


Dissecting a biodiversity hotspot: The importance of environmentally marginal habitats in the Atlantic Forest Domain of South America

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Abstract

Aim: We aimed to assess the contribution of marginal habitats to the tree species richness of the *Mata Atlântica* (Atlantic Forest) biodiversity hotspot. In addition, we aimed to determine which environmental factors drive the occurrence and distribution of these marginal habitats.

Location: The whole extension of the South American Atlantic Forest Domain plus forest intrusions into the neighbouring Cerrado and Pampa Domains, which comprises rain forests ("core" habitat) and five marginal habitats, namely high elevation forests, rock outcrop dwarf-forests, riverine forests, semideciduous forests and *restinga* (coastal white-sand woodlands).

Methods: We compiled a dataset containing 366,875 occurrence records of 4,431 tree species from 1,753 site-checklists, which were a priori classified into 10 main vegetation types. We then performed ordination analyses of the species-by-site matrix to assess the floristic consistency of this classification. In order to assess the relative contribution of environmental predictors to the community turnover, we produced models using 26 climate and substrate-related variables as environmental predictors.

Results: Ordination diagrams supported the floristic segregation of vegetation types, with those considered as marginal habitats placed at the extremes of ordination axes. These marginal habitats are associated with the harshest extremes of five limiting factors: temperature seasonality (high elevation and subtropical riverine forests), flammability (rock outcrop dwarf-forests), high salinity (*restinga*), water deficit severity (semideciduous forests) and waterlogged soils (tropical riverine forests). Importantly, 45% of all species endemic to the Atlantic Domain only occur in marginal habitats.

Main conclusions: Our results showed the key role of the poorly protected marginal habitats in contributing to the high species richness of the Atlantic Domain. Various types of environmental harshness operate as environmental filters determining the distribution of the Atlantic Domain habitats. Our findings also stressed the importance of fire, a previously neglected environmental factor.

KEYWORDS

campo rupestre, climate, conservation assessment, flammability, rain forests, restinga, stress gradients, variation partitioning

1 | INTRODUCTION

The Atlantic Forest of South America, or the *Mata Atlântica* as it is known in Brazil where it largely occurs, stretches for over 3,500 km across equatorial, tropical and subtropical latitudes, and is renowned world-wide for being one of the 35 biodiversity hotspots for conservation prioritization (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000). Its importance is also demonstrated by its designation as one of the five primary vegetation “Domains” of Brazil (Ab’Sáber, 2003; IBGE, 1993), the others being the Caatinga, Cerrado, Pampa and Amazon Domains. The Atlantic Forest Domain (hereafter Atlantic Domain) borders all the other Domains except for the Amazon. The prevailing land cover of these bordering Domains are semi-arid thorn woodlands in the Caatinga, woody savannas in the Cerrado and prairies in the Pampa. Species from rain forests, the habitat that originally prevailed in the Atlantic Domain, become a minor component of the landscape in these neighbouring Domains, and they are only found in riverine or high elevation forest enclaves.

Environmental restriction to the establishment of the rain forest habitat is certainly operating at the boundaries of the Atlantic Domain. In a seminal paper, Scarano (2009) proposed a list of five key factors limiting the occurrence and distribution of rain forest species in the Atlantic Domain, which at its harshest extremes give rise to distinct habitats (one for each factor), referred to as marginal habitats. Therefore, the rain forest is placed by Scarano (2009) as the “core” expression of the Atlantic Domain, where deep shade plays the chief role as a limiting factor for competing plants. The five marginal habitats are high elevation forests, rock outcrop dwarf-forests, riverine forests, seasonally dry forests and *restinga* (coastal white-sand woodlands). Most of these marginal habitats have a relatively high density of trees and can be considered forests, albeit not as well developed structurally as rain forests. High elevation forests are primarily associated with frost, with secondary limitation imposed by drought (leeward rain-shadow) and high-light intensity. Cloud forests and *Araucaria*-dominated forests are the main vegetation types of highlands in the Atlantic Domain. Rock outcrop dwarf-forests, found at lower elevations (and even at the seashore), are primarily limited by the paucity, or even lack, of soil and related poor water retention. Meanwhile, riverine forests are associated with waterlogging on lowland plains and riverbeds. Seasonally dry forests (either deciduous or semideciduous) replace rain forests where seasonal rainfall regimes bring regular periods of drought. Finally, environmental harshness for *restinga* is primarily associated with salinity, with secondary limitations imposed by drought and low fertility in mineral nutrients (Scarano, 2009) (Figure 1).

Within limited areas, some studies have confirmed the leading role of Scarano’s limiting factors as distribution filters for plants. These studies addressed tree species composition for particular

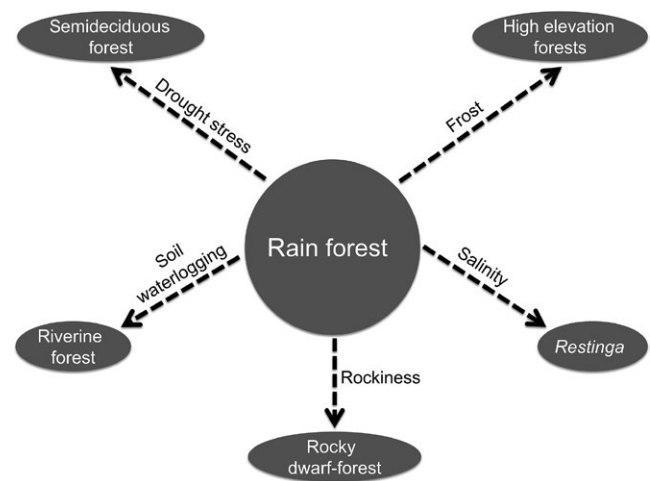


FIGURE 1 Environmental variables (arrows) hypothesized in Scarano (2009) as key factors limiting plant species distribution across the Atlantic Domain of South America. The harshest extremes give rise to distinct vegetation types, referred to as marginal habitats. Coastal white-sand woodlands are called *restinga* in Brazil

sectors of the Atlantic Domain, such as the south-east (Oliveira-Filho & Fontes, 2000; Eisenlohr & Oliveira-Filho, 2015), the subtropical South (Oliveira-Filho, Budke, Jarenkow, Eisenlohr, & Neves, 2015) and the highly biodiverse central region in eastern Bahia state, north-eastern Brazil (Saiter, Eisenlohr, Barbosa, Thomas, & Oliveira-Filho, 2016). However, the whole of the Atlantic Domain has only been investigated for epiphytic angiosperms (Menini-Neto, Furtado, Zappi, Oliveira-Filho, & Forzza, 2016). Also, the Atlantic Domain is affected by fire in much of its distribution (Archibald, Lehmann, Gómez-Dans, & Bradstock, 2013), though to a lesser extent than in surrounding Domains, such as in central (Cerrado woody savannas) and southern Brazil (Pampa prairies). Nevertheless, the potential effect of fire in limiting plant species distribution across the Atlantic Domain is yet to be investigated. Here we bring together a novel and comprehensive dataset assembled on the composition of tree communities across the whole Domain (c. 2,000 community surveys across core and marginal habitats, with >1,000 sites representing surveys not used in the aforementioned studies), combined with environmental data, focusing on testing Scarano’s proposed limiting variables as well as factors that were neglected in previous studies (e.g., fire).

Besides the importance for community ecology, understanding the degree to which limiting factors drive community differentiation is inherently relevant for conservation. The Atlantic Domain houses c.18,000 plant species (REFLORA, 2017), but the current high levels of fragmentation and the continuous habitat loss throughout the Domain have raised several concerns in the scientific community (Galindo-Leal, Jacobsen, Langhammer, & Olivieri, 2003; Joly, Metzger, & Tabarelli,

2014; Tabarelli, Pinto, Silva, Hirota, & Bedê, 2005; Tabarelli, Silva, & Gascon, 2004). Therefore, we believe the time is ripe for studies aiming to test the overall importance of environmental conditions in controlling the occurrence and distribution of plant species across the whole extent of the Atlantic Domain and, more importantly, across both its core and marginal habitats.

We addressed the following questions: (1) Are the patterns of tree species distribution across the Atlantic Domain, and its intrusions into neighbouring Domains, limited by factors associated with water deficit (via both soil depth and dry season), water excess (via water-logging), frosts (via low temperature) and soil salinity? If previously unrecognized environmental conditions are the main factors explaining the patterns of tree species distribution, Scarano's (2009) limiting factors should account for a small proportion of the variation in community composition explained by environmental factors; (2) are these limiting factors leading to floristically distinct marginal habitats? If the community composition of the marginal habitats is simply a nested subset of the more diverse Atlantic Domain rain forest, species turnover should account for a small fraction of the dissimilarity between rain forest and marginal habitats; and (3) what is the contribution of these marginal habitats to the overall high species richness of the Atlantic Domain?

2 | METHODS

2.1 | Study area

The Atlantic Forest, designated as one of the five phytogeographical "Domains" of Brazil (Ab'Sáber, 2003; IBGE, 1993), occurs primarily along the Atlantic coast and is bordered by the Pampa Domain (woody prairies) of southern Brazil and by the "dry diagonal," a corridor that includes three other phytogeographical Domains: Caatinga (largely semi-arid thorn woodlands) of north-eastern Brazil, Cerrado (largely woody savannas) of central Brazil, and Chaco (largely semi-arid thorn woodlands) of Paraguay–Argentina–Bolivia (IBGE, 1993, Prado & Gibbs 1993, Neves, Dexter, Pennington, Bueno, & Oliveira-Filho, 2015). The South American Atlantic Forest Domain (hereafter Atlantic Domain) has a history of controversies over its geographical circumscription and associated terminology. The controversy may be summarized by three main concepts of Atlantic Domain habitats: the sensu stricto, sensu lato and sensu latissimo concepts (Oliveira-Filho, Jarenkow, & Rodal, 2006). The first, and most restrictive concept, includes only the tracts of rain forests that occur as a narrow band along the coast (<100 km wide and up to 2500 m elevation) and stretches all through the Domain, though with two main interruptions, the São Francisco Gap and Campos dos Goytacazes Gap. The former is a semi-arid nucleus at the mouth of the São Francisco River (~10°30'S), and the latter is a seasonally dry region extending from southern Espírito Santo to northern Rio de Janeiro (RJ) States, with its driest extreme at Cabo Frio/RJ (~22°50'S).

The sensu lato concept of Atlantic Domain habitats, which is currently prevalent, includes other habitats adjacent to rain forests, such as the much more extensive semideciduous forests that cover

increasingly larger areas towards the south and become wide enough to reach eastern Paraguay and north-eastern Argentina. *Araucaria*-dominated forests are also a very important component of the sensu lato concept, followed by coastal woodlands on white-sand substrates (termed *restingas*) and three highland dwarf-forests: rocky cloud dwarf-forests, rocky semideciduous dwarf-forests and rocky highland savannas (termed *campos rupestres*).

The sensu latissimo concept of Atlantic Domain habitats proposed by Oliveira-Filho et al. (2006) surpasses the geographical limits of the Atlantic Domain to include riverine and deciduous forest tracts occurring in the neighbouring Domains as a secondary component of the landscape, though with a typically Atlantic Domain flora. In the present contribution, we adopt this concept because it allows a more complete inclusion of marginal habitats. However, deciduous forests found in the Cerrado and Pampa Domains, one of the forest types in the sensu lato concept (IBGE, 1993), were not included in this contribution because previous studies (e.g., Eisenlohr & Oliveira-Filho, 2015; Oliveira-Filho et al., 2006) have demonstrated that their flora is distinct and more closely related to that of semi-arid woodlands (e.g., in the Caatinga Domain).

2.2 | Dataset

We extracted the dataset from the NeoTropTree (NTT) database (<http://prof.icb.ufmg.br/treeatlan>), which consists of tree species checklists (trees defined here as freely standing woody plants >3 m in height) compiled for geo-referenced sites, extending from southern Florida (U.S.A.) and Mexico to Patagonia. NTT currently holds 5,126 sites/checklists, 14,878 woody plant species and 920,129 occurrence records. A site/checklist in NTT is defined by a single habitat, following the classification system proposed by Oliveira-Filho (2015), contained in a circular area with a 10-km diameter. Therefore, where two or more habitats co-occur in one 10-km area, there may be two geographically overlapping sites in the NTT database, each for a distinct habitat.

The data were originally compiled from an extensive survey of published and unpublished (e.g., PhD theses) literature, particularly those on woody plant community surveys and floristic inventories. Moreover, new species occurrence records obtained from both major herbaria and taxonomic monographs have been added to the checklists when they were collected within the 10-km diameter of the original NTT site and within the same habitat. All species and their occurrence records were checked regarding current taxonomic and geographical circumscriptions, as defined by the team of specialists responsible for the online projects *Flora do Brasil* and *Flora del Conosur* (available at <http://floradobrasil.jbrj.gov.br/> and <http://www.darwin.edu.ar/>, respectively). NTT does not, therefore, include occurrence records with doubtful identification, location or habitat, nor sites with an indication of high anthropogenic disturbance. The latter is assessed by taking into account the information available in the studies that comprise the checklists, and by direct observation of site surface on Google Earth©. It also excludes checklists with low species richness (<20 species), because this is often due to low sampling/collecting efforts, which results in poor descriptive power.

This study used a subset of tree inventories from the NTT database, consisting of 328 rain forest sites and 1,425 sites representing the limiting environmental factors and marginal habitats proposed by Scarano (2009), namely seasonally dry (663 semideciduous forests), high elevation (193 *Araucaria*-dominated forests and 61 cloud forests), rock outcrops (49 rocky cloud dwarf-forests, 31 rocky semideciduous dwarf-forests and 41 *campos rupestres*), high salinity (181 restingas—with only forests and dwarf-forests of the mosaic included) and waterlogged soils (133 tropical riverine forests and 73 subtropical riverine forests). Note that marginal habitats associated with seasonal drought and high salinity are represented by one vegetation type, whereas high elevation, rock outcrops and waterlogged soils are represented by more than one vegetation type. The final species matrix contained presence/absence data for 4,431 tree species across 1,753 sites, with a total of 366,875 presences (see Figure 2a and b).

The NTT database also included 26 environmental variables for all its sites, derived from multiple sources (at a 30 arc-second resolution; detailed below). The resolution used in this study was particularly appropriate (1 km²) because all sites are more than 1 km distant from each other (only 124 of 1,753 sites are less than 5 km distant from another site, and the mean distance between all sites is >1,000 km). Elevation at the NTT site centre was used as an integrative environmental variable. Mean annual temperature, mean daily temperature range, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, mean annual precipitation, precipitation of the wettest month, precipitation of the driest month and precipitation seasonality were obtained from WorldClim 1.4 data layers (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). WorldClim monthly temperatures and precipitation were also interpolated to obtain values for 5-day intervals by applying sinusoidal functions centred at day 15 of each month. These functions yielded values for days 1, 5, 10, 20, 25 and 30, which were used to generate Walter's Climate Diagrams (Walter, 1985) and, thus, four additional variables: duration (days) and severity (days) of both the water deficit and water excess periods. Frost frequency (days) and cloud interception

(mm) were obtained from interpolating known values as response variables (data obtained from 135 and 57 Brazilian Meteorological Stations measuring frost frequency and cloud interception, respectively) with elevation, latitude and the WorldClim layers as predicting variables. Potential evapotranspiration (mm) and the aridity index (annual precipitation/potential evapotranspiration) were obtained from Zomer et al. (2007), Zomer, Trabucco, Bossio, van Straaten, and Verchot (2008).

Surface rockiness (% exposed rock), soil coarseness (% sand), soil fertility (% base saturation) and soil salinity (ds/m) were obtained from the Harmonized World Soil Database v 1.2 (available at <http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/>) and ranked afterwards by mid-class percentage. The use of classes was adopted to add robustness to the data because of the high local soil heterogeneity that makes raw figures unrealistic. Soil drainage classes were obtained following EMBRAPA's protocol (Santos et al., 2013), which combines soil type, texture and depth with landforms. Soil drainage classes, mean annual precipitation (Hijmans et al., 2005) and the aforementioned indices of water deficit and excess were also combined to produce a hyperseasonality index. Grass coverage (%) was used as a proxy of fire return interval (i.e., frequency). Previous studies give support to grass coverage as a good proxy of fire frequency (Archibald et al., 2013; Hoffmann et al., 2012; Lehmann et al., 2014), although further quantification of fire regime is clearly needed (c.f. Archibald et al., 2013). Grass coverage was obtained by direct observation of site surface on Google Earth© images in five 100 × 100 m areas, one at the central coordinates of the NTT site and four at 2.5 km away from it and towards the NE, SW, NW and SE.

Further details of NTT history, products and protocols can be found at <http://prof.icb.ufmg.br/treetlan>.

2.3 | Analyses of community turnover

We first explored the patterns of floristic differentiation between rain forest and marginal habitats by performing non-metric multidimensional scaling (NMDS) (McCune & Grace, 2002). We then assessed

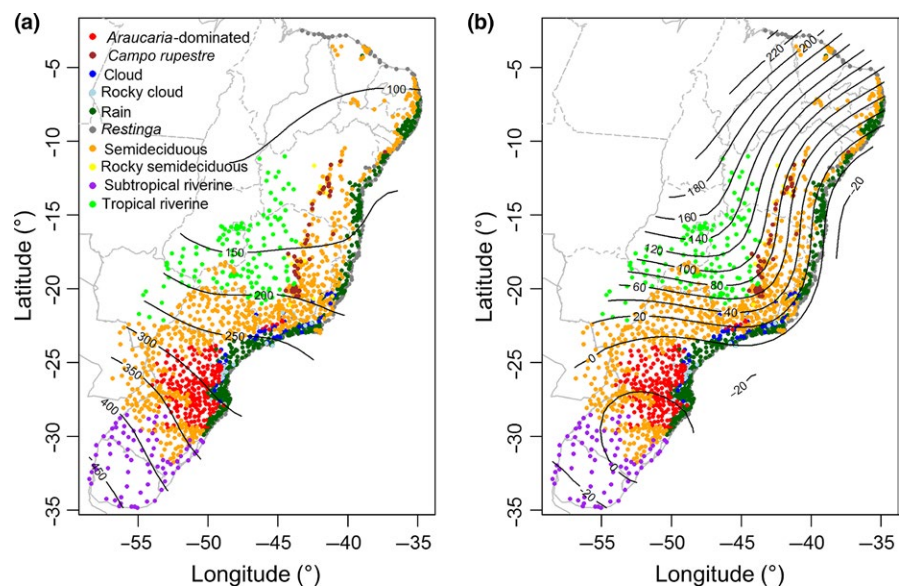


FIGURE 2 Distribution of 1,753 Atlantic Domain sites with their a priori classification into vegetation types (symbols). Variations in (a) temperature seasonality (standard deviation × 100) and (b) water deficit severity (mm) were fitted across geographical space by generalized additive models. Dashed lines represent Brazilian state borders

the relative importance of turnover and nestedness to floristic differentiation between rain forest and each of the marginal habitats. This analysis was performed by first calculating Jaccard pairwise distances, which range from 0 (identical in community composition) to 1 (completely different in community composition). These pairwise distances are then decomposed into dissimilarity due to species turnover (i.e., only compositional changes) and dissimilarity due to differences in species richness. The latter is the difference between Jaccard distance and the dissimilarity due to species turnover (Baselga, 2010). The ordination and the dissimilarity partitioning analyses were conducted in the statistical packages *vegan* (Oksanen et al., 2016) and *betapart* (Baselga & Orme, 2012), respectively, both in the R Statistical Environment (R Development Core Team, 2015).

We assessed whether Scarano's (2009) limiting factors are the key environmental factors driving variation in community composition, and then explored the results visually by plotting the habitats in geographical or ordination (NMDS) space and then fitting the values of the most important environmental variables via generalized additive models (GAM) and generalized linear models (GLM), respectively. This routine follows methods similar to those proposed by Blanchet, Legendre, and Borcard (2008) and Legendre, Borcard, and Roberts (2012), which comprise (1) the exclusion of 300 singletons (species found at a single site), as they commonly increase the noise in most analyses without contributing information (Lepš & Šmilauer, 2003); (2) the Hellinger transformation of the binary presence/absence data (Legendre & Gallagher, 2001), which reduces the effect of widespread species; (3) the independent compilation of significant spatial and environmental variables through a forward selection method for redundancy analysis (RDA), after first checking that the respective global models were significant (Blanchet et al., 2008); (4) an additional and progressive elimination of collinear variables based on their variance inflation factor (VIF) and ecological relevance, until maintaining only those with $VIF < 4$ (Quinn & Keough, 2002); and (5) an RDA-based partitioning of variation in the community composition matrix due to environmental variables, spatial autocorrelation and their combined, statistically indistinguishable effects. As spatial variables, we used principal coordinates of neighbour matrices (PCNMs; Borcard, Legendre, Avois-Jacquet, & Tuomisto, 2004), which represent the spatial structure of the sampling units at multiple spatial scales without considering any environmental variation (Borcard, Legendre, & Drapeau, 1992; Borcard et al., 2004; Legendre et al., 2002). We tested the overall significance of the environmental fraction (controlled for spatial autocorrelation) by applying ANOVA permutation tests (999 permutations) for RDA (Peres-Neto, Legendre, Dray, & Borcard, 2006). The variable selection, variation partitioning, NMDS, GLM and GAM analyses were conducted using the fields (Nychka, Furrer, Paige, & Sain, 2015), *spacemaker* (Dray, 2010) and *vegan* (Oksanen et al., 2016) packages in the R Statistical Environment (the variation partitioning script is available as supporting information). The maps were designed using the package *maptools* (Lewin-Koh & Bivand, 2012) in the R Statistical Environment.

We also calculated patch statistics to test whether floristic differentiation can be modulated by habitat quality (a proxy for anthropogenic effect). We used the *PatchStat* function—available in the

SDMTools package (VanDerWal, Falconi, Januchowski, Shoo, & Storlie, 2014) in the R Statistical Environment—and identified configuration metrics of landscapes (e.g., patch area, edge perimeter) for 95% of our sites using the vegetation map of the Brazilian Atlantic Domain (<http://mapas.sosma.org.br/>). We found that the effect of habitat quality was negligible in explaining variation in tree community composition across rain forests and marginal habitats (see Table S1 for further details).

2.4 | Conservation assessment

We assessed how well the floristic diversity is captured in our dataset by calculating the expected species accumulation curves for rain forest and marginal habitats, using sample-based rarefaction (Colwell et al., 2012) with the “*specaccum*” function in the statistical package *vegan* (Oksanen et al., 2016). We also explored levels of endemism for Atlantic Domain habitats. We obtained the lists of endemic species (woody + non-woody) from *Reflora* (<http://floradobrasil.jbrj.gov.br/>), which is the most comprehensive study of the patterns of plant species richness and endemism for phytogeographical Domains in eastern South America. Afterwards, we conducted an assessment of the conservation status of the Atlantic Domain habitats by overlaying the distribution of our 1,753 sites on to the coverage of protected areas across South America. We used conservation units from the World Database on Protected Areas (IUCN & UNEP—WCMC, www.protectedplanet.net) and *Cadastro Nacional de Unidades de Conservação* (Ministério do Meio Ambiente—Brazil, www.mapas.mma.gov.br). Species accumulation curves are provided for rain forest and marginal habitats as SI (Fig. S1).

Lastly, we used the main environmental variables emerging from the community turnover models to create site groups discriminating the marginal habitats and then processed the species matrix following the procedure proposed by Tichý and Chytrý (2006) to produce sets of diagnostic species, which are provided as supporting information (Table S2). This procedure is particularly suitable to quantify the fidelity of species to groups that have unequal sizes, that is, different numbers of sampling units, as is the case with our study. After the groups are equalized, a coefficient of fidelity is calculated and the significance of each diagnostic species is obtained with 999 Monte Carlo permutations.

3 | RESULTS

3.1 | Floristic patterns

The distribution of the sites in the ordination space yielded by NMDS (Figure 3a and b) largely segregated rain forests and marginal habitats. The ordination placed “marginal” vegetation types at the extremes of the first three ordination axes. Axis 1 segregated, at negative scores, the shoreline-associated *restinga* and, at positive scores, the vegetation types associated with low-temperature extremes of higher elevations and latitudes further from the equator (*Araucaria*-dominated forests and subtropical riverine forests). Axis 2 segregated, at positive scores, vegetation types associated with rock outcrops (rocky cloud dwarf-forests,

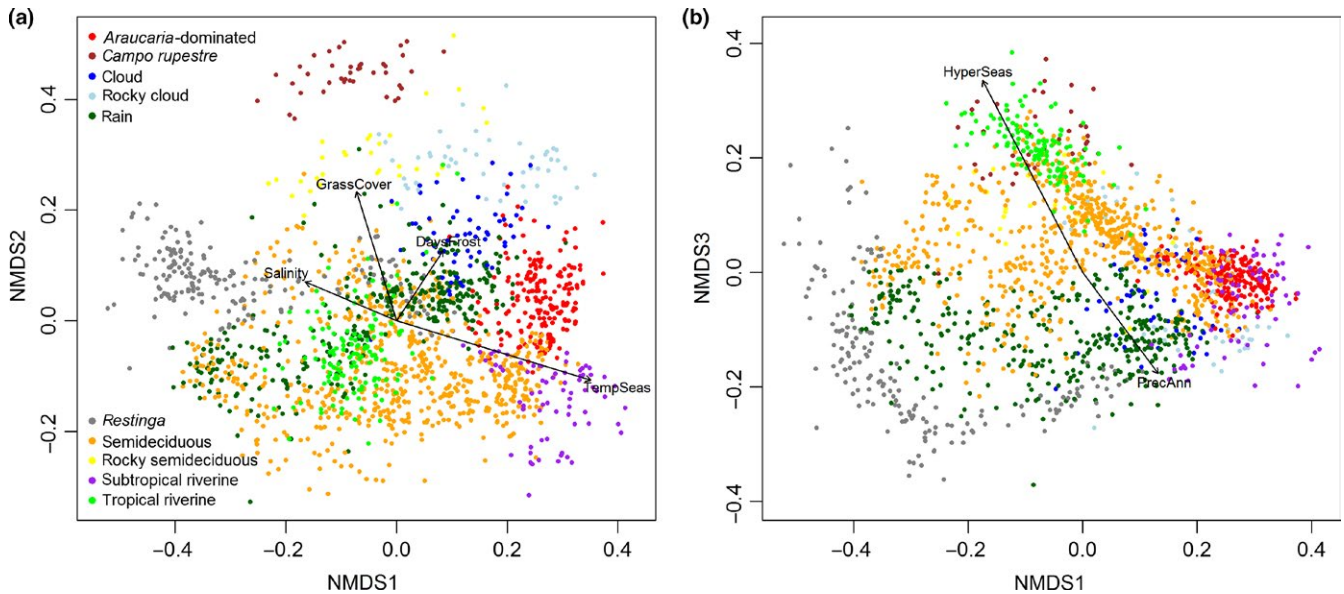


FIGURE 3 Ordination of 1,753 Atlantic Domain sites yielded by non-metric multidimensional scaling (NMS) of their tree species composition with their a priori classification into vegetation types (symbols). Diagrams are provided for axes 1×2 (a) and 1×3 (b). Arrows in each diagram represent the correlations between the most explanatory environmental variables and ordination scores. TempSeas, temperature seasonality; DaysFrost, days of frost; Salinity, soil salinity; GrassCover, grass coverage; HyperSeas, water hyperseasonality; PrecAnn, mean annual precipitation

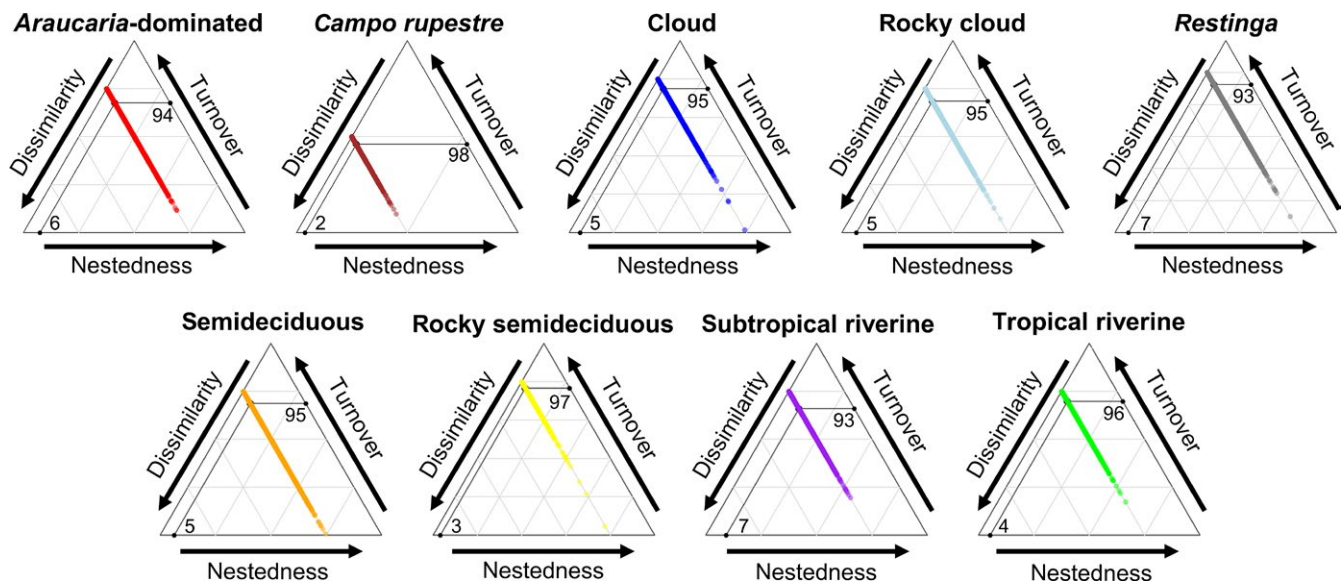


FIGURE 4 Decomposition of the pairwise floristic dissimilarity of rain forest and marginal habitat sites of the South American Atlantic Domain (e.g., bullets in the *Araucaria*-dominated triangle represent pairwise dissimilarities between each of the 193 *Araucaria*-dominated sites and all the 328 rain forest sites, i.e., 63,304 pairwise dissimilarity values). Numbers represent the mean turnover (%) and nestedness (%) components of the Jaccard dissimilarity for each marginal habitat

rocky semideciduous dwarf-forests and *campos rupestres*). Axis 1 further segregated rock outcrop vegetation types into warmer sites (rocky semideciduous dwarf-forests and *campos rupestres*), at positive scores, and colder sites (rocky cloud dwarf-forests), at negative scores. Axis 3 placed the habitat associated with seasonal drought (semideciduous forests) at intermediate scores and the habitat associated with water-logged soils at positive scores (tropical riverine forests).

The floristic composition of marginal habitats is not simply a nested subset of the more species rich rain forest. The turnover component accounts for most of the floristic dissimilarity of each marginal habitat in relation to rain forests (Figure 4). Nestedness is higher than the turnover component in very few cases (i.e., few marginal habitat sites are simply a subset of another rain forest site; see semideciduous forest triangle in Figure 4). More specifically, vegetation types associated

	adj. R ² cum.	ΔAIC	F	VIF
Temperature seasonality	0.068	-508.02	128.96	3.51
Grass coverage	0.174	-716.16	34.28	1.28
Salinity	0.199	-767.24	27	2.04
Water deficit severity	0.209	-787.86	22.65	3.13
Hyperseasonality	0.222	-816.58	15.42	3.82
Mean annual precipitation	0.234	-840.26	13.41	2.57
Days of frost	0.242	-856.91	8.87	1.76
Elevation	0.251	-863.48	8.52	3.83
Temperature daily range	0.251	-875.73	7.8	2.64
Cloud interception	0.257	-887	4.89	3.27
Soil fertility	0.26	-892.36	4.6	1.46
Water excess duration	0.263	-896.43	3.73	3.11
Sandiness	0.264	-897.48	3	1.74

The variables shown were selected through a forward selection method for redundancy analysis and are ordered by the amount of explained variation in species composition across rain forest and marginal habitats. Goodness-of-fit of the predictor variables was assessed through adjusted coefficients of determination, Akaike information criterion (AIC), F-values and significance tests ($p < .01$ in all cases). VIF, variance inflation factor, obtained using the r-squared value of the regression of one variable against all other explanatory variables. adj. R² cum. = cumulative adjusted coefficient of correlation.

with rock outcrops (including *campos rupestre*) have the highest fraction of dissimilarity attributed to turnover while *restinga* and subtropical riverine forest have the lowest fraction attributed to turnover.

3.2 | Variation partitioning analyses

The forward selection procedure retained 13 environmental variables in the model to explain the variation in tree species composition (Table 1). In partitioning the variation explained by the retained environmental and spatial predictors, we found that the environmental fraction explained 27% of the variation, 5% of which was independent of spatial autocorrelation ($p < .01$). The environmental predictors could not account for a spatially structured variation of 12% ($p < .01$), and 61% of the variation remained unexplained (see discussion for more details).

The harshest extremes of the retained environmental variables (Table 1) do lead to distinct habitats, treated here in the context of "marginal" vegetation types. A north to south increase in temperature seasonality was congruent with a latitudinal gradient in community turnover, which represents the floristic differentiation of *Araucaria*-dominated forests and subtropical riverine forests (Figures 2a and 3a) from all other vegetation types. Grass coverage, a proxy for fire frequency (see Methods), was congruent with the floristic differentiation of the vegetation types associated with rock outcrops (including *campos rupestres*) from all other vegetation types (Figure 3a). Within the rock outcrop habitat, the frequency of frost was associated with the floristic differentiation of rocky cloud dwarf-forests from the other rocky vegetation types. Soil salinity was congruent with a coast to inland gradient in community turnover, which represents the floristic differentiation of *restinga* from all other vegetation types (Figure 3a). Another coast to inland gradient is evident in the tropical section of

TABLE 1 Variables selected for the analysis of environmental controls of tree community composition in the Atlantic Domain of South America.

the Atlantic Domain, where water deficit severity and mean annual precipitation, proxies for drought-stress, explained the floristic differentiation of everwet vegetation types, namely rain forest, cloud forests and rocky cloud dwarf-forests, from *campos rupestres*, semideciduous forests, rocky semideciduous dwarf-forests and tropical riverine forests (Figures 2b and 3b). At the harshest extreme of the drought-stress gradient (Figure 3b), water-related hyperseasonality (i.e., ranging from water shortage to soil waterlogging) segregates *campos rupestres* and tropical riverine forests from semideciduous forests. These factors represent the seven most explanatory environmental variables (Table 1) and they accounted for a large fraction of the variation in community composition attributed to environmental predictors (adjusted R² = .242; Table 1), which is nearly the same as the value for all 13 variables retained in the variation partitioning model (adjusted R² = .264; Table 1).

3.3 | Conservation assessment

The species accumulation curves showed a levelling off at larger sample sizes for all vegetation types, although no curve actually reached an asymptote. Species accumulation curves levelled off less in vegetation types associated with rock outcrops (including *campos rupestres*) and in *Araucaria*-dominated forest (see Fig. S1). Because the overall floristic dissimilarity between cloud forests and rain forests was relatively low (Figure 3), we assessed the rates of endemism considering these two vegetation types as "core" habitats (wet forests in Table 2 and Figure 5). Despite the fact that wet forests have twice as much protection as marginal habitats (45% and 26%, respectively; Table 2 and Figures 5, 6 and 7), almost half of all species endemic to the Atlantic Domain are only found in marginal habitats (Table 2).

TABLE 2 Wet forests (rain forest + cloud forest) and marginal habitats of the South American Atlantic Domain ranked by their level of endemism in plant species (total endemics/total species richness).

	All						Endemics					
	Angiosperms	Pteridophyta	Gymnosperms	Total	Angiosperms	Pteridophyta	Gymnosperms	Total	Total endemics	%	PA (%)	
wet forests	8,938	755	2	9,695	3,740	199	-	3,939	41	45		
<i>campos rupestres</i>	4,936	57	-	4,993	1,953	15	-	1,968	39	54		
rocky cloud dwarf-forest	2,037	97	2	2,136	429	19	-	448	21	73		
<i>restinga</i>	2,490	38	2	2,530	297	1	-	298	12	51		
semideciduous forest	3,362	165	1	3,528	243	4	-	247	7	19		
rocky semideciduous dwarf-forest	878	21	1	900	8	-	-	8	1	52		
<i>Araucaria</i> -dominated forest	1,348	155	4	1,507	81	6	-	87	6	17		
tropical riverine forest	2,495	61	5	2,561	101	2	1	104	4	21		
subtropical riverine forest	231	2	1	234	-	-	-	-	-	1		

PA = percentage of NeoTropTree sites in protected areas (see Figures 5, 6 and 7). Lists of plant species (woody + non-woody) were obtained from the Reflora project (<http://floradobrasil.jbrj.gov.br>).

4 | DISCUSSION

Both the variation partitioning and the ordination support the importance of the set of limiting conditions proposed by Scarano (2009) as the factors controlling tree community composition of rain forests and marginal habitats, which are treated here in the context of “marginal” vegetation types (*question 1*). We also showed that these limiting factors lead to floristically distinct tree communities, thus indicating that the marginal habitats are not simply a nested subset of the more diverse Atlantic Domain rain forest (*question 2*). In fact, marginal habitats shelter nearly half the endemic plant species in the Atlantic Domain (*question 3*).

4.1 | Limiting factors

A north to south increase in temperature seasonality is the major factor associated with a wide-scale floristic differentiation between tropical habitats and those that are mainly comprised of cold-tolerant species (see Figure 2a and Table 1). Interestingly, this is consistent even within the subtropical section of the Atlantic Domain (Oliveira-Filho et al., 2015), where variation in community composition along the temperature seasonality gradient is congruent with increasing foliage deciduousness, a trait associated with frost-tolerance (Oliveira-Filho et al., 2015). A similar trend in species turnover and foliage deciduousness is also found in the tropical and equatorial sections of the Atlantic Domain, but the main driving force there is rainfall seasonality and the associated dry season (Eisenlohr & Oliveira-Filho, 2015; Saiter et al., 2016). Contrary to our expectations, temperature seasonality showed stronger explanatory power than the frequency of frosts, believed to be a chief factor limiting species distribution across temperature gradients (see Oliveira-Filho et al., 2015; Rundel, Smith, & Meinzer, 1994; Scarano, 2009; Zanne et al., 2014). Nevertheless, within rock outcrop habitats (Figure 3b), the occurrence of frost in rocky cloud dwarf-forests seems to be limiting the establishment of species from *campos rupestres* and rocky semideciduous dwarf-forests, suggesting that the frequency of frosts is an important factor underpinning the distribution of marginal habitats in the Atlantic Domain, though at smaller spatial scales.

Periods of water shortage represented by seasonal droughts are indeed the chief factor driving species turnover in the tropical and equatorial sections of the Atlantic Domain (see Figure 2b), while other local factors may also affect water availability to plants (Pontara et al., 2016). The substrate often either favours or restricts water drainage via landforms and soil depth and texture, while strong winds may add to the water deficit stress, particular nearer to the coast, where *restingas* occur. In this coastal marginal habitat, which was identified as one of the most floristically differentiated (see Figure 3a), the stress due to water deficit is increased by a sandy substrate with high salinity, and by salt spray coming directly from the ocean (Cerqueira, 2000). In addition, although nutrient-poor soils prevail all over the Domain, the edaphic conditions in *restingas* represent an extreme of particularly low soil fertility (most NTT sites of the dataset were classified as “dystrophic” while most *restingas* were “hyperdystrophic”).

When assessing whether soil waterlogging leads to a floristically distinct marginal habitat, we found that the intrusions of riverine

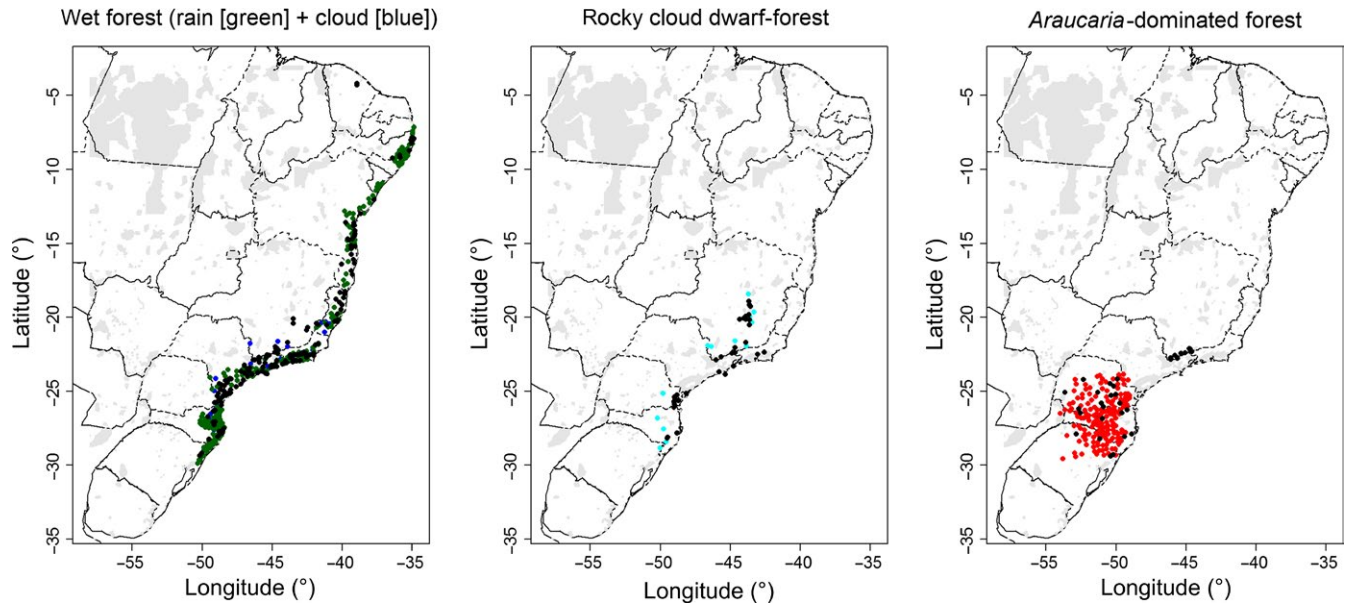


FIGURE 5 Conservation assessment of wet forests (rain + cloud), rocky cloud dwarf-forest and *Araucaria*-dominated forests of the South American Atlantic Domain. Black bullets represent woody plant communities occurring within protected areas. Grey areas represent the current network of protected areas across South America. Dashed lines represent Brazilian state borders

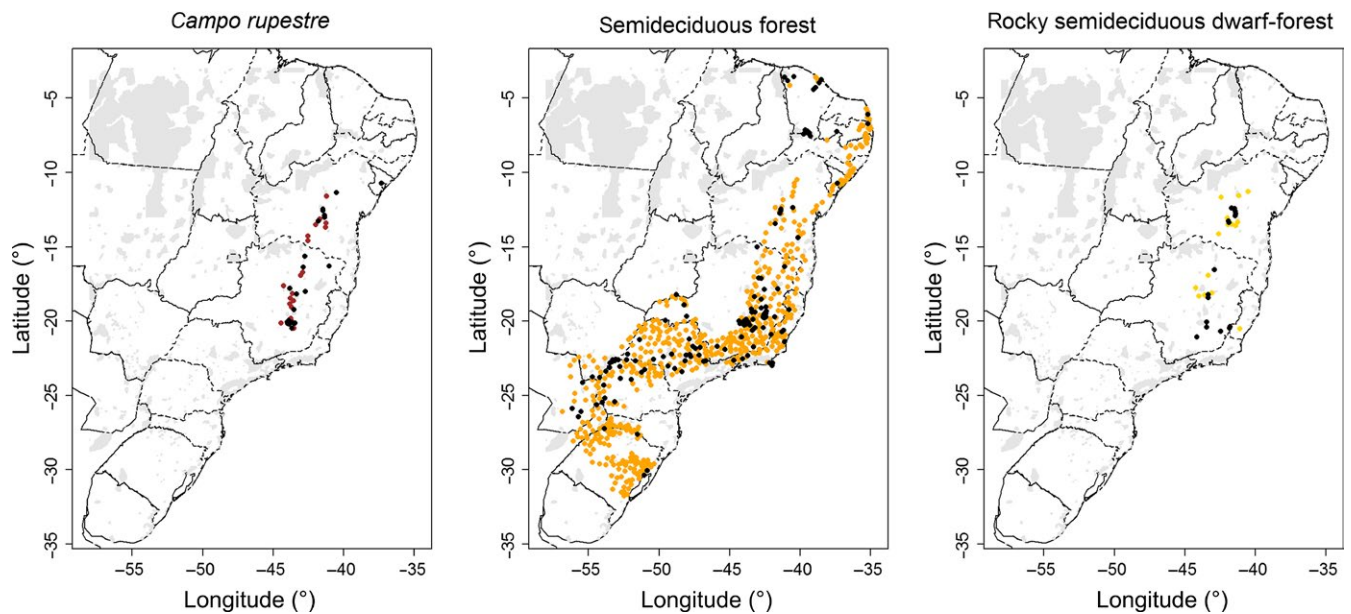


FIGURE 6 Conservation assessment of *campo rupestre*, semideciduous forests and rocky semideciduous dwarf-forests of the South American Atlantic Domain. Black bullets represent woody plant communities occurring within protected areas. Grey areas represent the current network of protected areas across South America. Dashed lines represent Brazilian state borders

forests into poorly drained soils of the Cerrado Domain showed only a weak differentiation from their neighbouring semideciduous forests (see Figure 3). Kurtz, Valentin, and Scarano (2015) also found that riverine habitats of the Atlantic Domain are indistinguishable as a floristic unit from non-flooded habitats, and that their flora is essentially an extract of the regional species pool. These trends may result from a particular feature of the Atlantic Domain. Unlike the Amazon Domain, where a wide net of rivers lead to large areas of seasonally flooded habitats, rivers in the Atlantic Domain represent a minor component of the landscape. In the Amazon, seasonal flooding over wide alluvial

beds is known as one of the main sources of floristic differentiation among habitat types and an important driver of tree species distribution patterns (Wittmann et al., 2013), whereas in the Atlantic Domain, the tiny areas of riverine forest are swamped with immigration from the non-flooded habitats. On the other hand, the intrusions of subtropical riverine forests into poorly drained soils of the Pampa Domain seems to have a comparatively stronger floristic differentiation (see Figure 3a), but primarily associated with high temperature seasonality.

For *campos rupestres* we were able to document fire as an important factor limiting tree species distribution across the Atlantic

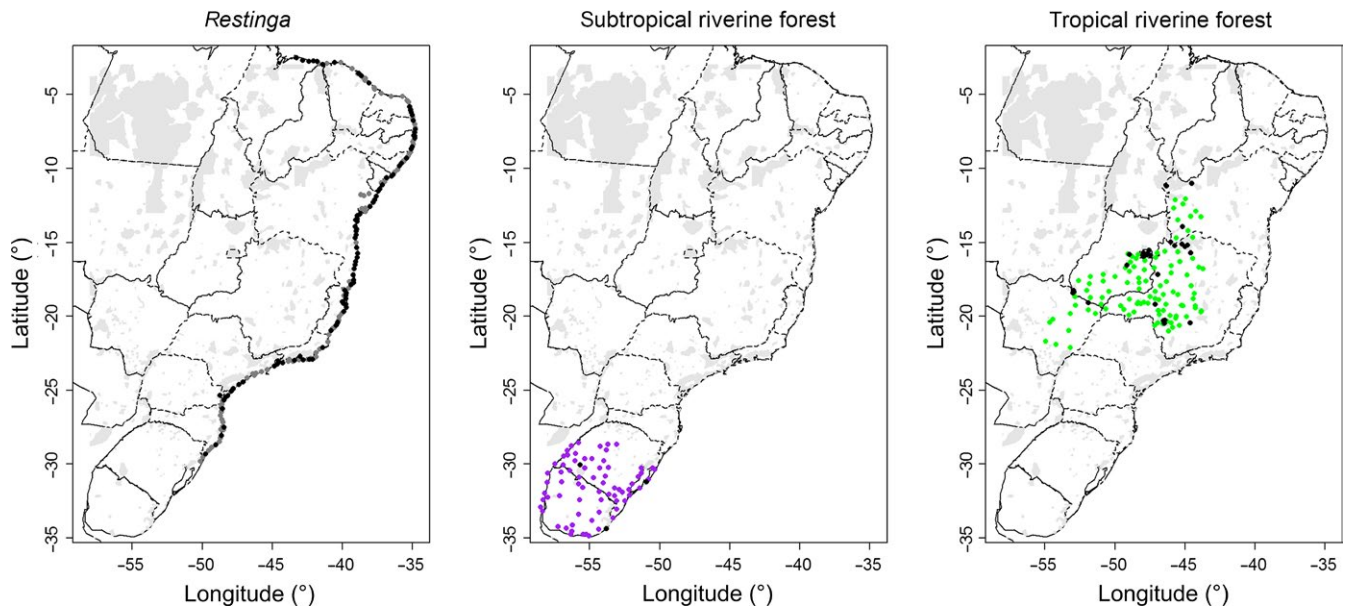


FIGURE 7 Conservation assessment of *restinga*, subtropical riverine forests and tropical riverine forests of the South American Atlantic Domain. Black bullets represent woody plant communities occurring within protected areas. Grey areas represent the current network of protected areas across South America. Dashed lines represent Brazilian state borders. Coastal white-sand woodlands are called *restinga* in Brazil

Domain (see Figure 3a). This is consistent with previous studies showing that forest-savanna boundaries in tropical savannas are driven by fire, though generally in interaction with other factors (Archibald et al., 2013; Dantas, Batalha, & Pausas, 2013; Hoffmann et al., 2012). Within the Atlantic Domain, however, fire frequency is low relative to the surrounding savanna formations (see detailed maps in Archibald et al., 2013) and has therefore been neglected in previous studies. Nevertheless, here we show that fire is actually an important component shaping macroscale patterns of floristic variation across the Atlantic Domain and thus deserves further attention. The congruence between floristic turnover and grass coverage, a proxy for fire frequency, across rocky semideciduous dwarf-forests and *campos rupestres* (Figure 3a) indicates that fire plays a key role in determining the mosaic of rock outcrop habitats in the Atlantic Domain. Rocky semideciduous dwarf-forests seem to represent a transition between rain forests and *campos rupestres* (see Figure 3a), which is likely to be mediated by fire history and local factors contributing to either increase or decrease flammability, particularly topography and soil depth.

4.2 | Spatial structure and unexplained variation

While the relevance of the environmental fraction in controlling community turnover was straightforward to interpret, the variation that either remained unexplained or was attributed to spatial structure independent of the measured environmental factors (61% and 12%, respectively) deserves further attention. Rain forests and marginal habitats are often geographically segregated (Figure 2), suggesting that there may be a role for spatially structured dispersal limitation and historical biogeography in driving some of the observed floristic differentiation. However, given the clear floristic segregation of rock outcrop dwarf-forests from semideciduous and rain forests, despite

their spatial interdigitation (e.g., in south-eastern Brazil; Figure 2), we believe it is more parsimonious to attribute the positive spatial autocorrelation, a proxy of distance decay in community similarity (Nekola & White, 1999), to niche-based controls (e.g., unmeasured spatially structured variables describing environmental conditions, natural enemies and competition). Regarding the large fraction of unexplained variation, it may suggest that ecological drift (cf. Hubbell, 2001) is driving stochastic rearrangements of species distribution ranges through time. However, a high proportion of unexplained variation, ranging from 40% to 80% (e.g., Legendre et al., 2009; Neves et al., 2015; reviewed by Sojininen, 2014), is a common outcome in studies of floristic composition over similar spatial scales, and could also be attributed to statistical noise (ter Braak, 1986; Guisan, Weiss, & Weiss, 1999) or unmeasured non-spatially structured environmental conditions.

4.3 | Conservation implications

Here we showed the uneven distribution of protected areas across the Atlantic Domain with wet forests having twice as much protection. Marginal habitats receive considerably lower protection, despite harbouring almost half of the 7,099 species endemic to the Atlantic Domain. These 3,160 endemic species are not found anywhere else in the world, including in the rain forests of the Atlantic Domain. This demonstrates that different marginal habitats, characterized by environmental harshness, underpin the patterns of high species richness across the Atlantic Domain as a whole. Therefore, we emphasize that these marginal habitats need better consideration by conservationists and biodiversity scientists, based on their (1) high level of endemism; (2) lower level of protection; and (3) less data (see species accumulation curves of vegetation types associated with rock outcrops in Fig. S1).

4.4 | Concluding remarks

The distribution of the Atlantic Forest marginal habitats is associated with low-temperature extremes (i.e., ranging from winter frosts to summer maxima higher than 40°C), soil salinity, drought-stress and soil waterlogging. Additionally, grass coverage, a proxy for flammability and a previously unappreciated environmental factor in the Atlantic Domain, is amongst the principal factors explaining the patterns of tree species distribution. For conservation purposes, the *restinga* is strikingly distinct both floristically and environmentally (see Figures 3a and b), suggesting the need for further investigation. If *restingas* are indeed a distinct phytogeographical region, instead of an extension of rain forests into saline white-sand environments, they may be much more threatened than assumed based upon classifications that places these two habitats together. *Restinga* has suffered massive fragmentation due to high human occupation in coastal areas and a rapidly developing tourism industry.

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AUTHOR CONTRIBUTIONS

A.O.F. compiled the database and conceived the idea; D.M.N. and K.G.D. designed the manuscript; D.M.N. analysed the data; D.M.N. and A.O.F. led the writing with substantial input from K.G.D. and R.T.P. All authors commented on the manuscript and approved the final version.

DATA ACCESSIBILITY

Additional accessibility data are provided as supporting information.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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