**Imprints of tropical niche conservatism and historical dispersal in the radiation of Tyrannidae**

**Running title: Imprints of historical factors in Tyrannidae assemblages**

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**ABSTRACT**

Historical events influence the diversity patterns that we observe in present day assemblages, and to understand the importance of these events we need to reconcile tools capable to access both past and present-day diversity patterns. Recently, was argued that phylogenetic clustering and overdispersion can shed light on the relative importance of in situ speciation and historical dispersal. In this work we showed that for a reliable assessment of the effects of historical events on present day communities we need to adopt an integrated framework that considers both present day phylogenetic patterns with ancestral character reconstruction. We tested two concurrent hypotheses (Tropical Niche Conservatism – TNC and Out of The Tropics - OTT) in which the distinction among them is only possible through the use of this integrated framework. We mapped Tyrannidae richness through the Americas and quantified the age and phylogenetic clustering of each assemblage based on a time-calibrated phylogenetic hypothesis. We found that the tropical assemblages were older than temperate ones, and that temperate assemblages are a result of closely related species that recently colonize this region. We conclude that recent events of historical dispersal realized by few lineages are important to determine the assembly of temperate communities, evidencing TNC as the most probable explanation to differences in phylogenetic structure between temperate and tropical assemblages of Tyrannidae.

**Keywords:** historical dispersal, in situ speciation, assemblage age, birds, phylogenetic patterns, tropical niche conservatism, out of the tropics.

**INTRODUCTION**

The increase in species richness from the poles to equator is one of the most striking patterns in ecology and biogeography (Hawkins, 2001; Hillebrand, 2004; Wiens & Graham, 2005; Jablonski, Roy, & Valentine, 2006). Although many hypotheses have been developed to explain this pattern (Rahbek & Graves, 2001; Bini, Diniz-Filho, & Hawkins, 2004), there is limited consensus about the mechanisms underlying the increase in biological diversity towards low latitudes (Duchêne & Cardillo, 2015; Pontarp *et al.*, 2019). For that reason, the search for the factors explaining the remarkable biological diversity in the tropics is a topic of great attention in the ecological agenda (Hawkins, 2001; Hillebrand, 2004; Wiens & Graham, 2005; Jablonski *et al.*, 2006). Ultimately, mechanisms affecting species richness are related to the evolutionary and biogeographic processes of speciation, extinction and dispersal (Wiens & Graham, 2005; Mittelbach *et al.*, 2007; Duchêne & Cardillo, 2015).Particularly, in situ speciation, extinction and historical dispersal are considered important factors to generate differences in diversity between tropical and temperate regions (e.g. Crouch et al. 2018, Pyron 2014).

Two concurrent evolutionary hypotheses highlight in situ speciation and historical dispersal of species as central mechanisms to explain the diversity in the tropics and its differences regarding temperate regions: Tropical Niche Conservatism (TNC) and the Out of the Tropics (OTT). The TNC hypothesis assumes that clades originated in the tropics diversified locally and then a subset of them spread to temperate biomes (Wiens & Donoghue 2004; Jansson *et al.* 2013; Duchêne & Cardillo 2015). Under TNC, gradients of species richness are generated by an old origin of tropical clades coupled with infrequent dispersal events, since only few species could have adapted and evolved to invade and persist in freezing temperatures. Such hypothesis implies that niche conservatism helped to keep the difference in species richness between the tropics and temperate regions over time (Pontarp *et al.*, 2019). On the other hand, the OTT hypothesis also suggests that most clades originated in the tropics, but these clades presented frequent dispersal to temperate zones (Jablonski *et al.* 2006; Mittelbach *et al.* 2007; Jansson *et al.* 2013; Duchêne & Cardillo 2015). Therefore, TNC and OTT differ in the timing and frequency of historical dispersal - infrequent and late in the former, frequent and continuous along diversification in the latter (Table 1).

Predictions for either TNC and OTT hypotheses can be analytically tested. Since both OTT and TNC hypothesis agree regarding the role of in situ speciation in the tropics, differentiating between them necessarily involves estimating a measure that explicitly consider the timing of migration events - specific time for TNC and diffuse for OTT (Jablonski *et al.* 2006; Duchêne & Cardillo 2015). Crouch et al. (2019) argued that the relative importance of in situ speciation and historical dispersal can be identified by calculating the Net Relatedness Index (NRI) (Webb *et al.*, 2002). Accordingly, since dispersal events are infrequent under TNC, temperate regions are predicted to show phylogenetically clustered assemblages (highly positive NRI), with greater contribution of in situ speciation to diversity (Figure 1A); on the other hand, more frequent events of dispersal are expected under OTT, and therefore temperate biomes are expected to show phylogenetically overdispersed assemblages (highly negative NRI), which are supposed to be assembled mainly by events of historical dispersal (Duchêne & Cardillo 2015). However, the phylogenetic structure of the assemblage does not indicate per se the ways in which diversity arose, if by means of historical dispersal or in situ speciation. This point is critical to differentiate between hypothesis that evoke historical processes underlying diversity, such as TNC and OTT. Figure 1 illustrates the problem regarding the use of NRI to infer the relative importance of past events of historical dispersal and in situ speciation. Suppose two communities (Island 1 and Island 2), both showing identical phylogenetic clustering (positive NRI values). Following the proposition of Crouch et al. (2018) both islands are shaped mainly by in situ speciation (Island 1), since the assemblages are composed of closely related species. However, historical dispersal can generate the same phylogenetic structure if the ancestors of present-day species came from other island than that we observed in the present distribution of species (Island 2). The information about ancestral areas, necessary to differentiate among the two historical process, would not be available if we use a phylogenetic structure metric that considers only present-day patterns.

Here, we investigated differences in the age and phylogenetic structure (clustered/overdispersed) of assemblages composed by Tyrannidae birds across the New World. For this, we propose a new methodological approach that explicitly considers the timing of ancestral migration events to differentiate among the two situations presented in Figure 1. Assemblages shaped mainly by in situ speciation must be occupied by species that presented a conservatism of the area of occurence during the evolutionary trajectory of the lineage (Figure 1, Island 1). Thus, older ages of tropical assemblages than temperate ones and the predominance of phylogenetic clustering of both tropical and temperate assemblages should provide support to TNC hypothesis. On the other hand, in assemblages where historical dispersal played a larger role to determine diversity, older temperate assemblages (or similar ages in both tropical and temperate assemblages) and phylogenetic clustering of tropical assemblages (or equal phylogenetic structure between tropical and temperate assemblages) give support to OTT hypothesis.

Here, we tested OTT and TNC as alternative hypotheses explaining diversity gradients across assemblages of bird species of the Tyrannidae family, which is a well-suited group to investigate the predictions of these two hypotheses because of its widespread geographic distribution and high species richness across the Americas. Tyrannids are members of the Suborder Suboscine; the latter 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 probably inside tropical rainforests in South America (Ohlson, Fjeldså, & Ericson, 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 and ecological roles that made them a good model for a series of studies on evolutionary radiations in a group of continental birds (Fitzpatrick, 1980).

Uma imagem contendo desenho

Descrição gerada automaticamente

Figure 1: Two assemblages in two islands with species represented by dots. Island 1 and 2 are identical regarding phylogenetic clustering, however, Island 1 are assembly by in situ speciation, whereas in Island 2 the assemblage is a result of a historical dispersal event (dotted arrow) in which ancestral of present-day species change their area of occurrence from Island 1 (green) to Island 2 (grey).

**METHODS**

*Species data*

The area of study is the American continent, since the geographic range of Tyrannidae species is restricted to this continent (Fiztpark 1980). The continent was subdivided in grid cells of 1 degree (~110 km² near the equator), excluding islands. These cells were classified as tropical (below 23° of latitude) and temperate (above 23° of latitude).

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). Based on these range maps, we generated assemblages for each grid cell. Evolutionary relationships among species were first taken form the BirdLife project (available at http://birdtree.org). We took 1000 time-calibrated phylogenetic hypotheses, randomly sampled from the Bayesian pseudo-posterior distribution (see Jetz et al., 2012 for details). Then, we created a consensus phylogenetic tree using Maximum Clade Credibility (MCC) method (Heled & Bouckaert, 2013). This method evaluates the frequency in which a clade is represented in a set of phylogenetic trees. The product of frequency values for the clades of a tree is the score of Clade Credibility for the phylogenetic tree. Therefore, the consensus phylogenetic tree is the tree with the highest product of clade frequency among the set of phylogenetic trees. The consensus tree was chose among 1000 trees using the *MaxCladeCred* function from phangorn package (Schliep 2011) in R (R Core Team, 2018).

*Ancestral area reconstruction*

Since OTT and TNC predictions specifies the timing and frequency in which species disperse from tropical to temperate regions we used reconstruction of ancestral areas of the Tyrannidae species based on its occurrence in South American biomes (Matzke, 2013). We adapted the biomes classification proposed by Olson et al. (2001), aggregating small and nearby biomes in order to reduce the number of biomes to ten. This was done to overcome limitations imposed by ancestral reconstruction methods with large numbers of character states.

We estimated the ancestral area of Tyrannidae species based on six models implemented in BioGeoBEARS: DIVA, DEC and BayArea, each model with and without the jump parameter. The parsimony‐based Dispersal‐Vicariance Analysis (DIVA) (Ronquist, 1997), emphasizes the vicariance process in speciation. DIVA assumes that the area of daughter species is a part of the areas of the ancestral species (vicariance), unless the ancestor occupies a single area, then sympatry is allowed. The Dispersal‐Extinction Cladogenesis (DEC) model (Ree & Smith, 2008) assumes that both vicariance and sympatry could origin daughter species. In DEC model the area occupied by a daughter species could be the same of its ancestor or a subset of the ancestor’s area. However, DEC model assumes that new species could occupy only one of the ancestor’s areas, in both sympatry and vicariance processes. The BayArea model (Landis *et al.*, 2013) assumes that speciation occurs only in sympatry, then the daughter species occupy the same areas of its ancestor, which can be single or multiple areas. Other three models are provided by including the founder effects to all models previous described. Thus, in these models a daughter species could ‘jump’ to a new area not occupied by its ancestor. These models are coded including a ‘+J’ to the model abbreviation.

We allowed species to belong to up to three biomes, based on the most frequent biomes that each species occurred. After running all six models we conduct model selection using Akaike Information Criterion to discriminate which one provides the best estimation of ancestral areas. The best ranked model of ancestral area estimation was used for the calculation of time arrival of species’ lineage in a biome.

*Quantifying phylogenetic patterns*

We quantified the phylogenetic clustering of the assemblages calculating net relatedness index (NRI) (Webb *et al.*, 2002). NRI is the standardized measure of the mean pairwise phylogenetic distance among species in an assemblage and quantifies how much cluster or overdispersed are the species of an assemblage. Negative NRI values indicates overdispersion, i.e. species in an assemblage are less related than expected by chance, and positive NRI values indicates clustering, species in an assemblage are more related than expected by chance (Webb *et al.*, 2002). NRI was calculated as follow:

where the is the mean phylogenetic distance between two taxa in the observed assemblage, is the mean phylogenetic distance between two taxa in the expected assemblage under null model*,* andis the standard deviation of (Webb *et al.*, 2002). We calculated NRI with *ses.mpd* function of the picante package (Kembel *et al.*, 2010), using 999 randomization of species identities in the phylogenetic tree (taxa shuffle null model).

*Average age of assemblages*

In order to evaluate if the observed NRI for assemblages resulted from in situ speciation or historical dispersal, we calculated the average age of assemblages from arrival times that each species´s lineages reach the assemblages. The arrival time was computed as the node age of the most ancient ancestor in which its descendants also occupied the biome of the assemblage. When the most recent ancestral of a species was estimated to occupy a different biome than that occupied by the current species in the assemblage of interest, we assign an arrival time of 1 x 10-5 Ma. Therefore, we adopt the premise that when the dispersal occurred after the last speciation event in the tree, the time of arrival was very recent. After obtaining the arrival age for all species in all biomes, the average age of the assemblages was calculated as the mean of the arrival age of all species presented in each assemblage.

*Data analysis*

To compare OTT and TNC hypotheses, we tested for differences in NRI and average age of assemblage between tropical and temperate assemblages with one-way ANOVA, in which p-value was calculated from a permutation test that freely shuffles the levels of predictor factor (temperate and tropical) in the response variable (NRI and average assemblage age) . We complemented that analysis with a regression model using latitude as a predictor of NRI values (Appendix 1, Figure S1). We also spatialized the results of NRI and average assemblage age for all Tyrannidae assemblages of America continent. All analyses were conducted in R environment (R Core Team, 2018) and all codes and functions used are available at https://github.com/GabrielNakamura/MS\_Tryranidae\_AgeAssemblage.

**RESULTS**

Tyrannidae assemblages presented a strong richness gradient with highest richness sites found near the Equator and at forested habitats (Amazonia and Atlantic Forest) (Appendix S1, Figure S2).

We selected the BayArea+J, since it was the model with the greatest support in AIC analysis, as the model to represent the ancestral biome of species (Appendix S2, Table S1 to see AIC results). Temperate regions showed stronger phylogenetic clustering than tropical assemblages (F= 1,426; p < 0.001) (Figure 3a). Also, temperate region showed more recent assemblages than tropical region (F= 4,171; p < 0.001; Figure 3b). In the tropical region we noted that the most ancient assemblages were located at tropical forests (Amazon and Atlantic forests ~35Mya), whereas temperate regions host the most recent assemblages (~4Mya). Furthermore, we identified an area with intermediate ages separating South and North America (Figure 4b).



Figure 3: Boxplots showing the NRI values (a) and mean age of assemblages (b) for temperate and tropical communities.

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Figure 4: NRI (a) and mean age of assemblages (b) for Tyranidae family in America continent.

**DISCUSSION**

Evaluation of the effects of deep past acting on contemporary community has been traditionally relied on analyzing patterns of phylogenetic diversity (Kraft *et al.*, 2007; Swenson, 2011; Gerhold *et al.*, 2018). However, such approach is limited regarding the mechanisms that can be evoked to explain the phylogenetic diversity patterns of present day assemblages (Gerhold et al. 2015). Here we show that analyzing only patterns of phylogenetic clustering and overdispersion does not allow to account for the relative importance of distinct historical processes (in situ speciation and historical dispersal), as stated in previous studies (Crouch *et al.*, 2019).

The methodological improvement presented in this study, that connect the phylogenetic diversity assessment with ancestral state reconstruction tools, allowed to infer TNC as the most probable explanation for to the diversity differences among tropical and temperate assemblages of tyranids. Without a framework that integrate the information brought by ancestral character reconstruction and current patterns of phylogenetic diversity, the differentiation between competing hypotheses relying fundamentally on past events become impossible by using only phylogenetic metrics that considers the occurrence of present-day species.

The rationale of combining the age of assemblage with community phylogenetic metrics was previously presented by Pinto-Ledezma et al. (2019) as an alternative to find for historical events that explain the phylogenetic structure of Furnariidae species. However, their approach differs from ours in operational and conceptual ways. Operationally, the age of assemblages was calculated as being the length of tip branches in the tree, without considering the area occupied by their ancestors (Pinto-Ledezma et al. 2019). That brings a conceptual difference regarding our assemblage age measure, that allows for a direct assessment of how long an assemblage is occupied by the lineages of species observed in the present. Pinto-Ledesma et al (2019) argues that the age of assemblage can be a proxy for diversification rates (*sensu* Jetz et al. 2012a), however, our measure of assemblage age holds a different meaning and can be viewed as a complementary approach for the study of the role of historical process in structuring assemblages.

Our results evidenced that the ages of temperate assemblages are most recent than pointed out in other studies. Duchêne and Cardillo (2015) defend that the dispersal events under TNC hypothesis occurred during the Eocene-Oligocene climate transition (around 34Mya). Despite the discrepancy among our results and that found by Duchene and Cardillo (2015), our findings are consistent with the fossil record of birds (Mayr, 2004; Manegold, Mayr, & Mourer-Chauviré, 2014) and woody angiosperms (Kerkhoff, Moriarty, & Weiser, 2014). Therefore, we support the idea that most of temperate lineages should have arisen after the Eocene-Oligocene climate transition, when the Earth began to cool and tropical environmental shrank in a relative comparison to temperate and boreal zones. As consequence, a few and recent lineages were found in temperate biomes, supporting the expectations of the TNC and less consistent with the expectations of OTT.

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 Mya) (Kennedy *et al.*, 2014). In the Cenozoic era South America continued isolated and only joined North America when the Isthmus of Panama are formed (~3-4 Mya) in the event known as “Great American Biotic Interchange- GABI” (Smith & Klicka, 2010). After that few lineages of Tyrannidae have colonized North America (Ricklefs, 2002). Our results are concordant to the history of colonization of Tyrannidae family, since we can note older assemblages in South America (with approximately 35Mya) and newer assemblages in North America (approximately 3Mya) with a transition area in the local that correspond to the Isthmus containing assemblages with intermediate ages between these two continents (Figure 4b). This result evidence the importance of in situ speciation in South America, recent historical migrations in North America and the connection among these two continents allowed by the Isthmus (Weir *et al.*, 2009).

Some caveats must be highlighted. First, the estimation of the ancestral area is based on the results of BioGEOBEARS that can present different outcomes depending on the model choose to perform the character reconstruction. In our case, the best support was found for BayArea+J model. We assumed that no range evolution occurs at cladogenesis, which means that the ancestral range is copied to both daughters’ lineages. Despite this caveat, our framework allows to use the results came from other models of character reconstruction, however the test of different models and its effects on the estimates of ages of assemblages is out of the scope of the present work. 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 from the phylogeny of Jetz, Thomas, Joy, Hartmann, & Mooers, (2012b). Finally, 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 different and maybe affect the results founded.

In summary, our study overcomes a problem related to the use of pattern-to-process approach to infer the role of historical mechanisms to shape ecological communities (in situ speciation and historical dispersal), by explicitly considering the information of ancestral states of species to interpret the present day phylogenetic information. Our study brings a different interpretation to explain the phylogenetic structure of Tyrannidae assemblages brought by Crouch et al (2019), in which the authors asserts that phylogenetic clustering is an indicative of in situ speciation process. The methodological improvement allows to evidence that TNC is the most probable process to explain the differences in phylogenetic patterns among temperate and tropical regions for Tyrannidae.

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Table 1: Differences between OTT and TNC regarding historical process and predicted patterns of NRI.

|  |  |  |  |
| --- | --- | --- | --- |
| **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 phylogenetically clustered in temperate biomes | Values of NRI are positive in temperate zones because only few ancestors arrived | (Wiens and Donoghue 2004, Jansson et al. 2013, Duchêne and 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 5º C (Liu et al. 2009), as a consequence of that permitted the emergence of new large areas with a temperate climate and then the dispersal of tropical lineages to temperate biomes | Values of age of assemblage will be younger in temperate assemblages | (Wiens and Donoghue 2004, Jansson et al. 2013, Duchêne and 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/or 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 and Cardillo 2015) |