

Chapter 5

Evolutionary Macroecology and the Geographical Patterns of Neotropical Diversification



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Abstract Over the last decades, the geographical distribution of species, as well as its associated patterns have been at the core of the macroecology research program. Gradients in geographic range size and shape, as well as range overlap (species richness), reveal broad-scale patterns that may help to infer underlying ecological processes, mainly related to climatic and environmental variation. However, it is clear now that evolutionary processes are at least equally important, demanding the inclusion of an evolutionary dimension to better understand such patterns. In this review, we discuss recent macroecological approaches to study evolutionary patterns at the geographical scale, and exemplify some of these approaches with data from a model group of Neotropical birds, the Furnariides.

Keywords Community phylogenetics · Latitudinal diversity gradients · Macroevolution · Niche conservatism · Species diversity · Speciation rates

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1 Introduction

Since the eighteenth century, broad-scale patterns of diversity called the attention of naturalists. Recognizing that tropical regions have higher species richness relative to temperate areas, Alexander von Humboldt was the first one to propose it to emerge from climatic differences (Hawkins 2001). This ubiquitous pattern has since then been known as the Latitudinal Diversity Gradient (LDG) and, although the global distribution of biodiversity is indeed far more complex than a simple unidirectional gradient (Hawkins and Diniz-Filho 2004), the difference in species richness between temperate and tropical regions tends to capture the most evident facet of the distribution of life on Earth: its geographic heterogeneity.

Early explanations for the LDG in the 1950s and 1960s followed von Humboldt's tradition and focused on the strong correlations observed between diversity (i.e., species richness) and components of current environmental variation—especially combinations of temperature and precipitation (Simpson 1964; Pianka 1966; O'Brien 2006; Hawkins et al. 2003; Brown 2012). These high correlations suggested a causal explanation, and spurred the development of hypotheses that aimed to identify the mechanisms affecting species distributions and hence driving geographical patterns (e.g., Currie et al. 2004). Although these diversity-environment correlations suggested “pure ecological explanations” that involved population-level processes tied to dispersal and aggregation of tropical organisms, it quickly became clear that deep-time evolutionary processes should also be taken into account to explain the LDG (Rohdes 1992; Ricklefs 2004). In fact, as early as 1937, Theodosius Dobzhansky had proposed that diversity gradients should be explained by an interaction between ecological and evolutionary mechanisms, in which evolution would drive the dimensions of the niche—the set of biotic and abiotic factors that allow a species to exist indefinitely—that would allow different patterns of niche packing throughout environmental gradients. Today, it is consensus that the LDG should be explained not only by current climatic factors, but also by the long-term dynamics of such climatic factors and by events happening throughout the evolution of the species (Fine 2015).

In the last 40 years, several papers have synthesized knowledge about LDG and discussed its potential causes at distinct spatial and temporal scales (e.g., Pianka 1966; Rohde 1992; Currie et al. 2004; Hillebrand 2004; Mittelbach et al. 2007; Fine 2015). Explanations gradually shifted from purely ecological mechanisms driving population-level processes to deep time evolutionary patterns and processes (Schemske and Mittelbach 2017). Currie et al. (2004) and Mittelbach et al. (2007), for instance, proposed two ways to couple evolutionary with ecological processes to generate the LDG. The first focused on the different ways by which speciation and extinction rates (and their balance; the diversification rate) vary geographically (see Schluter and Pennel 2017). The second emphasized how different regions are occupied at different moments in a clade's history, leading to different times for speciation-extinction events and creating gradients in the accumulated number of species. More recently, these two possibilities (speciation-extinction dynamics and

time for diversity accumulation) have been considered as evolutionary mechanisms to explain the LDG (Fine 2015). Indeed, both mechanisms are expressed in two of the most prominent hypotheses currently posed to explain the LDG: the tropical niche conservatism (Wiens and Donoghue 2004) and the out-of-the-tropics (Jablonski et al. 2006) hypotheses.

The tropical niche conservatism hypothesis (TNC) posits that most clades originated in the tropics and have occupied these regions for a longer time period compared to the fewer and more recent clades occupying temperate areas; this would have led to the accumulation of more species in the tropics relative to the temperate zone, resulting in the observed LDG (Wiens and Donoghue 2004). The TNC hypothesis does not explicitly predict differences in speciation and extinction rates, but focuses simply on the time available for speciation, tied to a limited dispersal from tropical to temperate regions. Alternatively, the out-of-the-tropics hypothesis (OTT) also postulates a tropical origin for most clades—but with additional higher dispersal out of (rather than into) the tropics, as well as comparatively higher and lower speciation and extinction rates, respectively, in these regions (Jablonski et al. 2006). Testing the predictions of both LDG hypotheses, whether related to time for speciation or evolutionary rates, requires comparisons between tropical and temperate regions in a spatial context. However, beyond more general difficulties related to scale effects, and considering that evolutionary (speciation-extinction) dynamics is a property of the clade, one of the main problems hindering our understanding of diversity gradients is that these dynamics are to be measured and evaluated in geographical space (Hawkins et al. 2006). It is still challenging to properly combine these two dimensions—space and time—in an analytical sense.

Our goal here is to review the application of alternative methodological approaches, under a macroecological perspective, to investigate evolutionary patterns and processes associated with the LDG in the Neotropics. To achieve this, we discuss the rationale behind these approaches, and their application in published studies that focused on or included the Neotropical region and clades. To illustrate their use, we apply them to available data from a model clade of passerine birds: the infraorder Furnariides. The Furnariides clade constitutes the largest continental radiation of vertebrates endemic to the Neotropics, comprising nearly 51% of suboscines species and 11% of all Passeriformes (Ricklefs 2002; Claramunt 2010). Furnariides present high levels of ecological diversity (e.g. morphology and life histories), and are distributed in nearly all major terrestrial habitats across the Neotropics. Highest concentrations of Furnariides species are found in forest habitats in the Amazon and the Atlantic Forest, whereas lowest species concentration can be found in open habitats such as the Andean and Patagonian deserts, and the Llanos of Venezuela and Colombia (Pinto-Ledezma et al. 2017). Furnariides thus show the classic latitudinal diversity gradient (Fig. 5.1a), and their ecological and evolutionary patterns make them an ideal system to review the use of macroecological approaches to study Neotropical diversification. All data used here to map species' geographic distributions (Furnariides range maps; see Pinto-Ledezma et al. 2017) come from Ridgely et al. (2012); the phylogenetic hypothesis inferred for the group follows Pinto-Ledezma et al. (2019). This phylogeny is a maximum clade credibility tree

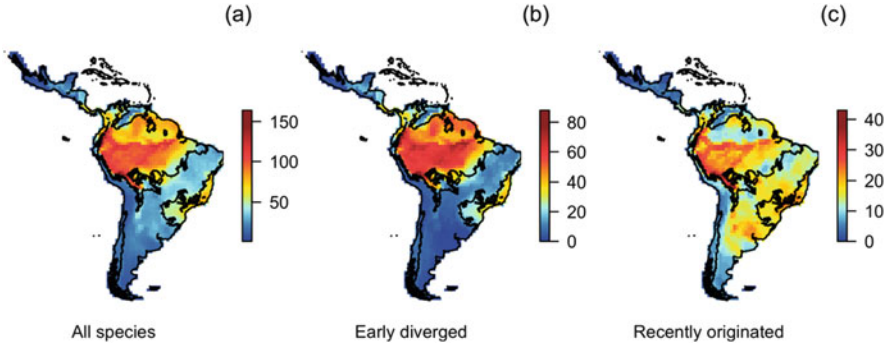


Fig. 5.1 Geographic patterns of species richness for different sets of species of the Furnariidae clade across the Neotropics; (a) all species, (b) early-diverged species and (c) recently-originated species. Map lines correspond to the division between forest and open habitats. Notice that to estimate the number of early-diverged and recently-originated species we ranked each species by calculating the number of nodes separating a species from the root of the tree (Root distance metric, RD). Then, using the 35% and 65% percentiles of RD across all species we defined, respectively, early-diverged species as those with few nodes from the root of the tree and recently-originated species as those with many nodes, yielding a balanced number of early-diverged (283) and recently-originated (236) species

obtained from a posterior distribution of trees built under a Bayesian framework and based on nine molecular markers (Pinto-Ledezma et al. 2019).

2 Mapping Phylogenetic History in Geographic Space

At broad spatial scales, diversity gradients are usually described from species' geographic ranges and their overlap (Gotelli et al. 2009). The standard methodology for doing so is to overlay a grid of cells onto the study area, wherein species richness (alpha diversity) is estimated by counting the (co)occurrence of species within each grid-cell. As a basic property describing species presence or absence within a cell, geographic ranges can be further used to describe diversity gradients beyond species richness. For instance, different spatial patterns can be derived by summarizing attributes of the species known (or assumed) to be present in each cell (Hawkins et al. 2017). This “assemblage-based” approach can be used to create a raster of a particular trait (e.g. body size) that is summarized across species, as commonly done in studies of ecogeographical rules (e.g. Bergmann's Rule; Olalla-Tárraga et al. 2010).

Following the current interest on evolutionary drivers of diversity patterns (Schemske and Mittelbach 2017), assemblage-based approaches now also include the creation of “evolutionary variables” from the species' phylogenetic information (Hawkins et al. 2017). Different phylogenetic metrics can be used to represent the evolutionary development of assemblages, such as their mean root distance (MRD;

Kerr and Currie 1999), relative phylogenetic diversity (rPD, Davies and Buckley 2011) or diversification rate (DR, Jetz et al. 2012). Mean root distance was one of the first evolutionary variable to be mapped (Kerr and Currie 1999), and it continues to be widely used despite its dependence on tree topology instead of branch lengths (Hawkins et al. 2012; Kennedy et al. 2014; Pinto-Ledezma et al. 2017). MRD quantifies the average distance of species as the number of nodes separating each taxon (one tip of the tree) to the root of the phylogeny, allowing the classification of assemblages along a continuum that spans from early-diverged to recently-originated assemblages (Pinto-Ledezma et al. 2017). Patterns in MRD have been useful to test hypotheses on diversity gradients related to evolutionary time, such as the Tropical Niche Conservatism (TNC) hypothesis, which posits that, for clades originated in the tropics, most lineages persist, diversify, and accumulate within the tropics—whereas few lineages are able to establish outside the ancestral conditions (e.g. temperate regions; Wiens and Donoghue 2004). Such pattern of lineage accumulation is expected to be discernable in the distribution of early-diverged (“old/basal”) and recently-derived (“young/derived”) species, with the former accumulating in the ancestral environment, and the latter doing so in different environments (Hawkins et al. 2006). Hawkins et al. (2006), for instance, explicitly used a “deconstruction” approach based on the distribution of root distance among species, and obtained richness for “basal” and “derived” clades for Neotropical birds. As expected under the TNC, current species richness is better explained by basal richness than by derived richness (Hawkins et al. 2006).

Kennedy et al. (2014) used a similar approach and showed different diversity patterns between the two suborders of passerine birds (oscines and suboscines). They used a measure related to the MRD, called the diversification rate (DR; Jetz et al. 2012), to rank species along the old-young continuum. The DR represents the number of diversification events along the history of a lineage (Jetz et al. 2012), and is highly correlated with the species root distances (Pinto-Ledezma et al. 2017). Kennedy et al. (2014) found that data from both oscines and subsocines support the TNC hypothesis, with young species preferentially accumulating in temperate regions, but young and old species doing so in the tropics. However, the spatial patterns in DR differed between these suborders, with oscines showing a southward pattern and suboscines a more tropical-temperate gradient. Such findings support the inferred biogeographic histories of both suborders, with a New World colonization from the north for the oscines, and colonization from the south for the suboscines. Later, Kennedy et al. (2016) expanded their approach to 10 large clades of passerine birds and confirmed the role of spatiotemporal differences in diversification in the establishment of current diversity gradients in the New World.

Claims about TNC influencing birds’ diversity gradients (Hawkins et al. 2006; Jetz et al. 2012; Kennedy et al. 2014, 2016) can also be extended to our study group, the Furnariides. Furnariids present similar patterns to those from the abovementioned studies, with high species co-occurrence in tropical areas being dominated by early-diverged species, and low species co-occurrence in subtropical to temperate areas, which are mainly dominated by recently-derived species (Fig. 5.1b, c). MRD and DR reveal a similar pattern (Fig. 5.2a, b). Furnariides

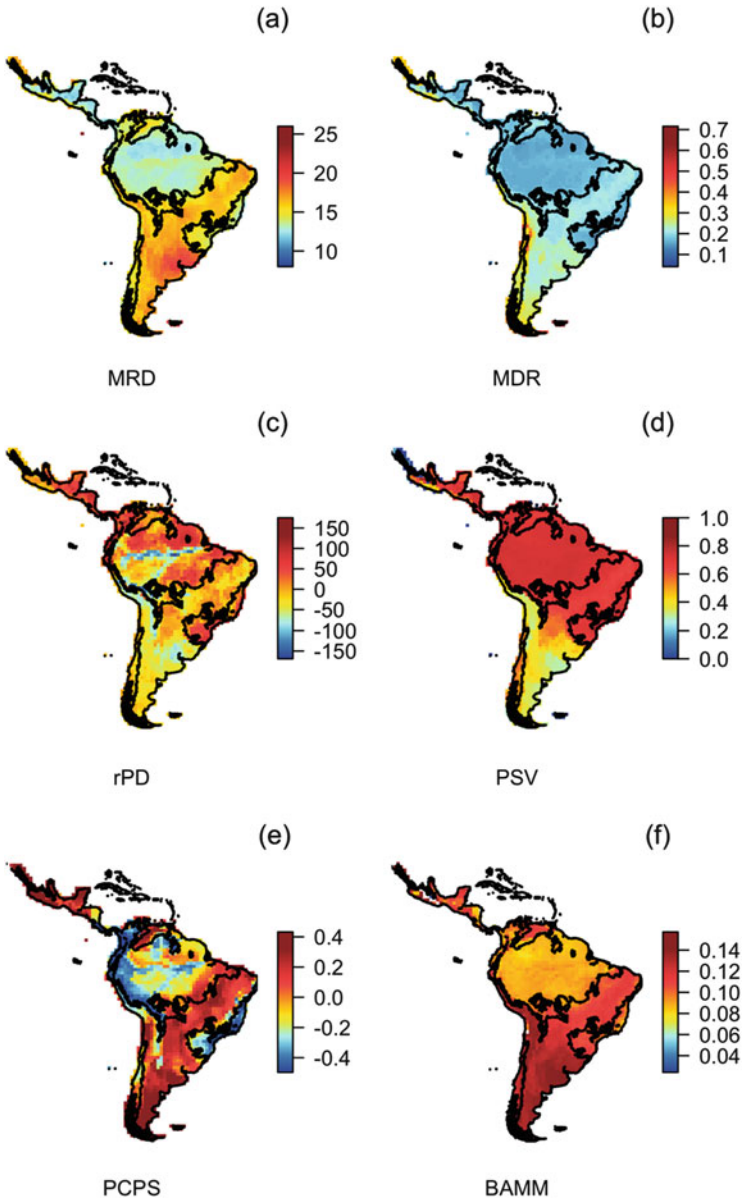


Fig. 5.2 Geographic patterns of evolutionary variables of Furnariid assemblages; (a) Mean Root Distance (MRD), (b) Mean Diversification Rate (MDR), (c) relative Phylogenetic Diversity (rPD), (d) Phylogenetic Species Variability (PSV), (e) first axis of the Principal Coordinates of Phylogenetic Structure (PCPS), (f) BAMM-derived speciation rates (BAMB). Map lines correspond to the division between forest and open habitats

patterns further show that both evolutionary variables, MRD and DR, are highly correlated ($r = 0.69$, $p < 0.001$) and thus may be used interchangeably when describing evolutionary patterns at the geographic scale (see also Pinto-Ledezma et al. 2017).

Another evolutionary variable commonly used is the phylogenetic diversity of assemblages. Phylogenetic diversity (PD) describes the sum of the branch lengths (estimated from a known phylogeny) that connect all species within an assemblage, and thus is highly correlated with the number of species considered (Faith 2013). Considering the relationship between species richness and PD, Davies and Buckley (2011) evaluated the spatial patterns of mammalian relative PD (rPD; the residual PD after controlling for species richness) to infer patterns of diversification and migration. They considered low rPD regions as evidence of rapid speciation and low immigration, and high rPD regions as those of low speciation rates and frequent long-distance immigration. Such different regions were clearly highlighted by a New vs Old World pattern, where the New World (specially the Neotropics) presented low rPD and the Old World (especially the Afrotropics) showed high rPD, consistent with the history of mammalian origin and dispersal (Springer et al. 2011; see also Fritz and Rahbek 2012; Volkamp et al. 2017 for a similar approach in amphibians and birds, respectively). Similarly, in Furnariides, mapping rPD shows that tropical areas (e.g., the Chocó ecoregion) tend to present low speciation rates, whereas temperate areas show mid- to high speciation rates (Fig. 5.2c). That being said, one can also identify tropical areas (e.g., the tropical Andes in Bolivia and Peru) consistent with high speciation rates (Fig. 5.2c), which may be linked to environmental variability (Morales-Barbero et al. 2018).

3 Expanding the Community Phylogenetics Framework to Macroecology

The development of a community phylogenetics (CP) framework (Webb et al. 2002) that explicitly integrates ecology and evolution renovated the interest in combining both disciplines to study diversity patterns (Cavender-Bares et al. 2012). The basis of such framework relies on studying the phylogenetic structure of species (i.e. their genealogical relationships) inhabiting an assemblage, under the assumption that species interact via traits that are not randomly distributed in the phylogeny (Vamosi et al. 2009). Accordingly, CP metrics represent an assemblage's phylogenetic structure in terms of overdispersion (i.e. species being more distantly related, on average, than expected by chance), clustering (i.e. species being more closely related, on average, than expected by chance) or randomness (Webb et al. 2002). A plethora of such metrics have been developed (Miller et al. 2017a), with recent proposals trying to clarify and guide the user based on their mathematical properties (Tucker et al. 2016).

The field of community phylogenetics has primarily focused on local-scale diversity patterns (e.g. within and among sampling plots; Cardillo 2011). However, about a decade ago, studies began to apply a CP approach under a macroecological perspective by evaluating the phylogenetic structure of assemblages within large geographical regions (Algar et al. 2009; Cardillo et al. 2008; Cardillo and Meijaard 2010; Cooper et al. 2008). The reasoning behind such an expansion of CP to macroecology is that the former allows a phylogenetically explicit evaluation of evolutionary hypotheses that seek to explain large-scale diversity patterns (Cardillo 2011; Tucker et al. 2016). In a macroecological context, the phylogenetic structure of an assemblage can be interpreted in terms of actual evolutionary processes such as geographic speciation and phylogenetic niche conservatism (Kissling et al. 2012; Villalobos et al. 2013).

One of the first applications of CP to macroecology, in which species' distributions were used to map phylogenetic structure, evaluated the Tropical Niche Conservatism (TNC) hypothesis as an explanation for the LDG of New World treefrogs (Hylidae; Algar et al. 2009). Under the TNC hypothesis, Algar et al. expected to find a correlation between species richness and phylogenetic structure (using the Phylogenetic Species Variability index; PSV, Helmus et al. 2007), as well as between each of these variables and a common set of explanatory climatic variables. However, they were unable to detect a correlation between species richness and phylogenetic structure, and found each one to be correlated with a unique climatic variable, thus not supporting TNC as an explanation for the LDG in treefrogs (Algar et al. 2009). Differently from Algar et al. (2009), however, studies of other biological groups—including Furnariides (Pinto-Ledezma et al. 2017)—were able to apply a similar approach and found support for TNC as one of the explanations for diversity gradients in the Neotropics. Indeed, there is broad correspondence between Furnariides species richness (Fig. 5.1a) and phylogenetic structure (PSV; Fig. 5.2d), with more related species co-occurring in species-poor subtropical/temperate areas, and more distantly related species co-occurring in species-rich tropical areas.

Another community phylogenetics tool that has been recently expanded to a biogeographical scale is the analysis of Principal Coordinates of Phylogenetic Structure (PCPS; Duarte et al. 2016). Given a map in which each grid-cell is associated with a list of species, and given a phylogenetic hypothesis relating all species, this method extracts eigenvectors from a matrix expressing the phylogeny-weighted species composition (i.e. species presence considering their phylogenetic similarity) for each cell (Duarte et al. 2016). These eigenvectors reveal orthogonal phylogenetic gradients across the studied region. Maestri et al. (2016) recently applied PCPS to model the body size variation (Bergmann's rule) among sigmodontine rodents in South America, with the first PCPS being used as an explanatory variable revealing assemblage phylogenetic structure. By doing so, Maestri et al. (2016) found that the combined influence of both phylogenetic composition and environmental factors is more important than each variable alone in driving Bergmann's rule in sigmodontine rodents. When we applied the PCPS approach to our Furnariides dataset, the spatial gradient derived from the first PCPS

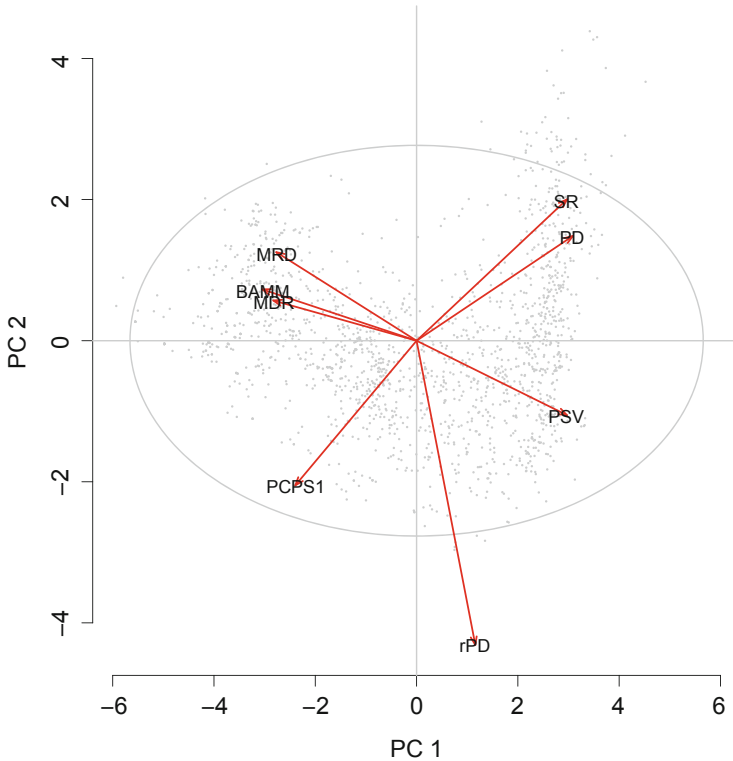


Fig. 5.3 Principal Component Analysis (PCA) biplot showing the ordination of Furnariides assemblages according to the grouping of their evolutionary variables. *SR* species richness, *PD* phylogenetic diversity; the rest of the acronyms correspond to those of Fig. 5.2

axis showed a clear distinction in phylogenetic structure between open and forest habitat assemblages—similar to those found for the other metrics (MRD, DR, PSV; Fig. 5.2e) and confirming our previous findings of differential phylogenetic structure between these habitats (Pinto-Ledezma et al. 2017, 2019).

Our analyses of the Furnariides in the Neotropics show that the alternative methods used to detect assemblage phylogenetic structure (Fig. 5.2) are, indeed, quite similar. This similarity is evident when we use a Principal Component Analysis (PCA) on the spatial correlation matrix among the maps of the six phylogenetic metrics and species richness. In this analysis, the loadings of the PCA were used to express the similarity in geographic space of the first two PCs, which accounted for 83% of the variation among the maps. In general, the alternative methods produced quite similar results (i.e., along the first axes of the PCA), with the exception of rPD—which showed mixed patterns between open and forest habitats (Fig. 5.3). As previously discussed, all methods tend to show the high level of “derivedness” of the Furnariides assemblages in open habitats.

Significant phylogenetic structure (clustering or overdispersion), the basis of the CP framework, depends on the scale of the sampling pool from which assemblages are composed, both spatially and phylogenetically (Cavender-Bares et al. 2009; Kissling et al. 2012; Graham et al. 2018). Indeed, evaluating assemblage phylogenetic structure in relation to sampling pools from different spatial extents can inform about the critical scales at which assembly processes act (Kissling et al. 2012). For instance, by studying a collection of palm assemblages across the world at the global, hemispheric, and biogeographic realm scales, Kissling et al. (2012) found that Neotropical assemblages show significant phylogenetic clustering within the first two spatial scales, but not the third. They interpreted such pattern as a strong signal of in situ diversification and geographic isolation. Considering different phylogenetic scales (a hierarchy of mutually nested clades; e.g. large clades containing subclades as in taxonomic families containing genera; Graham et al. 2018), can also lead to different findings regarding the phylogenetic structure of assemblages. For instance, in New World leaf-nose bats (Phyllostomidae), which are a major component of the Neotropical mammal fauna, assemblages showed high PSV values (thus phylogenetic overdispersion) towards the equator, which may be related to higher diversification in this region (Villalobos et al. 2013; Arita et al. 2014). However, another study showed opposite patterns when considering a higher-level taxon, the bat superfamily Noctilionoidea (Stevens et al. 2013), with lower PSV values and thus phylogenetic clustering towards the equator. Such opposite patterns across phylogenetic scales highlight the abovementioned need to consider the effect of scale (Graham et al. 2018).

Finally, another relevant scale component in a study of phylogenetic structure patterns is the unit of analysis—whether sites (site-based) or species (species-based). A site-based approach is most commonly used in community phylogenetics studies, whether at local, regional or global scales (Cardillo 2011; Kissling et al. 2012). However, considering individual assemblages as the study unit (site-based) is not necessarily equivalent to considering complete species' ranges (species-based) as such unit; especially when the former approach does not consider all sites where a particular species occurs (Villalobos et al. 2013). Given that the geographical coexistence among species (dictated by the size, shape and location of their whole ranges; Gotelli et al. 2009) ultimately determines large-scale biodiversity patterns, we should expect causal processes to be discernable at the level of species' ranges (Villalobos et al. 2013; Barnagaud et al. 2014). Thus, a species-based approach can be at least complementary to a site-based approach to evaluate evolutionary processes at biogeographic scales (Villalobos et al. 2017). So far, only one study has applied the phylogenetic field approach for a Neotropical clade (bat family Phyllostomidae; Villalobos et al. 2013), but studies at global and regional scales for birds (Barnagaud et al. 2014; Miller et al. 2017b) and mammals (Villalobos et al. 2017) have shown the potential of such approach in revealing interesting patterns and their potential evolutionary causes.

4 New Methods to Study Diversification at Macroecological Scales

In the last few years, there has also been an impressive increase in the availability of phylogenetic comparative methods (PCMs) to study evolutionary processes (Garamzegi 2014; Cooper et al. 2016)—mainly in terms of diversification rates (i.e. speciation minus extinction rates; Morlon 2014). While most diversification models provide estimates on speciation and extinction rates for the whole phylogeny (ies) under study, Rabosky (2014) introduced BAMM (Bayesian Analysis of Macroevolutionary Mixtures) to evaluate diversification rates at any point in time (including each of the individual species) across a time-calibrated phylogenetic tree. Given known limitations for accurately estimating extinction rates, BAMM-derived rates commonly focused solely on speciation rates (Rabosky et al. 2015).

Because BAMM allows us to estimate rates as a species-level attribute, they can be rasterized and mapped in geographic space by assigning rate values to the geographic distribution of the species, as explained above. Yet so far, few studies have mapped rates to evaluate, for instance, the presence of important areas of diversification (Perez-Escobar et al. 2017), or the museum/cradle role of diversity refugia (e.g. Morales-Barbero et al. 2018). For example, Perez-Escobar et al. (2017) mapped speciation rates of Neotropical orchid lineages and were able to identify speciation hotspots in different regions such as the Northern Andes and Central America. Their findings support geological events, such as the Andean uplift, in driving evolutionary processes of megadiverse groups like Neotropical orchids (see also Lagomarsino et al. 2016 for similar findings in bellflowers).

Contrary to those orchid and bellflower studies, our Furnariides maps do not flag the existence of speciation hotspot areas (Fig. 5.1f). Instead, they suggest that subtropical and temperate savannas, as a continuum, represent diversification arenas for this bird clade, supporting our previous findings using different approaches (Pinto-Ledezma et al. 2017). It is important to note, however, that mapping processes such as speciation rates also come with several caveats. For instance, assuming that speciation processes have occurred at sites where species are currently distributed can be particularly risky, especially given the dynamics of species ranges (Liow and Stenseth 2007).

All of the aforementioned approaches are based on mapping phylogenetic information of multiple species onto space, either by considering local inventories, or by rasterizing their geographic distributions. An alternative approach is to use the distributional information on multiple species and “map them” onto a phylogeny, by defining a “geographic trait” of species whose trait states depend on the particular location of each species within a geographic domain (e.g. tropical vs temperate distribution) (Goldberg et al. 2011; Jablonski et al. 2017). Indeed, recent phylogenetic comparative methods allow speciation and extinction rates to depend on species’ traits. These methods aim to disentangle the relationship between trait evolution and diversification rates, collectively referred as state-dependent speciation and extinction (SSE) methods (O’Meara and Beaulieu 2016). One such method

is the geographic state speciation and extinction (GeoSSE) model (Goldberg et al. 2011), which considers a species' geographic range as its trait, and includes spatial dynamics (i.e. dispersal rates) over two regions on the diversification process (Ramiadantsoa et al. 2017). Considering spatial dynamics, particularly range expansion and contraction (Goldberg et al. 2011), the GeoSSE model allows the inclusion of a third fundamental process responsible for the change in species numbers at a biogeographic scale, along with speciation and extinction: dispersal (Ricklefs 2004). In doing so, the GeoSSE model permits more complex exploration of evolutionary hypotheses.

Considering the tropical and temperate regions, for instance, recent studies have applied the GeoSSE model to evaluate predictions related to the Latitudinal Diversity Gradient in terms of speciation, extinction and dispersal rates. Based on existing interpretations of the LDG, species-rich areas (e.g. the tropics) would be expected to show higher speciation and/or dispersal rates relative to species-poor areas (temperate regions; Schluter and Pennel 2017). Yet, while some of studies have found support for higher rates in the tropics (mammals, birds, insects and flowering plants, Jansson et al. 2013; mammals, Rolland et al. 2014), others have found the opposite (reptiles, Pyron 2014). Such differences in macroevolutionary rates can also be observed between adjacent environments and habitats (Schluter and Pennel 2017), especially within species-rich regions such as the Neotropics (Pinto-Ledezma et al. 2017). Our previous work on Furnariides (Pinto-Ledezma et al. 2017) evaluated such rate differences between species-rich forest habitats and species-poor open habitats within the Neotropics, revealing a counterintuitive pattern where the latter habitats showed higher rates than the former habitats. This led us to suggest that the highest species richness in forest habitats depends upon the high diversification and rapid species colonization from open to forest habitats, as well as the stability of forest habitats through time, to allow for local species accumulation (Pinto-Ledezma et al. 2017).

Concerns on the use of SSE models have been raised recently, mainly related to interpretation of results and inflated Type I errors (Rabosky and Goldberg 2015; O'Meara and Beaulieu 2016; Alves et al. 2017). However, the few Neotropical studies published so far have applied a battery of methods to evaluate the robustness of their results (e.g. GeoSSE, BAMM, diversity-dependent models), showing that different methods were in fact consistent (Lagomarsino et al. 2016; Perez-Escobar et al. 2017; Pinto-Ledezma et al. 2017). Thus, despite well-founded concerns on SSE models, they appear to be useful exploratory tools.

5 Perspectives and Concluding Remarks

Our review discussed the advances and caveats of the distinct macroecological approaches currently available to investigate evolutionary processes associated with spatial gradients of species richness. Given that the multi-scale data needed to test these evolutionary processes have only been available in the last few years, or

decades at most (e.g. megaphylogenies, deep-time paleoclimatic data), several research avenues may still be explored.

Moreover, the analytical methods discussed here are not exhaustive. In addition to speciation and extinction processes, one may want to further focus on lineage dispersal over evolutionary time as a major contributor to geographic diversity gradients. To this aim, parametric biogeography has gained prominence, including methods implemented by software such as DIVA, DEC, LAGRANGE and BioGeoBEARS (see Ronquist and Sanmartín 2011; Albert and Antonelli 2017, and references therein). Parametric biogeography methods rely on the assumption that closely related taxa must have a similar geographic history (Ronquist and Sanmartín 2011), and are thus useful to disentangle the relative roles of cladogenetic and anagenetic processes driving diversity gradients. Different studies have used these approaches to evaluate dispersal as a driver of large scale patterns of species diversity, and to infer the ancestral areas (i.e. centres of origin) of clades (Wiens et al. 2011; Pyron 2014; Barker et al. 2015; Claramunt and Cracraft 2015; Dupin et al. 2017), or to support previous findings (Rolland et al. 2015). Integration with the overall research program on LDG is still missing, though, which opens an important research avenue (Albert and Antonelli 2017).

Another relevant framework to aid studies of spatial gradients is the simulation of biogeographical and macroecological patterns. Conceptually, one major difficulty in understanding the causes behind diversity patterns at large spatial and temporal scales is the inability to apply experimental approaches, leaving statistical analyses as an only option (Gotelli et al. 2009). Recently, however, macroecological approaches have bridged such difficulty by applying computer simulation models as an alternative to purely statistical analyses, allowing the explicit consideration of evolutionary dynamics in a spatial domain under changing environments. Rangel et al. (2007), for instance, applied a simulation model to evaluate the relative contribution of evolutionary mechanisms such as speciation and niche conservatism or evolution in creating the LDG for South American birds. They found that a Neotropical origin of species and strong conservatism of their niches generated an emergent diversity gradient that closely resembled the observed one (Rangel et al. 2007; see also Rahbek et al. 2007). While the complexity of the parameter space that the simulation models must explore may pose a computational challenge, more efficient programming and high-performance computers are overcoming these shortfalls (Cabral et al. 2017). A more complex model that couples empirical paleoclimatic data, dispersal, and adaptation to changing environments, while allowing for further parametrization regarding group-specific ecology and life history, has just been released (Rangel et al. 2018).

In summary, our review demonstrates that we now have multiple coherent metrics for capturing distinct components of evolutionary factors of diversity gradients. We have shown here that combining such evolutionary components into the study of diversity gradients—from species distributions and ages, to their phylogenetic structure and macroevolutionary rates—is not only possible, but also required for a comprehensive understanding of the most conspicuous pattern of biodiversity: its geographical variation. This is an exciting time for evolutionary macroecology.

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