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

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**ABSTRACT**

Past events can influence the diversity patterns that we observe in present day assemblages, and the understanding of the effects of historical process impose the need to integrate tools able to access both past and present-day patterns of communities. Recently, was argued that phylogenetic overdispersion and clustering can shed light on the relative importance of in situ speciation and historical dispersal. In this work we showed that for a correct assessment 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 tools. We tested two concurrent hypothesis (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 diversity of each assemblage based on a time-calibrated phylogenetic hypothesis. We found that the mean age of tropical assemblages is higher than temperate ones, and that temperate assemblages are a result of closely related species that recently colonize this region, indicating that Tyrannidae assemblages was strongly influenced by historical effect related to the older colonization of the tropical region compared to temperate regions, that presented recent and infrequent events of dispersal resulting in clustered recent assemblages, an evidence for TNC.

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

**INTRODUCTION**

The diversity observed in the tropics and the search for the factors that originated this diversity and its difference with temperate region is a topic of great attention in ecological agenda (Hawkins, 2001; Hillebrand, 2004; Jablonski, Roy, & Valentine, 2006; Wiens & Graham, 2005). In situ speciation and historical dispersion are supposed to generate the differences in diversity observed among tropical and temperate regions, and some empirical evidence based on diversity patterns supported the effects of these mechanisms in some groups (e.g. Crouch et al. 2018).

Particularly, two concurrent hypotheses highlight in situ speciation and historical movements of species (historical dispersal) as central mechanisms to explain the diversity in the tropics and its differences regarding temperate regions. While Tropical Niche Conservatism (TNC) assumes that the 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), Out of The Tropics (OTT) suggests that most clades originated in the tropics, but these clades presented frequent dispersion 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, in the first being infrequently and late, whereas the second being frequent and continuous during evolution of species.

Since both OTT and TNC hypothesis are concordant regarding the role of in situ speciation in the tropics, differentiating between them necessarily pass through the estimation of a measure that explicitly consider the timing of migration events (specific time for TNC and diffused for OTT. Crouch et al. (2019) argued that the relative importance of in situ speciation and historical dispersal can be identified by calculating a measure of phylogenetic diversity that estimate the mean phylogenetic distance among species in an assemblage (ses.MPD and ses.MNTD (Webb, Ackerly, McPeek, & Donoghue, 2002). The rationale behind the use of this metric is that assemblages that present low phylogenetic diversity (positive values of ses.MPD or ses.MNTD) are an indicative of great contribution of in situ speciation (Figure 1A), whereas communities with high phylogenetic diversity than expected by species richness are supposed to be assembled mainly by events of historical dispersal. However, the amount of phylogenetic diversity in an assemblage does not indicate the ways in which diversity arose, if by means of historical dispersion or in situ speciation, that is central to differentiate between hypothesis that evoke historical process, like TNC and OTT.

Figure 1 illustrate the problem regarding the use of MNTD or MPD to infer the relative importance of past events of historical dispersion and in situ speciation. Suppose two communities (island 1 and island 2), both presenting low phylogenetic diversity. Following the proposition of Crouch et al. (2018) both islands are shaped mainly by in situ speciation, since the assemblages are composed of closely related species. However, the same phylogenetic pattern could be obtained by events of historical dispersion (B) if the ancestors of present-day species came from other island than that we observed in the present distribution of species. The information of ancestral areas would not be available if we use a phylogenetic diversity metric that consider only present-day patterns.

In this work we proposed a new methodological approach that explicitly consider 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 occurrence area during the evolutionary trajectory of the lineage (Figure 1A), resulting in older assemblages than that in which historical dispersion plays an important role, since the ancestors changed their habitat to the new one that we current observe the occurrence of that species (Figure 1B) resulting in more recent assemblages. We applied the new framework to test the two hypothesis that explicitly consider the timing and frequency of historical dispersal: OTT and TNC. Expectations regarding phylogenetic patterns and assemblage ages accordingly OTT and TNC are presented in Table S1.

Uma imagem contendo texto, mapa

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Figure 1: Two scenarios showing assemblages in two islands. Both A and B presented low phylogenetic diversity accordingly to NRI metric (positive values), however, in A the assemblages are older than in B, indicating that in the second, the role of historical dispersal was more important than in situ speciation. Adapted from Crouch et al (2018).

**METHODS**

We test OTT and TNC using Tyrannidae family. Tyranidae is an ideal 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). Additionally, as ecology, behavior and life histories of birds are relatively accessible (ref), American tyrannids enable us to study the roles of phylogenetic conservatism and key innovations in the development of a regional fauna (Ricklefs, 2002).

The area of study is the America 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).

*Species 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). Based on these maps, we generate assemblages for each grid cell in the American continent. The evolutionary relationship among species was based in 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. For this, we used 1000 phylogenetic hypotheses randomly sampled from the Bayesian pseudo-posterior distribution, time-calibrated bird tree phylogenies (available at http://birdtree.org; see Jetz et al., 2012 for details). 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 the ancestral area of the Tyranidae species in South America continent based on its occurrence in biomes using BioGeoBEARS package (Matzke, 2013). We adapted the biomes classification proposed by Olson et al. (2001), aggregating small and near biomes in order to come up with 10 biomes. This was done to overcome limitations imposed by BioGeoBEARS, that allows the ancestral character reconstruction for a maximum of 10 character states.

We estimate the ancestral area of Tyranidae species based on six model presented in BioGeoBEARS. 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, Matzke, Moore, & Huelsenbeck, 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 new area, not occupied by its ancestor. These models are coded including a ‘+J’ to the model abbreviation.

We allowed that each species can belong up to three biomes, based on the most frequent biomes that a species occurs. 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 diversity 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, i.e. species in an assemblage are more related than expected by chance (Webb et al., 2002). NRI is 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).

*Mean age of assemblages*

In order to access if the observed NRI for assemblages is a result of in situ speciation or historical dispersal we calculate the mean 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 assume that when the dispersion occurred after the last speciation event in the tree, the time of arrival was very recent. After obtained the arrival age for all species in all biomes, the mean age of the assemblage was calculated as the mean of the arrival age of all species presented in each assemblage.

*Data analysis*

To evaluate the OTT and TNC hypothesis, we tested for differences in NRI and mean age of assemblage between Tropical and Temperate assemblages with one-way non parametric Anova (Legendre XXXX), and complementary with a regression model using latitude as a predictor of NRI values (Appendix 2, Figure S2). We also spatialized the results of NRI and mean assemblage age for all Tyranidae assemblages of America continent. All analysis was 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**

The Tyranidae assemblages presented a strong richness gradient with highest richness are found near the Equator and at forest habitats (Amazonia and Atlantic Forest) (Figure S1).

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Equator

Figure S1: Species richness gradient for the 392 species of Tyrannidae.

We selected the BayArea+J as the model to represent the ancestral biome of species (Table S2). We observed a difference in phylogenetic diversity among temperate and tropical regions (F= 1426, p<0.001 ), with a predominance of phylogenetic clustering in both temperate and tropical regions (Figure 3a). The mean age of assemblages also differed between tropical and temperate regions (F= 4171, p<0.001 ), with temperate presenting more recent assemblages than tropical region (Figure 3b). Particularly, in the tropical region, we also noted that the most ancient assemblages are located at tropical forests (Amazon and Atlantic forests ~35Mya), whereas temperate regions host the most recent assemblages (~4Mya), furthermore, we identify 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**

Understand the effects of deep past acting on contemporary community has as general methodological approach the description of patterns of phylogenetic diversity (Gerhold, Carlucci, Procheş, & Prinzing, 2018; Kraft, Cornwell, Webb, & Ackerly, 2007; Swenson, 2011), however, the process-by-pattern 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 the patterns of phylogenetic clustering and overdispersion does not allow to account for the relative importance distinct historical processes (in situ speciation and historical dispersion), as previous stated by previous works (Crouch et al., 2019).

The methodological improvement presented in this work, that joins the phylogenetic diversity assessment with ancestral state reconstruction tools, allowed to evidence TNC as the most probable explanation to the phylogenetic diversity patterns and historical events that conducted to differences among tropical and temperate assemblages of Tyranidae family. Without a framework that joins the information bring by ancestral character reconstruction and present patterns of phylogenetic diversity, the differentiation between competing hypothesis that have as fundamental information the 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 Furnaridae species. However, the approach adopted by the authors 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. That brings a conceptual difference regarding our assemblage age measure, that allows to 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 works. 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 results are consistent with the fossil record of avian (Manegold, Mayr, & Mourer-Chauviré, 2014; Mayr, 2004) and wood angiosperms (Kerkhoff, Moriarty, & Weiser, 2014), that 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 Tyranidae 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 among these two continents (Figure 4b). This result evidence the importance of in situ speciation in South America and recent historical migrations in North America.

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, Bermingham, & Schluter, 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 (ref aqui). Also, the characteristic of the most Suboscines, is that they are restricted to rainforest interiors (Kennedy et al., 2014) and explain why the dispersal event occur only when the Isthmus was closed (Weir et al., 2009). Thus phylogenetically clustered and recent assemblages in temperate biomes evidence that a few lineages managed to cross to North America after the connection with South America allowed by the Isthmus of Panama (Ohlson et al., 2008).

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 of 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 early that we expected and maybe affect the results founded.

In summary, our work overcome an problem relating 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 consider 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 Tyranidae assemblages bring 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 presented among temperate and tropical regions for Tyranidae.

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