gray 2016) and a few explicitly infer patterns of dispersion across latitudes (Duchêne & Cardillo 2015).

On this regard, by using the phylogenetic structure of the assemblage, we cannot explained if the *in situ* speciation is recent or old and assessing the age of the assemblage we are able to distinguish this. So, using phylogenetic plus biogeographical areas of occurrence, this intersection will allow estimating the time and directions of occurrence shifts over time. Then, we could use these estimates to define the age of species assemblages and properly test the second hypothesis.

In this work we have chosen a family of the Suborder Suboscine to test these hypotheses. The Suboscines originated in austral Gondwana and became isolated in South America when the continent was separated from Antarctica (about 40 Ma) (Kennedy *et al.* 2014). The family, Tyrannidae, has its origin inside tropical rainforests in South America (Ohlson *et al.* 2008) and presents a restricted distribution in the New World. This family is known to be one of the largest and most diverse bird families in the world. It shows a great diversity of body forms, ecological roles and the numerical dominance makes them a good model for a series of studies on evolutionary radiations in a group of continental birds (Fitzpatrick, 1980). Also, this family has the origin in South America and this continent was an isolated island throughout most of the Tertiary, a time in which passerine birds diversified throughout the world. This continent supported the evolutionary diversification of many unusual lineages of plants and animals. Additionally, as ecology, behavior and life histories of birds are relatively accessible, South America organisms enable us to study the roles of phylogenetic conservatism and key innovations in the development of a regional fauna (Ricklefs 2002).

Table 1: Differences between the two evolutionary hypotheses proposed to explain the latitudinal diversity gradient and the expected difference in the value of net relatedness index. For expanded version of this table, which include: process, assumption, geographic origin of the clade, composition of assemblage in temperate biomes, position in the phylogeny of switching events and frequency of dispersal see: Table S1-Supplementary information.

Hypothesis	Proposed patterns	Predictions	References
Tropical Niche Conservatism (TNC)	Tropical origins of major groups of organisms; only few species could evolve adaptations to invade and persist in freezing temperatures, implying that species are endemic and clustered phylogenetically in temperate biomes	Values of NRI are positive in temperate zones because only few ancestors arrived	(Wiens & Donoghue 2004; Jansson *et al.* 2013; Duchêne & Cardillo 2015)
	The dispersal event to temperate biomes is recent because during the Eocene-Oligocene Climate Transition (around 34 Ma) the average temperatures in high latitudes dropped by around 5° C (Liu *et al.* 2009), as a consequence of that, permitted a emergence of new large areas with a temperate climate and then the dispersal of tropical lineages to temperate biomes	Values of age of assemblage would be younger in temperate assemblages	(Wiens & Donoghue 2004; Jansson *et al.* 2013; Duchêne & Cardillo 2015)
Out of the Tropics (OTT)	Tropical biomes continually produce lineages and have a frequent net movement of species from tropical to temperate biomes and because that species would be less closely related and phylogenetically overdispersed in temperate biomes	Low value of NRI in biomes of temperate region	(Jablonski *et al.* 2006; Mittelbach *et al.* 2007; Jansson *et al.* 2013; Duchêne & Cardillo 2015)
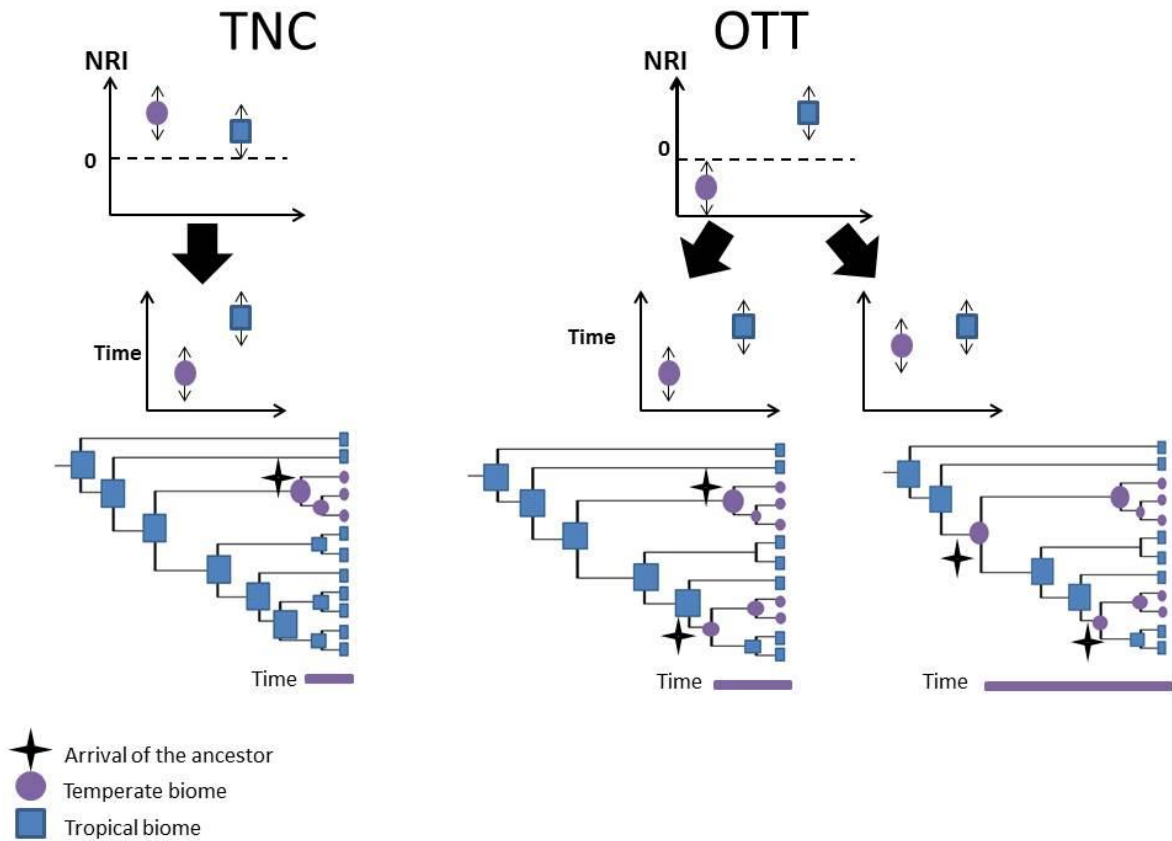
Figure 1: Predictions of values of net relatedness index and the age of the assemblage for temperate biomes. We expected for Tropical Niche Conservatism high values of NRI, indicative of clustering assemblages in temperate biomes. On the other hand, for Out of the Tropics, we expected low values of NRI in temperate assemblages. The image also shows that the value of NRI do not inform the age of the lineages' ancestor arrival. If, we have this information, we are able to distinguish if the arrival was recent (prediction of TNC) or if the arrival was old.

METHODS

Phylogenetic and geographic data

We compiled the geographic ranges of 392 species of the family Tyrannidae including both breeding and winter distributions from BirdLife International (BirdLife International and NatureServe 2017). This family is restricted to the New World (Fiztpark 1980). The taxonomy follows Jetz et al. (2012). We used 1000 phylogenetic hypotheses randomly sampled from the Bayesian pseudoposterior distribution, time-calibrated bird tree phylogenies (available at http://birdtree.org; cf. Jetz et al., 2012 for details). These trees are explicitly designed to be used as pseudo-posterior distribution and we constructed a consensus tree using the program R, with the function MaxCladeCred in the package phangorn (Schliep 2011). This approach evaluates each of the sample posterior trees and then computes the relative frequencies with which clade are represented across the set. After that, the product of these scores is taken as the tree's scores. The tree which has the highest product is the maximum credibility tree, and in this paper, we refer as consensus tree (MCC).

Species composition of assemblages were obtained by dividing the entire America in a gridded area of 110×110 km² (~$1° \times 1°$ at the equator), excluding islands. We choose this resolution because for well-known taxa, such as birds, the resolution recommended is 110×110 km² or higher (Hurlbert & Jetz 2007). We consider as tropical assemblages all the cells positioned between 0 and 23 degrees of latitude, and the cells that had values greater than 23 degrees were classified as temperate assemblages. Then, we rasterized the range maps of BirdLife, which contain the distribution of each species, and the overlap of these range maps gives us the composition of the assemblages and, summing species incidences of each assemblage, species richness.

Quantifying phylogenetic clustering within latitudinal zones

To quantify the degree of phylogenetic clustering of the assemblages we used the net relatedness index (Webb *et al.* 2002). Negative NRI values indicated overdispersion and positive values clustering (Webb *et al.* 2002). NRI is a standardized measure of the mean pairwise phylogenetic distance of a taxa in a sample, relative to a phylogeny of a species pool, and quantifies the average phylogenetic distance between co-occurring species. It is calculated by:

$$NRI = -1 * \frac{mn\,X_{obs} - mn\,X_N}{sd\,X_N}$$

Where the X_{obs} is the phylogenetic distance between two taxa in the phylogeny of the pool, mn (X_{obs}) is the mean of all possible pairs N taxa, $mn\,X_{(N)}$ and $sd\,X_N$ are the mean and standard deviation expected for N taxa randomly sampled on the phylogeny of the pool (Webb *et al.* 2002). We randomized species identities 999 times and using the R function ses.mpd in the package *picante* (Kembel *et al.* 2010) we calculated the z-values of mean pairwise distance and then we multiplied by -1 to turn them into NRI values. We used these values of NRI of each assemblage with the associated latitude of the same assemblage and then compare the values with temperate and tropical cells.

A framework for calculating assemblage age

To obtain when the ancestor arrived in the biome we merge the calculation of the ancestral range estimation with the information obtained through the present composition of each assemblage. Basically, our method requires 1) the ancestral biome for each ancestral 2) map in which biome each assemblage is and 3) calculate the age of the assemblages based only on the portion of evolutionary history that arose after the establishment of the ancestral in the biome in which the species are currently found. These steps are explained in detail in the next sections.

   1. *Ancestral range estimation*

The first step to construct this framework it is to find when the ancestor arrive in the biome. To access this information we estimated ancestral ranges with the package BioGEOBEARS (Matzke 2013) using a maximum likelihood approach. This analysis requires inform *a priori:* The biomes and the current biome in which the specie is found. So, we choose the classification of biomes proposed by (Olson *et al.* 2001) that consider global maps of floristic, zoogeographic provinces, broad vegetation types, regional maps of units based on the distribution of selected groups of plants and animals and the world's biotic province maps. This classification divided the terrestrial world into 14 biomes and eight biogeographic realms. For reasons of computational simplicity we aggregated the small and near biomes and after this procedure we have 10 biomes to estimate. If the geographic range of the current species was bigger than three biomes we excluded the biome with the lower occupancy. In BioGeoBEARS, the geographic range is not fixed to a single state; the method considers the combination of biomes. To make the estimative faster we limited the combination of biome to three. So, the package considered, in this situation, the combination of three, two and one biome to estimate the ancestral geographic range.

BioGEOBEARS permits evaluate six alternative models (DEC, DEC+J, DIVA, DIVA+J, BayArea, and BayArea+J) to infer the geographic range evolution. Each model makes some assumptions about the process of "dispersal" (range expansion), "extinction" (range contraction) and cladogenesis along phylogeny branches (Matzke 2013).

The difference among these models are: DEC model (Dispersal-Extinction-Cladogenesis) is a parametric method based on probabilities (Ree *et al.* 2005). At cladogenesis events assumes daughter lineages inherit the ancestral range if the ancestor lives in a single area or if the ancestral is widespread one the daughter lineage will live

in a subset of these areas, or one area will split off by vicariance. DEC assumes that one daughter lineage will always have a range of one area (Matzke 2013).

DIVA model (Dispersal-Vicariance Analysis) assumes that dispersal and extinction have value of one; otherwise vicariance events have zero cost (Ronquist 1997). So, the difference between DEC and DIVA is: the first, one of the daughter lineages inherits the whole area of its ancestor and the other inherits only a small portion. DIVA predicts the classical vicariance, a widely distributed ancestor generates two species in which each species inherits exactly the same number of areas (Ronquist & Sanmartín 2011). So, for that situation, DIVA estimates histories when the evolution of geographic range has been simple: where the speciation was driven by vicariance (Kodandaramaiah 2010).

BayArea (Bayesian Biogeographic Inference) is a Bayesian inference which has the principal advantage to include more areas *a priori* (Landis *et al.* 2013) and assumes that no range evolution occurs at cladogenesis events (Matzke 2013). Also, BioGEOBEARS permit to include the additional parameter +J which permit events for founder-event speciation (Jump-dispersal events) in these three models explained. Recently the DEC+ J received criticism because it is a poor model of founder-event speciation and not being statistically comparable to DEC model. Both differ in the relative allocation of explanatory power between cladogenetic and anagenetic events. So, statistical model selection between DEC and DEC+ J should not be done (Ree & Sanmartín 2018). The debate is still open and we think in the importance of jump-dispersal event, since birds can fly, and also because that estimations of ancestral distributions in passerines in South America have revealed that models which include jump-dispersal event present best evaluation (Batalha-Filho *et al.* 2014). So, we included this model in our evaluations.

After computing the log likelihood scores of all models, we used the Akaike Information Criteria (AIC) to select the best model of geographic range evolution and then we selected the highest value of the probability that the ancestral occupy the biome in this selected model. So, we constructed a matrix, called EcoNodes, In the rows, we have the node of the phylogeny, in the columns, the biome.

Matrix Nodes, express which species belongs to which node, in the lines the number of each node and the columns the presence or absence of the 392 species of Tyrannidae for each node. The matrix Econodes multiplied by Nodes resulted in a matrix that has the ancestral area associated with each node. In this resulting matrix, we do not have the association of the time the arrival. To access this information, we inserted the values of time using the dates extracted from the consensus tree (MCC) and the node affiliated (Matrix Time). After that, we had when the ancestors arrived and when the transition for another biome occurred.

2. *Mapping the current biome for each assemblage*

In this step, we tracked where the present species are. We constructed a matrix, Eco, which congregates each biome, has each assemblage. The classification of biome follows the same criteria used in the ancestral range estimation (Olson *et al.* 2001) and the assemblage is considered a gridded area of 1°x1° resolution resulting in 5565 cells (assemblages). We used a matrix, Composition (W), which gives us the composition of each assemblage. The multiplication of these matrixes (Eco and Composition) results in a matrix that has the correspondent biome associate of each assemblage.

Calculating the age of the assemblage

The age of each assemblage was calculated as being the mean period of time at which the ancestors spend in the biome which the currently species occur. Using the information of the past and the present, step 1 and 2, we calculated the arrival of the

ancestor. So, for each species we computed the age of the ancestor and thereafter we calculated the age of the assemblage for each cell.

In the case that the ancestor's transition occurs after the last-split event, this metric cannot infer the ancestor arrival. So, to indicate events like this, we adopted the value of 0.00001. If the position of the ancestor the same as the present species, we retrocede the occupation until we find the ancestor that is different from the current distribution of the species and then we calculated when the ancestor arrived in the biome.

Testing OTT and TNC hypothesis

To test the OTT and TNC hypothesis we applied the One-way Anova with permutation test since this test allowed to tested categorical descriptor (Tropical or Temperate biomes) with quantitative descriptor (NRI and Age of the Assemblages). So, if the test returns statistically significant result, we reject that the groups are equal. The value of *F,* give us, the variance between these two groups are significantly different and the *p-value*, for a given statistical model, the probability that, when the null hypothesis is true, the statistical summary would be greater than or equal to the actual observed result. Using both measures (value of *F* and *p-value*) we are able to distinguish if the null hypothesis is true, in that case, if the assemblages of temperate or tropical biomes are have same values of NRI and assemblages' age. So, we can test TNC and OTT hypotheses. We selected 10.000 permutations for each test: the first, using the values of NRI as variable response and the tropical or temperate biomes as predictors and the second test, we used the age of the assemblage as response variable and the tropical or temperate biomes as predictors.

RESULTS

Following the latitudinal diversity gradient, the 392 species of the family exhibit a strong richness gradient, where the sites with highest richness are found at forest habitats (Amazonia and Atlantic Forest).
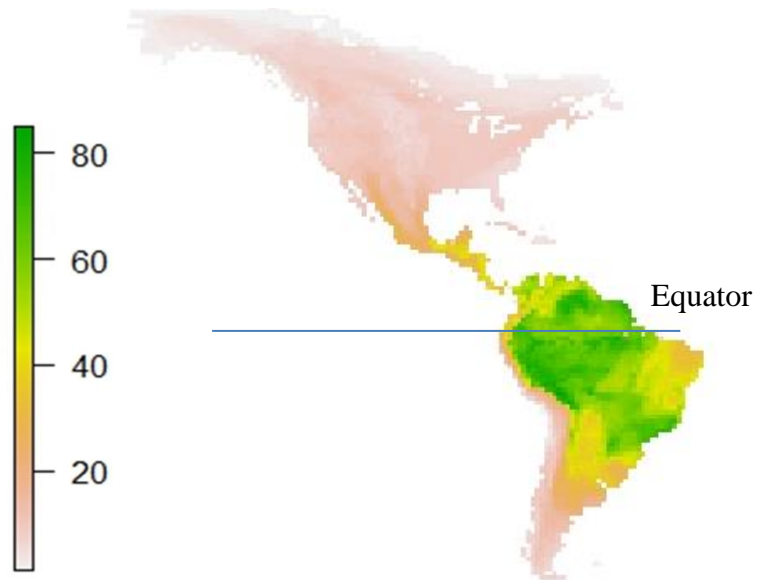

Figure 2: Species richness of 392 species of Tyrannidae The assemblage with the highest richness contain with 83 species. The lowest value was zero.

Phylogenetic clustering within latitudinal zones

We observed a range of NRI values, mostly positive, indicative of widespread clustering. But, the degree of phylogenetic clustering varies among latitudinal zones in which some latitudes show greater degree of clustering than others (Figure 3). The latitude 20º we have the highest values of clustering and the lowest value was in 0º. Temperate assemblages (latitude higher than 23º) we have a predominance of positive values of NRI, which are clustered assemblages (Figure 4). The One-way Anova returned the *F-value* corresponds a 2967.485, the degrees of freedom (DF) were 3830, the *p-value* were 0.00009 and R^2 0.4366.
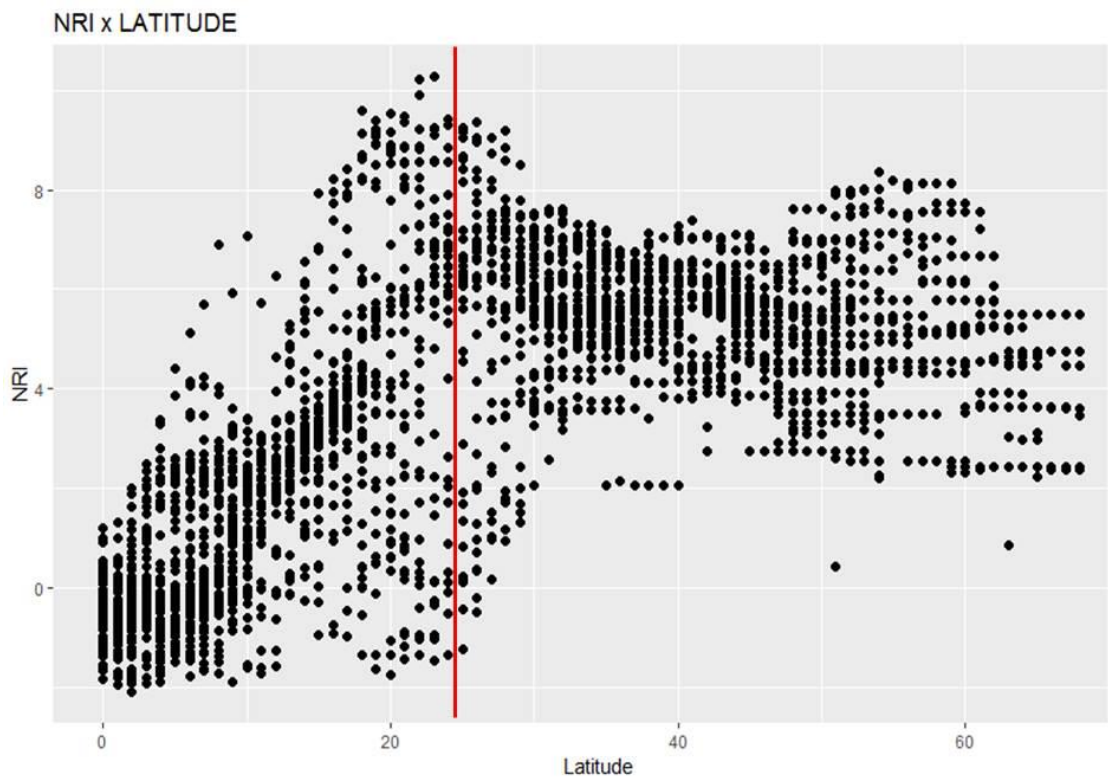

Figure 3: Values of NRI across different latitudes. In the equator, we have the lowest value of NRI. After the latitude 23º (Red line) we have a predominance of positive values.
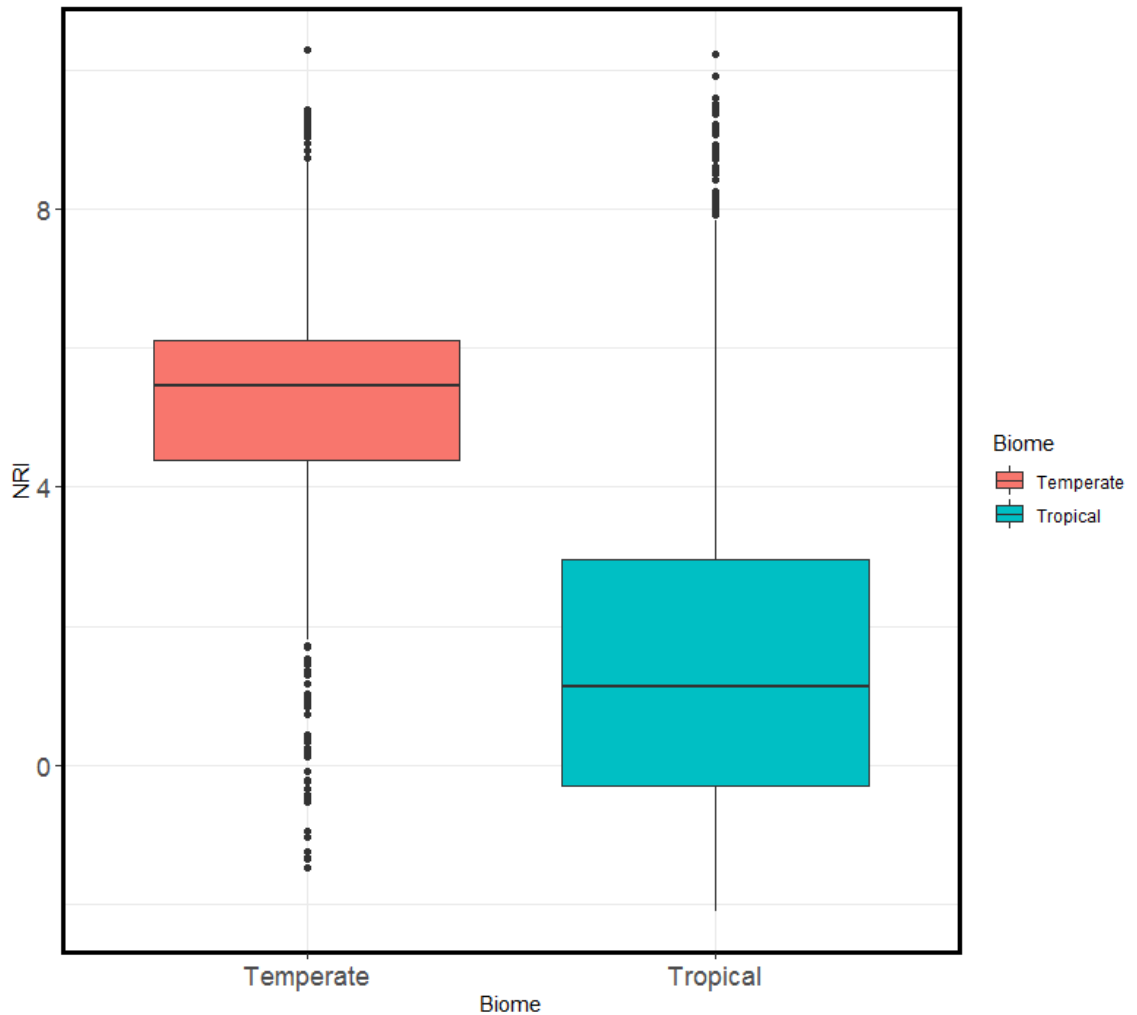
Figure 4: Values of NRI in the different biomes. Note that, in temperate assemblages, a predominance of positive values of NRI (clustered assemblages) and in tropical biomes a low value of NRI (overdispersed assemblages).

Age of the assemblage

Ancestral range estimation

We selected the model which received the lowest AIC score (Table S2) and extracted the highest probabilities of the ancestral to be occupying the biome in the selected model (BayArea+J).

After computing the age of assemblage, we observed that the recent assemblages are found in temperate biomes (Figure 5). The value of F was 724.011, DF was 3991, the *p-value* was 0.00009 and R^2 0.5421. Anova showed a lower value of F and a

significant value of p (lower than 0.05), which means, that these groups (tropical or temperate biomes) are different in both situations.
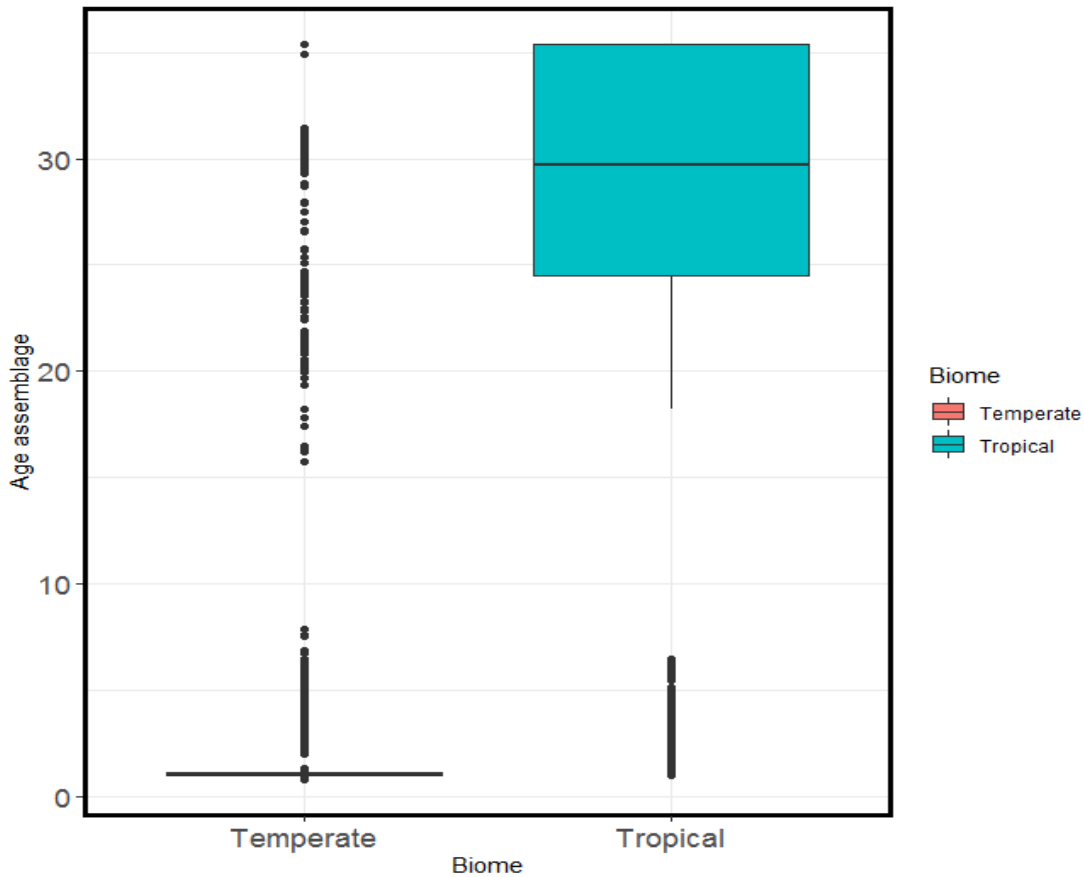
Figure 5: Values for age of the assemblages in the tropics and in temperate biomes. Tropic assemblages, in average, have the highest values of age assemblage in Ma while in temperate assemblages this value is low.

DISCUSSION

Both TNC and OTT assume that the major bird clades were originated in tropical environments and the temperate clades are derived from older tropical clades (Wiens & Graham 2005; Jablonski *et al.* 2006; Jansson *et al.* 2013). However, the TNC predicts a few dispersal events, while the OTT, in contrast, a continuous dispersal of lineages into temperate biomes. In other words, the temperate assemblages will be clustered for TNC and overdispersed for OTT (Duchêne & Cardillo 2015).

We were able to show that in temperate biomes there are clustered assemblages consistent with the expectations of TNC. Beside of that, further support is provided by the age of the assemblage, since the assemblages have a recent age in temperate biomes. However, for TNC the dispersal event is expected to have occurred during the Eocene-Oligocene Climate transition (around 34 Ma) (Duchêne & Cardillo 2015), while the values found for the age of assemblages in temperate biomes are lower than that. Nevertheless, our values are consistent with the evidence of fossil record of avian (Mayr 2004; Manegold *et al.* 2014) and woody angiosperms (Kerkhoff *et al.* 2014), which found that most of temperate lineages should have arisen after the Eocene-Oligocene Climate Transition, when the Earth began to cool and tropical environments shrank in a relative comparison to temperate and boreal zones. As consequence, a few and recent lineages were found in temperate biomes, broadly supporting the expectations of the TNC and less consistent with the expectations of OTT. Also, using the age of the assemblage, we are able to show that the richness found in temperate assemblages have originated recently and the phylogenetic structure indicates that *in situ* speciation are predominant in temperate assemblages. More specifically, age indicates that this *in situ* speciation was promoted recently.

It is interesting to note that the suborder Suboscines, appears to originate in austral Gondwana and became isolated in South America when the continent was separated from Antarctica (about 40 Ma) (Kennedy *et al.* 2014). In the Cenozoic era, South America, continued isolated and only joined when the Isthmus of Panama are formed (3-4 Ma), event known as "Great American Biotic Interchange- GABI" (Smith & Klicka 2010). After that, among the Suboscines, a few lineages of Tyrannidae have colonized North America (Ricklefs 2002). This explain why we have many lineages of Tyrannidae in South America (324 species) and a few in North America (125 species of

Tyrannidae) (Weir *et al.* 2009). The ability to colonize new regions should be difficulty for Tyrannidae because this family have a tropical forest-inhabiting and most families that have tropical forest-inhabiting required a completed land to cross (Weir *et al.* 2009). So, the interchange of species between South America to North America only succeeds when the Isthmus of Panama was closed since this event creates a completed land to cross. Also, the characteristic of the most Suboscines, is they are restricted to rain forest interiors (Kennedy *et al.* 2014) and explain why the dispersal event occur only when the Istmo of Panama are closed, even though bird have the capability of flying (Weir *et al.* 2009). Thus cluster assemblages in temperate biomes show that a few lineages managed to cross to North America (Ohlson *et al.* 2008). The old age of the assemblage in the tropics found could be explained by the fact that the origin of this family is in South America, more specifically, inside tropical rainforests (Ohlson *et al.* 2008).

To conclude, our work comes with two caveats. First, the estimation of the ancestral area is based on the results of BioGEOBEARS what could be controversial. In our case, the best probability of the data given the model was BayArea+J. We assumed that no range evolution occurs at cladogenesis, which means that the ancestral range is copied to both daughters' lineages. Also, prior to the ancestral range estimation, we had to classify the biomes. It is essential to note that the classification used (Olson *et al.* 2001) could express the history of occupation of the ancestor or not. Therefore, the first caveat is that the ancestral range estimation is based on the result of BioGEOBEARS which is a result of the biome classification adopted and the model used.

The second caveat is the lack of good fossil record, particularly in tropical biomes (Weir *et al.* 2009), since avian bones are thin and light as a consequence fossilize poorly (Smith & Klicka 2010). Also, more specifically, the fossil record of

New World Suboscines is very sparse (Batalha-Filho *et al.* 2014). For example, the results of (Oliveros *et al.* 2019) indicated that the rate shift within Passerida occurred several million years earlier than the expected of the phylogeny of (Jetz *et al.* 2012). In conclusion, the time-calibrated tree used in this study could express different information if we had more fossils in our backbone and, as a result, the time of the arrival of the ancestor could be early that we expected and maybe affect the results founded. Although we have these caveats, using phylogenetic plus biogeographical areas of occurrence, we estimated the time and the directions of occurrence shifts over time. These estimates permitted accessed the age of the assemblage and properly test the OTT and TNC hypotheses.

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Table S1. Differences between Tropical Niche Conservatism and Out of the Tropics

	Tropical niche conservatism	Out of the tropics
Processes	Diversification and dispersion	Diversification and dispersion
Assumption	Time to diversification is greater in the tropics than in temperate biomes	Time to diversification is greater in the tropics than in temperate biomes
Geographic origin of the clade	Tropical origins of major groups of organisms	Tropics continually produce lineages and have a frequent movement from tropical to temperate biomes
Composition of assemblages in temperate biomes	Endemic and clustered phylogenetically	Species are less closely related and Phylogenetically overdispersed
Position in the phylogeny of switching events	Recent, near tips	Anywhere
Dispersal	Is rare	Frequent to tropical to extra-tropical but rare in direction to temperate to tropical

References: (Wiens & Donoghue 2004; Jablonski *et al.* 2006; Mittelbach *et al.* 2007; Jansson *et al.* 2013; Duchêne & Cardillo 2015)

Table S2. Log likelihood (LnL), Number of parameters, AIC and AIC weight of the six models of ancestral range estimation evaluated from the BioGeoBEARS analyses.

Models	Log likelihood (LnL)	Number of parameters	AIC	AIC_wt
BAYAREALIKE+J	-1627	3	3260	1.00
BAYAREALIKE	-1660	2	3323	1.7e-14
DEC	-1872	2	3748	8.7e-107
DEC+J	-1872	3	3750	3.1e-107
DIVALIKE	-2002	2	4009	2.4e-163
DIVALIKE+J	-2003	3	4011	7.6e-164

CONCLUSÃO

Mostramos a importância de considerarmos os eventos de dispersão e de quando o ancestral de cada espécie chegou ao bioma. Concluímos que nossos resultados apoiam amplamente as expectativas da Conservação de Nicho Tropical e que os resultados são menos consistentes com as predições para a hipótese Fora dos trópicos. Indicando possivelmente que, o tempo disponível para diversificação, a dispersão e a conservação de nicho latitudinal são os mecanismos que explicam o gradiente latitudinal de diversidade para a família Tyrannidae. Isto traz implicações na distribuição atual da biodiversidade, uma vez que se os trópicos são as origens das linhagens e que se os eventos dispersivos contribuíram para a riqueza encontrada nas zonas temperadas, perdas de biodiversidade, nos biomas tropicais, trará consequências evolutivas para todos os biomas.