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LARISSA PEREIRA LEMES

Contingência histórica e o debate macroevolutivo generalismo-especialismo

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LARISSA PEREIRA LEMES

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Ata Nº **111** da sessão de Defesa de Tese de **Larissa Pereira Lemes** que confere o título de **Doutora em Ecologia e Evolução**, na área de concentração em **Ecologia e Evolução.**

Aos **oito dias do mês de dezembro de dois mil e vinte e um (08/12/2021)**, a partir das **13h30min**, por **webconferência, seguindo portaria CAPES no. 36 de 16 de março de 2020 e recomendação da UFG**, realizou-se a sessão pública de Defesa de Tese intitulada **"Contingência histórica e o debate macroevolutivo generalismo-especialismo"**. Os trabalhos foram instalados pelo Orientador, **Prof. Dr. Thiago Fernando Lopes Valle de Britto Rangel (Depto de Ecologia/ICB/UFG)**, com a participação dos demais membros da Banca Examinadora: **Profa. Dra. Luisa Mafalda Gigante Rodrigues Carvalheiro (Depto de Ecologia/ICB/UFG)**, membro titular interno; **Profa. Dra. Levi Carina Terribile (Depto de Ciências Biológicas/UFJ)**, membro titular interno; **Prof. Dr. Renato Bolson Dala Corte (Pós-Doc/ICB/UFG)**, membro titular externo; **Dr. Frederico Augusto Martins Valtuille Faleiro (Pós-Doc/ICB/UFG)**, membro titular externo. Durante a argüição os membros da banca **não fez** sugestão de alteração do título do **trabalho**. A Banca Examinadora reuniu-se em sessão secreta a fim de concluir o julgamento da Tese tendo sido a candidata **aprovada** pelos seus membros. Proclamados os resultados pelo **Prof. Dr. Thiago Fernando Lopes Valle de Britto Rangel**, Presidente da Banca Examinadora, foram encerrados os trabalhos e, para constar, lavrou-se a presente ata que é assinada pelos Membros da Banca Examinadora, aos **oito dias do mês de dezembro de dois mil e vinte e um (08/12/2021)**.

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DEDICATÓRIA

Dedico essa tese às minhas filhas Alice e Aurora, que a cada dia me salvam de mim mesma.

“... ♫♪♩... Tenho sangrado demais, tenho chorado pra cachorro
Ano passado eu morri, mas esse ano eu não morro ... ♫♪♩...”

AmarElo - Emicida

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Eu sempre tive uma inexplicável admiração por uma série chamada Sense8 (claro que odiada pelo meu esposo por motivos bastante explicáveis). Passava de adimiração. Era quase feitiço.

Depois de muito pensar, acabei descobrindo o motivo de tanta admiração. Na série, oito estranhos começam uma conexão surreal, compartilhando visões, sentimentos, sensações… como se fossem um. Você pode até achar hilário (eu também acho), mas eles eram a evolução da nossa espécie:

homo sensorium!

Imagina só? Alguém conseguir compreender os sentimentos cujas palavras inventadas para representá-los jamais chegarão perto de sua real imensidão. Eu, como singela *homo sapiens,* sigo esperando que alguma mutação me leve ao *sensorium* (assim como eu esperava minha carta de Hogwarts). Mas até lá, como detestadora de manifestações sentimentais públicas que sou, paro por aqui. Não é que eu não sinta. Ao contrário, tudo aquilo o que eu sinto é bem maior do que qualquer palavra jamais inventada pela nossa espécie. E eu espero que esse sentimento flutue até todas as pessoas que se fizeram presente, seja com palavras, olhares, abraços ou análises! Essas pessoas não só me ajudaram na construção dessa tese (a qual eu considero, devo dizer, de valor irrisório comparada a outras coisas). Elas ajudaram na construção dessa pessoa que nesse momento vos escreve tanta baboseira. Eu tive pessoas oferecendo o melhor delas a mim (de novo palavras, olhares, abraços ou análises) e hoje eu sou um pouco de cada uma delas. Eu só queria dizer, obrigada! por ter me oferecido a melhor parte de vocês!

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SUMÁRIO

RESUMO GERAL

Eventos contingentes são fenômenos imprevisíveis que aconteceram ao longo da história. Esses eventos afetam o curso da evolução, pois levam à contingência histórica. Contingência histórica é o termo utilizado para dizermos que a história evolutiva de uma linhagem e seus descendentes muda após a mesma ter passado por um evento contingente. De acordo, os eventos contingentes, em conjunto com a contigência histórica, ocasionaram em histórias evolutivas diversas, porém únicas. Portanto, se a contigência histórica evita que diferentes linhagens ou clados evoluam uniformemente perante os fatores determinantes de sua evolução, por que macroecólogos e macroevolucionistas procuram por padrões globais? Nessa tese eu mostro que ignorar efeitos locais na relação entre fatores determinantes e a dinâmica evolutiva das linhagens (i.e., não-estacionaridade) acarreta em contradições, conclusões equivocadas e perda de informação. No primeiro capítulo, eu mostro através de uma revisão que teorias tradicionais em Ecologia são acometidas e até mesmo invalidadas pela não-estacionaridade. Eu argumento que todas teorias macroecológicas e macroevolutivas exibem efeitos locais que devem ser considerados anteriormente durante a fundação teórica ou posteriormente durante as analises. No segundo capítulo, eu mostro que o enigma macroevolutivo generalismo-especialismo que dura mais de 150 anos surgiu devido à negligência da não-estacionaridade. Especificamente, eu esclareço no segundo capítulo que a evolução em ambas direções (generalismo e especialismo) é possível. O papel das diferentes regiões geográficas na evolução da dieta das linhagens, surpreendentemente não verificado até hoje, permite ambos enlarguecimento e estreitamento do nicho dietético, com linhagens tropicais evoluindo em direção ao generalismo e linhagens em regiões temperadas evoluindo em direção ao especialismo. Esse resultado não somente explica porquê o generalismo ainda existe como também levou à formulação de uma teoria nova e original para o gradiente latitudinal de riqueza de espécies. No terceiro capítulo, eu mostro que as regiões geográficas também mudam a relação entre dieta e as taxas de diversificação das espécies. Generalismo está correlacionado com maiores taxas de especiação apenas nos trópicos, com os descendentes conservando o nicho dietético generalista e consequente manutenção das maiores taxas de especiação nessa região. Eu também mostro que teorias de diversificação dependente do traço são acometidas pela não-estacionaridade filogenética devido à contingência histórica. Eu argumento que o futuro das teorias de diversificação dependente do traço consiste em, teoricamente ou analiticamente, relaxar o pressuposto de estacionaridade.

PALAVRAS-CHAVE: generalismo, especialismo, não-estacionaridade, amplitude de nicho, evolução da dieta.

ABSTRACT

Contingent events are unpredictable phenomena happening along lineages evolutionary history. These events have huge impact on evolution's course because it leads to historical contingency. Historical contingency is the term used to say that the evolutionary history of lineages and their descendants changes after it experiences random and unpredictable events. Accordingly, the several contingent events happening along history together with historical contingency led to several but unique evolutionary histories. Therefore, if historical contingency prevents lineages to respond evenly to drivers, why macroecologists and macroevolutionists search for global patterns? Here I show that ignoring local effects in the relationship between drivers and lineages evolutionary dynamics (i.e., non-stationarity) leads to contradictions, wrong conclusions and loss of information. On the first chapter of this thesis I show, through a review, traditional and well accepted macroecological theories commited and even invalidated by non-stationarity. I argue that every macroecological e macroevolutionary theories exhibit local effects and must consider them previously in theories formulation or during analyses. On the second and third chapter I show that the generalism-specialism macroevolutionary conundrum standing for over 150 years emerged due to non-stationarity neglecting. Specifically, I show in the second chapter that both evolution towards generalism and specialism is possible, conversely to what have been claimed until now. The surprisingly non verified role of geographic regions on lineages diet evolution allows both increasing and decreasing of the dietary niche breadth, with tropical lineages mostly evolving towards generalism and temperate lineages mostly evolving towards specialism. This result not only explains why generalism still exists but also lead to the proposition of a new and original theory for the species richness latitudinal gradient. On the third chapter I showed that space does also changes the relationship between species diet and their diversification rates. Generalism is correlated to higher speciation rates only in the tropics, with descendants conserving their ancestral's generalist dietary niche and consequent maintenance of higher speciation rates in this region. I also show that trait-dependent diversification theories are commited by phylogenetic non-stationarity due to their historical contingency. I argue that the future of trait-dependent diversification theories lies on, theoretically or analytically, relaxing the assumption of stationarity.

KEYWORDS: generalism, specialism, non-stationarity, niche breadth, diet evolution.

INTRODUÇÃO GERAL

Eventos contingentes são responsáveis por toda a biodiversidade que nós conhecemos (Gould 1989). Um dos significados da palavra contingente é “imprevisível”. Eventos contingentes são fenômenos imprevisíveis que acontencem ao longo da história e podem ser diversos, tais como mudanças ambientais, eventos catastróficos, novas interações bióticas ou mutações. Apesar desses eventos serem imprevisíveis e aleatórios, eles exercem grande impacto no curso da vida por levarem à contingência histórica. Contingência histórica é o termo utilizado para dizermos que a história evolutiva das linhagens possivelmente muda após elas terem experimentado eventos contingentes (Blount *et al.* 2008, 2018). Como um evento contingente não é filogeneticamente e espacialmente global, ele muda somente a história evolutiva das linhagens que passaram por ele, levando à emergência de efeitos locais. Como consequência, os diversos eventos contingentes que aconteceram ao longo da história da vida levaram a histórias evolutivas diversas e únicas. Portanto, se os eventos contingentes, em conjunto com a contingência histórica, produzem biodiversidade repleta de efeitos locais, porque macroecólogos e macroevolucionistas procuram por padrões globais?

Cientistas utilizam estacionaridade (o efeito constante do preditor sobre a variável resposta) como um pressuposto no intuito de verificar teorias globais. Entretanto, estacionaridade é uma quimera quando macroteorias estão em foco, pois os dados utilizados são extraídos de amplas escalas espaciais, temporais ou filogenéticas. É inevitável que dados de escalas amplas não exibam efeitos locais. Assumir estacionaridade e negligenciar os efeitos locais (i.e., não-estacionaridade) leva à contradições, conclusões equivocadas e perda de informações em diversas teorias macroecológicas tradicionais, como por exemplo, a Regra de Cope, Regra de Bergmann e o gradiente latitudinal na riqueza de espécies.

Outro campo de estudo repleto de contradições é o da diversificação dependente da dieta. O debate macroevolutivo generalismo-especialismo existe a mais de 150 anos (Price *et al.* 2012) e possivelmente a negligência da não-estacionaridade é responsável por grande parte das confusões nesse campo de estudo. A dieta de uma espécie (generalista ou especialista) é um traço funcional e uma medida ecológica importante para o estudo de interações bióticas e competição (Burin *et al.* 2016; Sexton *et al.* 2017). De acordo com sua importância, podemos assumir que a dieta de uma espécie ou linhagem determina a sua história evolutiva (Burin *et al.* 2016). Mas ainda não existe consenso sobre como a amplitude do nicho dietético afeta as taxas de especiação e extinção das linhagens. Diversos mecanismos permitem que o generalismo seja ligado tanto a altas como a baixas taxas de extinção. O mesmo acontece em relação às taxas de especiação (Day *et al.* 2016; Sexton *et al.* 2017). Uma segunda contradição involve a direção de evolução das linhagens. Se espécies com nicho dietético amplo estão em desvantagem quando competem com espécies com nicho dietético mais estreito (Dennis *et al.* 2011), porque ainda existem linhagens evoluindo em direção ao generalismo?

A hipótese macroevolutiva “generalista-especialista” (daqui em diante mencionada apenas como GTS [do inglês generalist-to-specialist]; Futuyma and Moreno 1988) prevê que as linhagens evoluam em direção ao especialismo como consequência de sua vantagem competitiva. Entretanto, essa hipótese falha em explicar as linhagens que evoluem em direção oposta. Uma segunda hipótese macroevolutiva sobre o gradiente latitudinal na amplitude do nicho (daqui em diante mencionada apenas como LNB [do inglês latitude-niche breadth]; MacArthur 1972), fornece a variável ausente responsável pelos efeitos locais e pela contradição envolvendo a GTS. Assim como na LNB, a direção de evolução das linhagens depende da região geográfica na qual elas evoluem. Surpreendentemente, o papel das regiões geográficas como contingentes da relação dieta-diversificação ainda não foi avaliado. Nós mostramos que parte da contradição sendo debatida no ultimo século ocorre como consequência de estudos sendo realizados em diferentes regiões geográficas sem explicitamente considerar essa informação nos modelos matemáticos. Além da não-estacionaridade espacial, as teorias da diversificação dependente da dieta também sofrem não-estacionaridade filogenética.

O intuito dessa tese é mostrar a importância dos efeitos locais para teorias macroecológicas e macroevolutivas, além de mostrar na prática como o uso da não-estacionaridade pode esclarecer as contradições no debate macroevolutivo sobre o generalismo-especialismo. Para alcançar esse objetivo nós utilizamos Aves como grupo de estudo. Aves é um grupo altamente diverso (c.10.300 espécies) cujos dados disponíveis incluem ocorrência geográfica, filogenias e traços das espécies (Barnagaud *et al.* 2014). Os dados utilizados nessa tese incluem 448 espécies de aves para as quais dados quantitativos sobre a dieta foram encontrados. Essas 448 espécies de aves estão distribuídas em 58 famílias, cuja máxima representatividade alcançou 27% do número total de espécies presentes na família (a porcentagem de representantes nas famílias estão representadas na figura 1 apresentada abaixo).

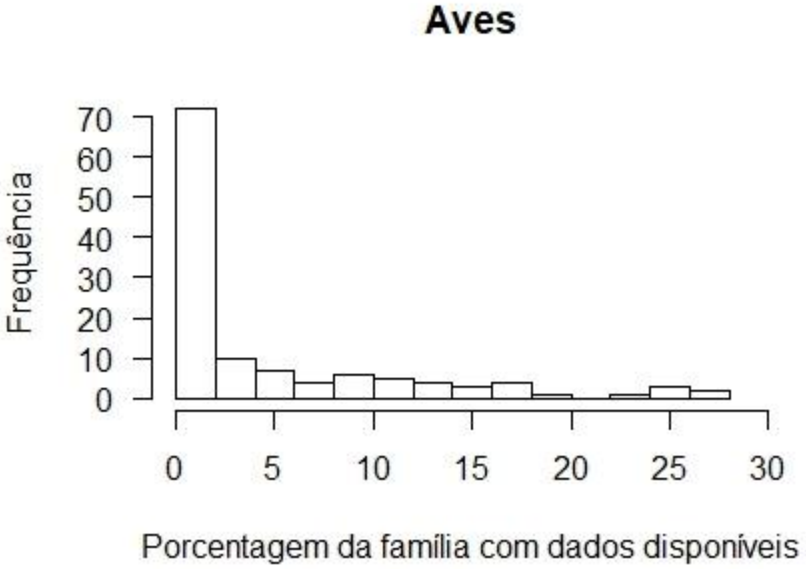

Fig.1. Distribuição de frequências da representatividade das famílias de Aves.

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CAPÍTULO 1

Raising Gods in Macroecology: is the search for general patterns making us blind?

Larissa Pereira Lemes, José Alexandre F Diniz-Filho, Matheus S Lima-Ribeiro, Thiago F Rangel

ABSTRACT

Since the dawn of the Ecology and Evolutionary Biology environmental sciences, researchers interested in natural processes have been seeking general explanations for global patterns. In an attempt to formulate omniscient, omnipotent and omnipresent theories, researchers generally use data from diverse taxa, regions and time periods. Hypotheses testing for universal theories are also based on comprehensive datasets and usually assumes homogeneous predictive effects over all data subsets. Notwithstanding, should we expect that a single predictor will have the same effect over multiple phylogenies, geological timescales and across the entire surface of the Earth? If not, our attempts to generalize may obscure opposite patterns and engender nonexistent global theories. Here, we review studies opposing general macroecological and macroevolutionary patterns (e.g. the latitudinal diversity gradient) and expose how ignoring non-stationarity may lead to incorrect results. We show that most macroecological and macroevolutionary patterns have their exceptions, and truly general patterns are indeed the exception. Hence, including the concept of non-stationarity in the development of environmental sciences is necessary to check the validity of global results, to identify factors structuring theories and to improve predictive models. We conclude that (i) incorporating non-stationarity, both conceptually and methodologically, is critical to help ecologists in unveiling missing variables and assessing the dynamics of nature unrevealed by generalizations; (ii) looking for non-stationary systems is desirable to tie together the multiple pieces of a synthetic theory of biodiversity and to make progress in environmental sciences; and (iii) even though not always totally blinded, ignoring non-stationarity and doing naïve generalization may be a potential genesis of errors and always a veil overshadowing our vision of the nature's complexity.

Key-words: Non-stationarity; generalization; local effects; phylogenetic non-stationarity; temporal non-stationarity; spatial non-stationarity

INTRODUCTION

The term “macroecology” was coined by James Brown and Brian Maurer in 1989 to describe the discovery and explanation of major patterns in species distributions, abundance and diversity at large spatial scales (Brown and Maurer 1989; see McGill 2019 for recent review). Although the name “macroecology” is relatively new, the goal of macroecological research is not (e.g. von Humboldt 1852). Recently, McGill (2019) has argued that macroecology mix two non-mutually exclusive goals, (i.e., to provide a conceptual expansion of ecology into large spatial, temporal and organizational scales), as well as an attempt to find general explanations from first principles. Also, there are several research programs in ecology attempting to theoretically expand ecology into macroecology, and then macroecology into evolutionary macroecology (McGill 2019; McGill *et al.* 2019). These research programms encompass biological agents as small as individuals or populations, or ecological systems as large as communities or ecosystems.

However, despite their diversity and width of scope, evaluating the numerous ecological and evolutionary theories invoked by these research programs require data at large spatial, temporal and/or taxonomic scales. Indeed, even research projects not conceptually concerned with deep-time and continent-wide ecological and evolutionary processes usually attempt to gather the largest possible dataset to evaluate hypotheses. Evaluating or expanding the generality of ecological and evolutionary hypotheses is the underlying philosophical motivation for all ecological research. For example, the role of evolutionary mechanisms has long been theoretically recognized as a driver of modern macroecological patterns (Brown 2014), but only recently have some of these mechanisms been methodologically incorporated into models designed to represent theoretical explanations (Diniz-Filho *et al.* 2013). Indeed, incorporating data from the fossil record in comparative phylogenetic methods gave rise to a new research field called ‘evolutionary macroecology’ (Diniz-Filho et al. 2013; see Morlon 2014 for more details), which is an attempt to expand the temporal dimension of evolutionary processes to link ecology with macroecology (McGill 2019).

The possibility of generalizations has long been advocated through the argument that patterns emerge only when details (i.e. idiosyncrasies) are omitted. The history of scientific progress clearly indicates that a key focus of natural sciences is achieving universal theories, potentially identifying general processes that drive as many biodiversity patterns, in as many places and epochs as possible. As pointed out by McGill (2019), this have been indeed one of the main goals of macroecology. But are there reliable universal theories or have they emerged from spurious generalizations? How the evolutionary contingencies and the complexity of patterns affect our ability to achieve these generalizations? To answer these questions, we have here searched for potential epistemic issues that underlie the process of generalizing macroecological theories.

1. How do scientists generalize?

Scientists often evaluate if one or several factors (“predictor” or “explanatory” variables, in statistical language) have spatial or temporal variation that is similar to those observed in another phenomenon of scientific interest (the “response” variable). Such analysis may emerge “a priori” from a prediction derived from a theory, or it may allow evaluating an existing theory. In macroecology, for instance, one could evaluate if variation in temperature tends to be correlated with variation in biodiversity. If a consistent correlation emerges between temperature and biodiversity within different taxonomic groups, across different regions and/or over different periods of time, then temperature acquires credibility among macroecologists as a general explanation for biodiversity patterns and the idea is to develop theoretical explanations underlying this general relationship (i.e., Storch et al. 2018). For instance, to verify if temperature drives biodiversity patterns, macroecologists compiled data on temperature and biodiversity across the globe and derived mathematical models that generalize the observed relationship. However, although this relationship allows generalization, the lines of this mathematical model keep the assumption that changes in the predictor are equivalently related to changes in the response along any data subsets. In other words, by building a mathematical model, macroecologists assume that the observed statistical relationship between temperature and biodiversity should remain unchanged across spatial, temporal and taxonomic scales, regardless of whether the pattern of correlation has been observed under multiple circumstances. A constant relationship between predictor and response variables within the scope of one study would allow us to apply the same single model (i.e. global model) to the entire data seta, a mechanism that constitutes the key scientific component to generalize. But is the assumption of a constant relationship logically consistent?

Imagine the following scenario: species S1, which has feature set F, coexists with species S2 and S3 in a region with climatic condition C. During climatic fluctuation F, a mutation M emerges and spreads within a population of S1. In this simplified world, many other species would have the same feature set, coexist with the same species, experience the same climatic conditions and fluctuations, and suffer the same mutation. This scenario confers a highly predictable world, in which a single theory and global model would fit almost perfectly to all data subsets (taxa or regions) within the entire data set. Notwithstanding, the real world is not as simple as this imaginary example. Instead, real species retain distinct features over the evolutionary history, occur across different communities and environments, and mutations are random. The non-fulfillment of one of the conditions A-F suffices to nullify the assumption of constancy in the relationships between predictor and response variables, challenging the accuracy of global models and the explanatory power of universal theories in macroecology. In this non-simplified scenario, which is the reality of nature, theories and mathematical models are actually contingent to circumstances.

Evolutionary history does not repeat itself, especially for distantly related species, with different geographic distributions, at different times. Historical contingency - the large influence of idiosyncrasies during species evolutionary history (Blount et al. 2018) - suggests that species relate to their environment and to one another in different ways. The outcome of contingency is amplified through speciation events, since descendants inherit the same evolutionary modification in the relationship with the environment and other species. Thereafter, when a small clade is under focus, shared idiosyncratic local effects accumulate over time and local effects comes to light. Concerned with the consequences of local effects on global models, researchers have focused on developing statistical methods to explicitly test for these local effects within global data sets. These statistical methods, developed to test for local effects, are designed to relax the assumption of stationarity, therefore identifying non-stationary patterns. Even though are few, were all announced upon the light of a mathematical term: non-stationarity.

The overall goal of this review is to review the meaning of non-stationarity to expose and discuss the consequences of ignoring non-stationarity in the development of generalization-based theories and of science itself. To achieve this main goal we establish four steps (*i*) address studies that have identified patterns that are different from the theoretical generalizations, (*ii*) summarize the processes evoked to explain these opposite patterns, (*iii*) identify the factors structuring the theories and how inference of mechanisms and processes evoked to explain emerging patterns may change in a non-stationary context, and finally (*iv*) based on the factors identified, propose non-stationary predictions from the theories to guide appropriate specification of global models.

2. Non-stationarity: from a mathematical concept to the complexity of nature

To understand non-stationarity, we have to first take a step back and define its precursor concept, stationarity. Stationarity is a mathematical term used to describe unchangeable values, variables or relationships, often implying *constancy*. Stationarity is an assumption of most statistical models. The term was first used by Kolmorogov (1931) to describe probability density functions that remain unchangeable through time. Maybe due to the simplified translation of stationarity as constancy, the concept of non-stationarity has also been simplified as the opposite idea, *lack of constancy*, or *inconstancy*. Nevertheless, non-stationarity is not purely lack of constancy (Koutsoyiannis & Montanari 2015), and this misconception of the term may lead to stagnation of scientific learning to a certain extent.

Non-stationarity is a statistical finding that the studied phenomenon is not constant. Concerning macroecological studies, non-stationarity is the term used to characterize data sets exhibiting local effects. Hence, non-stationarity within the macroecological context means that theoretical explanations for biological patterns and a corresponding mathematical model are not homogeneously accurate for all data subsets (Brunsdon *et al.* 1998; Fotheringham 2002). However, non-stationarity cannot be interpreted simply as the assumption of inconstancy in a model. A study system must be treated as non-stationary only if inconstancy in the data subsets are caused by factors subject to observation (Koutsoyiannis & Montanari 2015). The identification of missing variables cannot be neglected. Identifying factors structuring our theories within non-stationary study systems is of crucial importance to the scientific theoretical progress. Through the identification of missing variables, it is possible to disentangle the true relationship between the variables of interest and shed light into processes shaping different relationships to better inform our global models. More important, due to historical contingency, non-stationarity within macroecological data subsets should be an assumption previously considered to avoid potential mistakes, not a result *per se*.

At this point, it is clear that macroecological theories may be committed by non-stationarity. However, to our knowledge, there has been no systematic review of ecological and evolutionary literature to evaluate the potential impact of the mistaken assumption of non-stationarity. From now on, the major aim of this review is to show how major evolutionary and ecological theories might be influenced by non-stationarity. We explain how researchers' results may be mistaken when testing for stationarity assumption is neglected. The first step to accomplish this aim is to explain how mixing local effects into a global analysis may obscure the results.

3. How varying local effects may be hidden behind global results

Osborne et al. (2007) argued that global results mistakenly mirror average relationships between the predictor and response variables, masking local effects. Nevertheless, researchers may reach numerous errors from mistakenly applied global analysis. These mistaken results rely mostly on the strength and direction of local effects emerging from data subsets. In fact, global analysis may lead to (*i*) both increase and decrease of true coefficients of determination (Fig. 1A); (*ii*) partial type I error (Fig.1B); (*iii*) partial type II error (Fig. 1C); (*iv*) absolute type II error (Fig. 1D); and (*v*) partial directional error (Fig. 1E; Box 1).

4. Local effects and their related macroecological dimensions

Local effects within macroecological and macroevolutionary studies emerge in the dimensions in which these studies are conducted. Since macroecological theories are concerned with biodiversity patterns through time, space and phylogeny (McGill 2019), local effects can be seen in the temporal, spatial or phylogenetic data sets. The terms used to refer to emerging local effects on temporal, spatial and phylogenetic data sets are (not surprisingly) temporal, spatial and phylogenetic non-stationarity. But perhaps surprisingly, disentangling these three dimensions is not equally intuitive.

4.1. Temporal Non-Stationarity: local effects within temporal data

Studies concerned with local effects first appeared in the temporal dimension, in which theories made predictions about the apparently chaotic behavior of variables through time (e.g. Gregg and McPheeters 1913; Hunter 1928; Tomko and Crapper 1974). The data collected to assess theories that make predictions about changing variables through time is called *time series data*, from which the relationships between predictor and response are assessed across ordered temporal slices (see Sneyers 1990 for more details on time series analyses). Time series analyses became widespread in macroecology, mainly after the measurement of the temporal dimension became common in community ecology. Several research programs, of which main theme was succession ecology and their related biological and environmental drivers (or their missing variables leading to local effects), were developed based on time series analyses (Wolkovich *et al.* 2014).

Box 1 Types of errors emerging from global analysis

Overestimation-Underestimation error: emerges when local effects within the data set are similar in direction, but they vary in their strength. A global analysis that yields an averaged relationship may result in both underestimated correlations for data subsets exhibiting greater local effect strengths and overestimated correlation for data subsets exhibiting smaller local effect strengths (Fig. 1A). The coefficient of determination estimated through global analysis may potentially not mirror any of the local coefficients of determination.

Partial type I error (or false positive): emerges when one data subset exhibits a strong effect of the predictor upon the response variable, while the remaining data subset lacks correlation between the variables. Hence, a global analysis providing an averaged relationship between predictor and response variables results in a weak but significant correlation (Fig. 1B), which underestimates the coefficient of determination for one data subset, and yields a false positive result for the remaining data subset.

Partial type II error (or false negative): emerges when one data subset exhibits an effect of the predictor upon the response variable, while the remaining data subset lacks correlation between the variables. A global analysis providing an averaged relationship between predictor and response variables results in non-significant correlation (Fig. 1C), which confers the true absence of correlation between the variables for one group, but confers a false negative error for the remaining data subset.

Absolute type II error (absolute false negative): emerges when data subsets exhibit a high correlation between predictor and response variables, but in opposite directions of interaction (positive and negative). Similar to partial type II error, a global analysis providing an averaged relationship between the variables yields a non-significant correlation (Fig. 1D). Notwithstanding, because the two contrasting significant local effects cancel each other out, the global analysis results in non-significant correlation.

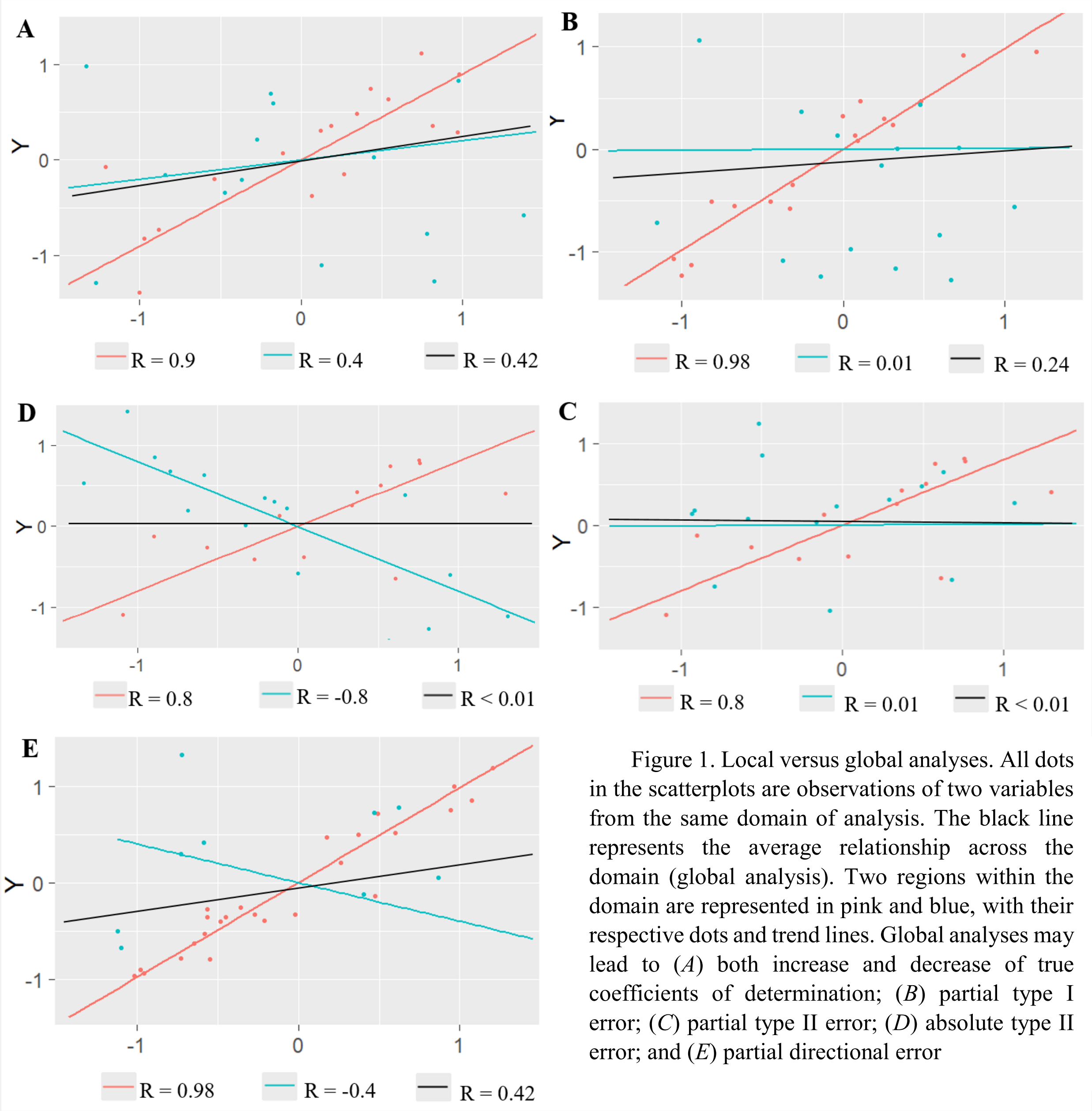


Figure 1. Local versus global analyses. All dots in the scatterplots are observations of two variables from the same domain of analysis. The black line represents the average relationship across the domain (global analysis). Two regions within the domain are represented in pink and blue, with their respective dots and trend lines. Global analyses may lead to (*A*) both increase and decrease of true coefficients of determination; (*B*) partial type I error; (*C*) partial type II error; (*D*) absolute type II error; and (*E*) partial directional error

<u>*Partial direction error*</u>: emerges when data subsets exhibit opposite directions of correlation, but the strength of the local effect for one group is greater. A global analysis yields a statistically significant relationship between predictor and response variables with the direction of interaction mirroring the relationship emerging from the data subset with stronger local effect (Fig. 1E). Such a result underestimates the local coefficient of determination of one group and masks the opposite local effect for the other group.

The types of errors emerging from ignoring local effects within non-stationary study systems were illustrated and distinguished using a simple example. Although the examples of stationary study systems given above are structured into only two data subsets, much more complex structures are possible and probable within macroevolutionary and macroecological studies. Furthermore, non-stationarity within study systems may arise from other dissimilarities than the direction and strength of the relationship between the variables. For instance, the best fitting model for different data subsets may also vary, with some data subsets better adjusted by linear functions, while other data subsets may adjust better to exponential, logarithm or quadratic functions. The error type emerging from mixing different functions (or not considering them) will rely on strength and type of functions combined.

Although the widespread usage of methods allowing non-stationarity within community ecology, studies accounting for local effects beyond human time scale are still lacking and, much of this gap is due to the lack of data. To overcome lack of data, researchers started to estimate the required variables through phylogenetic comparative methods. Together, the interplay between temporal and phylogenetic non-stationarity started. The tendency of increasing lineages' body size along their evolutionary history, named Cope's rule (Alroy 1998), is a good example for how temporal and phylogenetic non-stationarity are mixed. Although scientists were looking for temporal data (changes on body size over time), they were using higher-level phylogenies to estimate species body size along their evolutionary history. The usage of higher-level phylogenies, which means phylogenies encompassing several clades, inevitably added phylogenetic non-stationarity into an originally temporal theory such as Cope's rule.

It seems inconsistent that Cope's rule has been primarily derived from a phylogeny (Stanley 1973) while no phylogenetic data was needed to formulate it. In an ideal scenario, the evidence from fossil records would have been enough to formulate the Cope's rule and verify the tendency within a lineage to evolve towards bigger body sizes through time series. Indeed some studies analyzing Cope's rule were based only on fossil record (e.g. Jablonski 1997; Dommergues et al. 2002; Hone et al. 2005; Heim et al. 2015). However, fossil records mirroring complete lineages' evolution are scarce (Benton *et al.* 2000), making Cope's rule difficult to validate. Hence, the availability of current species' body size and phylogenetic hypotheses, together with phylogenetic comparative methods, allowed researchers to verify the validity of Cope's rule for the taxa lacking fossil data [although also had allowed the accumulation of facts against it; i.e. (Butler & Goswami 2008)]. Even though Cope's rule has been verified through phylogenies, it is committed by temporal non-stationarity because the local effects are seen in the time slices in which lineages' body size do not increase (Fig. 2).

Regardless the dimension in which non-stationarity affects Cope's rule, it may or may not be a valid general pattern. Some researchers agree that environmental pressures selected for larger species along evolutionary history (e.g. Baker *et al.*, 2015 for mammals; and Heim *et al.*, 2015 for marine species). However, it is also accepted that Cope's rule is not valid for some time periods (e.g. Macfadden, 1986; Alberdi *et al.*, 1995; Finarelli & Flynn, 2006; Butler & Goswami, 2008). Even though the agreement that lineages may not increase their body size during some time periods and that others may have switched their direction of size evolution, the factors leading to shifts and inverse patterns are poorly understood. However, the Lilliput effect is one clue to inquire about possible factors leading to temporal non-stationarity on Cope's rule.

The Lilliput effect was first described by Urbanek (1993) and concerns the tendency of species to reduce their body size after mass extinction events (Hansen et al. 1993; Harries and Knorr 2009). Differential extinction of larger taxa and survivorship of species capable of reducing their size more rapidly have been some of the ecological mechanisms proposed to explain the Lilliput effect (Harries and Knorr 2009; e.g. Guthrie 2003; Martin et al. 2018). Nevertheless, Sallan & Galimberti (2015) enlightened the importance of species' life-history traits to ensure their maintenance after mass extinction events through body size decrease. According to the authors, smaller sizes are selected after mass extinctions because it is also linked to other ecological features such as fast breeding, high abundance and low energetic requirement per individual, which decreases extinction and increases speciation probability of post-mass extinction events. Another known factor leading to decrease on lineages' body size is the release from predation pressure (Rozzi 2018; Wood & Erwin 2018). If mass extinction events extirpate large predators, the remaining prey species would evolve towards smaller sizes due to predatory release (Fig. 2).

The Lilliput effect is then important to enlighten Cope's rule because it reveals that mass extinction events are contingencies promoting local effects in the body size evolution of lineages. When the biota passes through a mass extinction event, a trigger is pulled, allowing some factors to reverse the trend in lineage's body size evolution. After mass extinction events, the status of the (i) predation pressure, (ii) food availability and, (iii) population density are conditions influencing the evolution of body size and producing temporal non-stationarity (Table 1). Although Cope's rule is pervasive at some degree across taxonomic and temporal scales, to avoid simplified and mistaken results these structuring factors must be considered when analyzing the overall pattern of lineages' body size evolution.

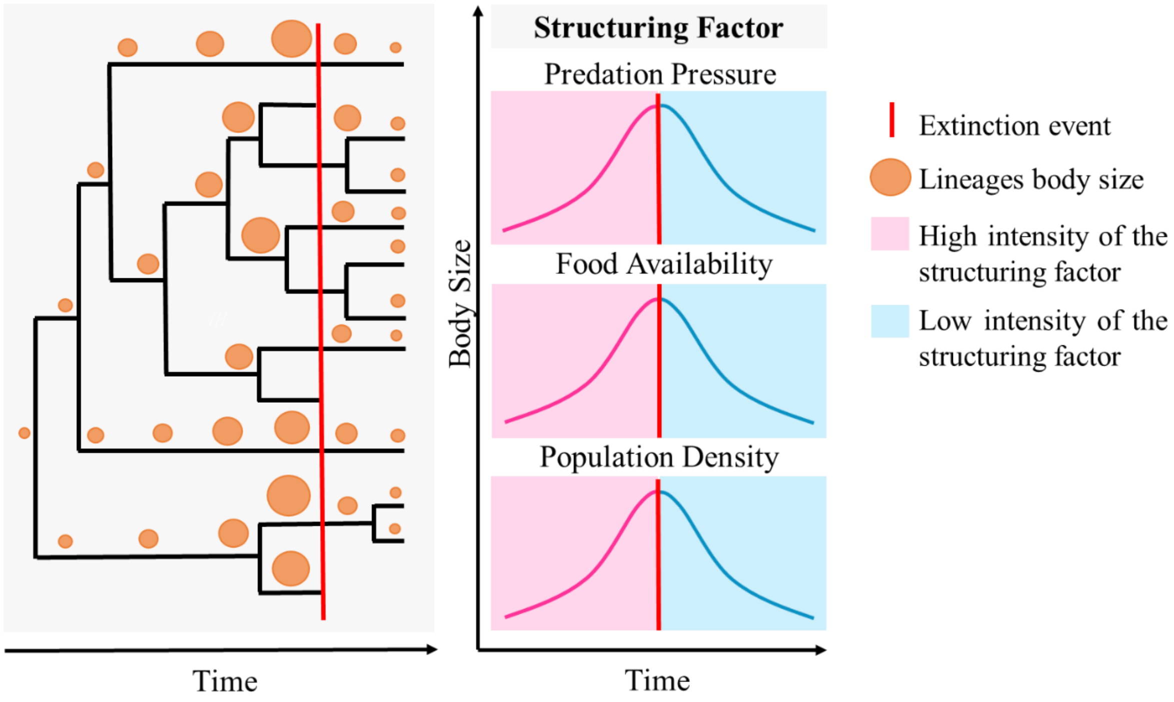


Figure 2. Mechanisms enabling temporal non-stationarity on Cope's rule. Cope deviates because structuring factors (predation, food availability and population density) operate in low intensity after mass extinction events, favoring the decrease of lineages body size along their evolution.

Confirming the dimension-tangled nature of non-stationarity, Cope's rule is commited by temporal (because it is not fulfilled at all time slices) and phylogenetic non-stationarity (because not all clades follows Cope's Rule). Cope's rule is a pattern generally accepted and emerged due to "partial direction errors", in which a general positive pattern is concluded, but with inverted temporal dynamics being obscured in global overviews. Ignoring the local effects within the temporal pattern of body size evolution does not only lead to mistaken generalizations, but also to stagnation of the theory because generalities mask low-level dynamics, which is crucial for us to improve the global model representing Cope's rule. This improved global model would be not only a model to confirm that lineages are becoming of bigger sizes, but also a global model to explain the dynamics of body size evolution, including growth, stasis and inversions.

Table 1. Factors reversing trends on lineages' body size evolution through time.

Structuring Factor	Non-stationary Prediction
Predation pressure	Species released from predation pressure (due to predator extinction after mass extinction events) might evolve towards smaller body sizes, while species undergoing predation pressure might evolve towards bigger body sizes as a mechanism of protection against predation.
Food availability	Species undergoing decreases in food availability (due to environmental changes during mass extinction periods) might evolve towards smaller body sizes to ensure population viability, while species inhabiting non-impacted high productive environments may achieve population viability without compromising the size of individuals.
Population density	Species suffering from drastic population declines might evolve towards smaller body sizes due to selection upon life-history traits such as earlier reproductive age, that allow fast population recovery, while stable populations will not undergo pressures selecting for these life-history traits.

4.2. Phylogenetic Non-Stationarity: clade-specific processes within phylogenies

The term 'phylogenetic non-stationarity' was proposed by Diniz-Filho et al. (2010) after adapting the spatial methods developed by Robert Sokal to deal with phylogenetic data (but see next section "spatial non-stationarity"; Sokal et al. 1998). Less than a decade ago, our research team was concerned with the problems of estimating niche conservatism without allowing parameter variation driving evolutionary changes across the phylogeny, called a phylogenetic stationarity assumption in the phylogenetic comparative methods. The goal was to evaluate if a 'global phylogenetic analysis' was able to provide accurate measures of the true niche evolution of some subgroup of species more prone to evolve their niche or remain in stasis. The exposure of the non-stationarity effect for niche evolution opened doors to other ways in which non-stationarity may affect evolutionary theories.

Although the terms 'non-stationarity' or 'local effect' are not commonly used, their concept have been extended to encompass the modified effect of one predictor variable upon the evolutionary responses of narrower clades (or groups of closely related species) inside phylogenies (Fig. 3). For instance, Rojas et al. (2018) recently found that the overall tendency of faster diversification for noctilionoids herbivore bats is biased by the great strength of correlation between these variable for the sub-family *Stenodermatinae*. The non-existent and reversed relationships between predictor and response emerging from other sub-families pertaining to the superfamily *Noctilionoidea* (comprising more than fifty percent of the superfamily) are obscured by the local effect from *Stenodermatinae*. This reversion is caused by ecological key innovations evolving from ancestral of each subfamily, such that the idiosyncratic evolutionary dynamics are not revealed in global analyses.

Reversion of patterns at lower taxonomic levels may also be caused by the spatial dimension. Species do not evolve in the same place, and the varying environmental conditions where they occur offer distinct selective pressures. Because the ecological meaning of a species' trait depends on the environmental pressures of the habitat in which it occurs traits should not equally affect the diversification dynamics of all species within a given clade. A simple classification of the landmasses between mainland and islands provides an example of how space may reverse relationships. Rojas et al. (2012) revealed that frugivory increases diversification rates of bat species occurring at the mainland, while it imposes a negative effect on diversification rates of bats occurring in islands. The authors link this reversal to the limited resources to frugivory on the islands.

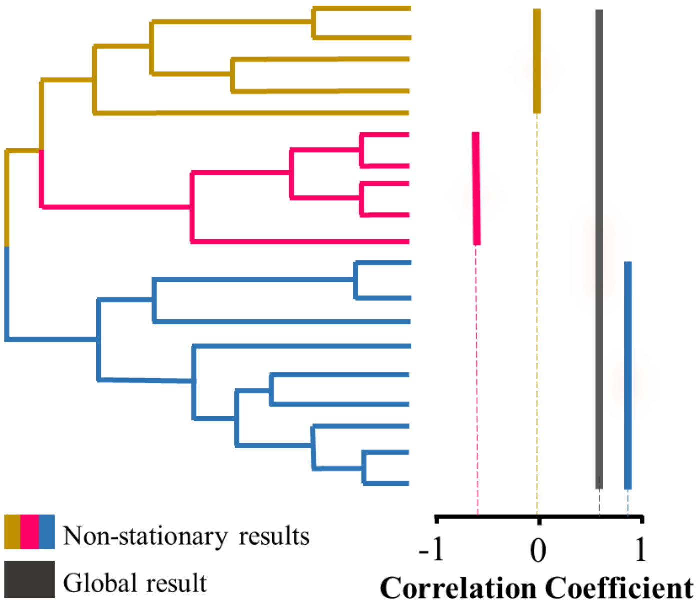


Figure 3. Non-stationarity in trait dependent theories of diversification. Correlation coefficients emerging from global analysis (gray line) do not mirror the true correlation coefficients of lower taxonomic ranks (blue, pink and golden lines).

The examples provided by Rojas et al. (2012 and 2018) constitute a piece of a larger macroevolutionary field, which is concerned with trait-dependent diversification theories. These theories search for differences between diversification rates of species exhibiting different traits that may explain why some taxa are so diverse, while others are so species-poor (Morlon, 2014; Scholl & Wiens, 2016). How species traits may enhance or depreciate their chance to survive date back to Darwin (Darwin 1859; Price *et al.* 2012). Nonetheless, only after the increasing availability of molecular phylogenies in the 1990s and the development of complex methods to estimate diversification rates, the studies aiming to correlate species traits with their macroevolutionary rates became abundant (Morlon 2014; Ng & Smith 2014). Examples of studies concerning trait-dependent diversification dynamics already comprise mutualistic interactions (Gómez & Verdú, 2012; Litsios *et al.*, 2012; Weber & Agrawal, 2014; Serrano-Serrano *et al.*, 2017), germinal development (Lambert & Wiens, 2013; Pincheira-Donoso *et al.*, 2013; King & Lee, 2015; Helmstetter *et al.*, 2016), antipredator defenses (Arbuckle and Speed 2015; Broeckhoven et al. 2016), diet (Barrett *et al.*, 2011; Wiens *et al.*, 2015; Davis *et al.*, 2016 and Rojas *et al.*, 2018; Burin *et al.*, 2016; Rojas *et al.*, 2012; Onstein *et al.*, 2017), and geographical occurrence (Moreau & Bell, 2013; Pyrcz *et al.*, 2013; Pyron, 2014; Rolland *et al.*, 2014; Antonelli *et al.*, 2015; Sánchez-Ramírez *et al.*, 2015; Rabosky *et al.*, 2018). Even though dozens of examples of trait-dependent diversification studies may seem many, they are whimsy compared to the thousands of studies published in the field of Macroevolution, and, unfortunately, non-stationarity is mostly neglected. This negligence imply that generalizations made in the trait-dependent diversification field may not reflect the real relationship between species' traits and their evolution.

Trait-dependent macroevolutionary theories are not the only ones suffering from a blinded attempt to globally explain the evolution of diverse taxa coming from diverse places. In the 1960s, the application of a statistical process of physics named Brownian motion (BM) into the macroevolutionary field gave rise to the first model of trait evolution (Cavalli-Sforza & Edwards 1967; Felsenstein 1984). The application of BM into combined phylogenetic trees and species' features estimates the evolution of the feature as a random process. After BM, some models of trait evolution considering non-randomness also emerged (e.g. Ornstein-Uhlenbeck (OU) - Hansen 1997; accelerating-decelerating (ACDC) - Blomberg et al. 2003; multi-peak OU - Beaulieu et al. 2012). Nowadays, the standard procedure when studying the evolution of a trait is to fit diverse models of trait evolution into the data and selecting the best-fit model. However, researchers simply assume BM with no model selection. Nevertheless, there is a chance that the mode of trait evolution has changed through the evolutionary history of a clade (Fig. 4). For instance, it is possible that body size of mammals passed through periods in which greater body sizes were selected for, and periods in which body sizes mainly changed during radiations, as well as periods of random evolution. Hence, choose a single best fitting model of trait evolution may not be a good estimate of evolutionary history of the entire clade. In addition, mode of evolution is an information required for other several phylogenetic comparative methods, such as PGLS (Phylogenetic Generalized Least Squares - Grafen 1989) and models to estimate ancestral character-state (Joy *et al.* 2016). Hence, generalization on the mode of trait evolution may potentially bias other phylogenetic estimates (i.e., Diniz-Filho et al. 2019).

The discussion about the implications of phylogenetic non-stationarity is still incipient and new methods accounting with reversion or annulment of patterns are just emerging (Castiglione *et al.* 2018). To account for phylogenetic non-stationarity within trait-dependent diversification theories, a phylogenetic weighted regression (PWR; Davies et al. 2018) was recently developed to account for local effects emerging from data subsets of a phylogeny. Although the methods to deal with phylogenetic non-stationarity are scarce, the approaches recently developed to estimate non-homogeneous macroevolutionary rates denote that the field already have developed much of the data

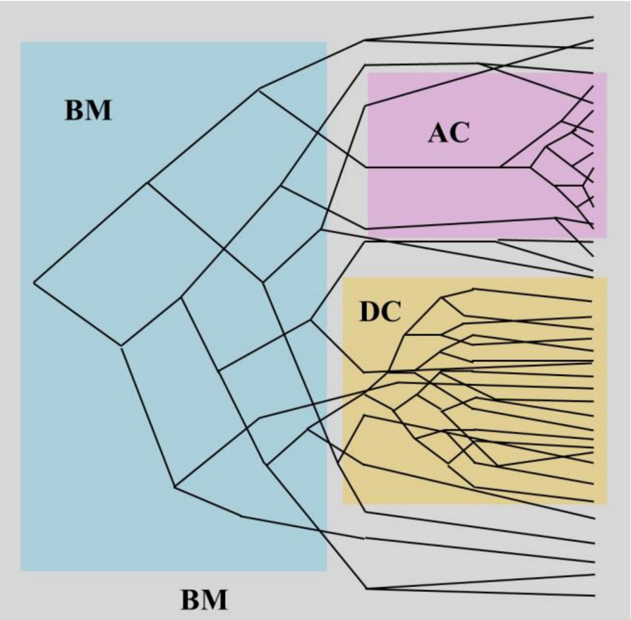


Figure 4. Phenogram exhibiting non-stationarity in the evolution mode of a given trait. Lower taxonomic ranks (golden and purple) and different time periods (blue) may show trait evolution distinguishing from mean mode of trait evolution estimated through a global analysis.

required to consider local effects across phylogenies. Prospective points giving attention to the development of non-stationary phylogenetic analyses must grow in the next years.

4.3. Spatial Non-Stationarity: local effects within spatial data

The simplest form of spatial non-stationarity is when a given pattern described across space is not homogeneous across the entire domain (Fig. 5). For instance, in 1847, Carl Bergmann proposed a theory to explain why endotherm species are usually larger at higher latitudes, called Bergmann's rule. Afterward, Bergmann's rule was extended to explain the inverse latitudinal gradient in ectotherm body sizes; species becoming smaller with increasing latitude (Muñoz *et al.* 2014b).

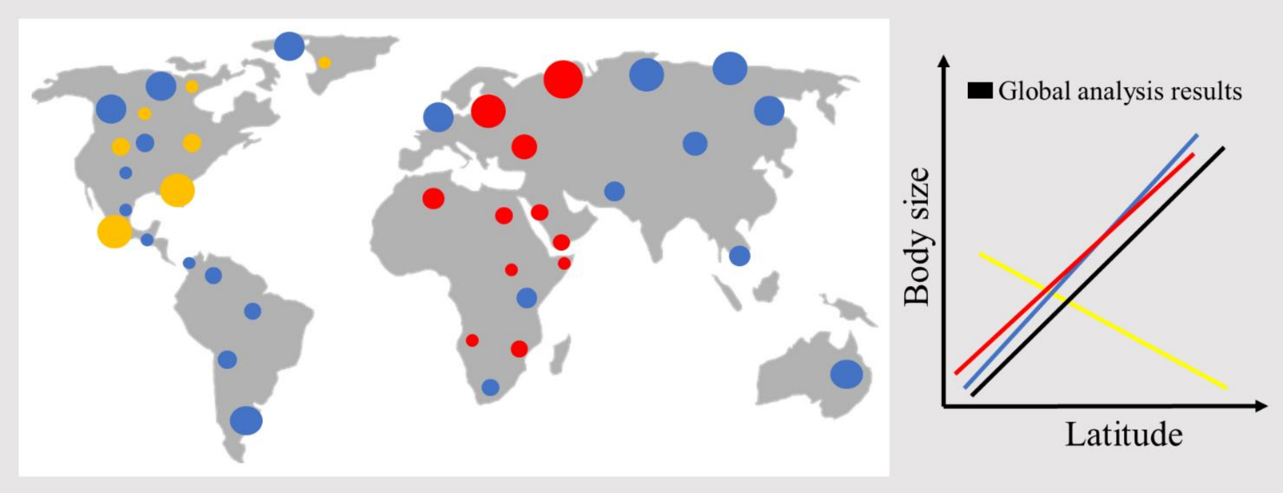


Figure 5. Spatial non-stationarity in Bergmann's rule. Most endotherm species (red and blue circles) show larger individuals in higher latitudes, while ectotherms (yellow circles) usually decrease their body size in high latitudes. A global analysis (black regression line) hide opposite patterns due to high number of species following Bergmann's rule.

One of the most evoked explanation for the reversion of Bergmann's rule is the existence of a threshold above which the relationship between latitude and body size reverses. High and cold latitudes do not select for ectotherm body sizes above a certain value due to the requirement of large periods of solar exposure required by large ectotherms, aiming to increase body heat (Ashton & Feldman 2003; Olalla-Tárraga *et al.* 2006). Besides reversal in thermal dynamics, the fulfillment of Bergmann's rule also depends on how life-history traits are affected in cold regions. For instance, individuals' growth rate decreases in cold temperatures and may lead to smaller adult sizes if the negative effect of temperature does also reach the survivor rate (Muñoz et al. 2014a). Finally, the spatial pattern on species body size may also depends on hibernation periods. Long hibernation periods cause high mortality of small individual with smaller capacity of fat storage in cold areas (Ashton 2001). Notwithstanding, non-hibernating or species displaying short periods of hibernation may be released from this selective pressure towards larger body sizes.

Many contingencies may lead to the reversion or annulment of the perceived global pattern. Actually, explanations for inverted Bergmann's rule has already claimed to be idiosyncratic (Shelomi 2012). Nevertheless, Queiroz & Ashton (2004) found that Bergmann's rule is ancestral for tetrapods and that phylogenetic signal is strong among species with classical or inverted Bergmann's rule. Queiroz & Ashton's (2004) results are crucial for us perceiving that species following opposite pattern (usually clustered in the phylogenies) probably conserved the body size throughout the spatial distribution where their common ancestor occurred, which may have reversed from Bergmann's rule into an inverse pattern due to some ecological innovation. The findings of strong phylogenetic signal do not mean that factors determining Bergmann's rule, or its inverse, are neither so idiosyncratic nor are globally identifiable, but require better understanding the theory behind thermal equilibrium in ecto- and endotherms. Indeed, this strong phylogenetic signal is the evidence of phylogenetic non-stationarity on Bergmann's rule.

The attempts to create a general pattern of body size distribution along the Earth's surface prevents us from perceiving factors responsible for the dynamics of species' spatial organization. Is there a theory general capable to explain the global distribution of species body size? To answer this question, currently missing variables must be identified and then added to complex and realistic models. As formulated until today, Bergmann's rule leads to direction error for species with opposite patterns and false positive results for groups lacking correlation between predictor and response variables.

5. Maintenance of processes as the cause of non-stationarity

Counter-intuitively stationary (maintenance) processes may also generate non-stationary patterns. Until now, we have discussed about contingencies allowing groups to deviate from the generality and promote non-stationarity on the patterns. It seems intuitive that the non-stationarity on the processes leads to non-stationary patterns. However, the maintenance of processes (i.e., stationary processes) may also lead to non-stationarity on the patterns. Indeed, stationary and non-stationary patterns and processes may be combined in a complex interplay framed in the Box 2.

The latitudinal diversity gradient (LDG) describes the spatial global pattern of species richness, in which species are more numerous at lower latitudes and becomes less numerous towards high latitudes (Kinlock *et al.* 2017). More than 30 not mutually exclusive theories aiming to explain the LDG were already developed (Brown 2014) but, in the "*integrative theory for biodiversity patterns*" of Wiens and Donoghue (2004), the role of the center of origin and niche conservatism were defined as main pillars to explain why the tropics are so species-rich. The tropics are older and more stable, so had more time to accumulate species through speciation events than temperate or polar regions. The tropical species were trapped due to the maintenance of ancestor's niche and the absence of features allowing migration to higher latitudes. Although many clades do exhibit higher species richness in tropical regions, there are many other clades exhibiting inverted pattern (more species in temperate areas) or no pattern at all (absence of relationship between latitude and species richness). But what could cause species to peak outside the tropics? This time, the same factors and maintenance of processes are responsible to generate non-stationarity in the pattern.

Imagine a species evolving traits to colonize high latitudes. By niche conservatism, descendants of that colonizer species will maintain the ancestor niche and have their diversification trapped on high latitudes, enabling the accumulation of species' in the temperate region via speciation events and promoting inverted LDG within its descendant clade (Stephens and Wiens 2003; Fig. 6). Hence, inverted LDGs may also be caused by the same factors and processes causing the common-type LDG. Inverted LDGs emerge through niche conservatism of ancestors originated at temperate regions, while common-type LDGs emerge through niche conservatism of ancestors originated at the tropics. The importance of the center of origin and subsequent niche conservatism has already been corroborated to innumerous common-type and inverted LDGs as well, such as the inverted species richness of turtles (Stephens and Wiens 2003), snakes (Pyron and Burbrink 2009), freshwater arthropods (Morinière *et al.* 2016), Holarctic treefrogs (Smith *et al.* 2005) and fungi (Sánchez-Ramírez et al. 2015). [Note that in this case with phylogenetic niche conservatism (and Bergmann's rule above), a non-stationarity at the phylogenetic level reflects in distinct LGDs for these groups, and may appear also as spatial non-stationarity].

The effort to develop a theory capable to explain the spatial pattern of species richness along the Earth's surface may be higher within macroecology. Notwithstanding, when efforts are based on global analyses, our results are committed by both direction error (for groups exhibiting inverted LDG - Fig. 1E) and type I error (for groups lacking correlation between latitude and species richness – Fig. 1B). Furthermore, global analyses mask the importance of the structuring factors in shaping the distribution of species. Biodiversity is generated and maintained by a complex machinery in which the functionality of an individual piece is controlled by another piece. Generalizations may represent different pieces of this machinery, but scientists will not be able to fit them together if they do not know the glue (or broader theory) capable to join them. We claim that attempts to develop a Synthetic Theory for the LDG would not succeed if the ones who develop them ignore the role of non-stationarity.

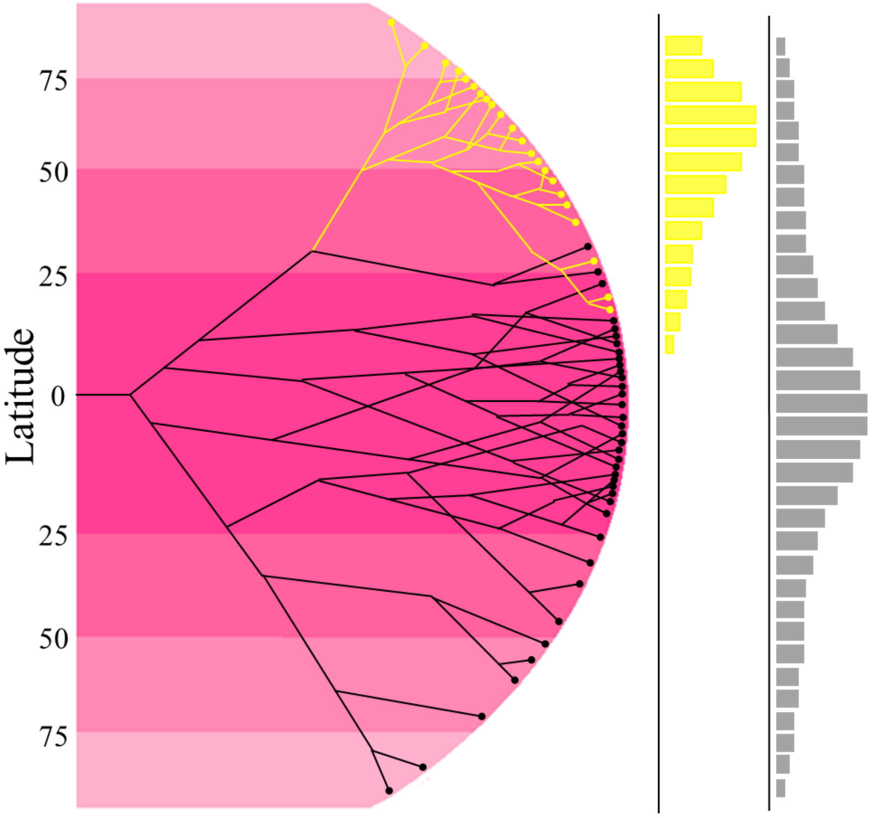


Figure 6. Patterns of the latitudinal diversity gradient. Most lineages are trapped in the tropics due to the conservatism of ancestor's tropical niche, enhancing the common-type LDG emerging from global datasets. Ecological innovations allow lineages to colonize cold regions (yellow lineages) and triggers pattern inversion due to the conservatism of the temperate ancestor's niche and subsequent species accumulation in high latitudes through speciation events. Distribution of richness frequencies are shown in gray for global datasets and yellow for local datasets. Adapted from Wiens and Donoghue (2004).

6. Non-stationarity within stationarity

Can scientists be free from the non-stationarity if they focus on small-scale stationary patterns? Stationary patterns do not have a unique explanation. Hence, even when the patterns are stationary, non-stationarity plays its role on the causes (Box 2). For instance, groups exhibiting higher species richness in the tropics may do so because the precipitation is higher, because the temperature is higher, because the regions is older, or because of any one of the more than thirty existing theories (Brown 2014). Does it mean that the total absence of non-stationarity a utopia? If non-stationarity is ubiquitous, even when generalizations do represent the overall, we would always lose a piece of the explanation for nature's dynamic, which is only revealed by the detection of missing variables.

7. The other side of the coin

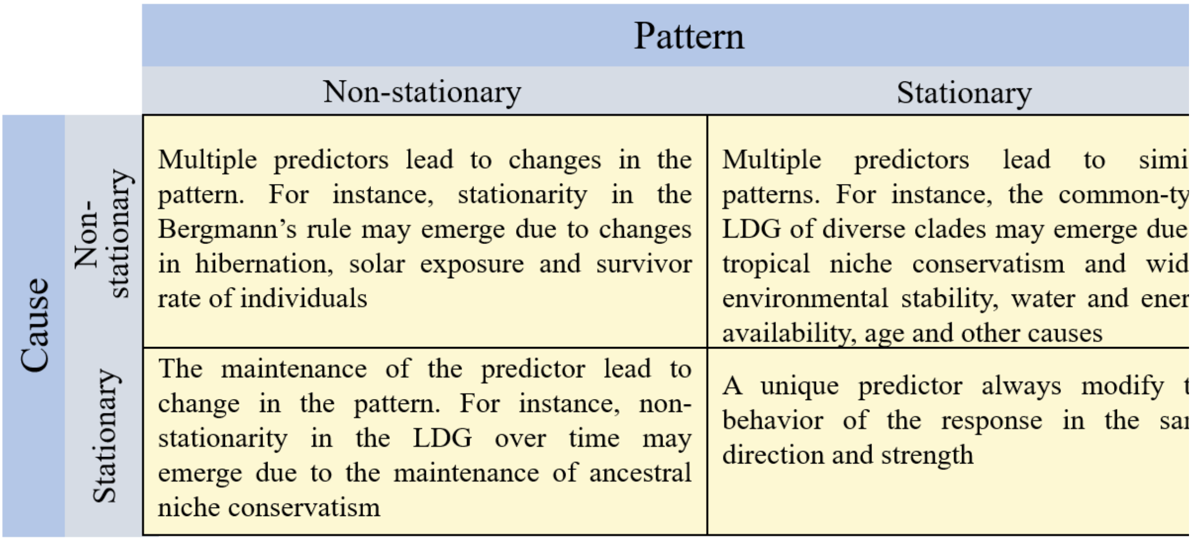
Generalizations are not the kill or cure to science. Although the many mistaken results and loss of information led by generalizations, scientists cannot neglect the importance of generalizations to science. When the knowledge about a system is short, as in the beginning of science, general theories about the system's functioning is the first and most informative step to uncover its overall features. The lack of information about unknown systems would make the formulation of non-stationary theories only speculative. Thus, precursor scientists followed generalizations as the most evident and fitting path to understand nature. However, while scientists followed this path, contradictions started to arise.

Conflicting results naturally appear together with sampling effort. When these contradictions emerged, scientists and philosophers begun to discuss their role in the progress of science. For most philosophers, the emergence of contradictions were the triggers for science to make progress. In the Popperian scientific method, initial theories are replaced by theories posteriorly corroborated (Godfrey-Smith 2021). Nevertheless, non-stationarity was not under the spotlight and to conciliate contradictions were not the philosopher's focus. Nowadays, scientists need to recognize non-stationarity's most role of binding together different theories that are initially seen as inconsistencies and uncover the dynamic of a system instead of its overall features. After all the benefits generalization has brought to scientific studies, non-stationarity is the natural way to continue the progress in science.

Box 2 Non-stationarity in the patterns, processes and multiple dimensions

Maybe because patterns are easier and faster to see than processes happening in nature, studies discussing non-stationarity usually concern patterns. However, non-stationarity may also exist in the processes causing such patterns. Although not explicitly, the interplay among stationarity and non-stationarity along the patterns and their causes has been thought in four frameworks. In the first framework, many triggers reverse patterns, meaning that factors or variables changing in nature lead to non-stationary patterns. One example for this framework is the Bergmann’s rule, in which inversion and absence, as well as the common Bergmann’s pattern, may be explained by different causes, such as hibernation, solar exposure and survivor rate of individuals. In the second framework, instead of studying the variety of patterns and their processes, the studies are focused in the multiple triggers of a unique pattern, meaning that multiple variables may be responsible for one stationary pattern. For instance, the higher species richness in tropical areas may emerge in response to several variables, such as tropical niche conservatism and width, environmental stability, water and energy availability, age and other causes. The third and rarely used framework consists in a stationary cause leading to non-stationary patterns. In other words, the maintenance of a process is responsible for inverted and uncommon patterns. For instance, the temporal non-stationarity in the latitudinal diversity gradient may be caused by the maintenance of ancestral niche conservatism along geological time. These three frameworks embrace most of the achievement of the researches. Notwithstanding, the fourth framework is the target of most studies: a stationary driver leading to a stationary pattern. This fourth framework mirrors the attempt to find a pattern governed by only one cause. But, is the existence of this undeviating effect of a trigger plausible?

The patterns and processes may not pertain to the same dimension. For instance, Bergmann`s rule and its deviations are, by definition, spatial patterns. However, the inversion of this spatial pattern in phylogenetically related species denotes that the non-stationarity in the



		Pattern	
		Non-stationary	Stationary
Cause	Non-stationary	Multiple predictors lead to changes in the pattern. For instance, stationarity in the Bergmann's rule may emerge due to changes in hibernation, solar exposure and survivor rate of individuals	Multiple predictors lead to simi patterns. For instance, the common-ty LDG of diverse clades may emerge due tropical niche conservatism and wid environmental stability, water and ener availability, age and other causes
	Stationary	The maintenance of the predictor lead to change in the pattern. For instance, non-stationarity in the LDG over time may emerge due to the maintenance of ancestral niche conservatism	A unique predictor always modify t behavior of the response in the sai direction and strength

phylogenetic dimension overruns to the spatial dimension, causing non-stationarity in the Bergmann's rule. In this example, the spatial non-stationarity in the pattern exists because different phylogenetic groups are affected by the environment in the same away. The non-stationarity in the Bergmann`s rule is a clear example of how non-stationarity is pervasiveness and tangible in the causes and patterns.

9. Uses and misuses of non-stationarity

Local regression approaches are a complement to global regression modeling (Jetz et al. 2005), and their potential depends on the researcher. Although the increasing usage of analyses developed to account with non-stationarity, there are many misuses of non-stationarity concept and methods. Mostly after the development of Geographically Weighted Regression (GWR, Fotheringham 2002; see also Barreto et al. 2019 and Coelho et al. 2019 for some empirical applications in macroecology), several studies have been published with the term non-stationarity without bringing any enlightenment about why and what is generating local effects within the study system. Macro scales are marked by non-stationarity and the existence of local effects should be an assumption instead of a study's main result. The misuse of non-stationarity leads to stagnation because these studies are not enhancing our knowledge about how nature works. Here, we should reaffirm the importance of disentangle the term non-stationarity from the meaning of simple inconstancy. Non-stationary study systems are the ones whose structuring factors are identifiable. To rescue non-stationarity's full concept might be the path to encourage researchers to go beyond of purely detecting non-stationary results and reach more realistic overall explanations for macroecological phenomena.

10. Prospects for macroecological and macroevolutionary theories

The centuries of scientific research provided information about the dynamics of several natural systems. Thereafter, science can make progress towards the understanding of how these pieces are fitted together through the lights of non-stationarity. Although the non-stationary analyses must receive even more attention, the available analytical tools are helpful to bring together different theories for the same pattern that may be pieces of the same true general theory.

Finally, we can answer if our search for general patterns is making us blind: It depends". Through the centuries of scientific research, the efforts were focused on attempts to generalize aiming to explain as much data as possible, and efforts did not go further that. This absence of attempts to validate global results led to a bifurcation in which one of the roads to follow finishes in error and the other finishes in unfulfilled potential. The error road was followed every time a researcher achieved an average relationship between the predictor and response variables that is inexistent in the real world. The unfulfilled potential road was followed every time the estimated average relationship truly reflects the relationship for most of the groups within the real world, but information about unfitting groups is lost. This lost information along decades of science would have enabled the identification of missing variables required to enhance our global models and achieve mathematical models representing the system's dynamics instead of only individual theories. Notwithstanding, the incomplete knowledge road had crucial importance to science because it enabled scientists to accumulate knowledge and understand how many different pieces of the biodiversity machinery works.

The search for general patterns and theories may blind us every time they follow the error road and consist in a veil overshadowing our vision every time we follow the unfulfilled potential road. Even though not always totally blinded, scientists have never seen clearly only through the lenses of generalization. Considering non-stationarity is crucial to avoid the solidification of unrealistic theories and most importantly, it is crucial for identify missing variables reversing or annulling patterns, which are the first clues to build synthetic theories of biodiversity. It may be necessary to lose focus on the generality aiming to correctly generalize.

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CAPÍTULO 2

A geographic perspective on the evolution of specialism and generalism

Larissa Pereira Lemes & Elisa Barreto

ABSTRACT

Together, macroecology and macroevolution can solve contradictions that emerges when seeing these fields in isolation. Here we merge the theoretical basis of the ‘latitude-niche breadth hypothesis’ (LNB – a theory with lacking mechanisms) and the ‘generalist-to-specialist hypothesis’ (GTS – a theory with many objections) to find that the evolutionary advantages of generalist vs specialist lineages depend on geographic region where it occurs. The GTS could not explain why some lineages are still evolving towards generalism since generalist species lose competiton when facing specialist species. We clarify that the GTS explains only lineages evolution in temperate regions where species must track and couple with variation in resource availability. Whereas the “specialist-to-generalist hypothesis’ (STG) explains lineages evolution in the tropics. Where resources are plentiful, it is less advantageous to be highly competitive and lineages may enlarge their niches. Together, the STG and the GTS compose what we term the “Region-dependent niche evolution” theory. The LNB still lacks a mechanism explaining tropical narrower niches. However, the LNB seems to be part of a higher-level dynamic where the modern pattern of narrower species niches is erased by evolutionary trends. Finally, we propose the ‘Specialization cage’, an original theory for the species richness latitudinal gradient. We argue that to bind macroecological and macroevolutionary theories may provide us clues to find missing variables in the theories and make progress in the fields.

Keywords: Specialism, generalism, niche breadth, dietary evolution, ‘latitude-niche breadth hypothesis’, ‘generalist-to-specialist hypothesis’, ‘Region-dependent niche evolution’, ‘Specialization Cage theory’

INTRODUCTION

The species richness latitudinal gradient is possibly the most studied spatial pattern in macroecology, with more than 30 proposed theories to answer "*Why are there so many species in the tropics?*" (Brown 2014). One of these theories is named 'latitude-niche breadth hypothesis' (MacArthur 1972; from now on quoted only as LNB) and has fascinated researchers since its proposition. The LNB proposes that the tropics are more species-rich because the greater environmental stability in tropical regions enables greater stability of tropical populations and consequent narrowing of species niches (Price 1991; Vázquez & Stevens 2004). This stronger niche packing at low latitudes would facilitate species coexistence due to small niche overlap and reduced competition, that otherwise could have brought species to extirpation (Forister *et al.* 2015; Gainsbury & Meiri 2017). Ultimately, facilitated coexistence would lead to greater species numbers. The assumptions to which the LNB is anchored have been widely accepted among scientists despite rarely being tested and not always supported (Vázquez & Stevens 2004; Schleuning *et al.* 2012).

Along with the emergence of population data, the assumptions of the LNB begun to be tested and neglected. Greater tropical variation in precipitation, which is a powerful boundary for tropical populations dynamics (Hawkins *et al.* 2003; Pearce-Higgins *et al.* 2015), weakens the first assumption of greater environmental stability in tropical region (Vázquez & Stevens 2004). The LNB's second assumption is also weakened by the scarcity of evidence linking greater stability of tropical populations to narrower species niche breadth (Vázquez & Stevens 2004). Despite the lack of evidence to support the LNB assumptions, the idea that species niche breadth triggers the species richness latitudinal gradient is still strong in macroecology. In fact, many of the more than 30 theories for the latitudinal gradient in species richness have the species niche breadth in its basis. Could the LNB be correct about in the mechanism shaping species richness (i.e., niche breadth) even when the assumptions are not supported (i.e., environmental and population stability)?

Another key assumption of the LNB is the negative relationship between species niche breadth and species efficiency in processing individual resources (Vázquez & Stevens 2004). Species with narrow niches (i.e., specialists) are expected to exploit individual resources more efficiently, making them superior competitors than species with large niches (i.e., generalists). This assumption in MacArthur's theory gave rise to new evolutionary hypotheses that may have played a role in the reinforcement of the niche breadth as driver of the species richness latitudinal gradient. Although the first use of the niche breadth-efficiency trade-off to test evolutionarily explicit hypotheses is hard to track, one precursor work of Futuyma and Moreno (1988) about *The Evolution of Ecological Specialization* is based on MacArthur's assumption to explain lineages evolutionary direction.

Futuyma and Moreno (1988) referenced MacArthur's statement "the jack of all trades is the master of none" to explain why lineages evolve towards specialism (or narrow their niches). This statement means that generalism does not confer advantages for species because they do not acquire energy efficiently from the resources used (Sexton *et al.* 2017). Therefore, generalist species would evolve towards niche narrowing due to gains at energetic acquirement efficiency and competitive superiority. This macroevolutionary theory is known as the 'generalist-to-specialist hypothesis' (Futuyma and Moreno 1988; hereafter quoted as GTS) and enlightens a possible mechanism promoting niche narrowing in the tropics, irrespective of climate or populations stability. Namely, that stronger competition push tropical lineages towards specialism (Carscadden *et al.* 2020). Niche narrowing may not be an outcome of environmental and populational stability, as stated by MacArthur, but a pattern emerged from advantages achieved through competitive superiority of more specialist species when facing generalist species. A consequence of this run is higher coexistence between specialists and consequent higher species richness in the tropics. Conversely, alleviated competition in temperate geographic regions would not push lineages towards niche narrowing.

The GTS provides the macroevolutionary mechanism enabling the macroecological LNB to still be a valid theory for the species richness latitudinal gradient. Likewise, the macroecological theory does also sheds light on the macroevolutionary theory. Both LNB and GTS use ecological processes to explain niche narrowing, although in different time scales. Hence, in a certain way, the GTS is a projection of MacArthur's ecological theory at the macroevolutionary scale. Therefore, similarly to MacArthur's LNB, the GTS may also depend on the geographic region (tropical versus temperate). As niche packing results from higher competition in species-rich regions (tropical regions), tropical lineages would be more prone to evolve towards specialism. Conversely, alleviated competition at species-poor regions (temperate regions), together with extinction vulnerability of specialist species occurring at locals with high paleoclimate variation, must allow lineages to evolve towards generalism. This tropical/temperate-dependent scenario for the GTS has potential to help unravel the generalism-specialism macroevolutionary conundrum that has been under debate for more than 150 years (Price *et al.* 2012). If species are evolving towards specialism because of the competitive superiority it confers, why many lineages had their niches enlarged through their evolutionary history? The key for this conundrum may be the different regions in which these lineages are evolving, that are, surprisingly, out of the focus of the generalism-specialism conundrum research.

Niche is a multidimensional entity in which several features, such as species habitat, physiology, environmental conditions and biotic interactions are involved (Carscadden *et al.* 2020). To measure species' full niche is a desire but still a chimera. Hence, studies concerning species niche commonly uses axes that best represent species ecology (Sexton *et al.* 2017). The dietary niche has been widely used as the chosen dimension of the species niche because it mirrors interspecific interactions, which is a major proxy for competition (Sexton *et al.* 2017). Through competition, populations or individuals of a species are pressured to displace their characters and become more prone to be isolated and evolve (Pigot 2013). Hence, dietary niche breadth is a potential driver of species evolution through competition and a proper axis of species niche to test the LNB and tropical/temperate-dependent GTS, since the mechanism of these theories is based on competition. Data on species diet has become more available in the last years, mainly for Aves, which is one of the most studied groups. Moreover, data sets on Aves include a whole-clade phylogeny (Jetz *et al.* 2012), which is crucial for the study of niche evolution. Therefore, Aves dietary niche breadth represents a good model system for elucidating the validity of the LNB and the dependence of the GTS on the geographic region, and more broadly, establish the interplay between these two theories.

In the last decades, approximating macroecological and macroevolutionary theories has improved our ability to answer biological questions (McGill *et al.* 2019) because, through the approximation of the real word's complexity, in which ecology and evolution interplay with each other, it enables us to include details previously unseen in our theories. The aim of this study is to validate both the LNB and the GTS through the coalescence of their theoretical basis. To verify the validity of the ecological LNB, even with the unfulfillment of its core assumptions (i.e. environmental and population stability), we tested if bird tropical lineages are narrowing their dietary niche breadth along their evolutionary history. We hypothesize that the direction of lineage's evolution depends on the geographic position of the lineage, with tropical lineages evolving towards specialism, and temperate lineages evolving towards generalism. The fulfillment of the same hypothesis does also support the validity of the evolutionary GTS as contingent to the geographic region. Hence, the 'generalist-to-specialist-hypothesis' would better describe the evolution of tropical bird lineages, while a 'specialist-to-generalist-hypothesis' would be a best approximation for the evolution of bird lineages occurring at temperate regions. However, we found the opposite, with tropical lineages evolving towards generalism while temperate lineages evolve towards specialism. This result weakens even more the LNB and supports an original theory for the species richness latitudinal gradient.

MATERIAL AND METHODS

To test if tropical species are evolving towards specialism in their dietary niche, we used three Aves datasets: (*i*) food networks, (*ii*) phylogenetic hypotheses and (*iii*) species distribution maps. Food networks were required to compute species dietary niche breadth, which were used, together with the phylogenetic hypotheses and phylogenetic comparative methods, to estimate species direction of evolution. Species distributions were required to compute its location (i.e., tropical or temperate) and range area, aiming to verify if dietary niche enlargement is due to range expansion along lineages' evolutionary history, what could bias the conclusions.

1. Dietary niche breadth

Dietary niche breadth is commonly estimated using dietary guilds (such as carnivores, omnivores and herbivores). Notwithstanding, categorical classifications for species diet may not mirror niche breadth, as species pertaining to the same guild may have the number of food resources varying from few to several resources. For instance, an herbivore may be specialized in one plant species, or consume numerous species. Hence, the classification of dietary niche breadth into guilds may not carry information on how specialized a species is. To avoid this issue, we estimated a continuous measure of dietary niche breadth based on ecological networks. We collected data on biotic interactions of Aves from the Web of life: ecological networks database (Fortuna *et al*. 2014; available at http://www.web-of-life.es/) and counted the number of interactions established by each bird species (or the number of food resources consumed by each bird species) as the species dietary niche breadth. We attained data for 523 bird species.

2. Phylogenetic data

We used the Aves phylogenetic hypothesis from Jetz *et al*. (2012), encompassing phylogenetic uncertainty through the usage of 1.000 randomly selected phylogenies. The increasing sequencing of species' genetic code in the last years has raised doubt about the reliability of phylogenies constructed based on species traits or the insertion of species lacking genetic data. Jonathan Losos, in his book "Improbable Destinies" (2017), gave numerous examples of how we have been deceived with species relationships when based on their morphology because the environment may build very similar species through convergent evolution, even though they are not phylogenetically related. Hence, we excluded the species lacking genetic data from the 1000 phylogenetic hypotheses. Finally, we pruned the 1000 phylogenies to include solely the species for which we have niche information, which resulted in 448 species of birds.

3. Distribution maps

We used the Aves distribution maps from BirdLife International and NatureServe (2015; available upon request at http://datazone.birdlife.org) in the *R software* (R Core Team 2018) to estimate species location at the globe and species range size. We used the boundaries of species distribution maps to classify species location as tropical (located within the tropical belt [between c. 23° north and c. 23° south]), temperate (located outside the tropical belt) and intertropical (distribution overlapping both tropical and temperate region). Lineages may be enlarging or narrowing their dietary niches in response to changes in species ranges size along their evolutionary histories. To control for this confounding factor, we also used species distribution maps to compute the size of their distributional areas [using the function *area()* from the *R package raster* (Hijmans 2017)] and to verify the existence of correlation between lineages dietary niche breadth evolution and the evolution of species range sizes. For a more enlightening discussion about the general dependence of species range and niche, see Slatyer et al. (2013).

4. Direction of evolution

We combined species dietary niche breadth with the 1000 pruned phylogenetic hypotheses and used phylogenetic comparative methods to reconstruct the ancestral state [using the *R package phytools* (Revell 2012)], while encompassing phylogenetic uncertainty. The lineages direction of evolution was defined based on the difference between the reconstructed niche breadth of the most recent common ancestral and the niche breadth of species at the tips. Species that interact with more species than the estimated for their ancestral were defined as evolving towards generalism, while lineages with more biotic interactions near the tree node than in the tips were defined as evolving towards specialism.

5. Correlation between niche breadth and range size

We used species dietary niche breadth and range size together with the 1000 pruned phylogenetic hypotheses and a phylogenetic method named *RRphylo* (Castiglione *et al.* 2017) to estimate rates of trait evolution through the phylogenies, separately, for dietary niche breadth and range size. *RRphylo* is based on phylogenetic ridge regression and estimates rates for each branch of the phylogeny (Castiglione *et al.* 2017). Hence, we obtained the branch-specific rates for dietary niche breadth evolution and correlated them with the branches-specific rates for range size evolution to verify the correlation between these two traits along Aves evolution. We accounted for the phylogenetic uncertainty by repeating the correlation 1000 times, for each phylogenetic hypothesis, in which we used the evolutionary rates for niche breadth and range size estimated through the same phylogeny in each iteration.

6. Statistical analysis

To verify if tropical lineages are narrowing their dietary niches while temperate lineages are enlarging their dietary niches, we used the lineages' direction of evolution (towards specialism and towards generalism) and location at the globe (tropical, temperate or intertropical) to perform a chi-squared test as the statistical analysis. The method, from the data collation to final analyses, is represented by the flowchart at figure 1.

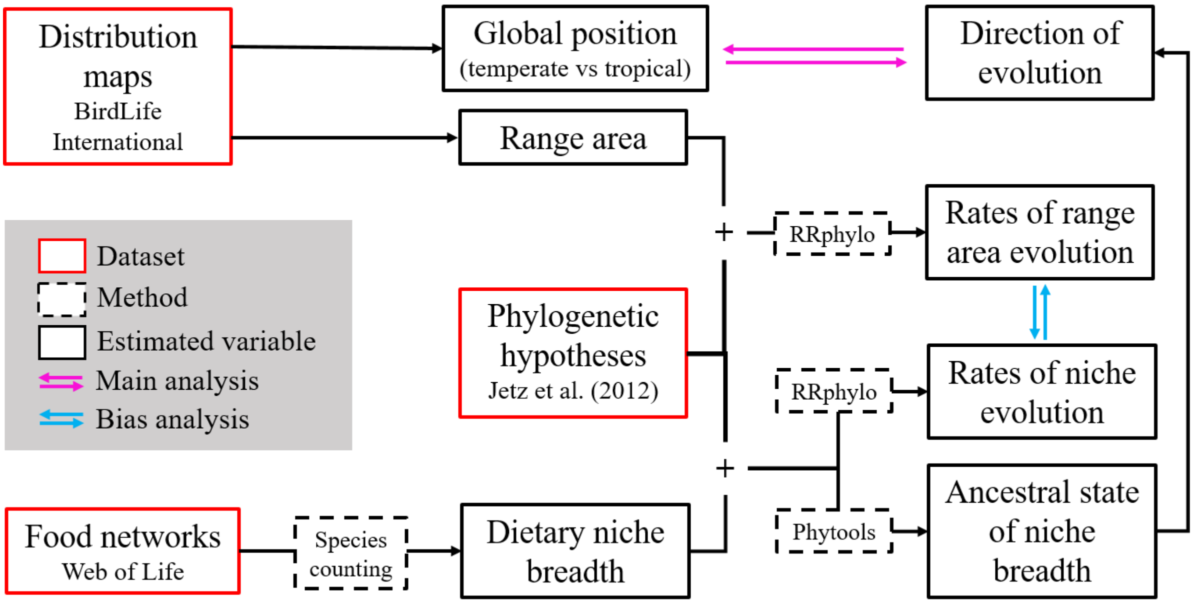

Fig. 1. Compiled datasets (red boxes) were used to estimate secondary variables (black boxes) through several methods (dashed boxes), which in turn are needed to verify the hypothesis of this study (represented by the double pink arrow) and possible biases in the results emerging from evolutionary correlation between rates of range area and niche breadth evolution (represented by the double blue arrow). Distribution maps were used to estimate species global position and range area, which in turn, was used together with 1000 phylogenetic hypotheses to estimate rates of range evolution through the usage of RRphylo package in the R software. Food networks were used to estimate dietary niche breadth, which in turn, was used together with the same 1000 phylogenetic hypotheses to estimate rates of niche evolution also through the usage RRphylo, and ancestral state of niche breadth through the usage of phytools R package. Rates of range area and niche breadth evolution were correlated to verify for potential biases, and species global position was tested as predictor of lineage's direction of evolution to verify if tropical lineages are mainly evolving towards specialism.

RESULTS

Correlation between dietary niche evolution and range size evolution were non-significant for all the 1000 phylogenetic hypothesis (mean p-value ± SD: 0.40 ± 0.24; mean r-squared ± SD: -0.03 ± 0.24). Hence, changes in lineages' dietary niche do not occur in response to changes in their range sizes. Concerning the hypothesis of lineages direction of evolution linked to the species geographic position, the statistical analysis showed a significant relationship between the direction of dietary niche evolution and the region in which the species occur (mean p-value ± SD: 0.02 ± 0.00; mean x-squared ± SD: 7.44 ± 0.07). Nevertheless, the relationship between direction of niche evolution and geographic location is the opposite of the predicted, with tropical lineages evolving towards generalism whereas temperate lineages are evolving towards specialism.

Table 1. Expected and observed frequencies for generalist and specialist lineages evolving in each global location

			Lineages' direction of niche evolution	
			Specialism	Generalism
Global position	Tropical	Observed	87	87
		Expected	103	70
		Residual (n)	-15	17
		Residual (%)	-15.5	24.2
	Temperate	Observed	27	8
		Expected	20	14
		Residual (n)	7	-6
		Residual (%)	35	-42.8
	Intertropical	Observed	135	103
		Expected	141	96
		Residual (n)	-6	7
		Residual (%)	-4.2	7.29
	Total	Observed	249	198
		Expected	264	180
		Residual (n)	-15	18
		Residual (%)	-5.6	10

Table 1 shows the observed number of lineages enlarging and narrowing their dietary niches in each region and the distribution of lineages evolution expected by a null relationship. Lineages evolving towards specialism are under a deficit of fifteen percent in the tropics, while they exceed the null expectation in thirty-five percent in the temperate regions. Concerning lineages evolving towards generalism, they are twenty-four percent above the expected in the tropics, and under a deficit of forty-two percent in the temperate regions.

The contrast between the number of lineages evolving towards generalism and specialism in each cell of the globe is illustrated at Figure 2. The Generalism/Specialism ratio is calculated as the number of lineages evolving towards generalism divided by the number of lineages evolving towards specialism in each cell, meaning that cells with values greater than one shelters more lineages evolving towards generalism. Conversely, cells with values smaller than one shelters more lineages evolving towards specialism. Some tropical regions harbor twelve times more lineages evolving towards generalism than lineages evolving towards specialism, while some places in the temperate region harbor eight times more lineages evolving towards specialism than lineages evolving towards generalism.

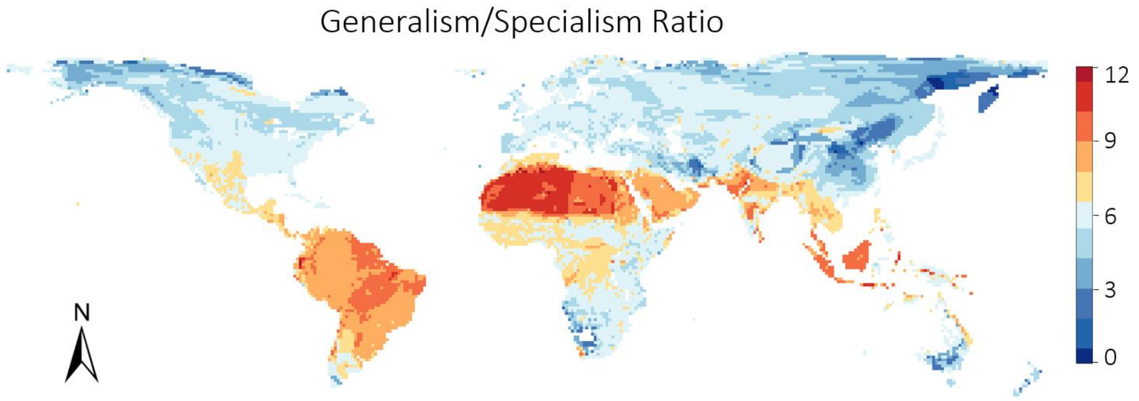

Fig. 2. Mapping of local discrepancies between the number of towards generalism and towards specialism lineages. Hotter colors indicate places harboring more species evolving towards generalism, while colder colors indicate places harboring more species evolving towards specialism.

DISCUSSION

Does the LNB still stand?

MacArthur proposed the LNB aiming to explain why the tropics are so species-rich assuming stability of tropical populations to predict species niche narrowing and consequent greater coexistence between tropical species. Nevertheless, MacArthur’s assumptions were rarely tested and sometimes refused (Vázquez & Stevens 2004), leaving the LNB upon weak foundations. Even the theoretical basis of the GTS could not save the LNB. Contrary to our expectation, tropical lineages are not more prone to evolve towards specialism. Instead, tropical locations harbor more lineages evolving towards generalism than the expected by a null relationship. Hence, MacArthur’s LNB has one more weakness and a mechanism to explain how niche of tropical species become narrower is still lacking.

Although dietary niche is enlarging along the evolution of tropical lineages, there is evidence for narrow niches in the tropics (e.g., Eeley and Foley 1999 for primates; Olesen and Jordano 2002 for plants; Forister et al. 2015 for insects; Dalsgaard et al. 2011, Gómez et al. 2016 and Sonne et al. 2020 for birds). Therefore, a mechanism breaking the macroevolutionary tendency of tropical species to become generalist must operate in short and recent time scales, enabling tropical narrower niche nowadays. We argue that the LNB composes a large-scale dynamic in which the modern tendency of narrower tropical niche is nullified by the evolutionary trend of tropical niche enlargement.

GTS contingency to geography

Lineages can evolve in both directions, “generalist-to-specialist” and “specialist-to-generalist”. The mysterious evolution towards generalism, even causing decreases in competitive strength of species, is possible because not always species need to be strong competitors. Since species evolve at different places imposing different environmental barriers and biotic interactions (Hawkins *et al.* 2003), it is expected that species located at distinct geographic regions evolve towards distinct directions. However, the corroboration of these two seemingly opposite patterns is local-specific and inverse to the expected.

Contrary to the logic argument that species should become more specialized to face the high competition in the tropics, these lineages showed to be more prone to evolve towards generalism than towards specialism. Although not studied in an evolutionary context, non-stationary relationship between dietary niche breadth and latitude was also reported for crabs, in which the dietary niche of temperate species was positively correlated with latitude, whereas relationship is lost for tropical species (Papacostas and Freestone, 2016). The authors argued that evolutionary history rather than latitude might play a greater role in governing the niche breadth of tropical species. Nevertheless, the absence of connection between species dietary niche breadth and latitude for tropical species may also emerge if competition for food resource does not impose limits for species coexistence in the tropics. Aves consists in a group featured by great establishment of biotic interaction with plants, which is an abundant group in the tropics. When resources are plentiful, as in tropical regions, low levels of competition breaks the advantages of higher competitive strength through specialization and allow species to coexist even with niche overlap (Schleuning *et al.* 2012). But why are tropical lineages enlarging their niches?

To become generalist confers advantages when competition is not a strong pressure. A study concerning generalism behavior in wasps colonies found that generalist individuals exhibit lower mortality risk while they invest less energy and time foraging for their resources (Santoro *et al.* 2019). Conversely to what MacArthur said, the jack of all trades might be the master of all when species are not under high competition pressures. Concerning temperate regions, higher proportion of lineages evolving towards specialism might be explained based on the advantages conferred by the ability of specialist species to track, acquire and couple with the resource in resource-scarce places (Godoy *et al.* 2014; Burin *et al.* 2016).

The spatial dependency of lineages direction of evolution helps us understand the lack of agreement among studies. The GTS proved to be one side of a coin ruled by strong competition in the tropics. The existence of seemingly contradictory evolution towards generalism is possible because lineages evolving towards such direction fall at the other side of the same coin. In the STG ("specialist-to-generalist" hypothesis) species are ruled by resource scarcity of temperate regions and, together with the GTS, compose the entire coin named "Region-dependent niche evolution" theory. The general theory for dietary niche evolution we propose formulates that the direction of evolution of a species or lineage's trait depends on the geographic region lineages are evolving (or the side of the coin they fall in).

Implications of the GTS contingency

The contingency of the GTS on the geographic region has implications for one of the most studied biological patterns: the species richness latitudinal gradient. Species cease to consume certain types of resources when they become more specialized. Along their evolution, as a result of neutral processes, these species going through specialization accumulate mutations that disable them to reverse the direction of phenotypic evolution towards generalism (i.e. species may lose physiological or morphological traits needed to feed on the resources previously used) (Futuyma & Moreno 1988). Therefore, species or lineages evolving towards specialism are decreasing their capability to expand their dietary niche, adapt in the face of new environmental pressures and their chances to go through adaptive radiations due to the irreversibility of specialization (Haldane 1951; Day *et al.* 2016). Accordingly, specialization of the species' dietary niche can lead to low rates of speciation within lineages (Haldane 1951; Day *et al.* 2016; Colles *et al.* 2009; Price *et al.* 2012).

Since specialization decreases speciation rates and lineages evolving towards specialism occur mainly in high latitudes, we can infer that these regions had experienced less speciation events due to the changes in the dietary niche breadth of species. The less species emerging, the less species accumulating in high latitudes, reinforcing the low number of temperate species and the species richness latitudinal gradient. Although differences in the diversification rates between tropical and temperate regions are far not the only explanation to the species richness latitudinal gradient, the poor speciation events in high latitudes caused by specialization of the lineages can be a powerful driver of the global species distribution. Here, we propose a new hypothesis to explain the current latitudinal gradient in species richness: Specialization Cage. Specialization Cage hypothesis is based on (i) the assumption of lower diversification rates of specialist lineages and (ii) the greater proportion of lineages evolving towards specialism in the high latitudes, as the greater proportion of species evolving towards generalism in the tropics. Our hypothesis perceives specialization as a cage (more numerous in high latitudes) preventing species to return to their original state (generalism) and hampering them to speciate.

The Specialization Cage hypothesis does not have the pretension to be a general theory or to fight the other more than 30 theories already developed to explain the species richness distribution. Instead, it is a piece of the puzzle that must be put together to frame a general theory for the latitudinal diversity gradient that stills need to be formulated. Although many may find that the Specialization Cage is just another theory, it has the uniqueness to place specialization of lineages as a driver of the global pattern in the species distribution.

Prospects and Conclusion

The dietary niche is one of the manifold dimensions of species niche. To consider other equally important dimensions for species evolution and distribution will bring even more clarity into the macroecological and macroevolutionary theories. Although the dietary niche of lineages is not becoming narrower in the tropics (what weakens MacArthur’s theory), the evolution of another niche dimension such as physiology or behavior may support the LNB. For instance, the specialization in any tropical species behavior may also decrease competition in the tropics and enable higher coexistence between species. Although the mechanism leading to narrower tropical niche is still unknown, it seems to operate in short time scales, compounding a higher-level dynamic in which the current spatial pattern we observe is erased by the evolutionary scale.

The GTS together with the STG hypothesis constitute a broad theory to explain contradictions emerging on the niche evolution field. The “Region-dependent niche evolution” theory brought us the answer for one of the big questions in the niche evolution field. If specialism confers competitive superiority, why does generalism still exist? Because competition is not the pressure driving species evolution in all geographic regions. The contradictions emerged because de specialist-to-generalist was still missing. Now that we propose the GTS and the STG together as pieces of the broader "Region-dependent niche evolution" theory, we expect that contradictions concerning the dietary niche evolution of lineages are now enlightened. Notwithstanding, the "Region-dependent niche evolution" theory may also be sensitive to niche dimension. Although dietary niche evolution may follow this pattern, it is necessary to verify the tendency of other species features.

Both MacArthur's and Futuyma and Moreno's hypotheses fit in higher-level dynamics. To unveil these two broader dynamics was only possible through the union the theoretical basis of these two distinct theories. To bring together macroevolutionary and macroecological theories has proved to be an enlightening pathway to fix and go forward with commonly used but still obscured theories. Moreover, to incorporate deeply discussed approaches of a field into another can bring enough clarity to develop unspoken biological theories, such as the Specialization Cage. We encourage the usage of the theoretical basis of one field to enlighten the other and promote advances in scientific research.

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CAPÍTULO 3

Space and lineages evolutionary history changes how diet drives Aves diversification

ABSTRACT

Is species diet driving diversification dynamics? The generalism-specialism macroevolutionary debate stands for more than 150 years and still engenders controversy. There is no consensus on the way dietary niche breadth is related to diversification rates. Both generalism and specialism have already been correlated to high extinction rates, but also to smaller extinction probability. The same holds to speciation rates. Here, I argue that conflicting results emerging in the trait-dependent diversification literature is due to spatial and phylogenetic non-stationary. Tropical lineages are mostly evolving towards generalism due to competition relaxation. Hence, the absence of the specialization run in the tropics may allow lineages to diversify and maintain their generalist dietary niche, increasing speciation rates only in this region and contributing to the emergence of local effects. Contingent events along lineages evolutionary history may also lead to the emergence of local effects on the relationship between diet and lineages diversification by changing the ecological meaning of diet niche breadth for the ancestral. The heritage of this new ecological trait meaning by descendants leads to local effects emerging in low-level clades (i.e., phylogenetic non-stationarity) when higher-level clades are under focus. Here, I use quantitative data on Aves diet (number of food resources consumed) combined with phylogenetic methods to estimate an evolutionary measure for dietary niche breadth and disentangle its effects upon Aves diversification dynamics. As expected, generalism increases speciation rates only in the tropics, leading to species accumulation at this region. Besides spatial non-stationarity, local effects emerging from low-level clades show that diet-dependent diversification is commited by phylogenetic non-stationarity. Although the overall effects of diet upon speciation and extinction rates, spatial and phylogenetic local effects must not be neglected because (i) it may be a way to achieve new explanatory or exploratory analyses to find which hidden variables shape the relationship between species diet and their diversification and, (ii) the neglection of the spatial and phylogenetic component on the diet-dependent diversification theories may have led to the inconsistent results on the literature. I argue that considering non-stationarity in trait-dependent diversification theories for high-level clades and broad geographic

areas is a promising task for future studies to enhance our knowledge about how diet (or any other species traits) drives lineages diversification dynamics.

Keywords: generalism; specialism; speciation rates; extinction rates; non-stationarity

INTRODUCTION

Is the dietary niche breadth of species driving their diversification? The dietary niche is a piece of species ecology and accordingly, must be a driver of lineages macroevolutionary dynamics (Burin *et al.* 2016). Nevertheless, the relationship between species diet and diversification is still obscure, with no consensus about how the dietary niche breadth correlates to speciation or extinction probabilities.

Species with narrow dietary niches – or specialist species are thought to have higher extinction rates and smaller speciation rates. Narrow niches increase species extinction risk due to high probabilities of resource scarcity and instability when facing harsh environmental conditions (Colles *et al.* 2009; Price *et al.* 2012). For instance, pollinators specialized on host-specific plants exhibits increased rates of extinction as a consequence of host extirpation (Day *et al.* 2016). Furthermore, the absence of variation on specialized lineages may also reduce speciation rates due to fewer available mechanisms for exploring and adapting to new ecological opportunities (Haldane 1951; Day *et al.* 2016). Although the disadvantages of being specialist, species with narrow dietary niches might be superior competitors (Patten 2008), granting some advantage of being specialist over generalists.

Broad dietary niches – or generalism is linked to higher extinction risk due to competitive disadvantage regarding more specialized species (Price et al. 2012 for mammals; Hardy & Otto 2014 for host-plant mutualism; Burin et al. 2016 for birds). Although the availability of diverse food resources, generalist species experience high niche overlap with other species and asymmetrically compete with specialists due to their higher efficiency on individual resources acquirement (Godoy *et al.* 2014; Burin *et al.* 2016). Accordingly, both generalism and specialism are hypothesized to have their advantages and disadvantages (check Hardy *et al.* 2020 for an informative review on the advantages and disadvantages of generalism), and conclusion about which of them leads to extinction or speciation is missing. This generalism-specialism macroevolutionary conundrum is under debate for more than 150 years (Price *et al.* 2012).

A piece of the generalism-specialism debate begun to be solved recently. Lemes & Barreto (in prep) found that evolution towards both generalism and specialism is possible due to the role of spatial non-stationarity at lineages evolution (i.e., geographic regions). While tropical lineages are mostly becoming more generalist, temperate lineages are evolving towards specialism. It occurs because, although generalism is, in general, seen as a prompter of competitive disadvantage leading to subsequent specialization run, plenty resources at the tropics may alleviate the competition at this regions and allow evolution towards generalism. This result is important because it shows that competition is a circuit breaker changing the effects of generalism. Here, I argue that this local effects of generalism, allowed by competition relaxation, reverberates at the diversifications dynamics of lineages. When competition is turned off, generalism affects lineages evolution differently than expected.

Competitive environments select for more specialized species (Dennis *et al.* 2011). In this scenario, generalism is followed by speciation generating species that are more specialized. In the absence (or low levels) of competition, such as in the tropics, speciation might occur without environmental selection for specialization. Hence, descendants may conserve their ancestor’s diverse dietary niche and have speciation probabilities increased. Accordingly, I hypothesize that dietary niche breadth drives speciation rates differently in tropical and temperate regions, with dietary niche breadth positively correlated to speciation rates in the tropics. The geographic regions may also affect the relationship between diet and extinction rates. Since the disadvantage of generalism (i.e., low competition strengh) is alleviated in the tropics, diverse food resource used by generalist species must decrease their extinction rates in this region. The relationship between dietary niche breadth and extinction rates is hard to predict in temperate regions. Both generalism and specialism may lead to low extinction rates. The former due to varied resource availability in harsh environmental conditions, and the latter due to species ability to couple and track food resource (Godoy *et al.* 2014; Burin *et al.* 2016). Hence, predictions concerning lineages extinction rates based on their dietary niche breadth would be powerless.

There is also a phylogenetic component in the non-stationary relationship between diet and diversification rates. Day et al. (2016) discussed this issue arguing that contrasting results are due to the differences in macroevolutionary processes in different groups. Rojas et al. (2018) found that the relationship between diet and diversification rates might differ even inside groups, deepening on the phylogenetic non-stationarity problematic. Here, I argue that generalism does not have global consequences on diversification rates due to historical contingencies lineages experience, which happens to change the meaning of narrowing or enlarging the dietary niche breadth for lineages. The general aim of this study is to show that the effect of dietary niche breadth on diversification rates is spatially and phylogenetically modulated. Specifically, I aim to investigate (i) if generalism is linked to high speciation rates and low extinction rates in the tropics, (ii) how generalism is linked to extinction rates in the temperate regions and, (iii) the phylogenetic non-stationarity commiting the relationship between diet and diversification rates. I used Aves as the model system to accomplish this study's aims. Data on Aves species has become increasingly available in the last years, including dietary information, distribution maps and a whole-clade phylogeny (Jetz *et al.* 2012), which is crucial for evolutionary questions.

MATERIALS AND METHODS

To elucidate the spatial and phylogenetic non-stationary effects on the relationship between diet and diversification rates, I used Aves (i) diet to estimate an evolutionary measure for lineages dietary niche breadth, (ii) phylogeny to estimate speciation and extinction rates and, (iii) distribution maps to estimate species geographic positions. Flowchart including the data, methods and main analyses is shown ahead in the figure 1.

Phylogenetic Hypothesis

I used the Maximum Clade Credibility phylogeny (MCC) from the 10,000 Aves phylogenetic hypotheses estimated with molecular data only (Jetz *et al*. 2012; available at birdtree.org). The MCC phylogeny was pruned to include only the species for which we have dietary information, resulting in 448 species of birds.

Diet

I estimated species diet based on ecological networks of Aves from the Web of life: ecological networks database (Fortuna *et al*. 2014; available at www.web-of-life.es/). Dietary niche breadth is usually estimated based on species current diet. However, species current diet may not portray species ecology at deeper time scales, which is crucial for evolutionary theories. Hence, instead of using species current diet, I used the lineages' direction of dietary niche evolution (from now on cited only as DDNE) as a measure for dietary niche breadth.

To estimate lineages DDNE, I (i) used the ecological networks to count the number of interactions established by each bird species (or the number of food resources consumed by each bird species); (ii) combined species numbers of interactions with the MCC phylogeny and used phylogenetic comparative methods to reconstruct the ancestral state [using the *R package phytools*

(Revell 2012)] and; (iii) used difference between the reconstructed trait and the dietary niche breadth of species at the tips as lineages DDNE. DDNE values greater than zero means that lineages established more biotic interactions near the tree tips than near the tree root (or evolving towards generalism). DDNE values smaller than zero means that lineages established more biotic interactions near the tree node than near the tree tips (or evolving towards specialism).

Speciation and extinction rates

I used Bayesian Analysis of Macroevolutionary Mixtures (BAMM, Rabosky 2014) together with the MCC phylogeny to estimate speciation (λ) and extinction (μ) rates at phylogeny tips. I used the R package *BAMMtools* (Rabosky *et al.* 2014) to specify priors for speciation and extinction rates and set the prior on the expected number of diversification-rate shifts equal to 1. I ran four independent MCMC chains of 60 million generations in BAMM and assessed convergence by computing effective sample sizes (ESS) of log-likelihoods and number of shifts using the R package *Coda* (Plummer *et al.* 2006) removing 20% of trees as burn-in. Finally, I calculated mean λ and μ per branch of 95% credible rate shift configurations using the R package *BAMMtools*.

Species Distribution Maps

I used the Aves distribution maps from BirdLife International and NatureServe (2015; available upon request at http://datazone.birdlife.org) in the *R software* (R Core Team 2018) to estimate species geographic position. Species were classified as tropical if their distribution maps were located within the tropical belt (between c. 23° north and c. 23° south), temperate (located outside the tropical belt) and intertropical (distribution overlapping both tropical and temperate region).

6. Statistical Analysis

To verify if the effect of DDNE on both speciation and extinction rates depends on the geographic region, I fitted generalized linear models (GLM) with gamma family using the R package *stats* (R Core Team 2021). All variables were square-root transformed. To verify the role phylogenetic non-stationarity on the relationship between DDNE and diversification rates (speciation and extinction rates separately), I fitted phylogenetic weighted regression (PWR, Davies *et al.* 2018). PWR was built accordingly to geographically weighted regression (GWR, Fotheringham *et al.* 1998), in which local regression coefficients are estimated through data weighting based on the geographical distances of observations. In PWR analysis, species-specific coefficients of determination are estimated by weighting species based on phylogenetic distances (Davies *et al.* 2018). I ploted species-specific coefficients of determination and the associated 95% confidence interval using the R package psychometric (Fletcher 2010).

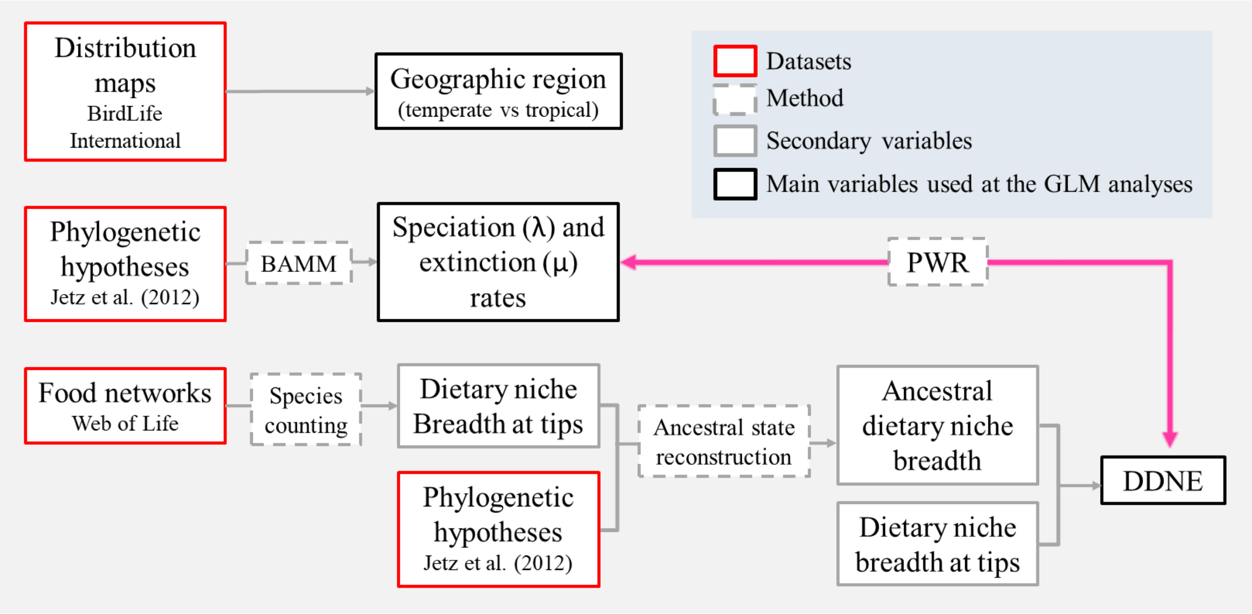

Fig. 1. Flowchart including the used data, methods and main analyses. Gray dashed boxes are the methods applied to the data (red boxes) to generate secondary or main variables. Gray boxes are secondary variables needed to generate DDNE. Black boxes are the main variables used to fit the GLM model. The pink arrow represents the PWR model, which was fitted using extinction and speciation rates (separately) linked to lineages direction of evolution.

RESULTS

The effect of DDNE upon speciation rates depends on the geographic regions (p-value < 0.05; t-value = 157.805). Speciation rates is positively correlated to DDNE in the tropics (p-value < 0.05; t-value = 2.479), while temperate lineages do not show their speciation rates correlated to DDNE. Concerning extinction rates, neither tropical nor temperate lineages are affected by DDNE.

Phylogenetic non-stationarity analysis

There is no overall pattern in the effect of lineages DDNE on their speciation and extinction rates (Fig. 2). Although global analysis show an overall positive correlation between DDNE and speciation rates (p-value <0.05; t-value = -2.276), some clades show no link between these two variables. Global analysis show no correlation between DDNE and extinction rates (p-value > 0.05). However, PWR analysis shows a weak, but extant, correlation between DDNE and extinction risk for some lineages. Species-specific r-squared estimated through PWR analysis ranged from 0.3^{-3} to 0.49 for λ and 0.5^{-3} to 0.24 for μ.

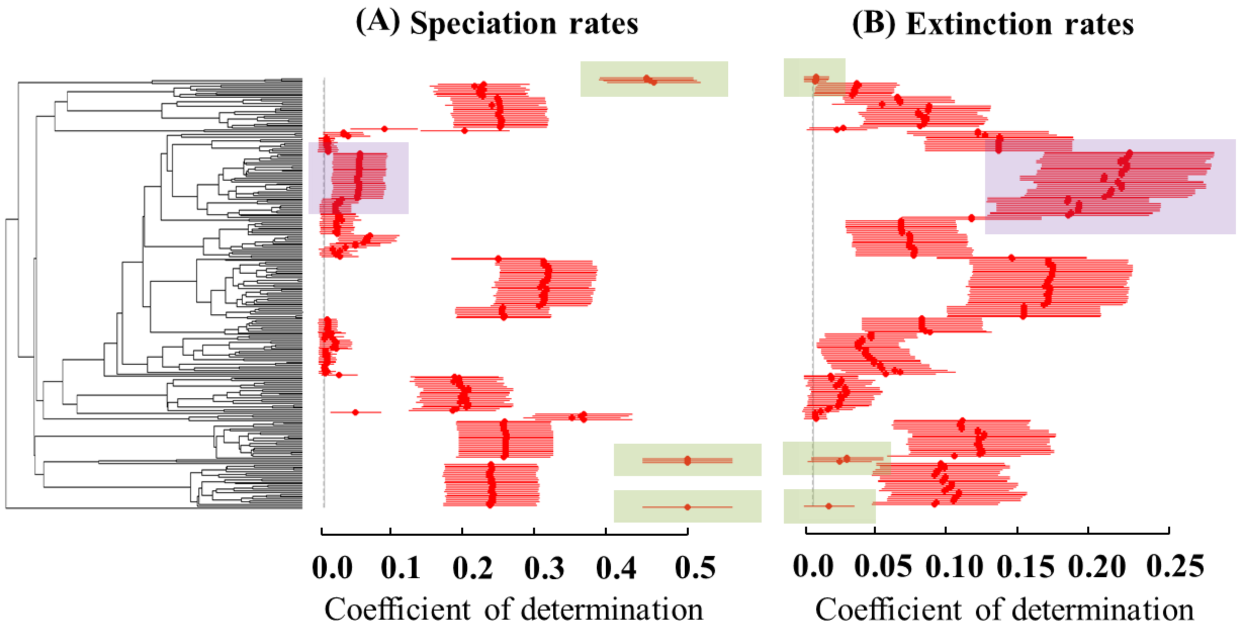

Fig. 2. Species-specific coefficients of determination between for the relationship between (A) speciation rates and DDNE and, (B) extinction rates and DDNE estimated using PWR. Red dots represents focal r-squared and horizontal red lines represents the associated 95% confidence interval. There is a strong phylogenetic signal in the relationship between diversification rates and dietary evolution, meaning that multiple past punctual events changed this relationship, which were conserved by the ancestor's descendant. Green and purple boxes highlights discrepancies in the relationship for the same clade. Green-highlighted clades have speciation rates impacted by DDNE while their extinction rates are not affected by it. Purple-highlighted clade shows opposite pattern, with extinction rates linked to DDNE instead speciation rates.

DISCUSSION

SPATIAL NON-STATIONARITY ON DIET-DEPENDENT SPECIATION

As predicted, the correlation between lineages diet and their speciation probability is modulated by space. I show that speciation probability increases with evolution towards generalism only in the tropics, while speciation probability of temperate lineages is not affected by their DDNE. This spatial-non stationarity might be, in part, responsible for inconsistent results on the literature showing distinct effects of diet upon speciation rates. Higher speciation probability of generalist tropical lineages strenghthens the assumption that tropical species conserve their dietary niche and speciate without specialization, since it is a mechanism capable to explain such result. There is evidence for higher environmental niche conservatism in the tropics (i.e., Wiens & Graham 2005; Khaliq *et al.* 2015; Shiono *et al.* 2018). However, studies about dietary niche conservation is scarse (i.e., Kamilar & Cooper 2013; Salinas-Ramos *et al.* 2015; Olalla-Tárraga *et al.* 2016; Manlick *et al.* 2019) and absent for tropical vs. temperate investigations. It is not only necessary, but promissing to investigate the dietary niche conservatism of species and how distinct geographic regions modulate it. I argue that although it is thought that specialization and speciation are bound together or even the same things (Futuyma & Moreno 1988; Patten 2008) there is a difference between speciation and specialization, mainly in the tropics.

Speciation and specialization have long been questioned as the same (i.e., Futuyma & Moreno 1988). Patten (2008) affirmed that 'they are one and the same thing'. Indeed, there is several studies showing that specialization may lead to speciation (i.e., Knudsen *et al.* 2010; Lenormand 2012; Rolland & Salamin 2016). However, speciation does not always leads to specialization. Tropical radiation events linked to the higher frequency of tropical lineages evolving towards generalism (Lemes & Barreto 2021) clarifies that speciation can occur without specialization.

The positive association between speciation rates and diet occurs because generalist species have more mechanisms to explore food resources previously unexplored, what is a trigger for adaptive radiations (Yoder *et al.* 2010). This process is maintained through time in the tropics due to dietary niche conservatism, with generalist descendants leading to new adaptive radiations. In temperate regions, speciation is attached to specialization (due to competition acquirement or higher specialist ability to track and couple with resource). Hence, generalism does not drive diversification rates in temperate regions. Instead, it leads to specialism.

Although temperate lineages usually follow the specialization path, there is still lineages evolving towards generalism in this region. Why these generalism-toward lineages do not have their speciation rates increased? Some authors have already proposed some mechanisms to explain why generalism does not increase speciation rates. Limited spatially distributed resources prevent species from fragmented distribution (Sexton *et al.* 2017), what could prevent species to increase their speciation rates even when they are generalists because fragmented and large distributions are recquired for allopatric and parapatric speciations (Dennis *et al.* 2011). New species may emerge through cladogenesis or they may change gradually through time, a processes we call anagenesis (Emerson *et al.* 2018). The emergence of generalism in temperate regions unlinked to higher speciation rates may be explained by differential anagenesis in these regions, while cladogenesis mainly occurs at the tropics. Also, a generalist species may be formed by true generalist individuals or by more specialized individuals with different uses of the niche (Sexton *et al.* 2017). In this case, if false and true generalist species distributions are biased through the globe, generalism may lead to increasing speciation rates only in the tropics. All these mechanisms are plausible to unlink generalism and speciation rates and they are worth testing.

SPATIAL NON-STATIONARITY ON DIET-DEPENDENT EXTINCTION

Neither tropical nor temperate lineages have their extinction probabilities affected by their DDNE. Contrary to the expected, even in the tropics where the disadvantages of generalism are break, its advantages do not decrease lineages extinction risk. However, does it make sense to affirm that generalism is better than the specialism? We argue that specialism and generalism are two different feeding strategies and one is not better than the other concerning protection against extinction. If tropical generalist species are less impacted due to food variety, tropical specialist species are less impacted due to environmental and resource stability although less varied resources (Schleuning *et al.* 2012). Likewise, both generalism and specialism may be risky in temperate regions. While specialists are under risk due to dependency on single or little food sources, generalists are under disadvantages competing with the higher frequency of lineages evolving towards specialism at this region or being affected by their possibly ineficiency in track and couple with food resource.

Lemes & Barreto (submitted) proposed a new theory to explain the latitudinal species richness gradient based on the higher frequency of temperate species evolving towards specialism. The ‘Specialization Cage’ theory proposes that species richness in the temperate region is lower because lineages in these regions are evolving towards specialism, which decreases their speciation rates. Hence, specialization is a cage mostly present in temperate regions. However, an underlying assumption on the ‘Specialization Cage’ theory concerns lineages’ speciation probabilities. For ‘Specializaton Cage’ to hold, tropical generalist lineages must have increased speciation rates to promote species accumulation at this region. Here, I show that ‘Specialization Cage’ is a promising theory with holding assumptions. In the tropics, lineages mostly evolve towards generalism (showed by Lemes & Barreto), which increases speciation rates (showed here) leading to generalist descendants due to dietary niche conservatism. This is an ongoing dynamic in the tropics, with new descendants conserving their niche, undergoing radiation events and leading to generalist descendants, which lead to species accumulation in the tropics. In temperate regions, lineages mostly evolve towards specialism, losing the variability needed to trigger speciation events and promote species accumulation.

PHYLOGENETIC NON-STATIONARITY ON DIET-DEPENDENT DIVERSIFICATION

Although global analysis show the existence of an overall explanatory power of diet on speciation rates, it does not hold for all lineages. Looking for global effects of DDNE on the macroevolutionary dynamics of whole clades, such as birds or mammals, is to ignore that some lineages respond to diet differently, or even are not been affected by it. The effect of DDNE on diversification dynamics is only a result of an asymmetry on the numbers of species been impacted by it. In our case, the global relationship between speciation rates and diet stands because the majority of the lineages have their speciation probabilities correlated to their DDNE. The same holds for extinction rates. Although the global analysis showed no relationship between DDNE and extinction rates, there are lineages whose extinction risk is affected their diet (Figure 2).

To look at phylogenetic local effects may provide us information about lineages diversification dynamics, including threatened clades (extinction mostly affected – highlighted with purple boxes in figure 2) and clades with high probability to undergo diversification (speciation mostly affected - highlighted with green boxes in figure 2). Local effects might also be key-measures for exploratory or even explanatory analyses concerning trait-dependent diversification theories. Currently most used models to verify trait-dependent diversification are the SSE (state-dependent speciation and extinction) models (O'Meara & Beaulieu 2016). SSE models have already been framed to fit many types of traits, since binary state traits (Maddison *et al.* 2007) to hidden traits (Beaulieu & O'Meara 2016). However, none of these models allows the verification of non-stationarity. Using lineages-specific measures of correlation (as provided by PWR analysis) as response variables allows to verify the effect of secondary variables hypothesized to change the relationship between diet (or any other trait) and diversification dynamics. This usage of PWR analysis is promising for trait-dependent diversification theories.

A new challenge is to enlighten the factors changing the expected relationship between species traits and their diversification. Is it space? Is it other traits with correlated evolution with focal trait? Is it the climatic variation in which species evolved? Past events, such as exposure to new environmental conditions or evolution of new traits, changed the meaning of being a generalist or specialist, and descendants inherit this trait ecological meaning. A task for future studies is to verify if changes promoted by this past events are idiosyncratic or not.

Although scientific knowledge enrichment over these 150 years of research on trait dependent diversification theories, we are losing a great amount of explanation. If a trait is important for species ecology, we must expect that this trait plays a role in the macroevolutionary dynamics of species (Ng & Smith 2014). If we want to go further and unscramble non-stationary effects of species features along their evolutionary history, we need to stop searching for unifying patterns in higher-level clades and start to focus at lineages levels. At this point, we need to detach local effects to determine what factors are shaping the relationship between lineages diet and diversification.

CONCLUSION

Species diet drives lineages diversification. However, the effect of species diet depends on space and lineages evolutionary history (i.e., the contingent events they experienced). Enlarging or narrowing the dietary niche does not decreases lineages extinction risk neither in the tropics nor in the temperate regions because one strategy is no better than the other is. However, generalism increases diversification rates only in the tropics, possibly due to niche conservatism. Higher speciation in the tropics allows species to accumulate in these regions, what strengths ‘Specialization Cage’ as a valid theory to explain the species richness latitudinal gradient.

Contingent events occurring through lineages evolutionary history changed the meaning of being generalist or specialist for some ancestral. Sequential heritage of new ecological trait meaning by ancestral’s descendants lead to phylogenetic non-stationarity, with local effects emerging in low-level clades. Mixing region-distinct and low-level clades (such as families and genus) without specifying these driving variables may lead to the conflicting results prevailing in the trait-dependent diversification literature. Hence, it is necessary to incorporate spatial and phylogenetic non-stationarity into trait-dependent diversification theories and analyses to solve contradictions in the field.

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SUPLEMENTARY MATERIAL

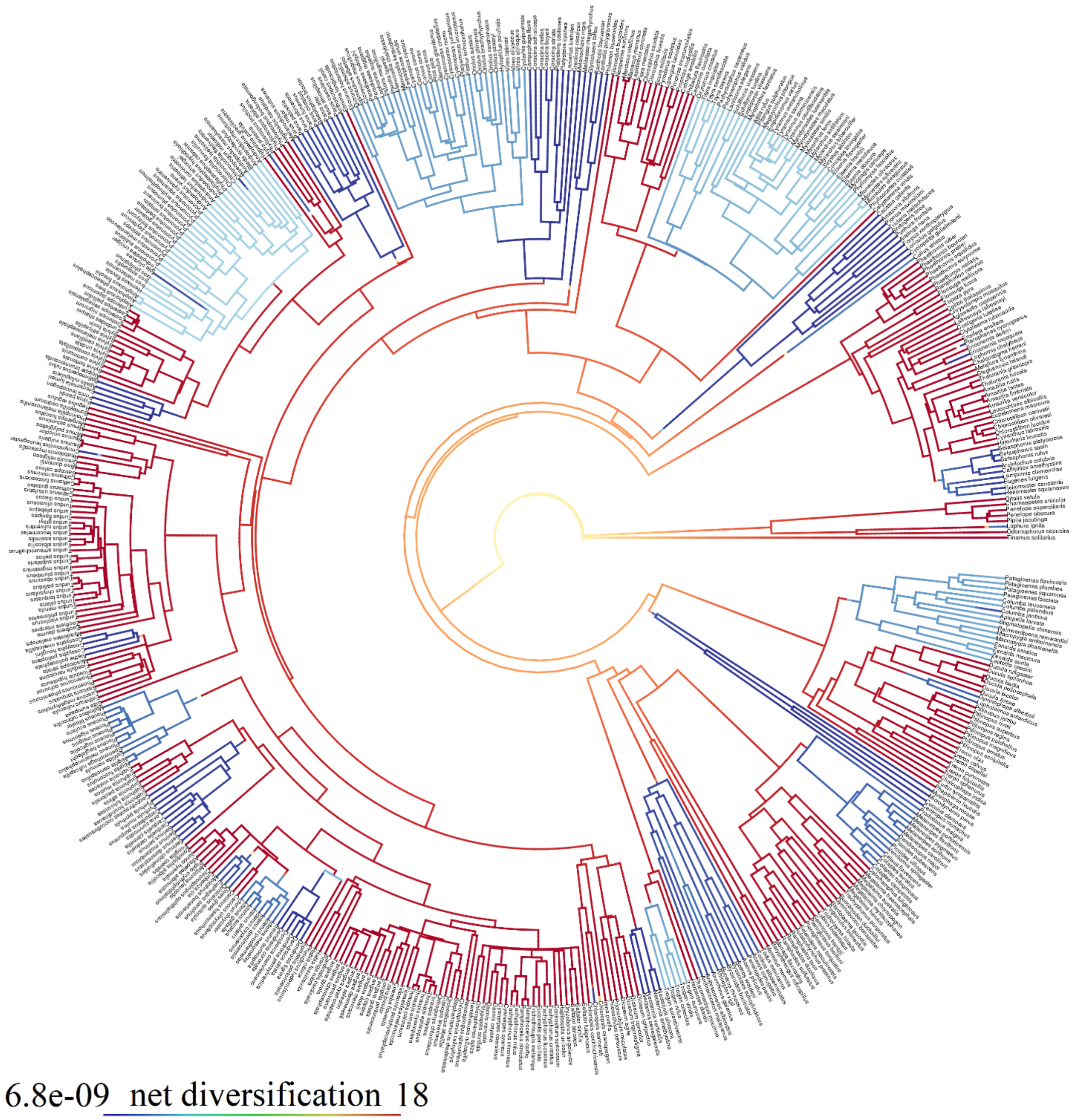

Fig. S1. Net diversification rates for Aves species.

Fig. S2. Ancestral reconstruction plot for species dietary niche Breadth.

CONSIDERAÇÕES FINAIS

As generalizações são responsáveis pela maioria do conhecimento científico atual. De fato, generalizar é o melhor caminho a seguir quando os mecanismos determinando os padrões biológicos são desconhecidos, assim como no início dos diversos campos científicos. Entretanto, todos esses campos cujas fundações estão ancoradas no generalismo são permeados pela não-estacionaridade. Portanto, agora que os benefícios das generalizações para a construção de teorias científicas já foram acessados, a não-estacionaridade é o melhor caminho a seguir para avançarmos no desenvolvimento científico. Já sabemos como mecanismos podem levar a padrões. Mas eles não possuem efeitos globais. Daqui em diante, é necessário que haja a unificação dos diversos mecanismos já conhecidos (através das generalizações) para que os modelos e teorias ecológicas e evolutivas sejam mais capazes de explicar o que acontece na natureza. Essa unificação é possível somente através da inclusão da não-estacionaridade.

Apesar de seus benefícios, as generalizações (ou negligenciamento da não-estacionaridade) também são responsáveis pelas contradições que encontramos em vários campos de conhecimento. As teorias de diversificação dependentes do traço compõem um desses campos. Por mais de um século e meio se discute por que linhagens linhagens ainda evoluem em direção ao generalismo e se a especialização é mesmo vantajosa para as linhagens. A resposta para essas questões está na inclusão da não-estacionaridade tanto na teoria quanto nos modelos criados para representá-las. As diferentes regiões geográficas e a própria história evolutiva das linhagens permite que haja evolução em ambas direções (generalismo e especialismo) e que ambos sejam vantajos, porém em regiões e clados distintos.

A inclusão da não-estacionaridade, que não está somente na utilização de métodos especificamente desenvolvidos para esse intuito, permite não somente o esclarecimento de contradições mas também nos fornece novas pistas para criar novas teorias como a ‘Evolução de nicho região-dependente’ e a ‘Jaula da especialização’. O desenvolvimento de novos métodos permite novas abordagens e compreensões sobre como encaixar os diversos mecanismos já conhecidos. Essa tese não é uma crítica ao caminho que a ciência seguiu até hoje, mas sim uma tentativa de mostrar que um novo caminho promissor existe.

MATERIAL SUPLEMENTAR

Tables S1. Species dietary niche breadth (estimated as the number of biotic interaction stablished by Aves species).

Species	Dietary niche breadth
Aegithalos caudatus	1
Aglaeactis cupripennis	8
Ailuroedus buccoides	2
Alcippe brunneicauda	7
Alethe poliocephala	2
Alophoixus bres	9
Alophoixus finschii	6
Alophoixus phaeocephalus	12
Amazilia fimbriata	3
Amazilia lactea	1
Amazilia rutila	17
Amazilia versicolor	16
Amazona albifrons	3
Andropadus ansorgei	2
Andropadus curvirostris	12
Andropadus gracilirostris	6
Andropadus importunus	11
Andropadus latirostris	22
Andropadus masukuensis	11
Andropadus virens	4
Anorrhinus galeritus	9
Anthoscopus caroli	2
Anthracoceros albirostris	1
Anthracoceros malayanus	17
Apalis rufogularis	5
Aplopelia larvata	1
Archilochus colubris	8
Atlapetes albinucha	7
Attila rufus	3
Aulacorhynchus prasinus	96
Baeolophus bicolor	4
Baeopogon indicator	5

Baryphthengus ruficapillus	3
Basilinna leucotis	8
Bathmocercus rufus	1
Bleda syndactylus	5
Bombycilla cedrorum	1
Brotogeris tirica	5
Buccanodon duchaillui	12
Buceros rhinoceros	13
Bycanistes bucinator	4
Bycanistes subcylindricus	9
Cacatua galerita	1
Cacicus chrysopterus	2
Cacicus haemorrhous	21
Calliphlox amethystina	4
Caloramphus fuliginosus	21
Calyptomena viridis	20
Campephaga flava	1
Cardinalis cardinalis	6
Carduelis carduelis	2
Carduelis citrinella	1
Carpodacus purpureus	1
Carpornis cucullata	48
Catharus fuscescens	6
Catharus guttatus	3
Catharus minimus	6
Catharus ustulatus	17
Celeus flavescens	6
Centropus monachus	2
Chalcophaps indica	14
Chalcostigma herrani	14
Chamaepetes unicolor	26
Chiroxiphia caudata	56
Chiroxiphia linearis	38
Chlorocichla flavicollis	1
Chlorocichla flaviventris	14
Chlorocichla laetissima	18
Chlorophanes spiza	15
Chlorophonia callophrys	14

Chloropsis cochinchinensis	5
Chloropsis cyanopogon	14
Chloropsis sonnerati	20
Chlorospingus ophthalmicus	29
Chlorostilbon canivetii	7
Chlorostilbon lucidus	32
Chlorostilbon olivaresi	7
Chrysolampis mosquitus	6
Cicinnurus magnificus	22
Cinnyricinclus leucogaster	3
Cissopis leverianus	13
Clytolaema rubricauda	21
Coccothraustes coccothraustes	6
Coeligena lutetiae	3
Coereba flaveola	21
Colaptes auratus	2
Colaptes campestris	1
Colaptes rubiginosus	7
Colibri thalassinus	4
Colius striatus	2
Columba janthina	4
Columba leucomela	4
Columba palumbus	6
Conirostrum speciosum	1
Conopias trivirgatus	1
Coracina boyeri	2
Coracina melas	1
Coracina schisticeps	2
Coracina striata	1
Corvus corax	1
Corvus corone	5
Corvus enca	3
Cossypha heuglini	1
Cossypha niveicapilla	1
Cossypha polioptera	1
Cotinga amabilis	1
Cracticus cassicus	1

Cuculus clamosus	1
Cyanerpes caeruleus	10
Cyanerpes cyaneus	8
Cyanocorax cristatellus	1
Cyanocorax yucatanicus	3
Cyanopica cyanus	9
Cyclarhis gujanensis	2
Cyclopsitta gulielmitertii	1
Cynanthus latirostris	9
Dacnis cayana	27
Dacnis venusta	4
Dendrocopos major	1
Dendroica caerulescens	1
Dendroica coronata	1
Dendroica pensylvanica	1
Dendroica striata	1
Dendroica tigrina	2
Dicaeum agile	3
Dicaeum concolor	2
Dicaeum ignipectus	1
Dicaeum trigonostigma	1
Dicrurus adsimilis	1
Dicrurus hottentottus	1
Dives dives	3
Ducula badia	2
Ducula bicolor	16
Ducula poliocephala	15
Ducula rufigaster	2
Ducula spilorrhoa	8
Ducula zoeae	2
Elaenia flavogaster	11
Elaenia frantzii	20
Elaenia mesoleuca	5
Elaenia obscura	4
Elminia longicauda	2
Emberiza cia	1
Empidonax virescens	2
Empidonomus varius	4

Ensifera ensifera	1
Epimachus albertisi	4
Eremomela turneri	2
Eriocnemis derbyi	11
Eriocnemis mosquera	25
Erithacus rubecula	29
Estrilda nonnula	2
Eucometis penicillata	2
Eugenes fulgens	8
Eupetomena macroura	12
Euphagus carolinus	1
Euphonia affinis	2
Euphonia fulvicrissa	1
Euphonia hirundinacea	7
Euphonia musica	8
Euphonia pectoralis	29
Euphonia violacea	22
Eupsittula nana	3
Ficedula hypoleuca	6
Ficedula narcissina	1
Florisuga fusca	4
Florisuga mellivora	1
Forpus xanthopterygius	1
Fringilla coelebs	27
Garrulus glandarius	5
Glycichaera fallax	1
Gracula religiosa	11
Gymnobucco bonapartei	7
Gymnophaps albertisii	1
Habia fuscicauda	3
Habia rubica	18
Haplospiza unicolor	2
Harpactes diardii	1
Heliomaster constantii	8
Heliomaster squamosus	11
Hemithraupis ruficapilla	10
Hemixos flavala	1
Hippolais pallida	8

Hylia prasina	1
Hylophilus poicilotis	4
Icterus auratus	2
Icterus cayanensis	1
Icterus chrysater	3
Icterus dominicensis	5
Icterus galbula	4
Icterus gularis	5
Icterus mesomelas	2
Icterus prosthemelas	2
Ilicura militaris	14
Iole olivacea	17
Irena puella	21
Iridosornis porphyrocephalus	10
Ixos amaurotis	13
Ixos malaccensis	3
Ixos philippinus	11
Junco hyemalis	4
Lafresnaya lafresnayi	3
Lampornis clemenciae	4
Laniarius luehderi	1
Laniisoma elegans	1
Lepidothrix coronata	14
Leptotila cassini	1
Leucochloris albicollis	8
Lipaugus lanioides	17
Lopholaimus antarcticus	1
Lophorina superba	12
Lophornis chalybeus	3
Lophura ignita	3
Loriculus galgulus	7
Loxia curvirostra	2
Loxigilla portoricensis	28
Luscinia megarhynchos	3
Macropygia amboinensis	22
Macropygia phasianella	9
Malimbus rubricollis	1
Manacus manacus	16

Manacus vitellinus	10
Manucodia chalybatus	12
Manucodia keraudrenii	21
Margarops fuscatus	15
Megalaima chrysopogon	21
Megalaima haemacephala	3
Megalaima henricii	17
Megalaima mystacophanos	18
Megarynchus pitangua	15
Melanerpes aurifrons	11
Melanerpes carolinus	2
Melanerpes flavifrons	5
Melanerpes portoricensis	3
Melanerpes pygmaeus	4
Melanocharis nigra	2
Melanochlora sultanea	2
Melilestes megarhynchus	1
Melozone leucotis	6
Metallura tyrianthina	12
Microdynamis parva	1
Mimus polyglottos	4
Mimus saturninus	2
Mino dumontii	1
Mionectes oleagineus	4
Mionectes olivaceus	9
Mionectes rufiventris	16
Molothrus bonariensis	2
Momotus momota	9
Monasa flavirostris	2
Muscicapa striata	3
Musophaga rossae	4
Myadestes melanops	51
Myiarchus antillarum	2
Myiarchus ferox	1
Myiarchus swainsoni	8
Myiarchus tuberculifer	8
Myiodynastes luteiventris	7
Myiodynastes maculatus	18

Myiopagis caniceps	1
Myiophobus fasciatus	2
Myiozetetes similis	11
Nectarinia amethystina	1
Nectarinia olivacea	1
Nectarinia senegalensis	1
Nectarinia verticalis	1
Neopelma aurifrons	1
Nesospingus speculiferus	3
Nigrita canicapillus	5
Nigrita fusconotus	1
Odontophorus capueira	1
Orchesticus abeillei	8
Oriolus auratus	1
Oriolus brachyrhynchus	4
Oriolus chinensis	7
Oriolus szalayi	3
Oriolus xanthonotus	8
Ortalis vetula	2
Orthogonys chloricterus	13
Oryzoborus angolensis	1
Oxyruncus cristatus	9
Pachyramphus castaneus	2
Pachyramphus validus	4
Paradisaea raggiana	19
Paradisaea rudolphi	11
Parotia lawesii	19
Parus albiventris	1
Parus ater	7
Parus atricapillus	1
Parus caeruleus	7
Parus cristatus	2
Parus funereus	5
Parus major	8
Parus palustris	7
Patagioenas fasciata	11
Patagioenas flavirostris	4
Patagioenas plumbea	12

Patagioenas squamosa	10
Penelope obscura	37
Penelope superciliaris	1
Penelopides panini	15
Phaethornis bourcieri	40
Phaethornis eurynome	53
Phaethornis malaris	15
Phaethornis pretrei	2
Phaethornis ruber	18
Phaethornis squalidus	28
Phainoptila melanoxantha	13
Phapitreron leucotis	14
Pharomachrus mocinno	40
Pheucticus ludovicianus	4
Phibalura flavirostris	1
Philemon buceroides	1
Phoenicurus ochruros	9
Phoenicurus phoenicurus	7
Phyllastrephus cabanisi	5
Phyllastrephus hypochloris	10
Phyllomyias fasciatus	1
Phylloscartes oustaleti	1
Phylloscopus budongoensis	9
Phylloscopus sibilatrix	2
Phylloscopus trochilus	11
Pica pica	2
Picoides pubescens	1
Picoides villosus	1
Pionus maximiliani	1
Pipile jacutinga	13
Pipilo erythrophthalmus	1
Pipra mentalis	15
Pipraeidea melanonota	1
Piranga rubra	4
Pitangus sulphuratus	12
Pitohui kirhocephalus	2
Platysmurus leucopterus	2
Platysteira castanea	2

Platysteira cyanea	1
Ploceus baglafecht	2
Ploceus bicolor	11
Ploceus insignis	2
Ploceus melanocephalus	1
Ploceus nigerrimus	1
Ploceus nigricollis	1
Ploceus ocularis	2
Pogoniulus bilineatus	36
Pogonornis bidentatus	1
Prinia bairdii	1
Prinia leucopogon	1
Prionochilus maculatus	9
Prionochilus percussus	14
Procnias nudicollis	7
Procnias tricarunculatus	30
Prodotiscus insignis	1
Psilopogon australis	20
Psilorhinus morio	17
Pteroglossus bailloni	22
Pteroglossus torquatus	5
Pterophanes cyanopterus	6
Ptilinopus jambu	6
Ptilinopus magnificus	48
Ptilinopus occipitalis	16
Ptilinopus ornatus	1
Ptilinopus pulchellus	2
Ptilinopus regina	12
Ptilinopus rivoli	2
Ptilinopus superbus	48
Ptiloris magnificus	6
Pycnonotus atriceps	7
Pycnonotus barbatus	32
Pycnonotus brunneus	16
Pycnonotus cyaniventris	12
Pycnonotus erythropthalmos	11
Pycnonotus eutilotus	14
Pycnonotus finlaysoni	1

Pycnonotus goiavier	12
Pycnonotus melanoleucos	1
Pycnonotus plumosus	1
Pycnonotus simplex	11
Pycnonotus squamatus	1
Pycnonotus zeylanicus	1
Pyroderus scutatus	7
Pyrrhula murina	5
Pyrrhula pyrrhula	3
Pyrrhura frontalis	6
Quiscalus quiscula	2
Ramphastos dicolorus	15
Ramphastos sulfuratus	20
Ramphastos toco	2
Ramphocelus carbo	32
Ramphocelus dimidiatus	1
Ramphodon naevius	2
Regulus regulus	1
Reinwardtoena reinwardtsi	1
Rhabdornis mystacalis	8
Rhabdotorrhinus waldeni	5
Rhinoplax vigil	9
Rhyticerus corrugatus	6
Rhyticerus plicatus	4
Saltator atriceps	4
Saltator fuliginosus	2
Saltator similis	22
Sarcops calvus	17
Saxicola torquatus	3
Schiffornis turdina	3
Schiffornis virescens	15
Seiurus aurocapilla	1
Selasphorus platycercus	4
Selasphorus rufus	4
Selasphorus sasin	4
Selenidera maculirostris	23
Semnornis frantzii	31
Serinus citrinelloides	2

Serinus dorsostriatus	1
Serinus mozambicus	4
Serinus serinus	6
Sirystes sibilator	1
Sitta europaea	5
Spermophaga ruficapilla	1
Spindalis portoricensis	30
Stactolaema leucotis	10
Stephanophorus diadematus	22
Stephanoxis lalandi	11
Stigmatopelia chinensis	8
Sturnus unicolor	4
Sturnus vulgaris	1
Sylvia atricapilla	65
Sylvia borin	15
Sylvia cantillans	8
Sylvia communis	8
Sylvia conspicillata	2
Sylvia hortensis	4
Sylvia melanocephala	14
Sylvia undata	2
Tachyphonus coronatus	43
Tachyphonus cristatus	3
Tachyphonus luctuosus	4
Tachyphonus rufus	25
Tangara cayana	3
Tangara cyanocephala	23
Tangara desmaresti	17
Tangara dowii	13
Tangara guttata	10
Tangara gyrola	26
Tangara icterocephala	4
Tangara mexicana	22
Tangara peruviana	1
Tangara seledon	16
Terpsiphone viridis	2
Thalurania furcata	16
Thalurania glaucopis	44

Thlypopsis sordida	3
Thraupis cyanoptera	35
Thraupis episcopus	18
Thraupis ornata	24
Thraupis palmarum	18
Thraupis sayaca	14
Tiaris bicolor	2
Tinamus solitarius	3
Tityra cayana	18
Tityra inquisitor	2
Tityra semifasciata	18
Tockus alboterminatus	1
Todus mexicanus	2
Topaza pyra	1
Trachyphonus purpuratus	4
Treron calvus	2
Treron capellei	12
Treron curvirostra	19
Treron fulvicollis	1
Treron olax	5
Treron sphenurus	5
Tricholaema hirsuta	5
Tricholestes criniger	5
Trichothraupis melanops	44
Triclaria malachitacea	1
Trogon aurantiiventris	14
Trogon citreolus	5
Trogon rufus	10
Trogon surrucura	14
Trogon viridis	13
Turdoides sharpei	1
Turdus albicollis	44
Turdus amaurochalinus	6
Turdus assimilis	12
Turdus chrysolaus	2
Turdus flavipes	22
Turdus grayi	12
Turdus iliacus	17

Turdus leucomelas	4
Turdus merula	63
Turdus migratorius	4
Turdus obscurus	1
Turdus olivaceus	2
Turdus pallidus	7
Turdus pelios	11
Turdus philomelos	17
Turdus pilaris	5
Turdus plebejus	44
Turdus plumbeus	13
Turdus rufiventris	41
Turdus subalaris	1
Turdus torquatus	12
Turdus viscivorus	18
Turtur tympanistria	6
Tyrannus caudifasciatus	2
Tyrannus dominicensis	9
Tyrannus melancholicus	13
Tyrannus savana	1
Veniliornis spilogaster	0
Vireo altiloquus	19
Vireo latimeri	3
Vireo olivaceus	16
Xanthotis flaviventer	1
Xanthotis polygrammus	1
Zenaida asiatica	1
Zenaida aurita	1
Zenaida macroura	2
Zonotrichia albicollis	7
Zoothera dauma	1
Zoothera interpres	2
Zosterops japonicus	5
Zosterops nigrorum	9
Zosterops pallidus	10
Zosterops senegalensis	15