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Seeing the forest through many trees: Multi-taxon patterns of phylogenetic diversity in the Atlantic Forest hotspot

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Abstract

Aim: We combine phylogenetic and point locality data from selected lineages of the Atlantic Forest flora and fauna to compare spatial patterns of biodiversity sustained by the current configuration of forest remnants to a scenario of complete forest preservation. We then ask the question "how much biodiversity is likely lost, already"? Specifically, we assess how habitat loss likely impacted the climatic spaces occupied by the local species, the inferred composition of local communities and the spatial distribution of phylogenetic diversity and endemism.

Location: Atlantic Forest, Brazil.

Methods: Using carefully curated point localities, phylogenetic data and parameterized models of species distributions, we generate maps of phylogenetic diversity, phylogenetic endemism and phylogenetic turnover for the entire Atlantic Forest. We map patterns of clade-specific diversity under complete preservation of forest and then incorporate present-day deforestation patterns to provide a more realistic scenario.

Results: Instead of a singular pattern, three different reoccurring syndromes described the flora and fauna of the Atlantic Forest. These patterns emerged irrespectively of clade age and life history traits. General turnover patterns were highly consistent with previous analyses of species composition and panbiogeographical studies. Deforestation has altered the availability of climatic spaces in the Atlantic Forest, its biological communities and the distribution of evolutionary lineages in space. However, approximately 60% of the pre-Columbian climatic space persists in forest remnants, and today's biological communities are estimated to be 45% similar to pre-deforestation times.

Main conclusions: The Atlantic Forest has been reduced to 8% of its once largely continuous range. However, the disproportionately large amounts of climate, community and lineage diversity that persist in remnants provide hope and support

for conservation efforts that combine species occurrence and phylogenetic data. Inclusion of evolutionary thinking into strategic approaches to restoring Brazilian ecosystems could further conservation effectiveness by incorporating the adaptive potential of local assemblages in the face of further environmental shifts.

KEYWORDS

Atlantic Forests, biogeography, comparative analyses, phylogenetic endemism, phylogenetic turnover, South America, spatial patterns

1 | INTRODUCTION

Understanding how biological diversity is distributed in geographical space and how it shifts in response to environmental change remain two of the most significant challenges facing conservation biologists, ecologists and biogeographers. For many regions, even despite anthropogenic habitat loss, there exists high congruence in diversity patterns across disparate taxonomic groups (Ackerly et al., 2010; Mannion, Upchurch, Benson, & Goswami, 2014). This suggests that biological communities are heavily influenced by similar evolutionary and ecological drivers, even if the latter act at distinct temporal, spatial or biological scales (Carnaval, Hickerson, Haddad, Rodrigues, & Moritz, 2009; Carnaval et al., 2014; Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). Mapping and contrasting biodiversity patterns across taxa and environmental conditions, such as climates or degree of habitat preservation, allow not only for the identification of flagship species whose diversity patterns are indicative of multi-taxon diversity shifts, but also for a more accurate assessment

of the biological impacts of anthropogenic global change (Brown, Cameron, Yoder, & Vences, 2014; Graham, Ron, Santos, Schneider, & Moritz, 2004). Both are essential for conservation planning and monitoring, especially in megadiverse, yet highly threatened tropical areas (Cardoso da Silva & Bates, 2002; Mittermeier, Myers, Thomsen, Da Fonseca, & Olivieri, 1998; Myers, 1988).

One critical knowledge gap concerning such at-risk tropical biomes, particularly given the need to adapt or mitigate future anthropogenic changes, pertains to their spatial patterns of evolutionary diversity (Faith, 1992; Moritz & Faith, 1998; Rosauer, Laffan, Crisp, Donnellan, & Cook, 2009). Going beyond species number and species identity, how is phylogenetic diversity, endemism and turnover represented in geographic space (Rosauer et al., 2009)—and how have anthropogenic habitat changes already affected these measures of biodiversity? Mapping phylogenetic diversity sheds light into the key mechanisms driving diversification (Mishler et al., 2014). Although generally correlated with spatial patterns of species richness, the geographic patterns of phylogenetic diversity can be
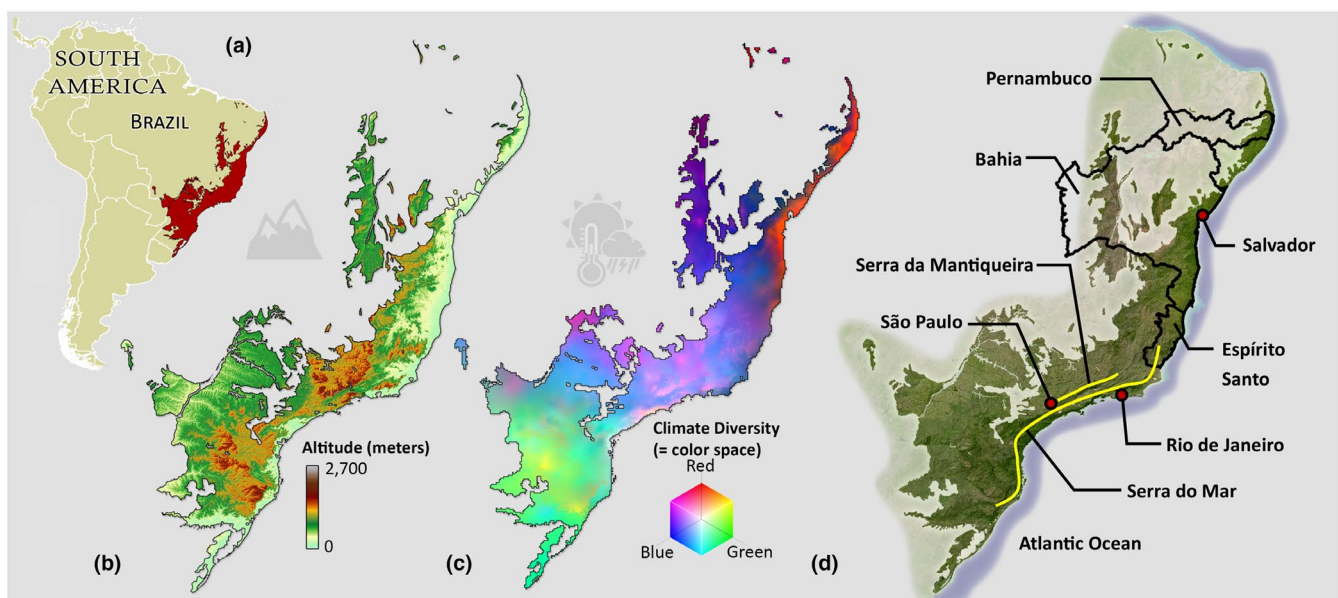
FIGURE 1 Geography, climate and key areas of the Atlantic Forest. Distribution of the Atlantic Forest in South America (a), its topography (b) and climate diversity (c). Key areas mentioned in the text (d): red dots depict cities, and yellow lines depict mountain ranges

especially insightful when they disagree with the former, signalling potential changes in speciation and extinction rates, or a legacy of biogeographic history (Davies & Buckley, 2011). Given the amount of information that it carries about the historical processes that underlie diversity patterns, and because it informs about the evolutionary potential of a community, phylogenetic diversity has been flagged as an important conservation currency (Davies & Buckley, 2011; Voskamp, Baker, Stephens, Valdes, & Willis, 2017). By extension, maps of phylogenetic endemism are particularly relevant to conservation by explicitly quantifying the amount of evolutionary uniqueness of a region (Rosauer et al., 2009).

Yet, while multiple studies have used species range information (especially from inventory lists and expert-drawn maps) to quantify and analyse broad taxon-centric patterns of richness, endemism and community turnover in tropical biodiversity hotspots (e.g. Durães & Loiselle, 2004; Moura, Argôlo, & Costa, 2017), relatively few analyses have incorporated knowledge about the evolutionary history that connects local communities to investigate patterns of accumulation of lineage diversity, across multiple taxonomic groups (e.g. González-Orozco et al., 2015). The addition of phylogenetic information to these biodiversity comparisons is particularly relevant in tropical systems where species descriptions still occur at high rates, and where the current state of taxonomy may not reflect true lineage diversity (Funk, Caminer, & Ron, 2011; Rosauer, Pollock, Linke, & Jetz, 2017).

To fill this knowledge gap in the megadiverse yet threatened Atlantic Forest of Brazil, we combine expertise across multiple research groups to provide the first broad comparative snapshot of spatial patterns of phylogenetic diversity of animals and plants of this tropical hotspot, given its present state of fragmentation. Extending over 1.3 million km^2 along the east coast of South America, the Atlantic Forest is rich in species and environments, showing high level of endemism (Morellato & Haddad, 2000). Known for its complex biogeographical history, high habitat heterogeneity and complex topography (Figure 1), it has been reported to host unique communities of plants and animals along the multiple climatic spaces it holds (Cardoso da Silva, Cardoso de Sousa, & Castelletti, 2004). Although the range of the Atlantic Forest is smaller than other tropical wet ecosystems such as Amazonia and the Congo forests (nearly 90% of the Atlantic Forest's pre-Columbian extent has been altered or destroyed by humans), it provides essential ecosystem services to the densely populated areas of coastal Brazil (Tabarelli, Aguiar, Ribeiro, Metzger, & Peres, 2010). As such, we have urgency in synthesizing regional biodiversity patterns and understanding how strongly they have changed in response to anthropogenic habitat loss.

Here, we gather and contrast carefully curated phylogenetic and point locality data from Atlantic Forest invertebrates, vertebrates and plants to (1) compare spatial patterns of biodiversity sustained by the current configuration of forest remnants and (2) assess how they compare to a scenario of complete preservation of the forest, asking the question of how much biodiversity we have likely already lost. To address the second point, we assess not only whether and how the climatic spaces occupied by evolutionary lineages of the local fauna and flora have changed due to habitat loss, but also how the composition of local communities and the distribution of phylogenetic diversity and endemism, inferred from correlative models based on climatic associations, may have been impacted from pre-Columbian times to this day.

2 | MATERIAL AND METHODS

2.1 | General framework

We quantified and compared phylogenetic biodiversity patterns of six taxonomic groups showing moderate to high biodiversity levels in the Atlantic Forest of Brazil. To ensure that our analysis reflected the most carefully curated locality and phylogenetic information available to date, we focused on two plant clades, one invertebrate clade and three vertebrate clades that have been extensively studied or analysed by the authors. This corresponds to bromeliads of the Bromelioideae subfamily (*n* = 18 species), melastomes of the Miconieae tribe (*n* = 177), butterflies of the Ithomiini tribe (*n* = 55), tree frogs of the genus *Boana* (*n* = 16), horned frogs of the genus *Proceratophrys* (*n* = 17) and tanager birds from family Thraupidae (*n* = 22; Aguirre-Santoro, Michelangeli, & Stevenson, 2016; Burns et al., 2014; Caddah, 2013; Goldenberg, Penneys, Almeda, Judd, & Michelangeli, 2008; Goldenberg, Reginato, & Michelangeli, 2018; Michelangeli et al., 2008; Reginato & Michelangeli, 2016; Vasconcelos, Prado, da Silva, & Haddad, 2014). The six taxonomic groups included here present high levels of species richness and endemism within the Atlantic Forest and, as such, are good candidates for understanding diversification patterns in situ. Each species was represented by a single terminal in their respective phylogenies. Newly generated sequences and their associated coordinates are available in GenBank (see Dryad: https://doi.org/10.5061/dryad.qz612jmbm).

We are aware that this final group of datasets is heterogeneous. First and foremost, our sampled clades have different levels of species richness and ages (published age estimates for these groups of bromeliads approximate 5–6 My (Givnish, Millam, Berry, & Sytsma, 2007), melastomes 13.3 My (Reginato, Vasconcelos, Kriebel, & Simões, 2020), butterflies 37 My (Garzón-Orduña, Silva-Brandão, Willmott, Freitas, & Brower, 2015), frogs 30–32 My (Feng et al., 2017) and birds 10 My (Sedano & Burns, 2010)). The clades also differ in dispersal abilities (e.g. high in birds vs. low in frogs), distinct reproductive systems (plants vs. animals) and differential metabolic strategies (ectotherms vs. endotherms). While a comprehensive comparison would require having multiple replicates of each category across taxonomic groups, we argue that this diversity of histories is still worthy of attention. Akin to comparative biogeography, which uses historical reconstructions of multiple lineages in a given region to generate insight about the evolution of that biogeographical area (e.g. Antonelli, 2017), we explore whether certain spatial patterns are consistent across a diverse set of groups, while ensuring uniformity across data collection protocols and analytical methods.

To present the first broad taxonomic assessment and one of the broadest comparisons for this region, we first map how clade-specific diversity patterns would look like if the forest had not been so heavily destroyed. For that, we project distribution models of all species onto the pre-Columbian extent of the forest, much like most biodiversity analyses of the Atlantic Forest are portrayed (e.g. Moura et al., 2017). To contribute to conservation efforts in the region, we then provide a more realistic portrait of the actual patterns of phylogenetic diversity, endemism, and turnover, by specifically incorporating present-day forest deforestation patterns into our maps. This allows us to coarsely quantify the effects of contemporary deforestation on local biodiversity—not only regarding the changes in the climate available for forest-dwelling species, but also quantifying inferred shifts in community composition and, by extent, the levels of phylogenetic diversity and phylogenetic endemism maintained in the environment. Through a comparison of species-specific ranges under the contemporary configuration of the forest, relative to its pre-deforestation extent, we discuss the major geographic shifts experienced by the local fauna and flora in response to habitat loss.

2.2 | Species distribution models

We opted to develop correlative species distribution models (SDMs; also commonly called ecological niche models) to obtain estimates of taxon-specific geographic ranges within the full (no deforestation, or pre-Columbian) extent of the Atlantic Forest. The reasons for this choice are threefold: (1) the ranges of multiple taxa had not been fully described, (2) information on pre-Columbian ranges of species is lacking, and (3) some distribution records are scattered. For that, we employed a total of 305 species and 39,672 unique locality points (bromeliads n = 3,774; melastomes n = 25,645; butterflies n = 3,269; tree frogs n = 227; horned frogs n = 2,065; birds n = 8,501; Aguirre-Santoro et al., 2016; Burns et al., 2014; Caddah, 2013; GBIF, 2017; Goldenberg et al., 2008; Goldenberg et al., 2018; Michelangeli et al., 2008; Reginato & Michelangeli, 2016; Vasconcelos et al., 2014; occurrence provided in Dryad), which were vetted by experts for spatial and taxonomic accuracy. Species distribution models were built with occurrence points from the entire range of each species within South America and later clipped to represent the pre-Columbian distribution of the Atlantic Forest. Species distribution models were generated in MaxEnt 3.3.3k (Phillips, Anderson, & Schapire, 2006), as implemented in SDMtoolbox 1.1c (Brown, 2014). To represent the extent of the Atlantic Forest, we built a shape file based on the vegetation elements identified by Fundação SOS Mata Atlântica (2019).

We generated SDMs for all species that had, at minimum, five unique occurrence points. Due to their controversial status as Atlantic Forest species, two bird species (*Gubernatrix cristata* and *Paroaria capitata*) were excluded from the analyses. Non-modelled species (i.e. species with fewer than five points; n = 73 in total; Pearson, Raxworthy, Nakamura, & Peterson, 2007) were still included in the quantifications of biodiversity metrics per grid cell. Because most SDM methods require input occurrence data to be

spatially independent, we used SDMtoolbox to randomly select one locality whenever multiple occurrence records per species existed within a 20-km radius. This locality was then used for species distribution modelling. This spatial filtering reduced the occurrence data from 39,672 to 19,316 unique localities.

To develop a climate-based correlative model of the distribution of each species, contemporary climate information was extracted for each locality in which each species occurs. For that, we used Hijmans's, Cameron, Parra, Jones, and Jarvis (2005) 19 bioclimatic variables at 30 arc-second resolution to describe local temperature and precipitation (Bioclim, available at: http://www.worldclim.org/), as well as 16 additional variables available at 2.5 arc-minute resolution pertaining to soil moisture and solar radiation (Hutchinson, Xu, Houlder, Nix, & McMahon, 2009; Kriticos et al., 2012; variables 20–35 downloaded from https://www.climond.org/ at 10 arc-minutes and downscaled to 2.5 arc-minutes as per Saiter, Brown, Thomas, & Carnaval, 2016; available at www.sdmtoolbox.org; see Dryad link for a complete list of environmental variables). Because soil and radiation variables were only available at a comparatively coarser resolution, they were downscaled to 30 arc-seconds using the ANUSPLIN method, as per Hijmans et al. (2005). A digital elevation model was used as a covariate in all the ANUSPLIN analyses (Hijmans et al., 2005). An additional covariate, annual precipitation, was used for the downscaling of variables pertaining to solar radiation (Bioclim 20–27). This incorporates the known dependences of solar radiation on cloud cover associated with rainfall, which gives rise to more complex solar radiation patterns in areas of topographic complexity (Hutchinson et al., 2009). Two additional covariates, slope and aspect (the compass direction that a slope faces), were used to downscale the variables pertaining to soil moisture (Bioclim 28–35). These were included because both affect the amount of solar radiation that habitats receive, hence directly influencing soil moisture and water retention (Geroy et al., 2011). The final downscaled variables are available for download at http://sdmtoolbox.org (Brown, Bennett, & French, 2017).

MaxEnt requires the sampling of background points, which were sampled from a minimum convex polygon built for each species, and defined as a 100-km buffer drawn around its occurrence localities. To parameterize the SDMs properly, we evaluated the performance of various combinations of five feature classes (linear; linear and quadratic; hinge; linear, quadratic and hinge; linear, quadratic, hinge and product) and ten regularization multipliers (from 0.5 to 5, in increments of 0.5; Brown et al., 2017). To this end, we evaluated the performance of SDMs built under each combination of model parameters, through a geographically structured k-fold cross-validation. In the latter, occurrence records were partitioned into k equal geographically clustered subsamples. Here, we used k = 3, and the models were trained with two of the groups and then evaluated with the excluded group until all group combinations were run. Model fit was assessed through inspections of the omission error rate, the area under the curve (AUC) and model feature class complexity. After optimum model parameters were determined (those leading to the lowest omission rate, highest AUC and lowest complexity, in the order

listed), a final SDM was built with all occurrence sites and converted into a binary (presence–absence) model, using the minimum training presence value as a threshold (Brown et al., 2017). Post-modelling, a minimum convex polygon defined as a 100-km buffer drawn around the occurrence localities was used to clip over-prediction in final MaxEnt models.

2.3 | Mapping species richness, phylogenetic diversity and phylogenetic-corrected weighted endemism

With the final SDMs in hand, maps were created for all biodiversity metrics in each one of the six taxonomic subsets. To estimate species richness within each taxonomic subset, the estimated occurrence (presence) of each species, sampled from binary SDMs, was counted throughout the entirety of the Atlantic Forest. To estimate phylogenetic diversity (PD; Faith, 1992), phylogenetic-corrected weighted endemism (herein refereed as phylogenetic endemism or PE; Rosauer et al., 2009) and phylogenetic turnover (PT, as per method described below), we used datasets that had both binary SDMs and genetic data, based on published and new DNA sequences (mitochondrial DNA sequences for the animal species, chloroplast DNA for plants).

Species richness, PD and PE were first calculated for each taxonomic group in Biodiverse 1.1 (Laffan, Lubarsky, & Rosauer, 2010) at a spatial resolution of 10 km. These maps were subsequently used to calculate total richness, total PD and total PE. To investigate the explicit relationships between species richness and PD, which tend to be quite similar, we performed a linear regression in which PD was set as a response variable, whereas richness, latitude and longitude were used as predictor variables (Davies et al., 2007; Figueiredo & Grelle, 2018; Fritz & Rahbek, 2012; Vale, Tourinho, Lorini, Rajão, & Figueiredo, 2018). The residuals were assessed for each site and plotted in as a map.

To reduce any biases associated with the different levels of species richness observed across taxonomic groups, as well as any potential differences caused by the evolutionary rate of the molecular markers available to generate the phylogenetic trees of the six target taxa, we standardized all per-group PD values before summing across them. These standardized values were calculated as a proportion of total tree length (as opposed to the total sum of branch lengths) present at each pixel, thus representing a relative measurement of PD that ranges from 1 to 0. In this case, 1 depicts a cell holding the total phylogenetic diversity of a given group (all taxa of the group present), and 0 represents no phylogenetic diversity, or no taxa present (Laffan et al., 2010). Hence, moderate PD values can either indicate, for a particular region, the presence of (1) many taxa, with many short branch lengths, (2) a few taxa with very long branch lengths or (3) some combination thereof. The summation of these proportional results provides a relative estimate of the total intra-group phylogenetic diversity observed in all taxonomic groups. It also enables the identification of those areas with highest phylogenetic diversity. We made identical adjustments to our combined measurements of PE

and summed the PE measurements of each separate group based on PE values representing a proportion of total tree length (vs. total tree length, as described above for PD).

By summing standardized PD and PE maps—as opposed to estimating PD and PE through a phylogenetic super-tree including all species—we avoided biasing the metrics by the fact that some of the major branches connecting the taxonomic groups were orders of magnitude greater than intra-group differences. Therefore, the synthesis maps presented here emphasize the patterns of PD and PE observed *within* each group, and all combined, rather than the distribution of higher-order taxa. This method also avoids issues associated with merging phylogenies generated from different molecular datasets.

2.4 | Mapping phylogenetic turnover

To map phylogenetic turnover per taxonomic group, we first calculated a matrix of compositional dissimilarities (CD) between pairs of sites throughout the Atlantic Forest, using a Sorenson Index in Biodiverse 1.1 (Laffan et al., 2010). We then applied multidimensional scaling in SPSS v22 (IBM, 2013), using the PROXSCAL function, to visualize these dissimilarities in space. The scaling reduced the data to three ordination axes, and each axis was represented by a unique RGB colour (red, green or blue) in a geographical information system software (ESRI, 2017). To avoid computational limitations associated with pairwise comparisons of very large datasets, we sampled the Atlantic Forest at 30 km^2 for the phylogenetic turnover analysis and then measured the absence or presence of each species within each 30-km^2 pixel (Brown et al., 2014). Visualization of phylogenetic turnover RGB value results was then downscaled from 30 to 10 km using a *k*-nearest neighbour classification with eight spatial covariates: latitude, longitude and six principal components outputs from a principal component analysis of the 35 high-resolution environmental layers used for the SDMs. To classify the phylogenetic turnover map, and therefore identify unique communities in geographical space, we used SPSS v22 and a two-step classification method that assesses the Akaike Information Criterion (AICc; IBM, 2013) of a range of class numbers to determine the optimum number of groups (here 1–30).

We opted not to estimate a total phylogenetic turnover map because phylogenetic diversity was highly correlated to species richness in all taxonomic groups ($r^2 > 0.95$). Also, group-specific phylogenetic turnover analyses result in n-dimensional matrices that cannot be easily merged. As a result, we here present a synthesis map of species-level turnover, instead of phylogenetic turnover. This map was built through a single analysis of all combined data, across taxa.

2.5 | Analyses of the impact of landscape change

To estimate the spatial patterns of diversity within each taxonomic group given the present state of forest preservation, every binary

SDM was (1) transformed to South America equal-area cylindrical projection in ArcMap 10.2 (ESRI, 2017) after undergoing correction for over-prediction, (2) downscaled to a spatial resolution of 1 km and (3) masked again with the most recent map of natural vegetation patches in the Atlantic Forest (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). Only patches that preserved ≥1 km² of the distribution of each species are shown here. To account for the spatial discord between the 1-km² resolution deforestation data and the 10-km pixel resolution of the biodiversity analyses, we classified all 10-km pixels as "forested" whenever they had at least 5 km of natural vegetation, as indicated by the 1-km² resolution forest cover map. Our final estimates are hence conservative estimates in regard to biodiversity and climate space loss due to habitat fragmentation. To flag areas of range contraction or no change, we subtracted these present-day (clipped) SDMs from the unclipped model of distribution of each species (i.e. the model projected into the continuous pre-Columbian range of the forest). We also calculated and connected the geographic centroids of those two binary SDMs in ArcGIS 10.1 using SDMtoolbox v1.1 (Brown, 2014) to examine the extent of species range shifts between the fragmented (clipped) and continuous (unclipped) range of the forest.

To measure the totality of climatic spaces available to Atlantic Forest species given the current state of deforestation, and to compare it against the climatic spaces that would be available if the forest had been fully preserved after the first European colonizers arrived in the country (respectively, referred to as the "pre-Columbian" and "current" from here on), we performed a principal component analysis on the 35 bioclimatic variables used for the SDMs. To that end, we sampled them from throughout the extension of the forest both prior to and post-fragmentation (i.e. sampling the climatic spaces within the fragments that remain). We extracted and plotted the first four PCs of the climatic space analysis, which represented 75.2% of the total variance observed in climate (PC1: 43.8%, PC2: 21.3%, PC3: 11.8%, PC4: 8.3%; Table S1 in Supplementary Material).

To measure and compare the impact of deforestation on modern community composition, we applied multidimensional scaling to our species-level turnover analysis in SPSS v22, using the PROXSCAL function as described above, and reduced the matrix to two ordination axes. Based on this map and the modern-day deforestation level of the forest, we created two community composition datasets: one reflecting the current state of the forest and one under a pre-Columbian (no deforestation) scenario. This multidimensional scaling analysis combined data from all taxonomic groups and did not include phylogenetic information.

To assess the explicit effect of deforestation on the amount of climate space available to each taxonomic group of focus, as well as on the spatial distribution of communities before and after deforestation, we modified a method originally devised to ask how statistically different are the spatial distributions of two species (Broennimann et al., 2012). Specifically, we adapted the pipeline proposed by Broennimann et al. (2012), using the R package Humboldt (https://github.com/jasonleebrown/humboldt.git) to assess whether the spatial distribution of climatic spaces (and communities) currently available in the Atlantic Forest, given its state of fragmentation, is significantly different from the totality of climatic spaces (and communities) that would have been available if the pre-Columbian range of the forest had been fully preserved. For these two comparisons, we performed an equivalency test (humboldt::humboldt.equivalency.test), employing Schoener's D statistic (Schoener & Schoener, 1982) to assess the overall match between the climatic spaces (and community composition) under the current and no deforestation scenarios. The equivalency test asked whether the observed overlap in climate or community distribution between the pre- and post-deforestation states (both the types and abundance of each type) lies within the density of 95% of D-values simulated from replicate (n = 300) reshuffling of the observed climate (or community) values from the pre- and post-fragmentation scenarios, jointly. Significant values (outside of the 95% range) indicate that the null hypothesis of equivalency is rejected, that is, that the climates (or the communities) of the pre- and post-deforestation are significantly different. When implementing the equivalency test, we used a kernel smooth parameter fixed at 0.4 to ensure that the unique climatic space communities lost due to deforestation remained empty in the analysis (i.e. unfilled by the kernel smooth parameter). The principal component (PC)/multidimension scaling (MDS) values were divided into 1,000 climate (or community) space bins, in two dimensions (100 by 100 bins). The use of a kernel smooth parameter >0.4 would have resulted in the filling of gaps due to missing information among neighbouring data points to create a smoother, uniform distribution. Because a continuous, uniform distribution is not central to our assumptions, we fixed it a single value to more accurately capture the changes between our two scenarios (before vs. after deforestation).

Finally, to assess the explicit effect of deforestation on the relative amount of spatial phylogenetic diversity and phylogenetic endemism, we performed Kolmogorov–Smirnov test in R, which compared the density curves of the two periods.

3 | RESULTS

3.1 | Biodiversity patterns within taxonomic groups

Spatial patterns of phylogenetic diversity were tightly correlated with patterns of species richness in all groups (Figure 2). In all six datasets, species richness dropped to lower levels in the northern and southern limits of the forest distribution. However, the six datasets differed in their spatial patterns of species accumulation. Generally, the richness patterns gravitated towards three major syndromes: (1) southern accumulation (particularly along the two mountain ranges that runs parallel to the Atlantic Ocean, the Serra do Mar and the Serra da Mantiqueira), (2) northern accumulation and (3) widespread. Three groups—the melastomes, tree frogs and tanagers—were predominantly montane, with several species accumulating along the Serra do Mar. Conversely, two groups had most of its species concentrated in the northern range of the forest (bromeliads in the coast, and horned frogs in the interior montane

areas). In the butterfly dataset, richness was fairly widespread along the forest, and although a high number of species is found both in the south and northern regions, richness showed a slightly northern accumulation.

In contrast to the diversity accumulation patterns, the relationship between species richness (and hence total phylogenetic diversity) and the spatial patterns of phylogenetic endemism varied considerably across taxa (Figure 2 rows 1–3). The tanagers, for instance, showed a tight correlation between the three metrics, whereas horned frogs showed no striking pattern of PE, despite having marked areas of high richness and high total PD. In the remaining groups, areas of high PE were located within regions of high total PD and high species richness, yet not all species or lineage-rich areas had high PE.

Our PD ~ SR residuals (hereafter called "Corrected PD") identified a mosaic of areas outside of the Serra do Mar region, with many taxa possessing higher Corrected PD in the margins of their distributions, particularly on the northern and southern edges of each group's distributions. However, unlike some of the other metrics (such as PD), there appears to be no widespread congruence between groups. Further, the areas with higher Corrected PD within each taxonomic group tend to be spatially dispersed (unlike other metrics, such as species richness, which exhibit a high level of spatial autocorrelation).

Patterns of lineage turnover were somewhat congruent across groups. All taxa show dissimilarities in the composition of lineages as one moves from the east to the west—both in the south and the northern regions of the forest (Figure 2 row 5, Figure 3). Moreover, in several of the taxa occupying the southern Atlantic Forest (e.g. melastomes, horned frogs, tree frogs, tanagers), a unique set of lineages is found to occupy the montane Serra do Mar region. Also common across many taxonomic groups is the existence of a unique combination of lineages in the northern range of the forest, particularly north of Salvador, Bahia. That said, fine-scale differences can be pointed out in the spatial patterns of phylogenetic turnover across groups. Butterflies and tree frogs, for instance, show more homogeneity relative to the remaining taxa (Figure 2 row 5; Figure S1). A classification protocol was able to identify two (in bromeliads), three (in tree frogs and horned frogs), four (in butterflies and melastomes) or five (in tanagers) unique sets of lineages distributed along the Atlantic Forest (Figure 3; Figure S1).

At a broad spatial scale, the data indicate three main regions of phylogenetic turnover along the coast of the Atlantic Forest, which we here call a southern, central and north group of turnover points (Figure 3). All taxonomic groups share one or two of these broad breaks. There is, however, discord in the exact placement of breaks among groups, particularly in the southern and central turnover regions. For instance, the unique group of lineages of melastomes that is broadly distributed along the Serra do Mar has a much larger geographic distribution relative to the Serra do Mar lineages of birds and frogs (Figures 2 and 3). Much higher spatial congruence is nonetheless observed in the northern turnover points, particularly among tree frogs, butterflies, melastomes and tanagers (Figure 3). Further

west, a concurrent break in phylogeographic turnover is observed between the coastal and the interior forests (Figure 3 break ii).

3.2 | Biodiversity patterns, all taxa combined

When all data are standardized and combined across taxonomic groups, total phylogenetic diversity is greatest along the mountain ranges that run parallel to the Atlantic Ocean, in the Serra do Mar (Figure 4c). Smaller mountain-top regions within this range hold the largest areas of high phylogenetic endemism (Figures 1b and 4e), followed by mid-montane and smaller, lowland regions further north.

The latitudinal gradient of climatic turnover observed along the Atlantic Forest (Figure 1) is broadly reflected in the geographical patterns of community turnover of the combined dataset (Figure 4), and clear differences in species composition are observed among the north, central and southern regions of the forest. Yet, at finer spatial scales (and often within region, e.g. the northern half of the forest), the patterns of community and climatic turnover are not identical (Figures 1d, 3 and 4a). Overall, the combined dataset flags distinct communities in the following five regions (from south to north; Figure 3): (1) the southern range of the forest (south of São Paulo; with further differentiation detected between the coastal and interior south), (2) the Serra da Mantiqueira mountain chain, (3) the central forest corridor, in the state of Espírito Santo, (4) the interior of the state of Bahia and (5) the north-eastern forests in the state of Pernambuco. A cluster analysis of community composition, once the data are merged across plants and animals, identifies nine unique community groups along the forest (Figure 5).

3.3 | Recent changes resulting from deforestation

A recent map of Atlantic Forest remnants (Ribeiro et al., 2009) illustrates that the domain has been reduced across most of its distribution, reaching, on average, 8.1% of its once continuous range (Figures 4). Inland regions of unique community composition (Figure 5) have suffered the highest deforestation rates, with 0.6%–3.1% of forests remaining (vs. 6.8%–12% in coastal areas; Figure 5).

Masked models suggest that all taxonomic groups represented in this study have experienced considerable range reductions due to deforestation (Figure 6a–c, Table 1, mean within-group reductions range from 83.2% to 90.7%; Figure 7). Two general movements were detected relative to individual species ranges: 1) several taxa had the centroids of their distributions displaced towards the Serra do Mar, while 2) others moved towards central lowland Bahia State (Figure S2).

Habitat fragmentation had a striking impact on the climatic spaces generally available throughout the forest, and on the way in which its communities are distributed. Only about 60.5% of the primary climatic components (PCs 1 and 2) and 66.3% of the
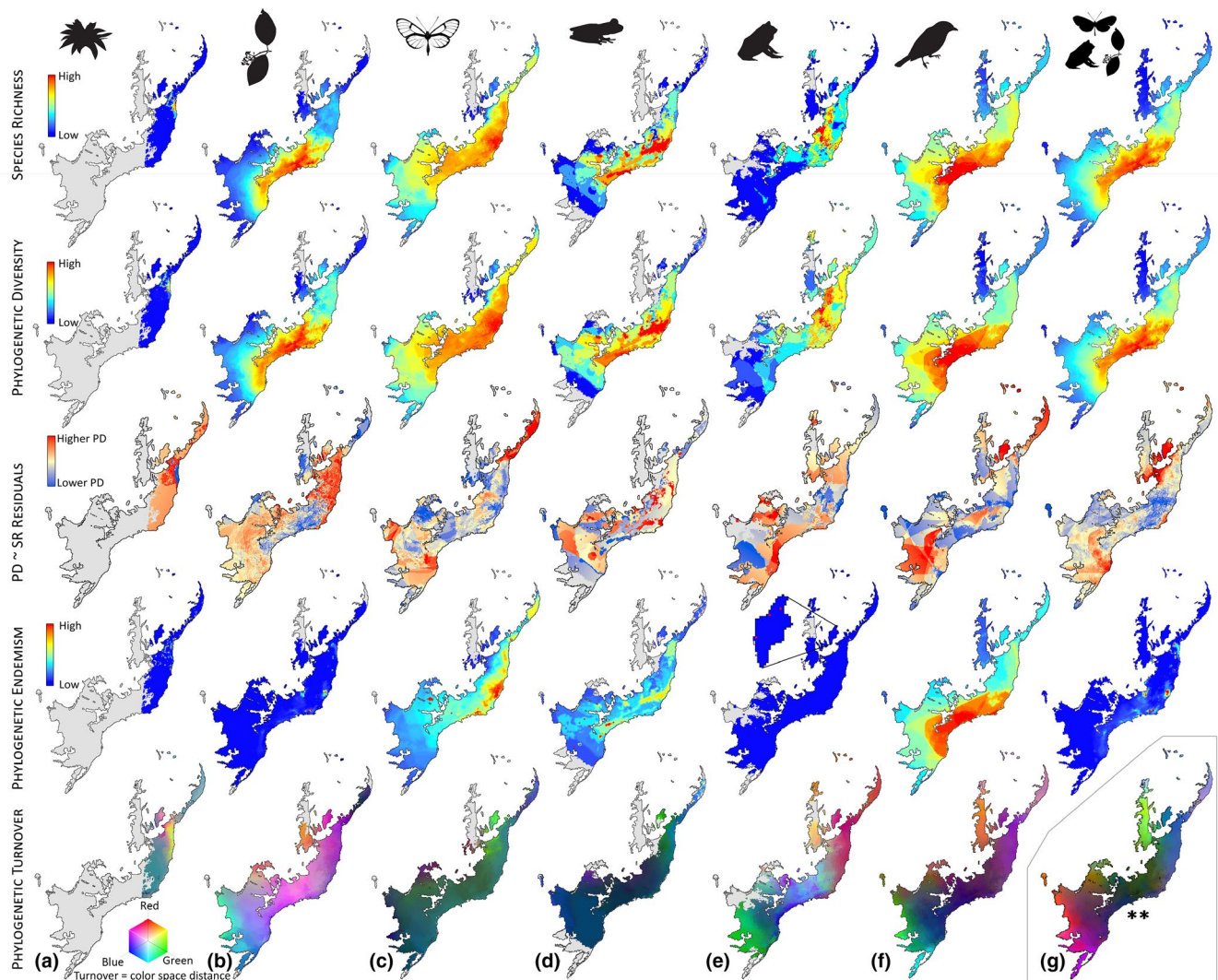
FIGURE 2 Biodiversity patterns of focal groups. Spatial biodiversity patterns for five metrics: species richness (SR), phylogenetic diversity (PD), PD ~ SR residuals* also called Corrected PD (*due to very high similarities between species richness and phylogenetic diversity, we present the residuals output from a linear regression in which PD was set as a response variable, whereas species richness, latitude and longitude were used as predictor variables), phylogenetic endemism (PE) and phylogenetic turnover for the six taxonomic groups: bromeliads (a), melastomes (b), butterflies (c), tree frogs (d), horned frogs (e) and tanagers (f). Last column depicts metrics for all groups combined (g). Overall turnover is based on alpha-taxonomy only (thus bottom right image depicts taxonomic turnover, not phylogenetic turnover, of all groups combined). Light grey areas indicate regions where subgroup is absent.

secondary climatic components (PCs 3 and 4) persist in the forest remnants that are left today (Figure 6). Not surprisingly, as a result of these reductions, the climatic spaces currently available are statistically different from the fully forested scenario ($p < .001$ in the equivalence test of climate space, Figure 6a, Figure S3). Likewise, the results suggest that habitat loss has resulted in highly significant ($p < .001$) differences in community composition, reflecting changes in the types of communities present (and the abundance of each type) in the current scenario relative to the fully forested (pre-Columbian) scenario (Figure 6b). By looking at community shifts caused by the removal of forest sites alone, the analysis estimates that today's communities are, maximally, 45.2% similar to pre-deforestation times (but see Discussion for other drivers potentially changing

these numbers). Lastly, a comparison of PE and PD values across the forest (Figure 6c,d) suggests a drastic shift caused by deforestation in the distribution of phylogenetic endemism (Figure 6c, $p < .001$) and total phylogenetic diversity (Figure 6d, $p < .001$) across the domain. Our results also revealed that there was a significant change in mean and mode of the distributions, with the current forest areas possessing higher PD (mean = 423.8 & 488.8, mode = 136 & 234, all significant at $p < .001$) and PE (mean = 0.292 & 0.437, mode = 0.039 & 0.108, all significant at $p < .001$). However, these changes in mode and mean should be not be overinterpreted, as our biodiversity measurements are biased towards the currently forested areas because endemics restricted to deforested areas would not be represented in our dataset.

FIGURE 3 Key turnover boundaries for each taxonomic subgroup. Phylogenetic turnover results characterize four marginal regions of concordant turnover (labelled i-iv). Dotted lines depict major turnover boundaries for climate data for tanagers (red), horned frogs (yellow), tree frogs (dark blue), butterflies (light blue), melastomes (light green) and bromeliads (dark green).

Comparative Map of Phylogenetic Turnover
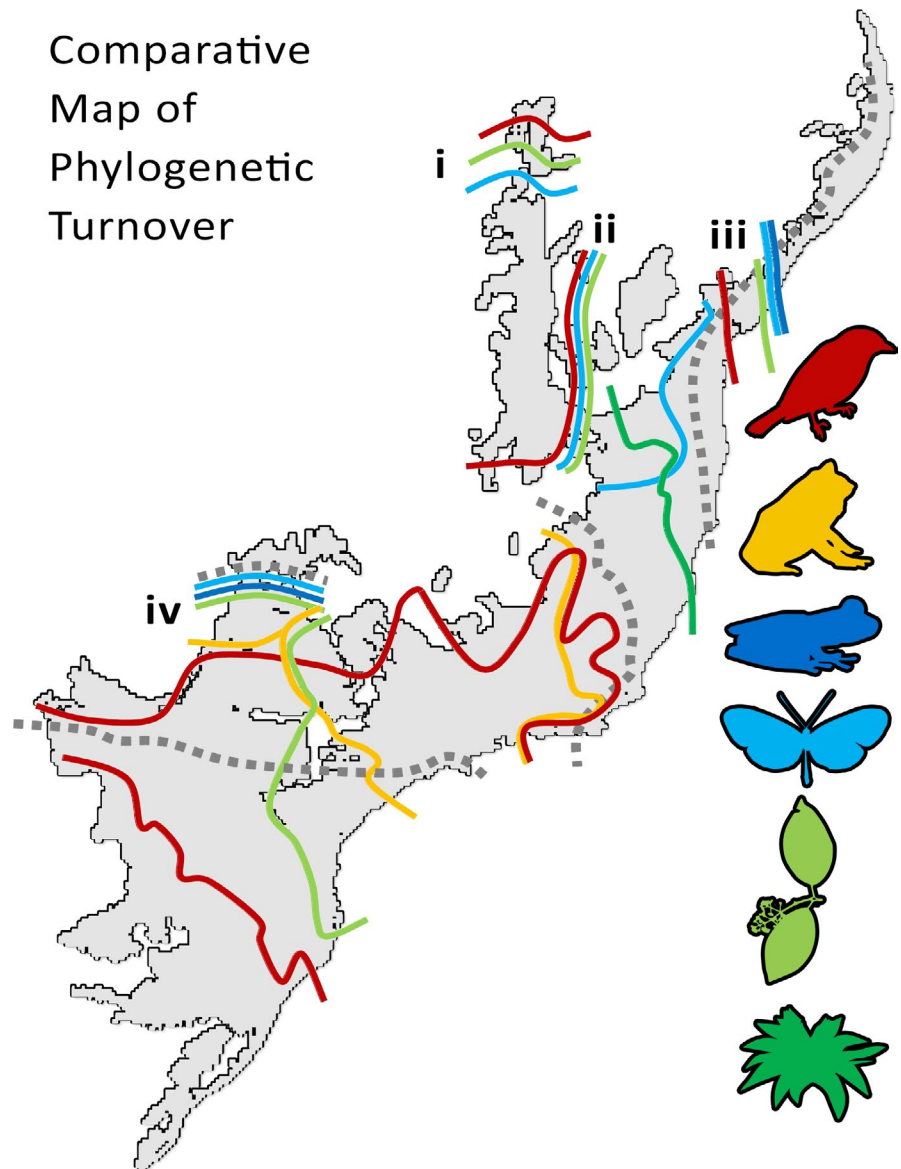
4 | DISCUSSION

4.1 | Biodiversity patterns among taxonomic groups

Our compilation has uncovered high diversity in the montane regions of the Atlantic Forest, a finding that aligns well with multiple taxon-specific studies in the region and elsewhere (e.g. Antonelli, 2017). Although simple comparisons would be inappropriate (as published studies vary widely in the scope, grain and level of biological sampling), a signal of higher species richness in the topographically complex areas of central Atlantic Forest is shared for most biological groups investigated to date. The latitudinal bands of 22–25°S, which include the coast and a portion of two mountain ranges in the states of São Paulo and Rio de Janeiro, have been identified to host the highest species richness of marsupials, rodents and primates of the Atlantic Forest (Costa, Leite, da Fonseca, & da Fonseca, 2000). These mountains have also been reported to hold high levels of species richness within other groups of butterflies (Brown & Freitas,

2000; Santos et al., 2020), birds (Vale et al., 2018) and plants (Lucas & Bünger, 2015). Further, available data from tiger moths likewise identify the mountains and coastal regions of Rio de Janeiro and São Paulo as most species-rich (Ferro & Melo, 2011).

Yet, no single pattern of biodiversity accumulation was observed across the fauna and flora. Instead, we are able to recognize at least three broad distribution syndromes: (1) clades that are mostly southern and montane (melastomes, tree frogs and tanagers), which are characterized by high species richness along the coastal mountain ranges; (2) clades that are essentially northern, often accumulating diversity in Bahia (either closer to the coastal lowlands, as the bromeliads, or in more inland montane areas, as the case of horned frogs); and (3) clades that are more widespread in latitude (and elevation) along the forest, such as the butterflies. These patterns suggest, at least casually, that the distinct animal and plant communities of the Atlantic Forest are not shaped or constrained by the same evolutionary and ecological drivers (e.g. Rangel et al., 2018). Instead, the forest encompasses different
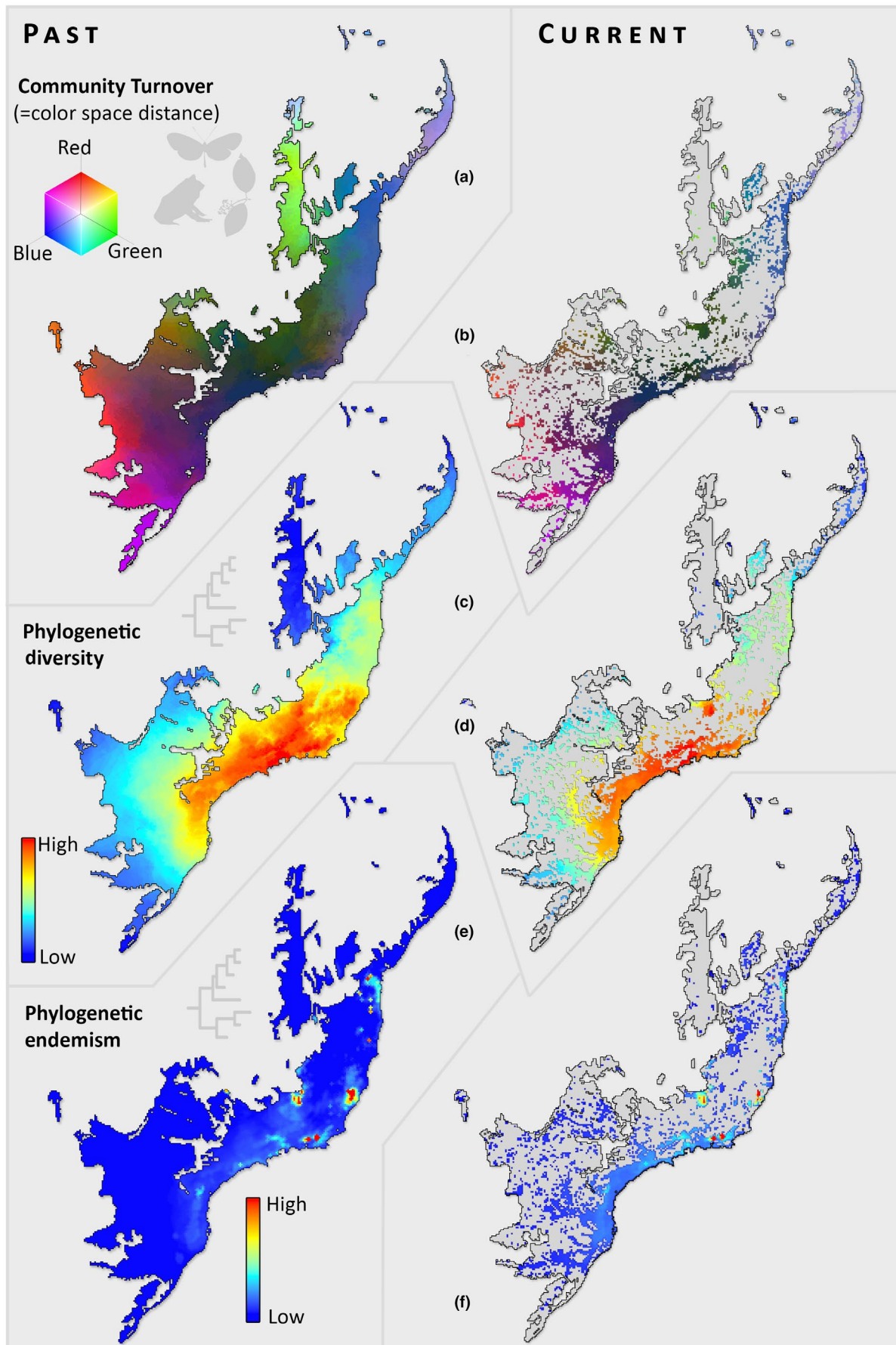
FIGURE 4 Estimated biodiversity patterns—now and then. Inferred pre-Columbian (a) and current (b) community turnover, total phylogenetic diversity (c and d, respectively) and phylogenetic endemism (e and f, respectively) of the six taxonomic groups combined. Left map depicts the no deforestation scenario, and the right map depicts the current forest scenario, where grey areas depict deforested habitats.

FIGURE 5 Areas of unique community composition and their percentage of remaining forests. Black boxes depict landscape extent averages measured in this study.
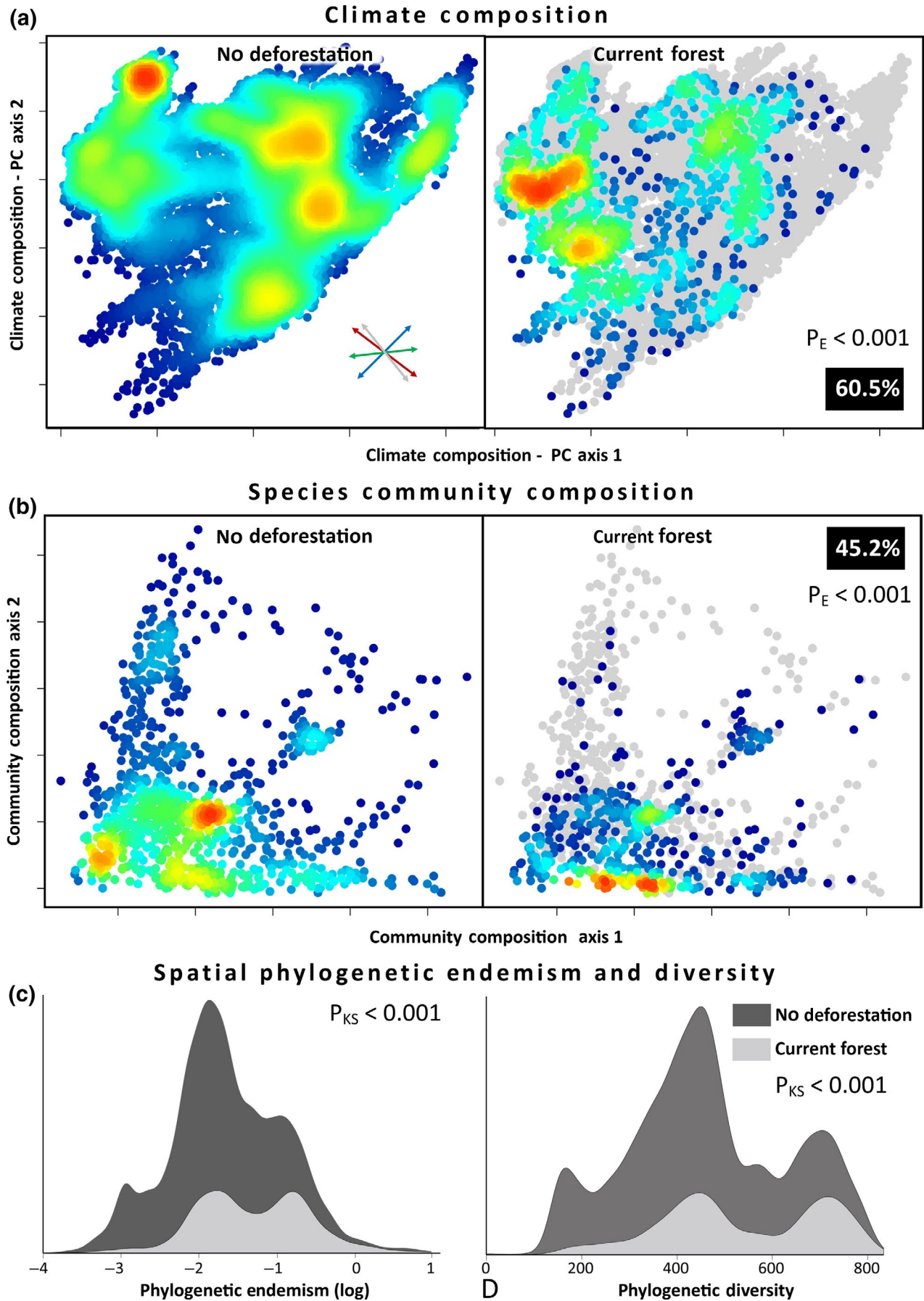

Remaining forests in areas of unique community structure
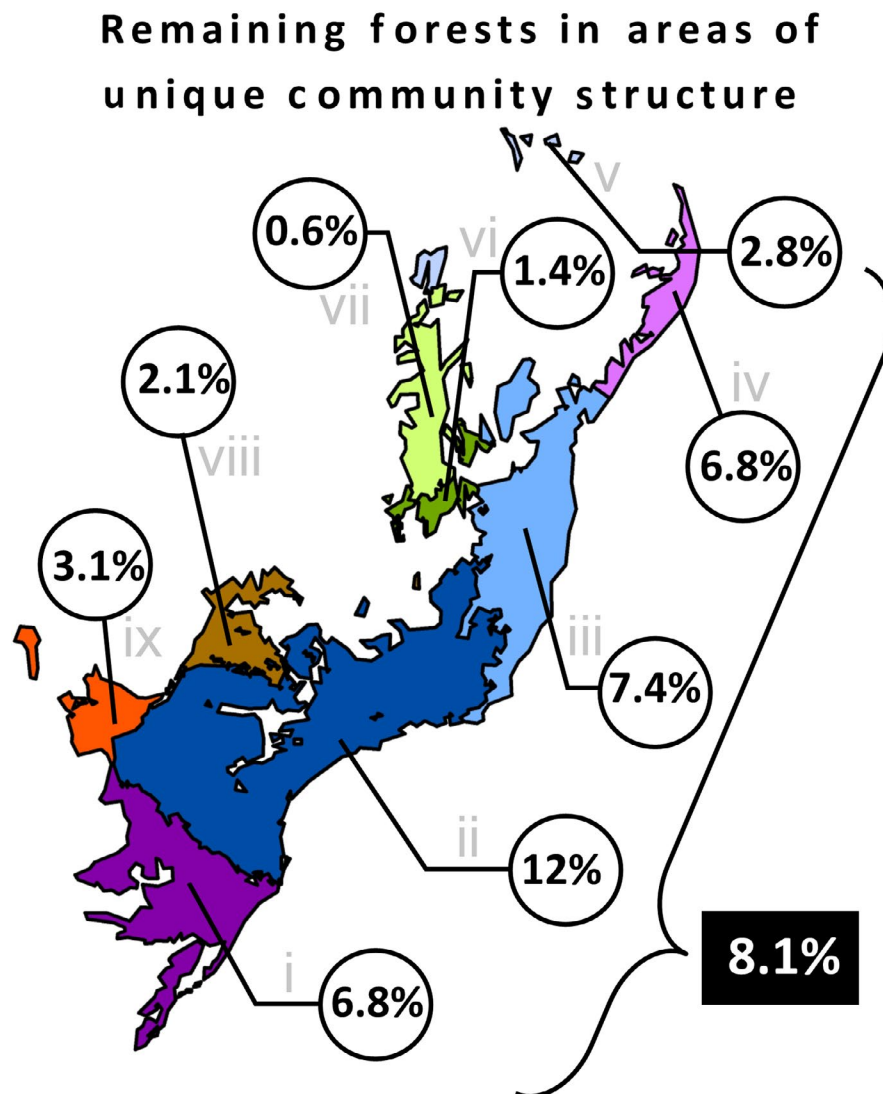
TABLE 1 Range Reductions by Taxonomic Group depicting the lower, mid, upper quartiles of taxa within each group

Taxonomic group	Lower (%)	Mid (%)	Upper (%)
Bromeliads	71.65	85.23	93.79
Melastomes	68.55	83.19	86.76
Butterflies	84.73	87.82	93.80
Tree frogs	80.61	88.55	91.00
Horned frogs	71.65	87.14	94.07
Tanagers	86.42	90.66	91.81

regional species pools, each reflecting unique biogeographic histories and links with other South American forests, or physiological or metabolic tolerances, or both, that are reflected in spatial patterns

(Batalha-Filho, Fjeldså, Fabre, & Miyaki, 2013; Brown et al., 2014; Carnaval et al., 2014; Costa, 2003; Silva, Moraes-Barros, Ribas, Ferrand, & Morgante, 2012). This lack of a unified biodiversity pattern across taxonomic groups highlights the necessity of biodiversity assessments that include multiple clades, environmental spaces or biogeographical tracks (in a way to represent a variety of species pools), to aid conservation planning and monitoring in the Atlantic Forest. To this extent, and given our sampling, we cannot pinpoint one flagship group that adequately acts as a single surrogate taxon for monitoring broad taxonomic changes in this system: given the taxa surveyed here, at least three flagship groups would be needed to represent the distinct diversity syndromes observed in the forest. Importantly, however, the observation that clades of varied dispersal abilities (e.g. birds and frogs), and distinct reproductive systems (plants and animals) share patterns of diversity accumulation speaks

(a)

Climate composition

No deforestation | Current forest

$P_E < 0.001$

60.5%

Climate composition - PC axis 2

Climate composition - PC axis 1

(b)

Species community composition

No deforestation | Current forest

45.2%

$P_E < 0.001$

Community composition axis 2

Community composition axis 1

(c)

Spatial phylogenetic endemism and diversity

$P_{KS} < 0.001$

No deforestation

Current forest

$P_{KS} < 0.001$

−4   −3   −2   −1   0   1

Phylogenetic endemism (log)

D

0   200   400   600   800

Phylogenetic diversity

FIGURE 6 Species composition and climates lost to deforestation. (a) Measurement of climate composition for current forested scenarios and a scenario of no deforestation (pre-Columbian extent). Warmer colours depict higher densities of each climate composition. Grey dots in the current plot depict climate space lost due to deforestation. (b) Measurements of species community composition for current and estimated no deforestation (pre-Columbian) communities. Warmer colours depict higher densities of each community composition. Grey dots in the current plot depict communities lost due to deforestation. Relative changes of phylogenetic endemism (c) and total phylogenetic diversity (d) between current and no deforestation scenarios. Density curves were rescaled to reflect relative abundances between the two scenarios.
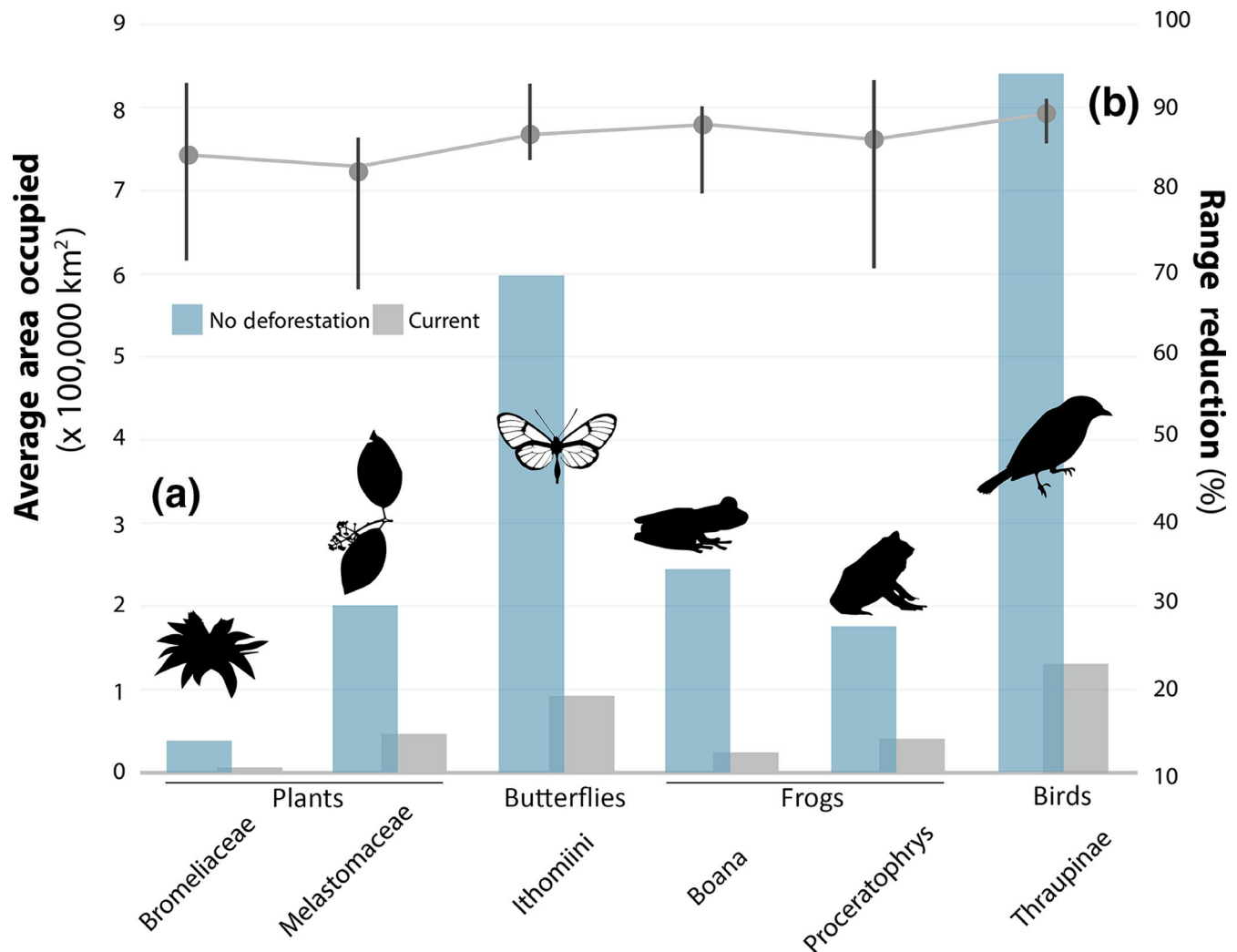
FIGURE 7 Deforestation and range loss. (a) Estimates of mean area occupied by species in each taxonomic group under the current and no deforestation scenarios (grey bars = current; blue bars = no deforestation). (b) Mean per cent range reduction for taxonomic subgroups (line).

to the possible role of history and historical biogeography—as opposed to ecological traits—as a central driver of these broad-scale diversity patterns (Silva et al., 2012). At finer spatial scales, however, the three broad syndromes begin to break down. This is particularly noticeable in the Corrected PD values (Figure 2 row 3), where we observe considerable spatial variation among taxonomic groups. The Corrected PD appears to identify lineage-specific nuances in phylogenetic diversity and appears to be particularly useful for lineage-based conservation prioritization. We hypothesize that life history traits and ecology may play increased roles in structuring the spatial biodiversity patterns at that level.

4.2 | Turnover breaks

Our analysis identified five areas of unique species composition (Figure 5) that largely agree with centres of species endemism previously reported in the literature. One such area (north of Salvador, Bahia; Figure 5, area v) largely matches the Pernambuco Center of Endemism recognized for passerine birds (Da Silva, de Sousa, & Castelletti,), woody plants (Prance, 1982) and butterflies (Brown & Freitas, 2000). Moving southward, a different set of communities is distributed along the state of Bahia (Figure 5, area iii), matching the Coastal Bahia Center of Endemism previously identified for birds (Da

Silva et al.,), woody plants (Prance, 1982), bamboos (Soderstrom, Judziewicz, & Clark, 1988), harvestmen (Da Silva, Pinto-da-Rocha, & DeSouza, 2015) and butterflies (Brown & Freitas, 2000). More inland (Figure 5, area vi), another region of unique communities approximates the location of the Central Bahia Center of Endemism, previously identified in birds (Cardaso da Silva et al.,) and butterflies (Brown & Freitas, 2000). South of Bahia, our analysis recovers another region of unique community composition (Figure 5, area ii) that largely matches the Serra do Mar centre of endemism identified in woody plants (Prance, 1982), bamboos (Soderstrom et al., 1988), harvestmen (Pinto-da-Rocha, da Silva, & Bragagnolo, 2005), amphibians (Vasconcelos et al., 2014), passerine birds (Da Silva et al.,), butterflies (Brown, 1987; Santos et al., 2020) and snakes (Moura et al., 2017). Lastly, a set of unique communities is identified at the southernmost extent of the forest (Figure 5, area i), much in agreement with data reported from studies of birds (Cracraft, 1985) in the Paraná Center of Endemism, tiger moths (Ferro & Melo, 2011), butterflies (Brown & Freitas, 2000), amphibians (Vasconcelos et al., 2014), harvestmen (Pinto-da-Rocha et al., 2005) and snakes (Moura et al., 2017). This ability to synthesize patterns observed across diverse taxonomic groups speaks to the representativeness of our dataset and reinforces the conclusion that generalized patterns of biotic distribution (generalized tracks, likely reflecting how local assemblages have responded to common geographical and environmental changes; e.g. Croizat, Nelson, & Rosen, 1974) can be identified in the Atlantic Forest. In fact, the patterns of biodiversity turnover identified by our study are remarkably similar to those identified by a panbiogeographical analysis of published datasets of Atlantic Forest vertebrates (Silva et al., 2012).

Yet, our analyses of phylogenetic turnover demonstrate the existence of fine-scale differences, across taxonomic groups, in the way that lineages are distributed in space. Although all sampled taxa have marked phylogenetic breaks along the Atlantic coast, they do not necessarily coincide in geography. Butterflies and tree frogs, for instance, show more homogeneity relative to the remaining taxa (Figure 2 row 5; Figure S1). In general, the taxa show marked phylogenetic breaks south and north of the Serra do Mar, and a northern break nearby Salvador (loosely shared by all groups with exception to horned frogs). These phylogenetic turnover zones often follow climatic breaks, as shown by grey dotted lines nearby the Espírito Santo Central Corridor break, and the northern break near Salvador (Figure 3).

4.3 | Recent changes resulting from deforestation

Our measurements likely underestimate pre-Columbian diversity and endemism and, as most analyses of this kind, are naturally biased to represent major patterns and processes relative to the more abundant and widespread species. As such, we acknowledge that our analysis of the potential impact of habitat loss is approximate, as non-random deforestation can introduce spatial biases in any contemporary sampling of species. While we implemented spatial

TABLE 2 Forested habitat within area of endemism in the Atlantic forest (see Map on Figure 5)

Area of endemism	Forest ≥ 5 km^2 (%)	Forest ≥ 1 km^2 (%)
i	4.56	6.75
ii	9.11	11.83
iii	4.21	7.42
iv	3.20	6.80
v	0.46	1.36
vi	2.44	2.75
vii	0.32	0.58
viii	0.89	2.07
ix	1.40	3.09
Entire biome	5.66	8.07

jackknifing and tuning experiments to avoid over-parameterization of the species distribution models and hence minimize intrinsic spatial biases in our occurrence data (please see Methods), we cannot exclude the possibility that each species' ecological tolerances (and ranges) are in fact larger than the ones we measured, particularly due to deforestation in areas of unique climate space. Further, our estimates include neither those species that have gone extinct over the past 500 years, nor include species that went undetected during field surveys. Lastly, we make the implicit assumption that our correlative species distribution models function as an adequate proxy for community composition. To this extent, nuances in species interactions not reflected in their contemporary distributions, and the causal correlations inferred from them, would only increase the complexity and number of community types (likely further fracturing unique communities grouped here into many more).

Still, when masked to reflect the contemporary state of forest fragmentation, our distribution models indicate that deforestation led to extreme, and pervasive, reductions in species ranges, with clade means ranging between 83.2% and 90.7% (Figure 7, Table 2). This number closely approximates recent landscape measures of total deforestation, which indicate that only ca. 8.1% of the forest remains today (i.e. 91.9% loss; Ribeiro et al., 2009). Slight differences in the amount of change across taxa may reflect the more coastal (vs. inland) distribution of several species, and the fact that these regions experienced distinct rates of deforestation (Table 2, Figure 5). The observation of centroid shifts towards the Serra do Mar in the south and towards southern Bahia in the north is not surprising (Figure S2): those areas have been more often spared from habitat degradation either due to their complex topography (in the south) and the shaded cocoa culture (in the north).

Importantly, however, our estimates suggest that nearly half of the unique community types inferred to have existed in pre-Columbian times may be able to persist today—and that while the distribution of total phylogenetic diversity and phylogenetic endemism values may have significantly changed, the forest still harbours a similar range of values as it did in the past. The disproportionate

persistence of unique communities, which is approximately five times higher than the remaining forests, tied to the persistence of phylogenetic diversity and endemism, bring renewed hope to ongoing and proposed restoration initiatives for the Atlantic Forest (e.g. Strassburg et al., 2019). They also highlight the potential role of the Serra do Mar and southern Bahia regions as biodiversity refugia, or stocks of biological diversity in the Anthropocene. Despite forest losses to date, cost-effective restoration practices can not only help offset extinction debts and the loss of ecosystem service in the Atlantic Forest (Strassburg et al., 2019), but also maintain evolutionary history and adaptive potential in the face of further environmental shifts.

DATA AVAILABILITY STATEMENT

All derived climate GIS layers, species distribution models, occurrence data, GenBank and phylogenetic trees used, and output maps of species richness, PD and PE are provided on Dryad (https://doi.org/10.5061/dryad.qz612jmbm).

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BIOSKETCH

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SUPPORTING INFORMATION

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