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Research

Extreme environments filter functionally rich communities of Atlantic Forest treefrogs along altitudinal and latitudinal gradients

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Understanding how environmental filtering and biotic interactions structure communities across elevational and latitudinal gradients is still a matter of debate. To provide insight into their relative importance, we explore the mismatch between three dimensions of biodiversity (taxonomic, functional and phylogenetic), and compare their patterns to null models of random community assembly. We focus on a highly diverse tropical group: the tree frogs (hylids) of the Atlantic Forest of Brazil. For that, we combined geographic distribution data with phylogenetic and trait information for 158 species to produce maps of the three dimensions of diversity. We show that communities of tree frogs of the Hylidae family tend to have high functional richness along the Atlantic Forest, potentially driven by niche partitioning. However, environmental filtering gains importance in extreme environments, both at high elevations and higher latitudes. In these areas of the forest, clustering of both functional and phylogenetic diversity is observed. Trait overdispersion is found in areas of contact between vegetation types, or of adjacent biomes, reflecting the encounter of amphibian species adapted to distinct environmental conditions and landscape configurations. Considering all three dimensions of diversity along with multiple axes of environmental variation allows for a more comprehensive understanding of the processes shaping amphibian community assembly in this biodiversity hotspot.

Keywords: community ecology, dimensions of biodiversity, functional diversity, phylogenetic diversity

Introduction

How ecological processes shape community assembly has been an open debate for decades. Support for the neutral assembly of communities, where dispersal is the main limiting factor, is found in several plant systems and species-rich communities, such as tropical islands (Hubbell 2005, 2006). However, the relative roles of two



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deterministic processes – environmental filtering and competition – vary across taxa, ecosystems and environmental pressures (Webb et al. 2002, Emerson and Gillespie 2008, Devictor et al. 2010, Swenson 2011). Under environmental filtering, phenotypes that ensure survival at local (usually harsh) conditions can persist and become prevalent, and the local assemblage is expected to be composed by species of similar morphological, physiological or behavioral traits (Webb et al. 2002, Cornwell et al. 2006). Competition, instead, reduces the overlap (and enables partition) of niches, leading to assemblages whose species differ in their phenotypic traits (Tilman 2004).

Spatial patterns of the distribution of two dimensions of biodiversity – species richness and functional diversity – can provide insight about the relative importance of environmental filtering and competition as drivers of community assembly. Functional diversity, which focuses on local phenotypes, reflects the ecological variation that exists between local species: taxa that are more different in their traits contribute more to local functional diversity than those with similar traits (Petchey and Gaston 2002). In this context, environmental filtering is expected to lead to lower functional diversity than expected by chance at a site given species richness (trait under-dispersion, or clustering; Cornwell et al. 2006). Competition, in turn, is expected to lead to higher functional diversity relative to species richness (trait over-dispersion, Safi et al. 2011, Boyce et al. 2019, Zhou et al. 2019).

Yet because the compilation of large trait databases is often unfeasible, and given that phylogenetic conservatism is relatively widespread (Wiens and Graham 2005, Wiens et al. 2010), several studies have utilized a third biodiversity dimension – phylogenetic diversity – as a proxy for functional diversity (Webb et al. 2002, Fritz and Rahbek 2012, Zupan et al. 2014, Voskamp et al. 2017, Paz et al. 2021). Phylogenetic diversity is a measure of evolutionary history that accounts for the genealogical relationship between all local lineages, with more closely related lineages contributing less to phylogenetic diversity than distantly related ones. The challenge faced by those studies, however, is that phylogenetic and functional diversity can differ in their spatial patterns (Devictor et al. 2010, Mazel et al. 2018, Oliveira et al. 2020): those mismatches between functional diversity and phylogenetic diversity often highlight communities where both environmental filtering and biotic interactions are acting, only upon different sets of traits related either to niche or competitive differences (Cavender-Bares et al. 2004, Mayfield and Levine 2010). A full understanding of the processes shaping community assembly thus requires measurements of all three dimensions of biodiversity rather than the use of one as a surrogate of the other (Cavender-Bares et al. 2004, Kraft et al. 2007).

While these complementary dimensions of diversity have been previously studied in temperate (Devictor et al. 2010, Cadotte et al. 2013, Calba et al. 2014) and tropical lowland communities (Kraft and Ackerly 2010), they have rarely been mapped to address the relative importance of environmental

filtering and competition in the assembly of montane elevational gradients – particularly along latitudinal gradients in the southern hemisphere (Montaño-Centellas et al. 2019). Given the levels of climatic and topographic variation, and the opportunity for contact between species pools that explore distinct environments (e.g. lowlands versus high elevations), tropical and subtropical altitudinal gradients provide an interesting and challenging system to explore the relative importance of ecological processes driving community assembly through patterns of mismatch across the three dimensions of biodiversity (Dehling et al. 2014, Chun and Lee 2018).

Studies that have focused on the mismatch between biodiversity dimensions along tropical–subtropical elevational gradients diverge in their conclusions about the relative importance of processes of community assembly (Weinstein et al. 2014, Dreiss et al. 2015, Zhou et al. 2019). One possible reason for this lack of convergence is that these studies seldom address how altitude and latitude interact to define local environmental variation, and either intensify or buffer environmental filters. For instance, lowland tropical species have narrower climatic tolerances than temperate species, and may find resistance to overcome montane barriers as temperatures decrease with increasing elevation (Janzen 1967, Ghalambor et al. 2006). As such, diversity patterns in the (least seasonal) tropical lowlands may be more strongly impacted by competitive interactions relative to lowland areas located in subtropical areas farther from the Equator. In turn, subtropical (more seasonal) regions are expected to reflect the increased effect of environmental filters (Algar et al. 2011). Moreover, while high elevations are expected to show increased environmental filtering, tropical mountaintops may experience milder conditions than subtropical mountaintops – hence resulting in comparatively less filtering and more functional diversity (Fig. 1a, b).

To test if and how latitudinal gradients interact with elevation in a Neotropical montane system and impact the strength of environmental filtering and inter-species competition, we quantify and contrast spatial patterns of functional, phylogenetic and taxonomic diversity in the Brazilian Atlantic Forest hotspot. This region includes a striking latitudinal gradient of ca 25 degrees, and elevations ranging from 0 to 2000 m above sea level (a.s.l.) along most of the Atlantic coast of South America (Fig. 1c, Veloso et al. 1991). Within the Atlantic Forest domain, climate varies latitudinally and with distance to the coast, and across elevational gradients (Supporting information). Colder temperatures and higher temperature seasonality are reached in the southern (subtropical) half, particularly at higher elevations (Fig. 1c, Supporting information). In contrast, precipitation reaches its lower values, and higher seasonality, in the interior deciduous forests at northern (tropical) latitudes, and in the interior semi-deciduous forests along the central domain of the forest (Fig. 1d, Supporting information).

In this system, we studied frogs of the Hylidae family, one of the most widely distributed and diverse family of anurans

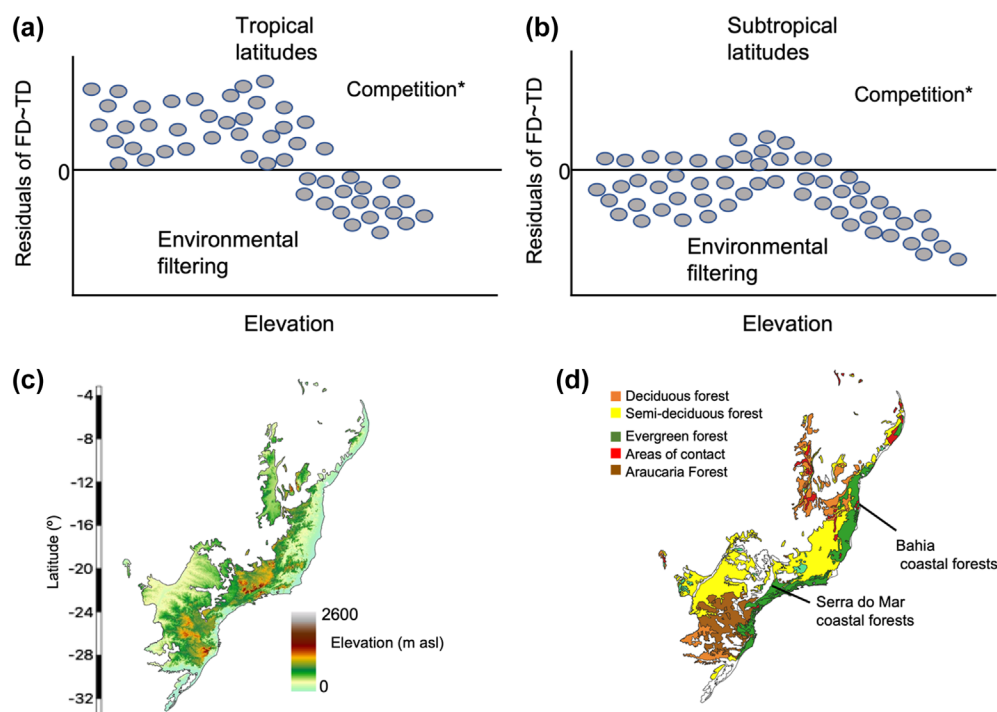


Figure 1. (a and b) Expected changes in the mismatch between taxonomic diversity (TD) and functional richness (FD_{rich}) across elevation at different latitudes: (a) tropical and (b) subtropical. Mismatch is represented by the residuals of pairwise models of TD on FD. In this case, positive residuals represent more functional diversity than expected given species richness (a potential signal of competition), and negative residuals represent less functional diversity than expected given species richness (a potential signal of environmental filtering). These expectations assume no environmental variation within latitudes. * Ecotones or areas of contact of distinct environmental spaces are also expected to have positive residuals of the $FD \sim TD$ regression. (c) For contextualization, an elevation map of the Atlantic Forest domain and (d) a map of vegetation and regions discussed in this paper are provided. Coastal evergreen forests in green, semi-deciduous forests in yellow, deciduous forests in orange, mixed (*Araucaria*) forests in brown and vegetation contact zones in red. Elevation data obtained from the WorldClim database (Hijmans et al. 2005). Simplified vegetation classification based on IBGE (2006).

(733 species, Frost 2020). Hylid frogs have distinct distribution patterns, constituting an appropriate group for the questions asked here. More than 500 species of hylids occupy a variety of habitats along the elevational gradients of South America; of those, ca 200 inhabit the Brazilian Atlantic Forest (Haddad et al. 2013). Although hylids are referred to as tree frogs, this group includes pond-breeders, stream specialists and arboreal species, as well as the subfamily Pseudinae which represents tree frogs that, in the course of evolution, returned to the aquatic environment, assuming a ranid morphology. Body size is the main axis of phenotypic variation in hylids (Moen et al. 2009) and species in this family range from ca 20 mm to 10 cm+ long. Moreover, hylids are found in a diversity of environmental conditions, and several species have adaptations to the cold extremes at both high latitudes and high elevations (Navas 1997).

Based on what is currently understood about the relationships between the ecological processes of competition and ecological filtering and the spatial patterns of taxonomic, phylogenetic and functional diversity, we hypothesize that, in the Atlantic Forest system:

1) Higher trait similarity, and hence lower functional diversity relative to species richness, should be prevalent at higher elevations of the Atlantic Forest where species

experience colder temperatures – and particularly strong in mountaintops at the southern, subtropical latitudes (Fig. 1a, b). We expect this given that environmental filtering is known to be a dominant process driving community assembly in areas of challenging environmental conditions. Assuming that traits are conserved across the Hylid phylogeny, we also expect to find lower phylogenetic diversity relative to species richness in these areas.

- 2) Reduced functional and phylogenetic diversity relative to species richness should also be observed as precipitation regimes become harsher in the deciduous and semi-deciduous (inland) forests of the Atlantic Forest. Similarly to (1), we expect this to happen as a function of environmental filtering, only now in relation to water availability as opposed to cold temperatures.
- 3) Higher functional and phylogenetic diversity than expected by chance should occur at low and mid-elevations of the more northern, tropical latitudes of the Atlantic Forest. We expect this given that environmental filtering should be relaxed, and competitive interactions to play a larger role, in these areas of high energy availability and productivity.
- 4) Contrasting patterns of functional and phylogenetic diversity should be detected in lowland areas of the

subtropical latitudes. Although seasonal, these sites should experience conditions that are milder than those in the subtropical highlands. In these areas, we expect both competitive interactions and environmental filtering to be acting (Fig. 1b), resulting in high phylogenetic diversity (because of competition between conspecifics), but low functional diversity (given that a more homogeneous set of traits facilitates survival in these more dynamic, sometimes extreme, environments – such as the deciduous forests; Fig. 1d).

- 5) Higher functional and phylogenetic diversity should occur in mid-elevation regions of the Atlantic Forest and ecotones, such as the deciduous forest regions in the mountain blocks to the northwest (Peres et al. 2020), which border the adjacent savannahs of the Cerrado (Fig. 1b, red). We expect that any sites of contact of different environmental spaces will show high diversity of traits and evolutionary histories relative to species richness because their communities will have a mix of species with distinct biogeographic histories and adaptations to different environmental conditions (cool versus warm environments along a mountain; wet versus seasonally dry in latitude).

Methods

Occurrence data

To select the species to be included in this study, we used the list of amphibians of the Atlantic Forest provided by Haddad et al. (2008), but excluded what is now recognized as the Phyllomedusidae family (which was then included as Hylidae) and island endemics, for a total of 182 species. A dataset of species occurrences was built from the Célio F. B. Haddad amphibian collection (CFBH) in the Departamento de Biodiversidade, I.B., Universidade Estadual Paulista, Rio Claro, SP, Brazil, The Global Biodiversity Information Facility (GBIF 2019) and the speciesLink database (CRIA 2020). To vet the occurrence data, we ensured they corresponded to the locality being described and not to centroids of municipalities or states. Species records were checked against the distribution maps provided by the International Union for Conservation of Nature (IUCN et al. 2006), both visually and through a coded script, to highlight outliers (available in the GitHub repository for this manuscript). Flagged localities were verified carefully for validity (coordinate accuracy, associate publications and identifier name) and kept if deemed trustworthy. Species classified as micro-endemics by the IUCN (restricted to one specific location), or which had no available or trustworthy locality information after validation, were excluded from the analysis. After this process, our analysis included data for 158 species, representing 87% of the 182 species in the family in the Atlantic Forest (Supporting information), and a total of 17 836 occurrence points (GitHub repository).

Trait and phylogenetic information

For all species with appropriate occurrence data, we compiled information on reproductive mode as per Haddad and Prado (2005), along with species size (snout vent length, SVL), head width and tibia length as per Watters et al. (2016). These morphometric traits relate to habitat use, diet and dispersal, respectively (Cortés Gomez et al. 2016). This strategy excluded those traits that are mostly conserved within the family, such as the type of larvae, presence of adhesive discs and arboreal habits (Vitt and Caldwell 2013). For SVL and reproductive mode, most data were extracted from Haddad et al. (2008) and complemented with Melo et al. (in prep.). For head width and tibia length, information was complemented from original species descriptions, as needed. For those species for which we could not find information, we used data imputed phylogenetically by Melo et al. (in prep.). All morphological data were log-transformed for further analyses. Detailed information on trait sources can be found in the Supporting information. To estimate phylogenetic diversity, we downloaded and used the consensus amphibian phylogeny from VertLife; this tree had been generated with Phylogenetic Assembly with Soft Taxonomic Inferences (Jetz and Pyron 2018), including all available molecular data for amphibians and the taxonomic backbone of AmphibiaWeb.

Species distribution maps

For species with more than five occurrence points, we created species distribution models using a presence/background method in Maxent V3.4.4 (Phillips et al. 2021). We first generated sets of occurrences for each species that were spatially separated by spatially thinning the data to 5 km (i.e. if more than one point was present in a 5 km radius, only one was kept). For that, we used the *spThin* package for R (Aiello-Lammens et al. 2015). Nineteen bioclimatic variables from the WorldClim database (Hijmans et al. 2005), which describe trends in temperature and precipitation, were downloaded at 30" (~1 km) resolution and used as environmental data for model building (~1 km, Hijmans et al. 2005). All models were trained with 10 000 background points for each species, and sampled from within a minimum convex polygon that included all occurrences and a 100 km buffer.

For model tuning, we used the *ENMeval* ver. 0.3.1 package for R (Muscarella et al. 2014). For each species, we tested different combinations of feature classes, allowing for different responses to predictor variables (Linear, Linear Quadratic, Hinge and Linear Quadratic Hinge features) and different regularization multipliers penalizing model complexity (with values ranging from 0.5 to 4, in 0.5 steps). For model testing, we used two different approaches. For species with more than 20 occurrence points, we used random-k-fold validations with five groups (k=5). For species with 20 points or less, we used a special case of the random-k-fold method, where the number of groups equaled the number of observations, referred to as the n-1 jackknife method (Pearson et al. 2007). To identify the best model

among those compared, we used sequential criteria and selected the model with the lowest omission test rate (OR) and then the highest test area under the curve (AUC) for each species. For all downstream analyses, we applied the species-specific 10th percentile training presence threshold (T10, Pearson et al. 2007) to transform the models to a binary (suitable/unsuitable) prediction. Because threshold selection can affect the downstream analyses (Pearson et al. 2007), we also used an alternative threshold – the minimum presence threshold (MPT, Pearson et al. 2007) – to assess the robustness of the results.

For species with fewer than five occurrence points, or with very poor model statistics (AUC of less than 0.5 and very high OR), we opted not to use a species distribution model in our analysis. Instead, those species were added as rasterized points, with pixels mapped as present if they contained an occurrence point. In total, we created 118 species distribution models (representing 75% of the total number of species), of which 14 had inadequate performance and were not used. A total of 104 species models were used (66% of the total number of species) and 54 species (34%) were represented in our maps as points. The use of points to represent these very narrowly distributed species can potentially underestimate their distribution; however, we employed them because expert range maps are not available for all of them or might misrepresent their distributions. Further, including those species as polygons built from a very small number of occurrence points would likely overestimate their distributions, especially at the resolution used here (and would only be possible for species with at least three occurrence points, which still leaves at least half out). Our species distribution models were therefore based on 5–153 points, depending on the species (Supporting information), and had an average test AUC of 0.78 and an average test OR_{MPT} of 0.19 (Supporting information). The script used to generate models and map points is available in the GitHub repository for this manuscript.

Diversity maps

To create diversity maps we used the R software; the script is available in the GitHub repository for this manuscript. For that, all binary distribution maps (thresholded species distribution models, and rasterized occurrence points) were stacked and summed, and the sum was used as a proxy for the number of species present in each pixel (~1 km pixel) – hereafter referred as taxonomic diversity. We are aware that the use of stacked SDMs can overestimate richness (Graham and Hijmans 2006, Hurlbert and Jetz 2007). However, recent studies show they perform better than alternatives such as joint SDMs; although probabilistic stacking reduces bias in the estimation of species richness, it loses vital information on community composition (Zurell et al. 2020). There is no survey of every pixel at every time point in the Atlantic Forest to ground-truth our predicted communities. However, a data paper compiling surveys of amphibians in the forest, the ATLANTIC-Amphibians (Vancine et al.

2018), allowed us to compare our predicted communities to ground observations. As expected, we found that our method detects more species than the surveys (because of different temporal and geographical scale of analyses) but that they are very good at predicting the species detected by the surveys (on average only 2 are missed).

We then converted the species distribution stack into a community composition matrix, with each column representing one species and each row representing one pixel. Using this community composition matrix and the phylogenetic tree of the group, we computed a per-pixel phylogenetic diversity index PD (Faith 1992), using the *pd* function in the R package *picante* (Kembel et al. 2010). For each pixel, the PD index was computed as the sum of branch lengths leading to all present lineages.

Lastly, using the community matrix and the compiled trait database (Supporting information), we computed indices of functional richness (Villéger et al. 2008) and functional dispersion (Laliberté and Legendre 2010) for each pixel, using the *dbFD* function in the R package *FD* (Laliberté et al. 2014). This allowed us to obtain information on both the amount of trait diversity and the overall differences between species in each community. Functional richness (FD_{rich}) for each community (here, each pixel) was calculated as a convex hull volume representing the richness of trait space in the community. In turn, functional dispersion (FD_{dis}) was computed from a species-species trait distance matrix, representing the dispersion of traits in the community (and thus independently of species richness). Because the computation of functional dispersion requires that the trait distance matrix be Euclidean, we corrected it using the ‘cailliez’ method (Cailliez 1983). When analyzing reproductive modes, which are a categorical variable, the computation of functional richness requires the reduction of data dimensionality via a principal coordinate analysis (PCoA) and the use of a reduced number of axes, resulting in data loss. Because we observed substantial data loss after running the PCoA analyses on the total trait data (which include information on reproductive modes plus morphology, resulting in a quality of reduced representation of only 0.22), we also computed functional richness based solely on the continuous traits, ensuring very little data loss (quality of the reduced representation 0.98). We nonetheless kept both results for functional richness to explore whether the inclusion of reproductive mode provides unique insight into the distribution of diversity.

Detection of mismatch between diversity dimensions and elevational patterns

To identify areas of potential non-random assembly of communities of tree frogs in the Atlantic Forest, we compared the observed values functional diversity against a null model of random assembly of the community. For that, in each pixel, we randomly selected *x* species without replacement (where *x* is the per pixel taxonomic diversity) from the list of species of hylids included in this study (Supporting information).

This procedure was repeated 10 000 times for each pixel. For each of the 10 000 randomizations, we computed indices of functional richness (both with and without reproductive mode) and functional dispersion per pixel. We then compared the observed functional diversity indices against the null distribution in a two-tailed test (with alpha 0.05) to obtain a p-value and identify the direction of the difference: higher or lower index value than expected under null distribution. A map was then created for each of the three functional diversity indices, highlighting those pixels with significant departures of neutrality (p-values lower than 0.05). Because the null model of random assembly is dependent on the species pool (Kraft et al. 2007), and given that the Atlantic Forest domain includes multiple species pools of distinct biogeographic histories, we divided the forest roughly into a Northern and Southern climatic space, as defined in Carnaval et al. (2014) based on an environmental PCA. Each one of these divisions is bioclimatically unique and has been shown to have different vertebrate community composition (Carnaval et al. 2014). As such, we defined two species pools and created null models for each of the two climatic spaces of the forest separately, following previously described steps for the entire forest null model. We also defined species pools using dispersion fields (Lessard et al. 2012): in this case, the pool is defined by the range of all species present in the community. Because this method is more computationally intensive, the dispersion field analysis was repeated 1000 times (instead of 10 000 times) for each pixel, and was done for pixels of 10 km resolution (instead of 1 km).

Although functional and phylogenetic diversity are expected to increase with a higher number of species, they not always do so linearly. Areas where a mismatch between different dimensions of diversity is detected often indicate the influence of one or more ecological processes. For example, when there is less functional or phylogenetic diversity than expected given species richness, environmental filtering may be at play (Fig. 1a, b). On the other hand, areas with higher functional or phylogenetic diversity than expected given species richness might be indicative of competition (Fig. 1a, b). To detect areas where different dimensions of biodiversity were not fully congruent, we produced generalized additive models (GAM) of different pairwise combinations of diversity indices, and computed the residuals of each model. In total, we computed the residuals of four different GAM models: between 1) functional richness (FD_{rich}) and taxonomic diversity (TD), 2) functional richness (FD_{rich}) and phylogenetic diversity (PD), 3) functional dispersion (FD_{dis}) and phylogenetic diversity (PD) and 4) phylogenetic diversity (PD) and taxonomic diversity (TD). Since functional dispersion is not affected by species richness, we did not model that relation. We mapped the residuals of each model to pinpoint areas of positive or negative residuals in the forest. Areas of positive residuals have more functional or phylogenetic diversity than expected given species richness, whereas areas of negative residuals have less functional or phylogenetic diversity than expected given species richness.

Finally, we used an elevation raster from the WorldClim 2.0 database at a 1 km resolution (Fick and Hijmans 2017) to explore the relation between the mismatch of different dimensions of biodiversity and elevation. Because the Atlantic Forest encompasses such a wide latitudinal gradient, we divided the forest in latitudinal bands corresponding to deciles of latitude. The two extreme latitudinal bands (1 and 10) encompass only a very small fraction of forest and were not studied further. We then plotted the changes in the mismatch between dimensions of biodiversity across elevational gradients in eight different latitudinal bands. To quantify the effect of both latitude and elevation on the residuals of the different pairwise combinations of diversity measures, we created GAM models than included elevation, latitude and their interaction as predictors of the residuals. The GAM models were built using the *mgcv* package for R (Wood 2011) and were fit using the *ti* smooth for modeling interactions.

Results

While the diversity of hylid species and evolutionary lineages is concentrated along the coast of the Atlantic Forest (broadly matching the location of the Serra do Mar and Bahia coastal forests; Fig. 1d and 2a, b), functional diversity is much more widespread (Fig. 2c, d). These general patterns were similar to those based on species distribution models to which a different threshold (minimum presence threshold) was applied (Supporting information). The richness of morphological traits (functional richness based on body measurements only) is not only elevated along the coastal forests, but also in inland regions occupied by semi-deciduous forests (Fig. 2c). When morphology and reproductive modes are combined, functional richness is even higher along the coast and through most of the interior (Fig. 2d). However, when the trait data are summarized as a function of how different the traits are to each other (i.e. representing functional dispersion, instead of functional richness), it becomes clear that the communities with the largest difference in trait values are found in the deciduous forests in the mountain ranges to the northwest, where the forest borders the seasonally dry Cerrado. It should be noted that this gradient nonetheless shows much less variation than the others (Fig. 2e).

A comparison of these patterns against null models of random community assembly (Fig. 3) confirms that the Atlantic Forest is composed of hylid communities that have significantly higher functional richness than expected, both for size and reproductive modes. This holds irrespectively of how the species pool is defined in the randomization exercise: they are evident when all species pools are defined as dispersion fields (Fig. 3), when all species are combined into a single pool (Supporting information), and when they are split into northern and a southern species group (Supporting information), and). Furthermore, when including reproductive mode in the analysis, the coastal forests of the Serra do Mar and the Bahia Coastal Forests not only have significantly more functional diversity, but

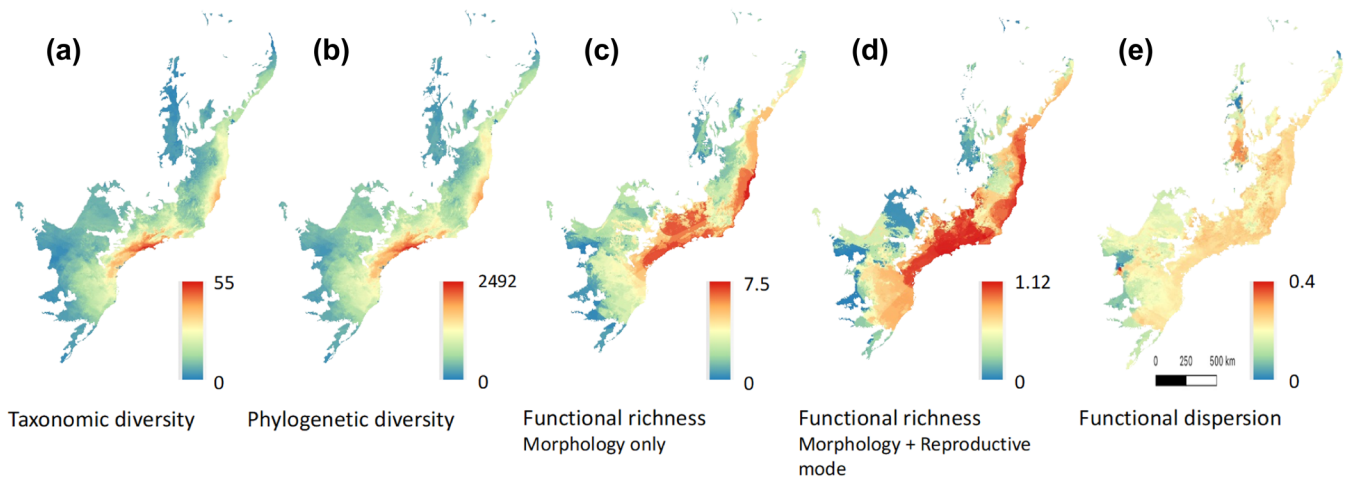


Figure 2. Patterns of hylid biodiversity in the Atlantic Forest. (a) Taxonomic (species) richness, (b) phylogenetic diversity, (c) functional richness measured from morphology, (d) functional richness measured from morphology and reproductive modes and (e) functional dispersion. Warmer colors represent higher diversity, colder colors depict lower diversity.

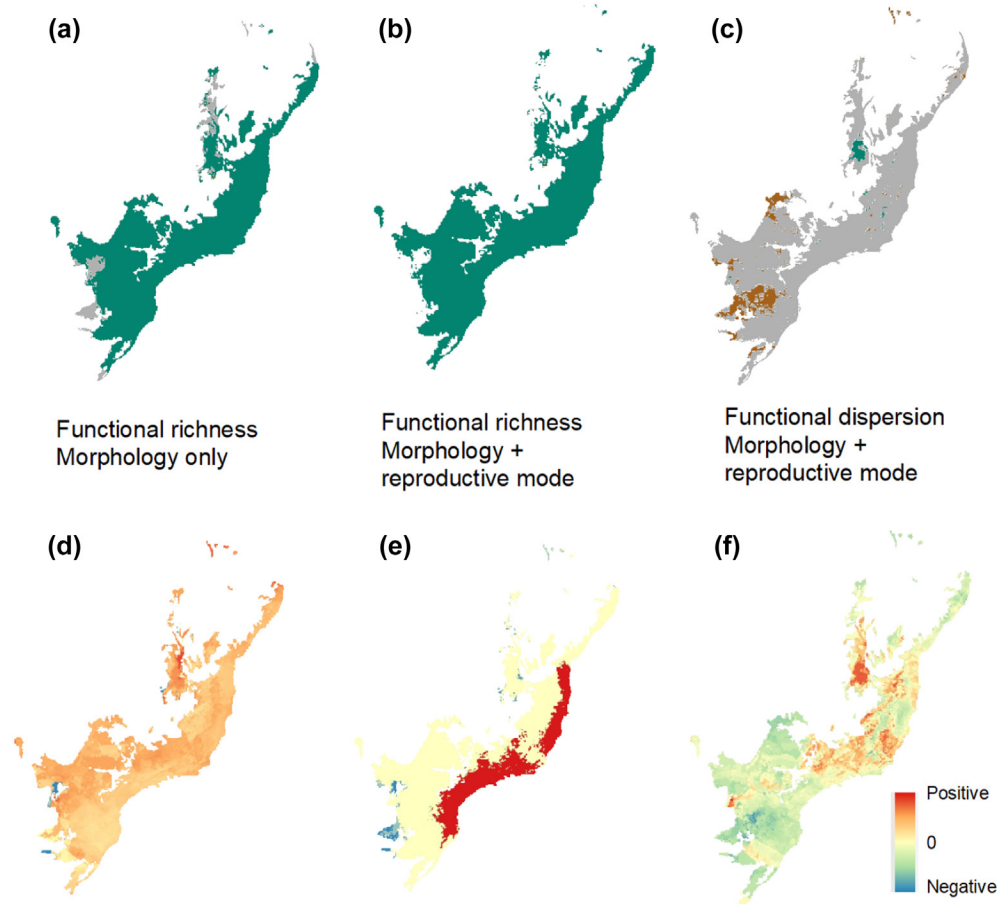


Figure 3. Results from comparisons against null models created based on dispersion fields for each community (pixel). In the first column (a, d), functional richness is derived from morphological traits only. In the middle column (b, e), functional richness is derived from morphology and reproductive mode. In the last column (c, f), functional dispersion is derived from morphological traits and reproductive mode. Panels a–c depict Atlantic Forest regions with higher (green) and lower (brown) functional diversity relative to expected under null models. Areas in grey did not present significant differences from null model expectations. Panels d–f depict the z-values of the null models, with warmer colors depicting positive z-values and colder colors depicting negative z-values. The z-values vary from (d) -1 to 39.5 , (e) -1.1 to $2.2e^{35}$ and (f) -4.28 to 2.9 .

also the greatest magnitude of difference (Fig. 3e). When functional dispersion is compared against the null models, two reasonably large and several small regions of non-random assembly are detected. In agreement with the distribution maps (Fig. 2), more functional dispersion than expected under random assembly is detected in the patch of deciduous forests in the tropical northwestern region, adjacent to the Cerrado domain (Fig. 3c, f). Small areas of similarly high functional dispersion are also observed in the northern half of the forest, in sites where the humid coastal forest meets the semi-deciduous forest (Fig. 1d and 3c, f). On the other hand, less functional dispersion than expected is found in the southern and cooler (subtropical) part of the forest domain, where the *Araucaria* forests are commonly found (Fig. 3c, f). This general pattern also holds when the models of non-random assembly are run separately for the northern and southern frog species pools (of 118 and 128 species respectively), although the size of the regions detected as having more and less functional dispersion notably decreases (Supporting information).

Maps of the mismatch between pairwise diversity metrics (Fig. 4) illustrate that functional richness is particularly higher than expected given the observed taxonomic diversity along

the northern coast and the inland semi-deciduous forests. Lower functional richness than expected is observed in the cold forest spaces occupied by the *Araucaria* Forest in the south, in the southern arm of the Serra do Mar mountain range, and in the seasonally dry deciduous forests in the northwest (Fig. 4d). Because a strong correlation between taxonomic diversity and phylogenetic diversity is observed (Fig. 4b), the relationship between functional richness and phylogenetic diversity is very similar to that between functional richness and taxonomic diversity (Fig. 3a; Supporting information), and so is the spatial distribution of their residuals (Fig. 3d; Supporting information).

Phylogenetic diversity is very tightly correlated with taxonomic diversity along most of the Atlantic Forest and broadly agrees with the functional diversity patterns, except in the *Araucaria* Forest (Fig. 4b, Supporting information). Because of this tight correlation, the observed relation between functional richness and taxonomic diversity is almost identical to that between functional richness and phylogenetic diversity (Fig. 4a, d and Supporting information). In agreement with the functional richness patterns, phylogenetic diversity is lower than taxonomic diversity in the northwestern mountain ranges at the border of the Cerrado, and

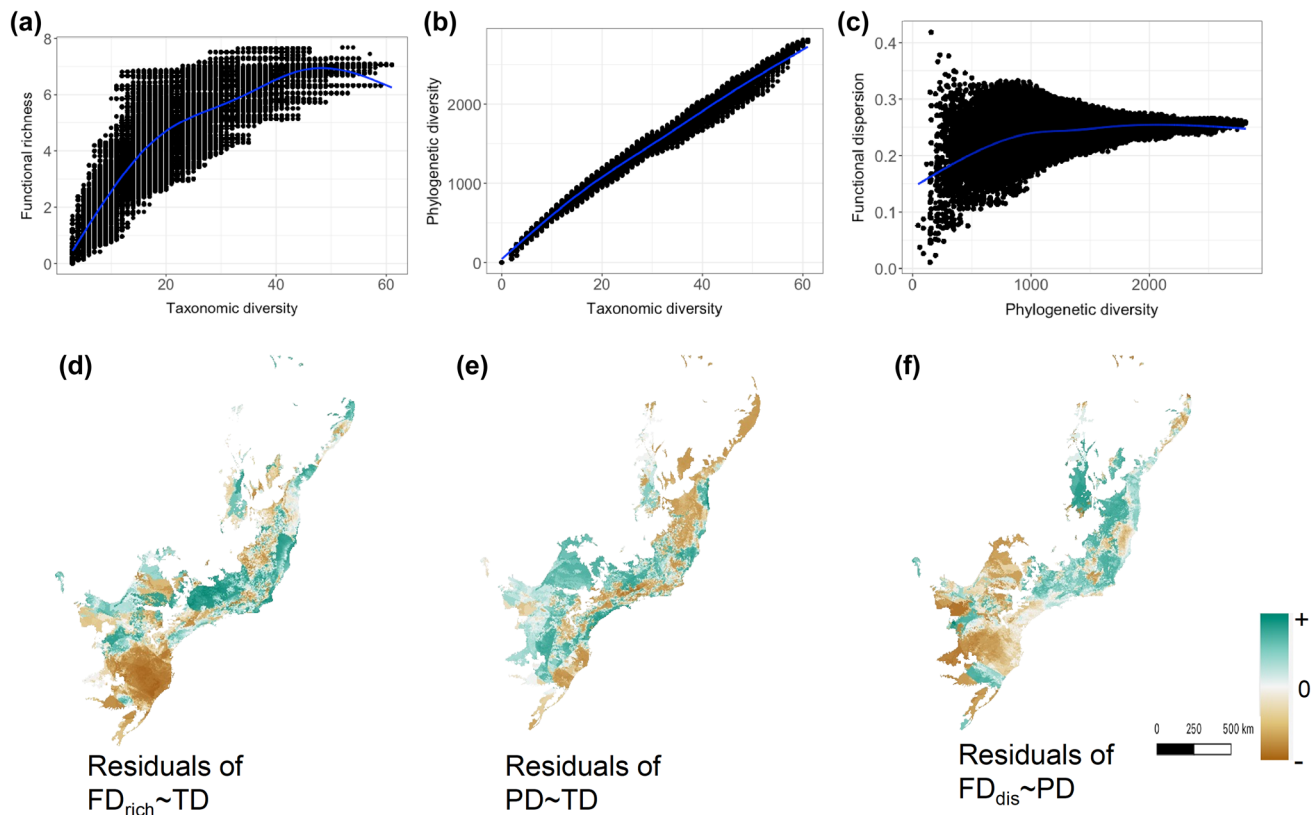


Figure 4. Relationship between dimensions of diversity in hyliid frogs of the Atlantic Forest. Panels a–c depict the following relationships: (a) taxonomic diversity versus functional richness, (b) taxonomic versus phylogenetic diversity and (c) phylogenetic diversity versus functional dispersion. Panels d–f map the residuals of the pairwise GAM models of the diversity measures shown in the first row. Maps depict the residuals of the GAM model of taxonomic diversity (TD) and functional richness (FD_{rich} ; d), the residuals of the GAM model of taxonomic diversity (TD) and phylogenetic diversity (PD; e), and the residuals of the GAM model of phylogenetic diversity (PD) and functional dispersion (FD_{dis} ; f). Each map is scaled to maximum/minimum values of the residuals of the corresponding model.

along the southern arm of the Serra do Mar. Other areas of lower phylogenetic diversity relative to taxonomic diversity are found in the very northern and southern limits of the domain (Fig. 4e). However, the subtropical Araucaria Forest, which has relatively low functional diversity and dispersion relative to the number of species, has higher phylogenetic diversity given local taxonomic diversity (Fig. 4e, Supporting information).

The relationship between functional dispersion and phylogenetic diversity differs from the previous comparisons. Functional dispersion stops varying once a certain threshold of PD is achieved (around $PD=2000$, Fig. 4c). Below that threshold, communities have either higher or lower functional dispersion than expected. Higher functional dispersion is observed in the northern part of the forest (Fig. 4f), and lower functional dispersion is more prevalent in the southern half (Fig. 4f), similar to the spatial patterns of functional richness (Fig. 4d).

Elevational and latitudinal patterns

In the Atlantic Forest, as you climb up, functional richness decreases towards expected values or lower (Fig. 5a, Supporting information). However, this pattern is not apparent with functional dispersion (Fig. 5c, Supporting information). The highest – and the lowest – levels of mismatch between functional richness and taxonomic diversity in the Atlantic Forest are observed in mid-elevation areas, around 1000 m a.s.l. (Fig. 5a). While functional richness is generally high across the forest (Fig. 2 and 3), these values decrease in areas of high elevations (above 2000 m a.s.l.) when compared to taxonomic diversity (Fig. 5a), and relative to phylogenetic diversity (Supporting information). The residuals of the GAM model between phylogenetic diversity and taxonomic diversity also decrease above 1500 m even more markedly than the prior pattern (Fig. 5b). Functional dispersion levels match those expected given phylogenetic

diversity, with residuals close to 0, in these high elevations (Fig. 5c).

The mismatch between functional richness and taxonomic diversity in the low- and mid-elevation areas, as well as that between phylogenetic and taxonomic diversity, varies with latitude (Fig. 6). When modeling the effect of elevation and latitude on the residuals of pairwise comparisons between different dimensions of diversity we found that elevation, latitude and their interactions can predict the residuals in a statistically significant way. Elevation and latitude explain 26.1% of the variance in $PD \sim TD$ residuals, 42.9% of the variance in $FD_{rich} \sim TD$ residuals and, 32.2% of the variance in $FD_{dis} \sim PD$ residuals. Low- and mid-elevation areas of the northern forests have higher functional richness than expected (latitudinal bands 9, 8, 7 and partially 6, Fig. 6). In the south, however, those altitudinal bands have lower functional richness than expected (latitudinal bands 2 and 3, Fig. 6). Phylogenetic diversity shows the opposite pattern, with lineage clustering in the north, and overdispersion in the south (Fig. 6). Low and mid-elevation species in the northern communities are thus closely related, but differ in their traits; those in the south, in contrast, have more homogeneous traits, but represent a diversity of evolutionary histories. The residuals of the GAM model of functional dispersion and phylogenetic diversity show a similar pattern: more functional dispersion than expected given the relatedness of the species is seen in the north, which thus has more divergent traits. In the south, a trend towards less dispersion of traits is only observed at low- to mid-elevations; no decoupling is seen at higher elevations (Fig. 6).

The filtering impacts of elevation are most strongly detected at latitudinal band 4 (Fig. 6). This area includes the northern part of the Serra do Mar coastal forests, as well as part of the semi-deciduous forests (Fig. 6). Together with latitudinal band 5, this region shows the broadest altitudinal gradient in the forest domain, and they jointly determine most of the general patterns observed for the forest as a whole

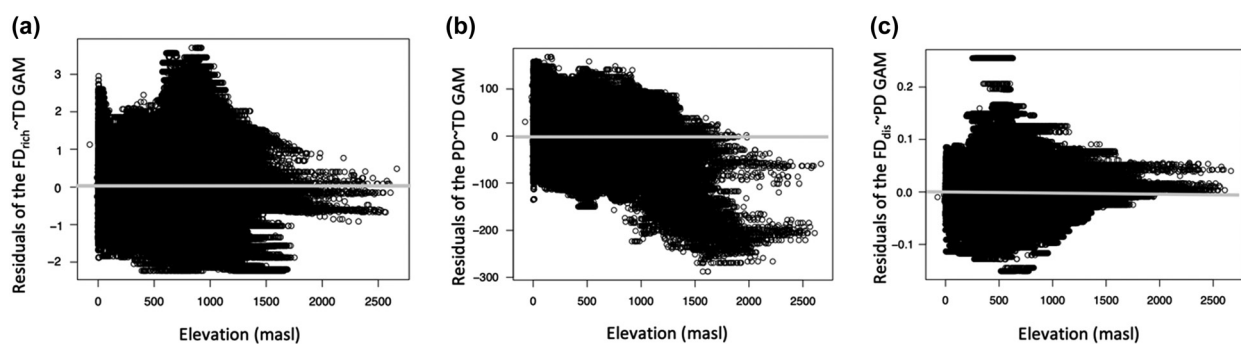


Figure 5. The relationship between elevation and the residuals of GAM models between pairwise dimensions of biodiversity. The grey line represents $y=0$ (no residuals). (a) Change in the residuals of the GAM model of functional richness (FD_{rich}) and taxonomic diversity (TD) across elevations; points below the grey line represent areas with less functional richness than expected given taxonomic diversity. (b) Change in the residuals of the GAM model of phylogenetic diversity (PD) and taxonomic diversity (TD) across elevations; points below the grey line represent areas with less phylogenetic diversity than expected given taxonomic diversity. (c) Change in the residuals of the GAM model of functional dispersion (FD_{dis}) and phylogenetic diversity (PD) across elevations; points below the grey line represent areas with less functional dispersion than expected given phylogenetic diversity.

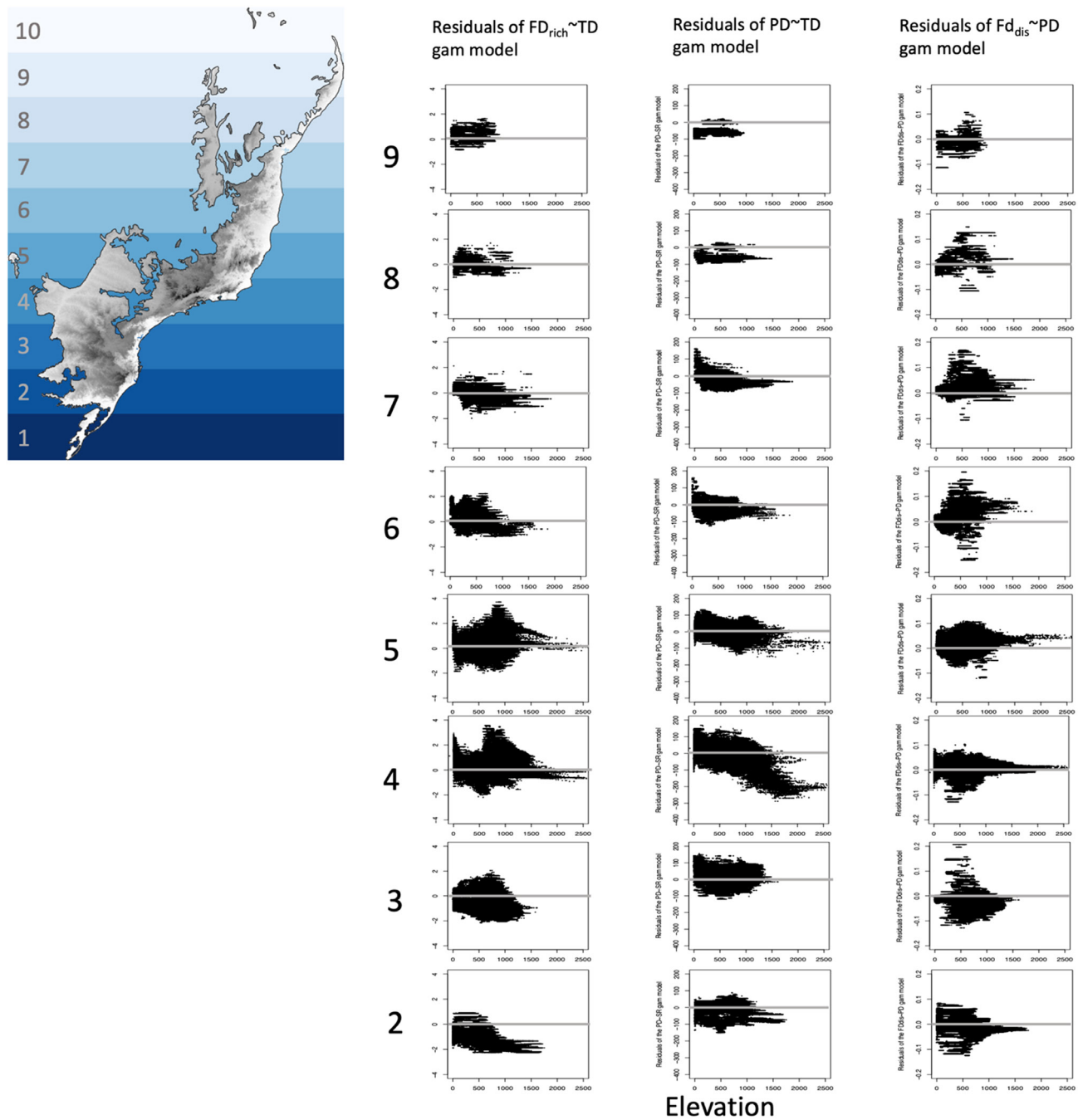


Figure 6. Residuals of the GAM models between biodiversity measures and their changes along elevation, across different latitudinal bands. Map on the upper left shows ten latitudinal bands in the Atlantic Forest in different shades of blue; each band is numbered. In the map, lower elevations are depicted in white, higher elevations in darker colors. Plots, from left to right, represent the change in the residuals of the GAM model of phylogenetic diversity (PD) and taxonomic diversity (TD) across elevations, the change in the residuals of the GAM model of functional richness (FD_{rich}) and taxonomic diversity (TD) across elevations, the change in the residuals of the GAM model of functional richness (FD_{rich}) and phylogenetic diversity (PD) across elevations, and the change in the residuals of the GAM model of functional dispersion (Fd_{dis}) and phylogenetic diversity (PD) across elevations. Each row represents a latitudinal band, as numbered. No plots are shown for latitudinal bands 1 and 10, for lack of data. In all plots, the grey line represents $y=0$ (no residuals); points below the line represent areas with negative residuals, those above the line represent sites with positive residuals.

(Fig. 5). Reductions in functional and phylogenetic diversity across elevation is hardly seen in the other latitudinal bands (Fig. 6, columns 1 and 2).

Discussion

Contrary to our expectations of pervasive signatures of environmental filtering (and thus relatively low functional diversity) in high elevations, subtropical latitudes and inland regions of the Atlantic Forest, we found that the functional richness of hylid communities is high across a large portion of this ecosystem – including sites that experience cooler temperatures or higher precipitation seasonality. This is reflected 1) in diversity patterns based solely on morphological data and on combined observations of morphology and reproductive mode (Fig. 2c, d), 2) in the patterns of mismatch between functional richness and taxonomic diversity (Fig. 4a) and 3) in comparisons against null models of functional richness. Not only the majority of the forest harbors more functional richness than expected in a randomly assembled community (Fig. 3a, b, d, e), but areas of higher functional richness than taxonomic diversity are observed in many elevations and latitudes (Fig. 6). The fact that distinct communities of Atlantic Forest hylids show a wide variety of body types and reproductive modes is consistent with observations of niche partitioning in amphibians (Toft 1985, Moen and Wiens 2009) and with studies of hylid diversification (Moen et al. 2009). This result is also aligned with the hypothesis that competitive interactions more strongly drive the assembly of communities in the tropics, even in the presence of altitudinal gradients (Boyce et al. 2019). Here, we suggest that competitive interactions may be a dominant process in community assembly in the Neotropics even in the presence of significant latitudinal gradients. This finding is robust even when community randomization tests are implemented in a way to allow for multiple regional species pools (Supporting information; Carnaval et al. 2014).

Nevertheless, we do encounter signals of environmental filtering in the system and demonstrate that the decoupling of the different dimensions of biodiversity changes with elevation and latitude (Fig. 6). In harsh environments – both at high elevations and at low- and mid-elevations in the cooler (subtropical) southern areas – environmental filtering appears to play some role in the assembly of hylid communities. This is shown by a trend towards decreased functional richness at the highest elevations (Fig. 5a), which is particularly evident along the sharp elevational gradient of the Serra do Mar in the southern half of the Atlantic Forest (Fig. 6). In these areas, decreased functional diversity is matched by a relative decrease in phylogenetic diversity (Fig. 6), suggesting an environmentally imposed filtering of traits and lineages. Similar patterns to this have been observed in Andean gradients and the African tropics (Dehling et al. 2014, Dreiss et al. 2015, Zhou et al. 2019). Reduced functional diversity in amphibians has also been shown in areas of high aridity (Ochoa-Ochoa et al. 2019).

The same environmental filtering process over traits is inferred to be present at low- to mid-elevations in the subtropical southern half of the Atlantic Forest, where functional richness is lower than expected relative to taxonomic and phylogenetic diversity (Fig. 6). However, and consistent with our prediction of multiple processes acting at lower elevations in subtropical latitudes, the filter is not apparent for communities with higher phylogenetic diversity relative to taxonomic diversity in the same area (Fig. 6). This mismatch between the patterns of functional diversity and phylogenetic diversity is likely the result of the expected intervention of different processes in the same community. It is likely that biotic interactions or secondary contact between separately evolving pools explain the presence of distantly related species in communities such as these, despite the homogenizing role of environmental filtering on functional diversity (Cavender-Bares et al. 2004).

Further evidence of environmental filtering is found at mid to high elevations in the colder (subtropical) latitudes, this time related to the magnitude of variation in observed traits (functional dispersion; Fig. 3). Null models of community assembly demonstrate that the values of trait dispersion in hylids living in the Araucaria Forest, measured for morphology and for reproductive modes, are significantly smaller (although with varying magnitude) than expected in a randomly assembled community (Fig. 3c, f). This observation is similar to those of Calixto (2018) showing the amphibian communities in the Araucaria Forest resemble those of temperate regions. Interestingly, the extent and location of these areas of low functional dispersal change when the null model is based only on the pool of amphibian species that occupy the southern half of the Atlantic Forest. While the latter recovers areas of the Araucaria Forest with lower trait dispersion than expected, those regions are much smaller in geographical extent relative to those flagged by the all-species null model (Supporting information). This suggests that two levels of environmental filtering are reflected in the communities that occupy this most subtropical region: a first (latitudinal) filter appears to be impacting the entire southern range of the forest, reducing functional diversity as a whole; then, for those species that can occupy the southern half of the forest, a second filter (probably related to elevation) appears to exist in relation to the Araucaria Forest.

Our hypothesis of relaxed environmental filtering in the warmer and more climatically stable northern latitudes was also confirmed: we found more functional richness and functional dispersion in the north than expected given the observed taxonomic and phylogenetic diversity, even with phylogenetic diversity being slightly lower than expected given the number of species (Fig. 4). We also found little variation of the residuals of the regression of functional richness and taxonomic diversity with elevation in those areas (Fig. 6); this is consistent with the fact that the local mountains are not as tall or steep as those in the south, likely reducing the role of environmental filtering. This pattern is consistent with an increased effect of biotic interactions, and has been found at the lower end of Andean elevational

gradients (Dreiss et al. 2015) and contact regions that enable the encounter of different biogeographical pools (Kraft et al. 2007, Cavender-Bares et al. 2009).

In contrast to our expectations, the hypothesis that diversity patterns at mid-elevations reflect the contact between different species pools, thus showing more overdispersion of traits and evolutionary histories, was not fulfilled. While mismatches between diversity dimensions were common at mid-elevations, they happen in no particular direction (Fig. 5). Only at mid-latitudes (Fig. 6, bands 5 and 6) there seems to be overdispersion of functional diversity (in both richness and dispersion) possibly explained by contact between species pools – either occurring at different elevations, or largely distributed in the northern versus southern portions of the forest. We did find evidence of higher functional diversity than expected given species richness in the northern forests, particularly in the northwest deciduous forests that border the Cerrado savannas, and in small areas of contact between vegetation types (Fig. 1d and 3c, f). However, those areas have lower phylogenetic diversity than expected given the taxonomic diversity (Fig. 4b, Supporting information). Collectively, these observations suggest that, in Atlantic Forest hylids, contacts between groups of species occupying different elevations do not seem to erase the signal of other ecological processes driving community assembly – but contact areas between different vegetation types are bringing together species with traits adapted to different environments, yet closely related to each other.

We illustrate how studies of the processes driving community assembly in the Atlantic Forest can benefit from the inclusion of all three dimensions of biodiversity and a broader characterization of environmental constraints that go beyond elevational gradients. Similar to other studies (Stevens and Tello 2014, Barreto et al. 2019), we point to the complementarity of the different measures of biodiversity dimensions, and how the regions where they are not fully redundant help us understand the drivers of biological patterns. In the Atlantic Forest, we find that phylogenetic diversity is not always a good proxy for functional diversity; using the former to represent the latter can obscure the interplay of multiple ecological processes in community assembly, in agreement with previous experimental work in other ecosystems (Germain et al. 2018). Biotic interactions appear to be the most prevalent force explaining the large levels of functional richness observed in local hylid communities. However, altitudinal and latitudinal structuring of communities is influenced by environmental filtering, which is reflected in mismatches between different dimensions of diversity, particularly in the geographic structure of functional dispersion. We show that the strength of the processes impacting community assembly at different elevations change with latitudinal gradients (Montaño-Centellas et al. 2019). Although signatures of some level of environmental filtering are present at high elevations, the drivers of community assembly at low- and mid-elevations appear very different between tropical and subtropical latitudes, with filtering dominating at subtropical latitudes. We also show that secondary contacts between species pools

distributed in northern versus southern latitudes, or in adjacent ecosystems, appear to impact the patterns of functional and phylogenetic diversity more strongly than secondary contacts along elevation.

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Andrea Paz: Conceptualization (lead); Data curation (supporting); Formal analysis (lead); Methodology (lead); Writing – original draft (lead). **Leyla Hernandez:** Data curation (equal). **Lilian S. O. Melo:** Conceptualization (supporting); Data curation (equal); Formal analysis (supporting). **Mariana Lyra:** Data curation (equal). **Célio F. B. Haddad:** Data curation (equal); Funding acquisition (supporting); Writing – review and editing (supporting). **Ana C. Carnaval:** Conceptualization (equal); Funding acquisition (lead); Supervision (lead); Writing – original draft (supporting).

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Data availability statement

Data is available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.kpr4xh6p>> (Paz et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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