



THE UNIVERSITY *of* EDINBURGH

## Edinburgh Research Explorer

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

### Citation for published version:

Neves, DM, Dexter, K, pennington, T, Valente, ASM, Bueno, M, Eisenlohr, PV, Fontes, MAL, De Miranda, PLS, Moreira, SN, Rezende, VL, Saiter, FZ & Oliveira-Filho, AT 2017, 'Dissecting a biodiversity hotspot: the importance of environmentally marginal habitats in the Atlantic Forest Domain of South America' Diversity and Distributions. DOI: 10.1111/ddi.12581

### Digital Object Identifier (DOI):

[10.1111/ddi.12581](https://doi.org/10.1111/ddi.12581)

### Link:

[Link to publication record in Edinburgh Research Explorer](#)

### Document Version:

Peer reviewed version

### Published In:

Diversity and Distributions

### General rights

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

### Take down policy

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact [openaccess@ed.ac.uk](mailto:openaccess@ed.ac.uk) providing details, and we will remove access to the work immediately and investigate your claim.



1

2 Article type: Biodiversity Research

3

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

6

7 Danilo M. Neves<sup>1\*</sup>, Kyle G. Dexter<sup>2,3</sup>, R. Toby Pennington<sup>3</sup>, Arthur S. M. Valente<sup>4</sup>,  
8 Marcelo L. Bueno<sup>5</sup>, Pedro V. Eisenlohr<sup>6</sup>, Marco A.L. Fontes<sup>7</sup>, Pedro L. S. de  
9 Miranda<sup>2</sup>, Suzana N. Moreira<sup>8</sup>, Vanessa L. Rezende<sup>8</sup>, Felipe Z. Saiter<sup>9</sup>, Ary T.  
10 Oliveira-Filho<sup>8</sup>

11

12 *<sup>1</sup>Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ*  
13 *85721, USA. <sup>2</sup>School of Geosciences, The University of Edinburgh, Edinburgh EH9*  
14 *3JN, UK. <sup>3</sup>Royal Botanic Garden Edinburgh, Edinburgh EH6 5LR, UK. <sup>4</sup>Instituto*  
15 *Estadual de Florestas – Minas Gerais, Ubá 36500-000, Brazil. <sup>5</sup>Laboratório de*  
16 *Ecologia e Evolução de Plantas, Departamento de Biologia Vegetal, Universidade*  
17 *Federal de Viçosa, Viçosa 36570-000, Minas Gerais, Brazil. <sup>6</sup>Laboratório de*  
18 *Ecologia, Universidade do Estado de Mato Grosso, Alta Floresta 78580-000, Brazil.*  
19 *<sup>7</sup>Departamento de Ciências Florestais, Universidade Federal de Lavras, Lavras*  
20 *37200-000, Brazil. <sup>8</sup>Programa de Pós-Graduação em Biologia Vegetal, Universidade*  
21 *Federal de Minas Gerais, Belo Horizonte 31270-090, Brazil. <sup>9</sup>Instituto Federal do*  
22 *Espírito Santo, Santa Teresa – Espírito Santo 29660-000.*

23

24 **Running head:** Stress gradients across the Atlantic Forest Hotspot

25

26 **\*Correspondence:** Danilo M. Neves, *Department of Ecology and Evolutionary*  
27 *Biology, University of Arizona, Tucson, AZ 85721, USA.*

28 E-mail: dneves@email.arizona.edu and danilormn@gmail.com

29 **Number of words in the Abstract:** 289

30 **Main text word count:** 5,282

31 **Number of references:** 59

32

33

34 **ABSTRACT**

35

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

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

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

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

59 marginal habitats.

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

65

66 **Keywords:** campo rupestre, climate, conservation assessment, flammability, rain  
67 forests, restinga, stress gradients, variation partitioning

68

69

70 **(A) INTRODUCTION**

71

72           The Atlantic Forest of South America, or the *Mata Atlântica* as it is known in  
73 Brazil where it largely occurs, stretches for over 3,500km across equatorial, tropical  
74 and subtropical latitudes, and is renowned worldwide for being one of the 35  
75 biodiversity hotspots for conservation prioritisation (Myers *et al.*, 2000). Its  
76 importance is also demonstrated by its designation as one of the five primary  
77 vegetation 'Domains' of Brazil (IBGE, 1993; Ab'Sáber, 2003), the others being the  
78 Caatinga, Cerrado, Pampa and Amazon Domains. The Atlantic Forest Domain  
79 (hereafter Atlantic Domain) borders all the other Domains except for the Amazon.  
80 The prevailing land cover of these bordering Domains are semi-arid thorn woodlands  
81 in the Caatinga, woody savannas in the Cerrado and prairies in the Pampa. Species  
82 from rain forests, the habitat that originally prevailed in the Atlantic Domain, become  
83 a minor component of the landscape in these neighbouring Domains, and they are  
84 only found in riverine or high elevation forest enclaves.

85           Environmental restriction to the establishment of the rain forest habitat is  
86 certainly operating at the boundaries of the Atlantic Domain. In a seminal paper,  
87 Scarano (2009) proposed a list of five key factors limiting the occurrence and  
88 distribution of rain forest species in the Atlantic Domain, which at its harshest  
89 extremes give rise to distinct habitats (one for each factor), referred to as marginal  
90 habitats. Therefore, the rain forest is placed by Scarano (2009) as the 'core'  
91 expression of the Atlantic Domain, where deep shade plays the chief role as a  
92 limiting factor for competing plants. The five marginal habitats are high elevation  
93 forests, rock outcrop dwarf-forests, riverine forests, seasonally dry forests and

94 *restinga* (coastal white-sand woodlands). Most of these marginal habitats have a  
95 relatively high density of trees and can be considered forests, albeit not as well  
96 developed structurally as rain forests. High elevation forests are primarily associated  
97 with frost, with secondary limitation imposed by drought (leeward rain-shadow) and  
98 high light intensity. Cloud forests and *Araucaria*-dominated forests are the main  
99 vegetation types of highlands in the Atlantic Domain. Rock outcrop dwarf-forests,  
100 found at lower elevations (and even at the seashore), are primarily limited by the  
101 paucity, or even lack, of soil and related poor water retention. Meanwhile, riverine  
102 forests are associated with waterlogging on lowland plains and riverbeds. Seasonally  
103 dry forests (either deciduous or semideciduous) replace rain forests where seasonal  
104 rainfall regimes bring regular periods of drought. Finally, environmental harshness  
105 for *restinga* is primarily associated with salinity, with secondary limitations imposed  
106 by drought and low fertility in mineral nutrients (Scarano, 2009) (Fig. 1).

107         Within limited areas, some studies have confirmed the leading role of  
108 Scarano's limiting factors as distribution filters for plants. These studies addressed  
109 tree species composition for particular sectors of the Atlantic Domain, such as the  
110 South-east (Oliveira-Filho & Fontes, 2000; Eisenlohr & Oliveira-Filho, 2015), the  
111 subtropical South (Oliveira-Filho *et al.*, 2015) and the highly biodiverse central region  
112 in eastern Bahia state, northeastern Brazil (Saiter *et al.*, 2016). However, the whole  
113 of the Atlantic Domain has only been investigated for epiphytic angiosperms (Menini-  
114 Neto *et al.*, 2016). Also, the Atlantic Domain is affected by fire in much of its  
115 distribution (Archibald *et al.*, 2013), though to a less extent than in surrounding  
116 Domains, such as in central (Cerrado woody savannas) and southern Brazil (Pampa  
117 prairies). Nevertheless, the potential effect of fire in limiting plant species distribution  
118 across the Atlantic Domain is yet to be investigated. Here we bring together a novel

119 and comprehensive dataset assembled to date on the composition of tree  
120 communities across the whole Domain (c. 2,000 community surveys across core and  
121 marginal habitats, with > 1,000 sites representing surveys not used in the  
122 aforementioned studies), combined with environmental data, focusing on testing  
123 Scarano's proposed limiting variables as well as factors that were neglected in  
124 previous studies (e.g., fire).

125         Besides the importance for community ecology, understanding the degree to  
126 which limiting factors drive community differentiation is inherently relevant for  
127 conservation. The Atlantic Domain houses c.18,000 plant species (REFLORA,  
128 2017), but the current high levels of fragmentation and the continuous habitat loss  
129 throughout the Domain has raised several concerns in the scientific community  
130 (Galindo-Leal *et al.*, 2003; Tabarelli *et al.*, 2004; 2005; Joly *et al.*, 2014). Therefore,  
131 we believe the time is ripe for studies aiming to test the overall importance of  
132 environmental conditions in controlling the occurrence and distribution of plant  
133 species across the whole extent of the Atlantic Domain and, more importantly,  
134 across both its core and marginal habitats.

135         We addressed the following questions: (i) are the patterns of tree species  
136 distribution across the Atlantic Domain, and its intrusions into neighbouring Domains,  
137 limited by factors associated with water deficit (via both soil depth and dry season),  
138 water excess (via waterlogging), frosts (via low temperature), and soil salinity? If  
139 previously unrecognized environmental conditions are the main factors explaining  
140 the patterns of tree species distribution, Scarano's (2009) limiting factors should  
141 account for a small proportion of the variation in community composition explained  
142 by environmental factors; (ii) are these limiting factors leading to floristically distinct  
143 marginal habitats? If the community composition of the marginal habitats is simply a



144 nested subset of the more diverse Atlantic Domain rain forest, species turnover  
145 should account for a small fraction of the dissimilarity between rain forest and  
146 marginal habitats; and (iii) what is the contribution of these marginal habitats to the  
147 overall high species richness of the Atlantic Domain?

148

## 149 **(A) METHODS**

150

### 151 **(B) Study area**

152

153 The Atlantic Forest, designated as one of the five phytogeographical  
154 'Domains' of Brazil (IBGE, 1993; Ab'Sáber, 2000), occurs primarily along the Atlantic  
155 coast and is bordered by the Pampa Domain (woody prairies) of southern Brazil and  
156 by the 'dry diagonal', a corridor that includes three other phytogeographical  
157 Domains: Caatinga (semi-arid thorn woodlands) of northeastern Brazil, Cerrado  
158 (woody savannas) of central Brazil, and Chaco (semi-arid thorn woodlands) of  
159 Paraguay–Argentina–Bolivia (IBGE, 1993, Prado & Gibbs 1993, Neves *et al.* 2015).  
160 The South American Atlantic Forest Domain (hereafter Atlantic Domain) has a  
161 history of controversies over its geographical circumscription and associated  
162 terminology. The controversy may be summarized by three main concepts of Atlantic  
163 Domain habitats: the *sensu stricto*, *sensu lato* and *sensu latissimo* concepts  
164 (Oliveira-Filho *et al.*, 2006). The first, and most restrictive concept, includes only the  
165 tracts of rain forests that occur as a narrow band along the coast (<100 km wide and  
166 up to 2500 m elevation) and stretches all through the Domain, though with two main  
167 interruptions, the São Francisco Gap and Campos dos Goytacazes Gap. The former  
168 has a semi-arid nucleus at the mouth of the São Francisco River (~10°30'S), and the

169 latter is a seasonally dry region extending from southern Espírito Santo to northern  
170 Rio de Janeiro (RJ) States, with its driest extreme at Cabo Frio/RJ (~22°50'S).

171 The *sensu lato* concept of Atlantic Domain habitats, which is currently  
172 prevalent, includes other habitats adjacent to rain forests, such as the much more  
173 extensive semideciduous forests that cover increasingly larger areas towards the  
174 south and become wide enough to reach eastern Paraguay and north-eastern  
175 Argentina. *Araucaria*-dominated forests are also a very important component of the  
176 *sensu lato* concept, followed by coastal woodlands on white-sand substrates (termed  
177 *restingas*) and three highland dwarf-forests: rocky cloud dwarf-forests, rocky  
178 semideciduous dwarf-forests and rocky highland savannas (termed *campos*  
179 *rupestres*).

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

191

## 192 **(B) Dataset**

193

194 We extracted the dataset from the NeoTropTree (NTT) database  
195 (<http://prof.icb.ufmg.br/treetlan>), which consists of tree species checklists (trees  
196 defined here as freely standing woody plants >3 m in height) compiled for geo-  
197 referenced sites, extending from southern Florida (U.S.A.) and Mexico to Patagonia.  
198 NTT currently holds 5,126 sites/checklists, 14,878 woody plant species and 920,129  
199 occurrence records. A site/checklist in NTT is defined by a single habitat, following  
200 the classification system proposed by Oliveira-Filho (2015), contained in a circular  
201 area with a 10-km diameter. Therefore, where two or more habitats co-occur in one  
202 10-km area, there may be two geographically overlapping sites in the NTT database,  
203 each for a distinct habitat.

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

219 often due to low sampling/collecting efforts, which results in poor descriptive power.

220 This study used a subset of tree inventories from the NTT database,  
221 consisting of 328 rain forest sites and 1,425 sites representing the limiting  
222 environmental factors and marginal habitats proposed by Scarano (2009), namely  
223 seasonally dry (663 semideciduous forests), high elevation (193 *Araucaria*-  
224 dominated forests and 61 cloud forests), rock outcrops (49 rocky cloud dwarf-forests,  
225 31 rocky semideciduous dwarf-forests and 41 *campos rupestres*), high salinity (181  
226 restingas - with only forests and dwarf-forests of the mosaic included) and  
227 waterlogged soils (133 tropical riverine forests and 73 subtropical riverine forests.  
228 Note that marginal habitats associated with seasonal drought and high salinity are  
229 represented by one vegetation type, whereas high elevation, rock outcrops and  
230 waterlogged soils are represented by more than one vegetation type. The final  
231 species matrix contained presence/absence data for 4,431 tree species across 1,753  
232 sites, with a total of 366,875 presences (see Fig. 2a-b).

233 The NTT database also included 26 environmental variables for all its sites,  
234 derived from multiple sources (at a 30 arc-second resolution; detailed below). The  
235 resolution used in this study was particularly appropriate (1 km<sup>2</sup>) because all sites  
236 are more than 1 km distant from each other (only 124 out of 1,753 sites are less than  
237 5 km distant from another site and the mean distance between all sites is > 1,000  
238 km). Elevation at the NTT site centre was used as an integrative environmental  
239 variable. Mean annual temperature, mean daily temperature range, isothermality,  
240 temperature seasonality, maximum temperature of the warmest month, minimum  
241 temperature of the coldest month, temperature annual range, mean annual  
242 precipitation, precipitation of the wettest month, precipitation of the driest month and  
243 precipitation seasonality were obtained from WorldClim 1.4 data layers (Hijmans *et*

244 *al.*, 2005). WorldClim monthly temperatures and precipitation were also interpolated  
245 to obtain values for 5-day intervals by applying sinusoidal functions centered at day  
246 15 of each month. These functions yielded values for days 1, 5, 10, 20, 25 and 30,  
247 which were used to generate Walter's Climate Diagrams (Walter, 1985) and, thus,  
248 four additional variables: duration (days) and severity (days) of both the water deficit  
249 and water excess periods. Frost frequency (days) and cloud interception (mm) were  
250 obtained from interpolating known values as response variables (data obtained from  
251 135 and 57 Brazilian Meteorological Stations measuring frost frequency and cloud  
252 interception, respectively) with elevation, latitude and the WorldClim layers as  
253 predicting variables. Potential evapotranspiration (mm) and the aridity index (annual  
254 precipitation/potential evapotranspiration) were obtained from Zomer *et al.* (2007,  
255 2008).

256         Surface rockiness (% exposed rock), soil coarseness (% sand), soil fertility (%  
257 base saturation) and soil salinity (ds/m) were obtained from the Harmonized World  
258 Soil Database v 1.2 (available at [http://www.fao.org/soils-portal/soil-survey/soil-](http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/)  
259 [maps-and-databases/harmonized-world-soil-database-v12/en/](http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/)) and ranked  
260 afterwards by mid-class percentage. The use of classes was adopted to add  
261 robustness to the data because of the high local soil heterogeneity that makes raw  
262 figures unrealistic. Soil drainage classes were obtained following EMBRAPA's  
263 protocol (Santos *et al.*, 2013), which combines soil type, texture and depth with  
264 landforms. Soil drainage classes, mean annual precipitation (Hijmans *et al.*, 2005)  
265 and the aforementioned indices of water deficit and excess were also combined to  
266 produce a hyperseasonality index. Grass coverage (%) was used as a proxy of fire  
267 return interval (i.e., frequency). Previous studies give support to grass coverage as a  
268 good proxy of fire frequency (Hoffmann *et al.*, 2012; Archibald *et al.*, 2013; Lehmann

269 *et al.*, 2014), although further quantification of fire regime is clearly needed (c.f.  
270 Archibald *et al.*, 2013). Grass coverage was obtained by direct observation of site  
271 surface on Google Earth<sup>®</sup> images in five 100×100m areas, one at the central  
272 coordinates of the NTT site and four at 2.5 km away from it and towards the NE, SW,  
273 NW and SE.

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

276

## 277 **(B) Analyses of community turnover**

278

279 We first explored the patterns of floristic differentiation between rain forest and  
280 marginal habitats by performing non-metric multidimensional scaling (NMDS)  
281 (McCune & Grace, 2002). We then assessed the relative importance of turnover and  
282 nestedness to floristic differentiation between rain forest and each of the marginal  
283 habitats. This analysis was performed by first calculating Jaccard pairwise distances,  
284 which ranges from 0 (identical in community composition) to 1 (completely different  
285 in community composition). These pairwise distances are then decomposed into  
286 dissimilarity due to species turnover (i.e., only compositional changes) and  
287 dissimilarity due to differences in species richness. The latter is the difference  
288 between Jaccard distance and the dissimilarity due to species turnover (Baselga,  
289 2010). The ordination and the dissimilarity partitioning analyses were conducted in  
290 the statistical packages *vegan* (Oksanen *et al.*, 2016) and *betapart* (Baselga &  
291 Orme, 2012), respectively, both in the R Statistical Environment (R Development  
292 Core Team, 2015).

293 We assessed whether Scarano's (2009) limiting factors are the key

294 environmental factors driving variation in community composition, and then explored  
295 the results visually by plotting the habitats in geographic or ordination (NMDS) space  
296 and then fitting the values of the most important environmental variables via  
297 generalized additive models (GAM) and generalized linear models (GLM),  
298 respectively. This routine follows methods similar to those proposed by Blanchet *et al.*  
299 *al.* (2008) and Legendre *et al.* (2012), which comprises (i) the exclusion of 300  
300 singletons (species found at a single site), as they commonly increase the noise in  
301 most analyses without contributing information (Lepš & Šmilauer, 2003); (ii) the  
302 Hellinger transformation of the binary presence/absence data (Legendre &  
303 Gallagher, 2001), which reduces the effect of widespread species; (iii) the  
304 independent compilation of significant spatial and environmental variables through a  
305 forward selection method for redundancy analysis (RDA), after first checking that the  
306 respective global models were significant (Blanchet *et al.*, 2008); (iv) an additional  
307 and progressive elimination of collinear variables based on their variance inflation  
308 factor (VIF) and ecological relevance, until maintaining only those with  $VIF < 4$   
309 (Quinn & Keough, 2002); and (v) an RDA-based partitioning of variation in  
310 community composition matrix due to environmental variables, spatial  
311 autocorrelation and their combined, statistically indistinguishable effects. As spatial  
312 variables, we used principal coordinates of neighbour matrices (PCNMs; Borcard *et al.*  
313 *al.* 2004), which represent the spatial structure of the sampling units at multiple  
314 spatial scales without considering any environmental variation (Borcard *et al.*, 1992;  
315 Legendre *et al.*, 2002; Borcard *et al.*, 2004). We tested the overall significance of the  
316 environmental fraction (controlled for spatial autocorrelation) by applying ANOVA  
317 permutation tests (999 permutations) for RDA (Peres-Neto *et al.*, 2006). The variable  
318 selection, variation partitioning, NMDS, GLM and GAM analyses were conducted

319 using the fields (Nychka *et al.*, 2015), spacemakeR (Dray *et al.*, 2010) and vegan  
320 (Oksanen *et al.*, 2016) packages in the R Statistical Environment (the variation  
321 partitioning script is available as supporting information). The maps were designed  
322 using the package maptools (Lewin-Koh & Bivand, 2012) in the R Statistical  
323 Environment.

324 We also calculated patch statistics to test whether floristic differentiation can  
325 be modulated by habitat quality (a proxy for anthropogenic effect). We used the  
326 PatchStat function - available in the SDMTools package (VanDerWal *et al.*, 2014) in  
327 the R Statistical Environment - and identified configuration metrics of landscapes  
328 (e.g., patch area, edge perimeter) for 95% of our sites using the vegetation map of  
329 the Brazilian Atlantic Domain (<http://mapas.sosma.org.br/>). We found that the effect  
330 of habitat quality was negligible in explaining variation in tree community composition  
331 across rain forests and marginal habitats (see SI for further details).

332

## 333 **(B) Conservation assessment**

334

335 We assessed how well the floristic diversity is captured in our dataset by  
336 calculating the expected species accumulation curves for rain forest and marginal  
337 habitats, using sample-based rarefaction (Colwell *et al.*, 2012) with the 'specaccum'  
338 function in the statistical package vegan (Oksanen *et al.*, 2016). We also explored  
339 levels of endemism for Atlantic Domain habitats. We obtained the lists of endemic  
340 species from Reflora (<http://floradobrasil.jbrj.gov.br/>), which is the most  
341 comprehensive study of the patterns of plant species richness and endemism for  
342 phytogeographical Domains in eastern South America. Afterwards, we conducted an  
343 assessment of the conservation status of the Atlantic Domain habitats by overlaying



344 the distribution of our 1,753 sites on to the coverage of protected areas across South  
345 America. We used conservation units from the World Database on Protected Areas  
346 (IUCN & UNEP - WCMC, [www.protectedplanet.net](http://www.protectedplanet.net)) and *Cadastro Nacional de*  
347 *Unidades de Conservação* (Ministério do Meio Ambiente - Brazil,  
348 [www.mapas.mma.gov.br](http://www.mapas.mma.gov.br)). Species accumulation curves are provided for rain forest  
349 and marginal habitats as SI (Figs. S1).

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

359

## 360 **(A) RESULTS**

361

### 362 **(B) Floristic patterns**

363

364 The distribution of the sites in the ordination space yielded by NMDS (Fig. 3a-  
365 b) largely segregated rain forests and marginal habitats. The ordination placed  
366 'marginal' vegetation types at the extremes of the first three ordination axes. Axis 1  
367 segregated, at negative scores, the shoreline-associated *restinga* and, at positive  
368 scores, the vegetation types associated with low-temperature extremes of higher

369 elevations and latitudes further from the equator (*Araucaria*-dominated forests and  
370 subtropical riverine forests). Axis 2 segregated, at positive scores, vegetation types  
371 associated with rock outcrops (rocky cloud dwarf-forests, rocky semideciduous  
372 dwarf-forests and *campos rupestres*). Axis 1 further segregated rock outcrop  
373 vegetation types into warmer sites (rocky semideciduous dwarf-forests and *campos*  
374 *rupestres*), at positive scores, and colder sites (rocky cloud dwarf-forests), at  
375 negative scores. Axis 3 placed the habitat associated with seasonal drought  
376 (semideciduous forests) at intermediate scores and the habitat associated with  
377 waterlogged soils at positive scores (tropical riverine forests).

378         The floristic composition of marginal habitats is not simply a nested subset of  
379 the more species rich rain forest. The turnover component accounts for most of the  
380 floristic dissimilarity of each marginal habitat in relation to rain forests (Fig. 4).  
381 Nestedness is higher than the turnover component in very few cases (i.e., few  
382 marginal habitat sites are simply a subset of another rain forest site; see  
383 semideciduous forest triangle in Fig. 4) More specifically, vegetation types  
384 associated with rock outcrops (including *campos rupestre*) have the higher fraction of  
385 dissimilarity attributed to turnover while *restinga* and subtropical riverine forest have  
386 the lower fraction attributed to turnover.

387

## 388 **(B) Variation partitioning analyses**

389

390         The forward selection procedure retained 13 environmental variables in the  
391 model to explain the variation in tree species composition (Table 1). In partitioning  
392 the variation explained by the retained environmental and spatial predictors, we  
393 found that the environmental fraction explained 27% of the variation, 5% of which

394 was independent of spatial autocorrelation ( $P < 0.01$ ). The environmental predictors  
395 could not account for a spatially structured variation of 12% ( $P < 0.01$ ), and 61% of  
396 the variation remained unexplained (see discussion for more details).

397         The harshest extremes of the retained environmental variables (Table 1) do  
398 lead to distinct habitats, treated here in the context of 'marginal' vegetation types. A  
399 north to south increase in temperature seasonality was congruent with a latitudinal  
400 gradient in community turnover, which represents the floristic differentiation of  
401 *Araucaria*-dominated forests and subtropical riverine forests (Figs. 2a and 3a) from  
402 all other vegetation types. Grass coverage, a proxy for fire frequency (see Methods),  
403 was congruent with the floristic differentiation of the vegetation types associated with  
404 rock outcrops (including *campos rupestres*) from all others vegetation types (Fig. 3a).  
405 Within the rock outcrop habitat, the frequency of frost was associated with the  
406 floristic differentiation of rocky cloud dwarf-forests from the other rocky vegetation  
407 types. Soil salinity was congruent with a coast to inland gradient in community  
408 turnover, which represents the floristic differentiation of *restinga* from all other  
409 vegetation types (Fig. 3a). Another coast to inland gradient is evident in the tropical  
410 section of the Atlantic Domain, where water deficit severity and mean annual  
411 precipitation, proxies for drought-stress, explained the floristic differentiation of  
412 everwet vegetation types, namely rain forest, cloud forests and rocky cloud dwarf-  
413 forests, from *campos rupestres*, semideciduous forests, rocky semideciduous dwarf-  
414 forests and tropical riverine forests (Figs. 2b and 3b). At the harshest extreme of the  
415 drought-stress gradient (Fig. 3b), water-related hyperseasonality (i.e. ranging from  
416 water shortage to soil waterlogging) segregates *campo rupestres* and tropical  
417 riverine forests from semideciduous forests. These factors represent the seven most  
418 explanatory environmental variables (Table 1) and they accounted for a large

419 fraction of the variation in community composition attributed to environmental  
420 predictors (adjusted  $R^2 = 0.242$ ; Table 1), which is nearly the same as the value for  
421 all 13 variables retained in the variation partitioning model (adjust  $R^2 = 0.264$ ; Table  
422 1).

423

## 424 **(B) Conservation assessment**

425

426 The species accumulation curves showed a levelling off at larger sample  
427 sizes for all vegetation types, although no curve actually reached an asymptote.  
428 Species accumulation curves levelled off less in vegetation types associated with  
429 rock outcrops (including *campos rupestres*) and in *Araucaria*-dominated forest (see  
430 Fig. S1). Because the overall floristic dissimilarity between cloud forests and rain  
431 forests was relatively low (Fig. 3), we assessed the rates of endemism considering  
432 these two vegetation types as 'core' habitats (wet forests in Table 2 and Fig. 5).  
433 Despite the fact that wet forests have twice as much protection as marginal habitats  
434 (45% and 26%, respectively; Table 2 and Figs. 5, 6 and 7), almost half of all species  
435 endemic to the Atlantic Domain are only found in marginal habitats (Table 2).

436

## 437 **(A) DISCUSSION**

438

439 Both the variation partitioning and the ordination support the importance of the  
440 set of limiting conditions proposed by Scarano (2009) as the factors controlling tree  
441 community composition of rain forests and marginal habitats, which are treated here  
442 in the context of 'marginal' vegetation types (*question i*). We also showed that these  
443 limiting factors lead to floristically distinct tree communities, thus indicating that the

444 marginal habitats are not simply a nested subset of the more diverse Atlantic Domain  
445 rain forest (*question ii*). In fact, marginal habitats shelter nearly half the endemic tree  
446 species in the Atlantic Domain (*question iii*).

447

#### 448 **(B) Limiting factors**

449

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

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

482           When assessing whether soil waterlogging leads to a floristically distinct  
483 marginal habitat, we found that the intrusions of riverine forests into poorly drained  
484 soils of the Cerrado Domain showed only a weak differentiation from their  
485 neighbouring semideciduous forests (see Fig. 3). Kurtz *et al.* (2015) also found that  
486 riverine habitats of the Atlantic Domain are indistinguishable as a floristic unit from  
487 non-flooded habitats, and that their flora is essentially an extract of the regional  
488 species pool. These trends may result from a particular feature of the Atlantic  
489 Domain. Unlike the Amazon Domain, where a wide net of rivers lead to large areas  
490 of seasonally flooded habitats, rivers in the Atlantic Domain represent a minor  
491 component of the landscape. In the Amazon, seasonal flooding over wide alluvial  
492 beds is known as one of the main sources of floristic differentiation among habitat  
493 types and an important driver of tree species distribution patterns (Wittman *et al.*,

494 2013), whereas in the Atlantic Domain, the tiny areas of riverine forest are swamped  
495 with immigration from the non-flooded habitats. On the other hand, the intrusions of  
496 subtropical riverine forests into poorly drained soils of the Pampa Domain seems to  
497 have a comparatively stronger floristic differentiation (see Fig. 3a), but primarily  
498 associated with high temperature seasonality.

499         For *campos rupestres* we were able to document fire as an important factor  
500 limiting tree species distribution across the Atlantic Domain (see Fig. 3a). This is  
501 consistent with previous studies showing that forest-savanna boundaries in tropical  
502 savannas are driven by fire, though generally in interaction with other factors  
503 (Hoffman et al., 2013; Archibald et al., 2013; Dantas et al., 2013). Within the Atlantic  
504 Domain, however, fire frequency is low relative to the surrounding savanna  
505 formations (see detailed maps in Archibald et al., 2013) and has therefore been  
506 neglected in previous studies. Nevertheless, here we show that fire is actually an  
507 important component shaping macroscale patterns of floristic variation across the  
508 Atlantic Domain and, thus, deserves further attention. The congruence between  
509 floristic turnover and grass coverage, a proxy for fire frequency, across rocky  
510 semideciduous dwarf-forests and *campos rupestres* (Fig. 3a) indicates that fire plays  
511 a key role in determining the mosaic of rock outcrop habitats in the Atlantic Domain.  
512 Rocky semideciduous dwarf-forests seem to represent a transition between rain  
513 forests and *campos rupestres* (see Fig. 3a), which is likely to be mediated by fire  
514 history and local factors contributing to either increase or decrease flammability,  
515 particularly topography and soil depth.

516

## 517 **(B) Spatial structure and unexplained variation**

518

519           While the relevance of the environmental fraction in controlling community  
520 turnover was straightforward to interpret, the variation that either remained  
521 unexplained or was attributed to spatial structure independent of the measured  
522 environmental factors (61% and 12%, respectively) deserves further attention. Rain  
523 forests and marginal habitats are often geographically segregated (Fig. 2),  
524 suggesting that there may be a role for spatially structured dispersal limitation and  
525 historical biogeography in driving some of the observed floristic differentiation.  
526 However, given the clear floristic segregation of rock outcrop dwarf-forests from  
527 semideciduous and rain forests, despite their spatial interdigitation (e.g., in  
528 southeastern Brazil; Fig. 2), we believe it is more parsimonious to attribute the  
529 positive spatial autocorrelation, a proxy of distance decay in community similarity  
530 (Nekola & White, 1999), to niche-based controls (e.g., unmeasured spatially  
531 structured variables describing environmental conditions, natural enemies and  
532 competition). Regarding the large fraction of unexplained variation, it may suggest  
533 that ecological drift (cf. Hubbell, 2001) is driving stochastic rearrangements of  
534 species distribution ranges through time. Although, a high proportion of unexplained  
535 variation, ranging from 40% to 80% (e.g. Legendre et al., 2009; Neves et al., 2015;  
536 reviewed by Soininen, 2014), is a common outcome in studies of floristic composition  
537 over similar spatial scales, and could also be attributed to statistical noise (ter Braak,  
538 1986; Guisan et al., 1999) or unmeasured non-spatially structured environmental  
539 conditions.

540

## 541 **(B) Conservation implications**

542

543           Here we showed the uneven distribution of protected areas across the Atlantic



544 Domain with wet forests having twice as much protection. Marginal habitats receive  
545 considerably low protection, despite harbouring almost half of the 7,099 species  
546 endemic to the Atlantic Domain. These 3,160 endemic species are not found  
547 anywhere else in the world, including in the rain forests of the Atlantic Domain. This  
548 demonstrates that different marginal habitats, characterised by environmental  
549 harshness, underpin the patterns of high species richness across the Atlantic  
550 Domain as a whole. Therefore, we emphasize that these marginal habitats need  
551 better consideration by conservationists and biodiversity scientists, based on their (i)  
552 high level of endemism; (ii) lower level of protection; and (iii) less data (see species  
553 accumulation curves of vegetation types associated with rock outcrops in Fig. S1).

554

## 555 **(B) Concluding remarks**

556

557 The distribution of the Atlantic Forest marginal habitats is associated with low  
558 temperature extremes (i.e. ranging from winter frosts to summer maxima higher than  
559 40°C), soil salinity, drought-stress and soil waterlogging. Additionally, grass  
560 coverage, a proxy for flammability and a previously unappreciated environmental  
561 factor in the Atlantic Domain, is amongst the principal factors explaining the patterns  
562 of tree species distribution. For conservation purposes, the *restinga* is strikingly  
563 distinct both floristically and environmentally (see Figs. 3a-b), suggesting the need  
564 for further investigation. If *restingas* are indeed a distinct phylogeographical region,  
565 instead of an extension of rain forests into saline white-sand environments, they may  
566 be much more threatened than assumed based upon classifications that places  
567 these two habitats together. *Restinga* has suffered massive fragmentation due to  
568 high human occupation in coastal areas and a rapidly developing tourism industry.

569

570 **(A) ACKNOWLEDGEMENTS**

571

572 D.M.N. and R.T.P. were supported by the National Environmental Research Council  
573 (grant NE/I028122/1). AOF and MLB were supported by the Conselho Nacional de  
574 Desenvolvimento Científico e Tecnológico - Brazil (CNPq) (grants 301644/88-8 and  
575 151002/2014-2, respectively). ASMV and SNM were supported by the Fundação de  
576 Amparo à Pesquisa de Minas Gerais - Brazil (FAPEMIG). PLSM. thanks the  
577 Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brazil (CAPES)  
578 for supporting a full PhD at the University of Edinburgh under the Science Without  
579 Borders Programme (grant BEX 13197-13-4).

580

581 **(A) REFERENCES**

582

583 Ab'Sáber, A.N. (2003) *Os domínios de natureza no Brasil: potencialidades*  
584 *paisagísticas*. Ateliê Editorial, São Paulo.

585 Archibald, S., Lehmann, C.E.R., Gómez-Dans, J.L. & Bradstock, R.A. (2103)  
586 Defining pyromes and global syndromes of fire regimes. *Proceedings of the*  
587 *National Academy of Sciences U.S.A.*, **110**, 6442-6447.

588 Baselga, A. (2010) Partitioning the turnover and nestedness components of beta  
589 diversity. *Global Ecology and Biogeography*, **19**, 134–143.

590 Baselga, A. & Orme, D.I. (2012) betapart: an R package for the study of beta  
591 diversity. *Methods in Ecology and Evolution*, **3**, 808-812.

592 Blanchet, F.G, Legendre, P & Borcard, D. (2008) Forward selection of explanatory  
593 variables. *Ecology*, **89**, 2623-2632.

594 Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component

595 of ecological variation. *Ecology*, **73**, 1045-1055.

596 Borcard, D., Legendre, P., Avois-Jacquet, C. & Tuomisto, H. (2004) Dissecting the  
597 spatial structure of ecological data at multiple scales. *Ecology*, **85**, 1826-1832.

598 ter Braak, C.J.F. (1986) Canonical correspondence analysis: a new eigenvector  
599 technique for multivariate direct gradient analysis. *Ecology*, **67**, 1167–1179.

600 Cerqueira, R. (2000) Biogeografia das restingas. *Ecologia de restingas e lagoas*  
601 *costeiras* (ed. by F.A. Esteves and L.D. Lacerda), pp. 65-75. NUPEM/UFRJ,  
602 Macaé, Brasil.

603 Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S-Y, Mao, C.X., Chazdon, R.L. & Longino,  
604 J.T. (2012) Models and estimators linking individual-based and sample-based  
605 rarefaction, extrapolation and comparison of assemblages. *Journal of Plant*  
606 *Ecology*, **5**, 3–21.

607 Dantas, V.L., Batalha, M.A. & Pausas, J.G. (2013) Fire drives functional thresholds  
608 on the savanna–forest transition. *Ecology*, **94**, 2454-2463.

609 Dray, S. (2010) *spacemakeR: spatial modelling*. R package version 473 0.0–5/r101.  
610 Available at: <http://R-Forge.R-project.org/projects/sedar/>.

611 Eisenlohr, P.V. & Oliveira-Filho, A.T. (2015) Revisiting patterns of tree species  
612 composition and their driving forces in the Atlantic forests of southeastern  
613 Brazil. *Biotropica*, **47**, 689-701.

614 Galindo-Leal, C., Jacobsen, T.R., Langhammer, P.F. & Olivieri, S. (2003) State of  
615 the hotspots: the dynamics of biodiversity loss. *The Atlantic Forest of South*  
616 *America: biodiversity status, threats, and outlook* (ed. by C. Galindo-Leal C  
617 and I.G. de Câmara), pp. 12–23. Center for Applied Biodiversity Science and  
618 Island Press, Washington.

619 Guisan, A., Weiss, S.B. & Weiss, A.D. (1999) GLM versus CCA spatial modeling of

620 plant species distribution. *Plant Ecology*, **143**, 107–122.

621 Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L.,  
622 Haridasan, M. & Franco, A.C. (2012) Ecological thresholds at the savanna-  
623 forest boundary: how plant traits, resources and fire govern the distribution of  
624 tropical biomes. *Ecology Letters*, **15**, 759-768.

625 Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*.  
626 Princeton University Press, Princeton, NJ.

627 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high  
628 resolution interpolated climate surfaces for global land areas. *International*  
629 *Journal of Climatology*, **25**, 1965–1978.

630 IBGE (1993) *Mapa de Vegetação do Brasil*. Fundação Instituto Brasileiro de  
631 Geografia e Estatística, Ministério da Agricultura, Rio de Janeiro.

632 Joly, C.A., Metzger, J.P. & Tabarelli, M. (2014) Experiences from the Brazilian  
633 Atlantic forest: ecological findings and conservation initiatives. *New*  
634 *Phytologist* **204**, 459–473.

635 Kent, M. & Coker, P. (1992) *Vegetation description and analysis: a practical*  
636 *approach*. Belhaven, London.

637 Kurtz, B.C., Valentin, J.L. & Scarano, F.R. (2015) Are the Neotropical swamp forests  
638 a distinguishable forest type? Patterns from Southeast and Southern Brazil.  
639 *Edinburgh Journal of Botany*, **72**, 191-208.

640 Legendre, P. & Gallagher, E.D. (2001) Ecological meaningful transformations for  
641 ordination of species data. *Oecologia*, **129**, 271-280.

642 Legendre, P., Dale, M.R.T., Fortin, M.J., Gurevitch, J., Hohn, M. & Myers, D. (2002)  
643 The consequences of spatial structure for the design and analysis of  
644 ecological field surveys. *Ecography*, **25**, 601-615.

- 645 Legendre, P., Mi, X., Ren, H., Ma, K., Yu, M., Sun, I. & He, F. (2009) Partitioning  
646 beta diversity in a subtropical broad-leaved forest of China. *Ecology*, **90**, 663-  
647 674.
- 648 Legendre, P., Borcard, D. & Roberts, D.W. (2012) Variation partitioning involving  
649 orthogonal spatial eigenfunction submodels. *Ecology*, **93**, 1234–1240.
- 650 Lehmann, C.E.R., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S.,  
651 Hoffmann, W.A., Hanan, N.P., Williams, R.J., Fensham, R.J., Felfili, J.M.,  
652 Hutley, L.B., Ratnam, J., San Jose, J., Montes, R., Franklin, D., Russell-  
653 Smith, J., Ryan, C.M., Durigan, G., Hiernaux, P., Haidar, R., Bowman, D.M.J.  
654 S. & Bond, W.J. Savanna vegetation-fire-climate relationships differ among  
655 continents. *Science*, **343**, 548-552.
- 656 Lepš, J. & Šmilauer, J.P. (2003) *Multivariate analysis of ecological data using*  
657 *CANOCO*. Cambridge University Press, Cambridge, UK.
- 658 Lewin-Koh, N.J. & Bivand, R. (2012) *maptools: tools for reading and handling spatial*  
659 *objects*. R package version 0.8–17/ r238. Available at: [http://R-Forge.R](http://R-Forge.Rproject.org/projects/maptools/)  
660 [project.org/projects/maptools/](http://R-Forge.Rproject.org/projects/maptools/).
- 661 McCune, B. & Grace, J.B. (2002) *Analysis of ecological communities*. MjM Software  
662 Design, Gleneden Beach, Oregon.
- 663 Menini-Neto, L., Furtado, S.G., Zappi, D., Oliveira-Filho, A.T. & Forzza, R.C. (2016)  
664 Biogeography of epiphytic Angiosperms in the Brazilian Atlantic forest, a world  
665 biodiversity hotspot. *Brazilian Journal of Botany*, **39**, 261–273.
- 666 Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., Kent, J. (2000)  
667 Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.
- 668 Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography  
669 and ecology. *Journal of Biogeography*, **26**, 867-878.

670 Neves, D.M., Dexter, K.G., Pennington, R.T., Bueno, M.L. & Oliveira-Filho, A.T.  
671 (2015) Environmental and historical controls of floristic composition across the  
672 South American Dry Diagonal. *Journal of Biogeography*, **42**, 1566-1576.

673 Nychka, D., Furrer, R., Paige, J. & Sain, S. (2015) *fields: Tools for Spatial Data*. R  
674 package version 8.3-5. Available at: [http://CRAN.R-](http://CRAN.R-project.org/package=fields)  
675 [project.org/package=fields](http://CRAN.R-project.org/package=fields).

676 Oliveira-Filho, A.T., Jarenkow, J.A. & Rodal, M.J.N. (2006) Floristic relationships of  
677 seasonally dry forests of eastern South America based on tree species  
678 distribution patterns. *Neotropical savannas and dry forests: plant diversity,*  
679 *biogeography and conservation*. (ed. by R.T. Pennington, J.A. Ratter and G.P.  
680 Lewis), pp. 151-184. CRC Press, Boca Raton, USA.

681 Oliveira-Filho, A.T., Fontes, M.A.L., Viana, P.L., Valente, A.S.M., Salimena, F.R.G. &  
682 Ferreira, F.M. (2013) O mosaico de fitofisionomias do Parque Estadual do  
683 Ibitipoca. *Flora do Parque Estadual do Ibitipoca e seu entorno* (ed. by R.C.  
684 Forzza, L. Menini-Neto, F.R.G. Salimena and D. Zappi), pp. 53-93. Editora  
685 UFJF, Juiz de Fora, Brazil.

686 Oliveira-Filho, A.T. (2015) Um Sistema de classificação fisionômico-ecológica da  
687 vegetação Neotropical. *Fitossociologia no Brasil: Métodos e estudos de*  
688 *casos, volume 2* (ed. by P.V. Eisenlohr, J.M. Felfili, M.M.R.F. Melo, L.A.  
689 Andrade and J.A.A. Meira-Neto), pp. 452-473. Editora UFV, Viçosa, Brazil.

690 Oliveira-Filho, A.T., Budke, J.C., Jarenkow, J.A., Eisenlohr, P.V. & Neves, D.R.M.  
691 (2015) Delving into the variations in tree species composition and richness  
692 across South American subtropical Atlantic and Pampean forests. *Journal of*  
693 *Plant Ecology*, **8**, 242-260.

694 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B.,

695 Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2016) *vegan*:  
696 *community ecology package*. R package version 2.0–3. Available at:  
697 <http://CRAN.R-project.org/package=vegan>.

698 Peres-Neto, P.R., Legendre, P., Dray, S. & Borcard, D. (2006) Variation partitioning  
699 of species data matrices: estimation and comparisons of fractions. *Ecology*,  
700 **87**, 2614-2625.

701 Pontara, V., Bueno, M.L., Garcia, L.E., Oliveira-Filho, A.T., Pennington, R.T.  
702 Burslem, D.F.R.P. & Lemos-Filho, J.P. (2016) Fine-scale variation in  
703 topography and seasonality determine radial growth of an endangered tree in  
704 Brazilian Atlantic forest. *Plant Soil*, **403**, 115-128.

705 Quinn, G.P. & Keough, M.J. (2002) *Experimental design and data analysis for*  
706 *biologists*. Cambridge University Press, Cambridge, UK.

707 R Core Team (2015) *R: a language and environment for statistical computing*.  
708 Version 3.1.0. R Foundation for Statistical Computing, Vienna. Available at:  
709 <http://www.Rproject.org/>.

710 REFLORA, 2017. Lista de espécies da flora do Brasil. Jardim Botânico do Rio de  
711 Janeiro, Brazil. <http://floradobrasil.jbrj.gov.br/> (accessed 19.01.17).

712 Rundel, P.W., Smith, A.P. & Meinzer F. C. (1994) *Tropical alpine environments:*  
713 *plant form and function*. Cambridge University Press, Cambridge, UK.

714 Saiter, F.Z., Eisenlohr, P.V., Barbosa, M.R., Thomas, W.W. & Oliveira-Filho, A.T.  
715 (2016) From evergreen to deciduous tropical forests: how energy-water  
716 balance, temperature, and space influence the tree species composition in a  
717 high diversity region. *Plant Ecology & Diversity*, **9**, 45-54.

718 Santos, H.G., Jacomine, P.K.T., Anjos, L.H.C., Oliveira, V.A., Lumberras, J.F.,  
719 Coelho, M.R., Almeida, J.A., Cunha, T.J.F. & Oliveira, J.B. (2013) *Sistema*

720 *brasileiro de classificação de solos*, 3rd edn. Embrapa, Brasília.

721 Scarano, F.R. (2009) Plant communities at the periphery of the Atlantic rain forest:  
722 Rare-species bias and its risks for conservation. *Biological Conservation*, **142**,  
723 1201-1208.

724 Soininen, J. (2014) A quantitative analysis of species sorting across organisms and  
725 ecosystems. *Ecology*, **95**, 3284–3292.

726 Tabarelli, M., Silva, J.M.C. & Gascon, C. (2004) Forest fragmentation, synergisms  
727 and the impoverishment of neotropical forests. *Biodiversity and Conservation*,  
728 **13**, 1419–1425.

729 Tabarelli, M., Pinto, L.P., Silva, J.M.C., Hirota, M. & Bedê, L. (2005) Challenges and  
730 opportunities for biodiversity conservation in the Brazilian Atlantic Forest.  
731 *Conservation Biology*, **19**, 695–700.

732 Tichý, L. & Chytrý, M. (2006) Statistical determination of diagnostic species for site  
733 groups of unequal size. *Journal of Vegetation Science*, **17**, 809-818.

734 VanDerWal, J., Falconi, L., Januchowski, S., Shoo, L. & Storlie, C. (2014).  
735 *SDMTools: Species Distribution Modelling Tools: tools for processing data*  
736 *associated with species distribution modelling exercises*. R package version  
737 1.1-221. Available at: <https://CRAN.R-project.org/package=SDMTools>

738 Walter, H. (1985) *Vegetation of the earth and ecological systems of the geo-*  
739 *biosphere*, 3rd edn. Springer-Verlag, Berlin.

740 Wittmann, F., Householder, E., Piedade, M.T.F., Assis, R.L., Schöngart, J., Parolin,  
741 P. & Junk, W.J. (2013) Habitat specificity, endemism and the neotropical  
742 distribution of Amazonian white-water floodplain trees. *Ecography*, **36**, 690-  
743 707.

744 Zanne, A.E., Tank, D.C., Cornwell, W.K., Eastman, J.M., Smith, S.A., FitzJohn, R.G.,



745 McGlinn, D.J., Moles, A.T., O'Meara, B.C., Royer, D.L., Wright, I.J., Aarssen,  
746 L., Bertin, R.I., Govaerts, R., Hemmings, F., Leishman, M.R., Oleksyn, J.,  
747 Reich, P.B., Sargent, R., Soltis, D.E., Soltis, P.S., Stevens, P.F., Swenson,  
748 N.G., Warman, L., Westoby, M. & Beaulieu, J.M. (2013) Three keys to the  
749 radiation of angiosperms into freezing environments. *Nature*, **506**, 89-92.

750 Zomer, R.J., Bossio, D.A., Trabucco, A., Yuanjie, L., Gupta, D.C. & Singh, V.P.  
751 (2007) *Trees and water: smallholder agroforestry on irrigated lands in*  
752 *northern India. IWMI Research Report 122*. International Water Management  
753 Institute, Colombo, Sri Lanka.

754 Zomer, R.J., Trabucco, A., Bossio, D.A., van Straaten, O. & Verchot, L.V. (2008)  
755 Climate change mitigation: a spatial analysis of global land suitability for clean  
756 development mechanism afforestation and reforestation. *Agriculture*  
757 *Ecosystems and Environment*, **126**, 67-80.

758

## 759 **(A) BIOSKETCH**

760 Danilo M. Neves is a postdoctoral research fellow at the University of Arizona. He is  
761 interested in the evolutionary dimension of community ecology, with an emphasis on  
762 historical biogeography of terrestrial biomes.

763

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

768

769 **Table 1** Variables selected for the study of environmental controls of tree community  
770 composition in the Atlantic Domain of South America. The variables shown were  
771 selected through a forward selection method for redundancy analysis and are  
772 ordered by the amount of explained variation in species composition across rain  
773 forest and marginal habitats. Goodness-of-fit of the predictor variables were  
774 assessed through adjusted coefficients of determination, Akaike Information Criterion  
775 (AIC), F-values and significance tests ( $P < 0.01$  in all cases). VIF, variance inflation  
776 factor, obtained using the r-squared value of the regression of one variable against  
777 all other explanatory variables. adj.  $R^2$  cum. = cumulative adjusted coefficient of  
778 correlation.

	adj. $R^2$ cum.	$\Delta$ AIC	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

**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). PA = percentage of NeoTropTree sites in protected areas (see Fig. S2, S3 and S4). Lists of plant species were obtained from the Re flora project (<http://floradobrasil.jbrj.gov.br>).

	All				Endemics					
	Angiosperms	Pteridophyta	Gymnosperms	Total	Angiosperms	Pteridophyta	Gymnosperms	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	-	1968	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

## Figure Captions

**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.

**Figure 2** Distribution of 1,753 Atlantic Domain sites with their *a priori* classification into vegetation types (symbols). Variation in (a) temperature seasonality (standard deviation x100) and (b) water deficit severity (mm) was fitted across geographic space by generalized additive model. Dashed lines represent Brazilian state borders.

**Figure 3** Ordination of 1,753 Atlantic Domain sites yielded by non-metric multidimensional scaling (NMDS) of their tree species composition with their *a priori* classification into vegetation types (symbols). Diagrams are provided for axes 1 x 2 (a) and 1 x 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.

**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.

**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.

## **DATA ACCESSIBILITY**

Additional accessibility data is provided as supporting information.

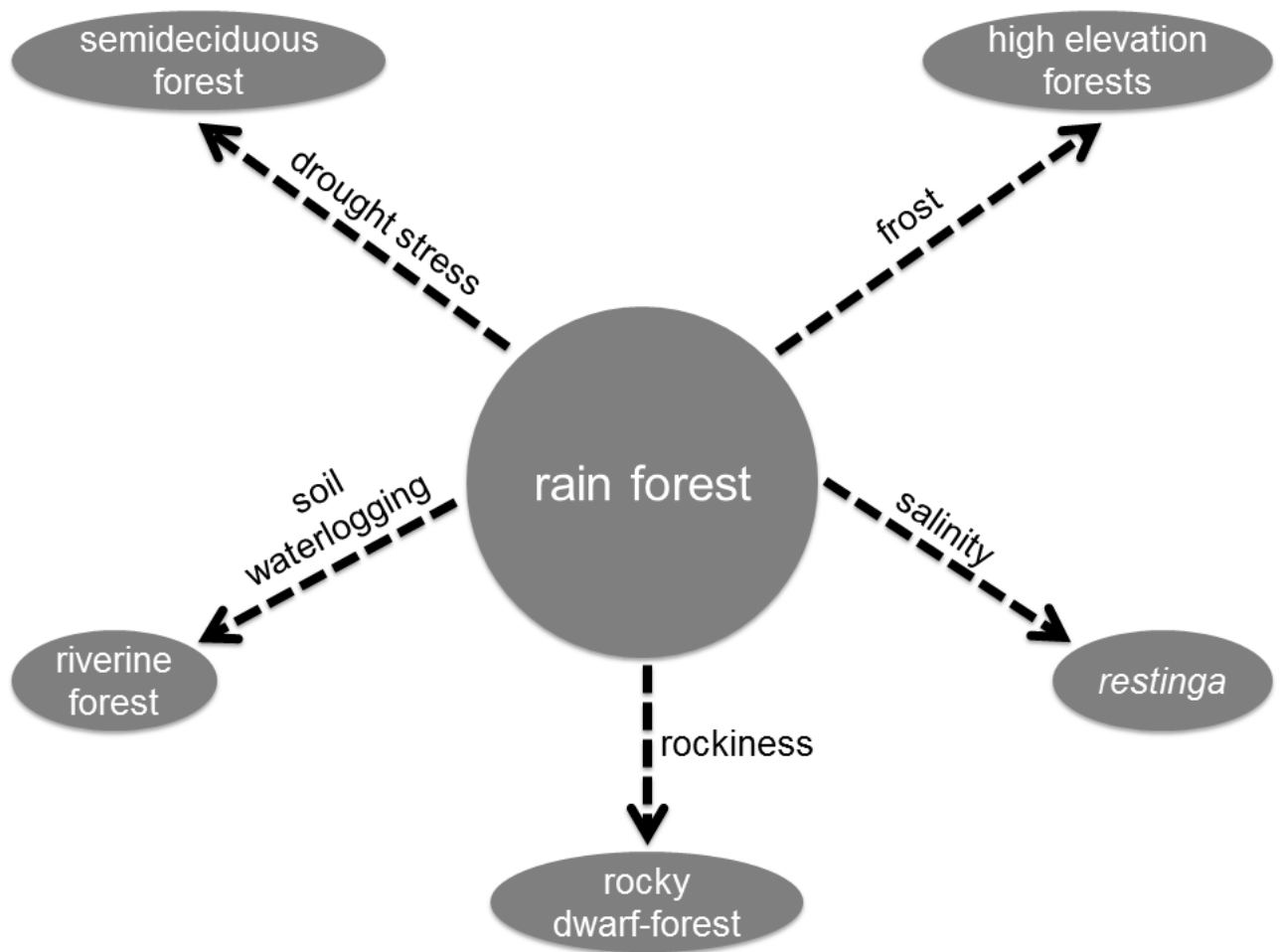
## **SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of this article:

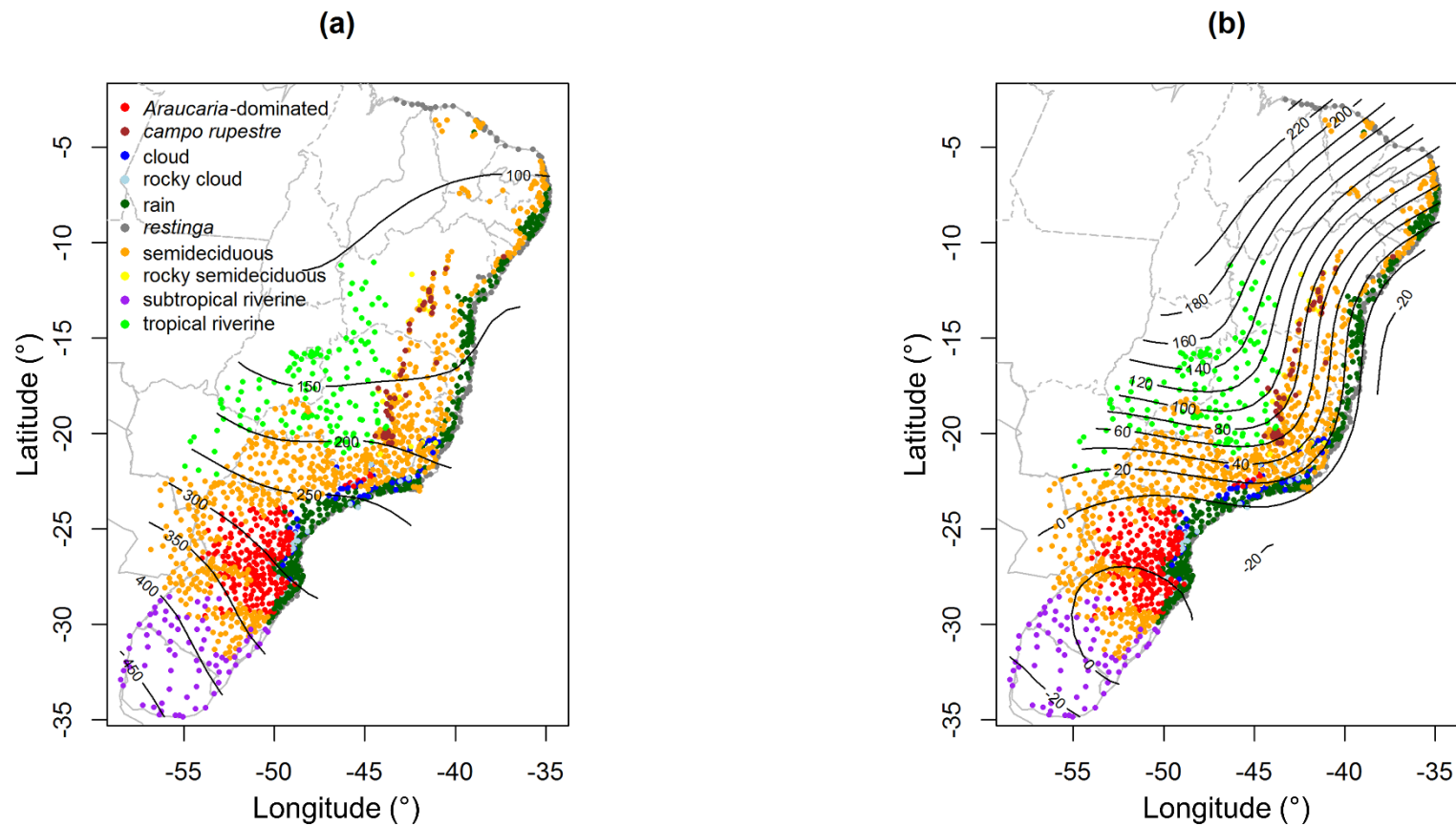
**Figure S1** Species accumulation curve per vegetation type, using a sample-based rarefaction method. Grey shadow shows confidence intervals from standard deviation.

**Table S1** Relationship between habitat quality and variation in tree community composition across the Atlantic Domain of South America. 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 variation across rain forests and marginal habitats. Goodness-of-fit of the predictor variables were assessed through adjusted coefficients of determination, Akaike Information Criterion (AIC), F-values and significance tests ( $P < 0.01$  in all cases). adj.  $R^2$  cum. = cumulative adjusted coefficient of correlation.

**Table S2** Top 50 diagnostic species of the five marginal and stressing habitats of the Atlantic Domain defined by the main explanatory environmental emerging from the community turnover models. The top 50 diagnostic species of the non-stressed habitat (i.e. wet habitat) of the Atlantic Domain are also given.

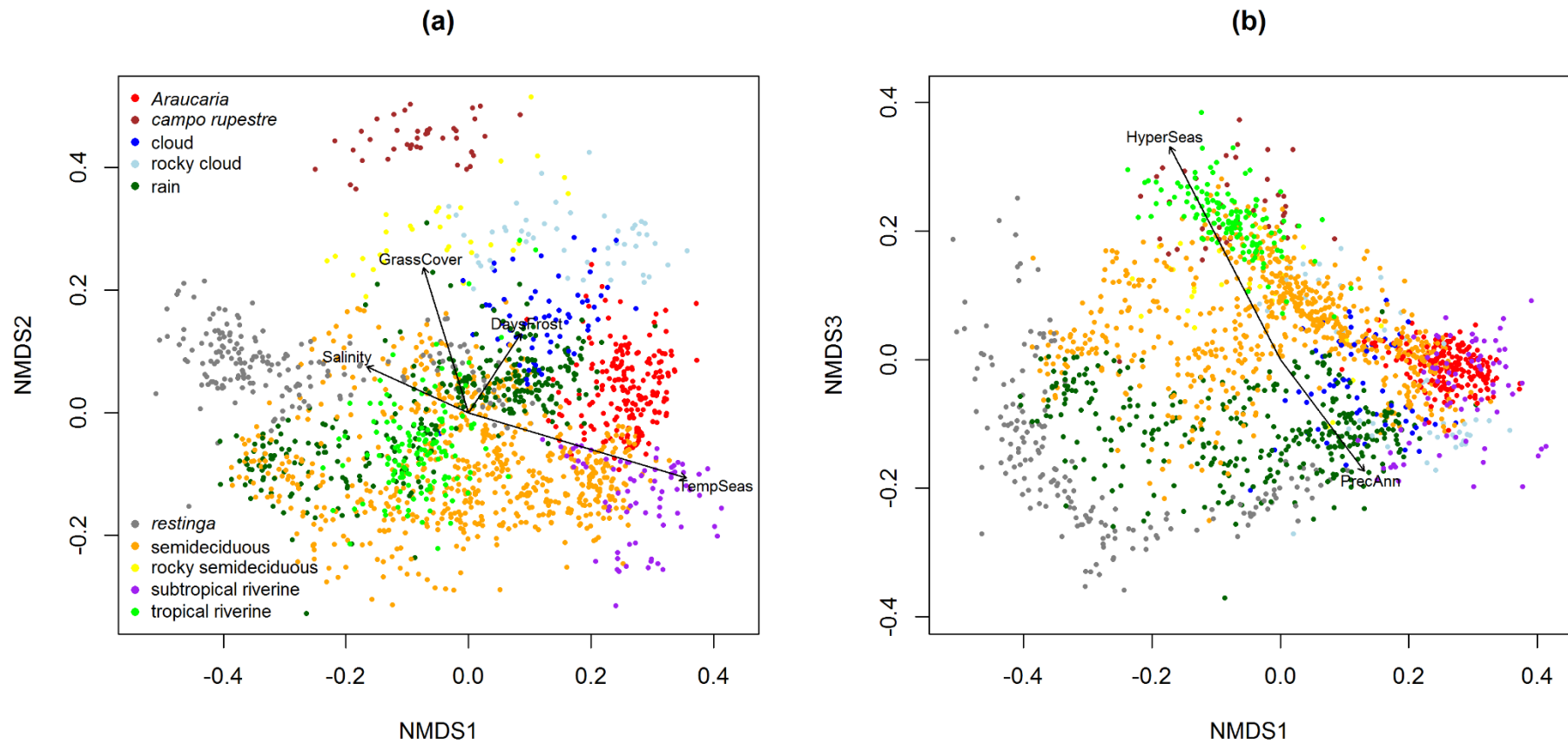


**Figure 1** Environmental variables (arrows) hypothesized in Scarano (2009) as key factors limiting plant species distribution across the Atlantic Domain of South America. The harshest extremes give rise to distinct vegetation types, referred to as marginal habitats. Coastal white-sand woodlands are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

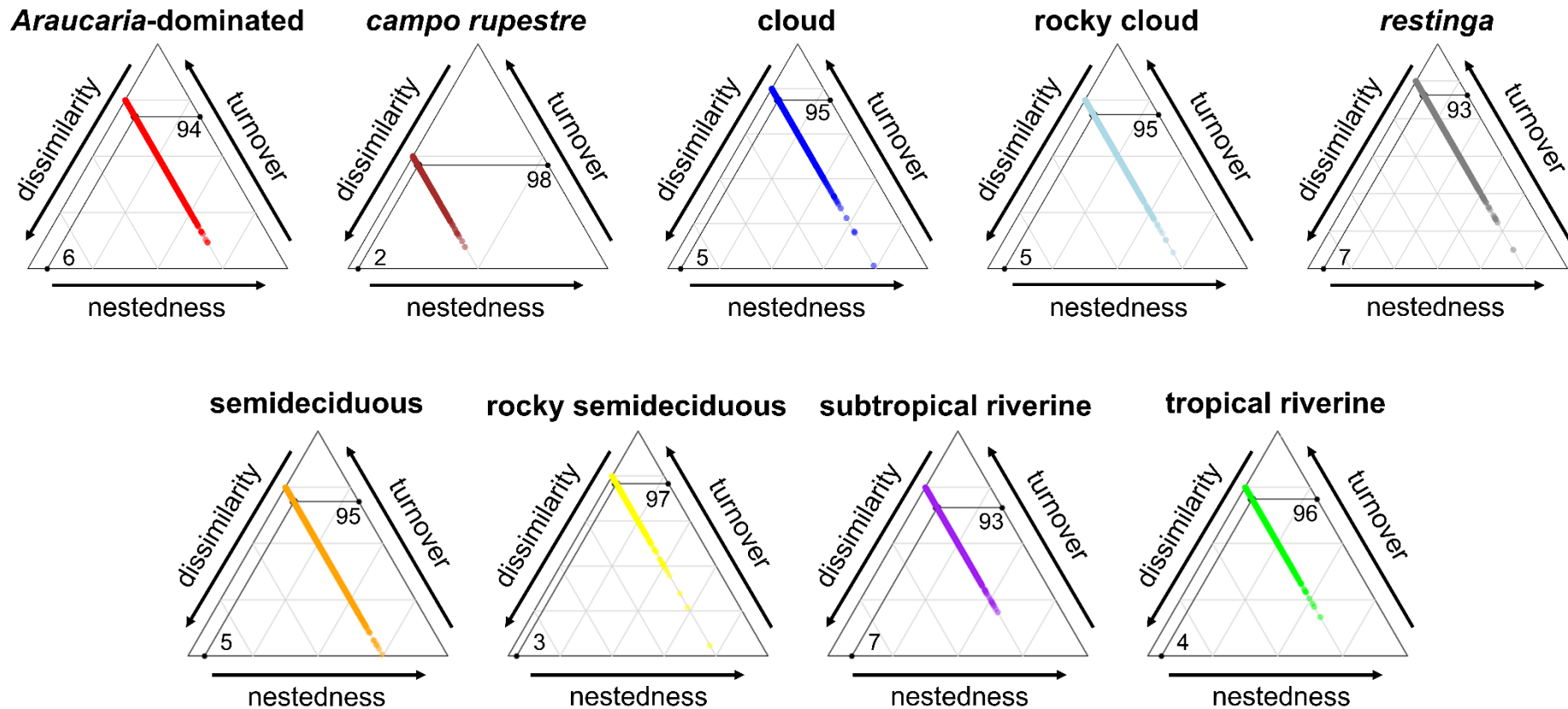


**Figure 2** Distribution of 1,753 Atlantic Domain sites with their *a priori* classification into vegetation types (symbols). Variation in (a) temperature seasonality (standard deviation \*100) and (b) water deficit severity (mm) was fitted across geographic space by generalized additive model. Dashed lines represent Brazilian state borders.

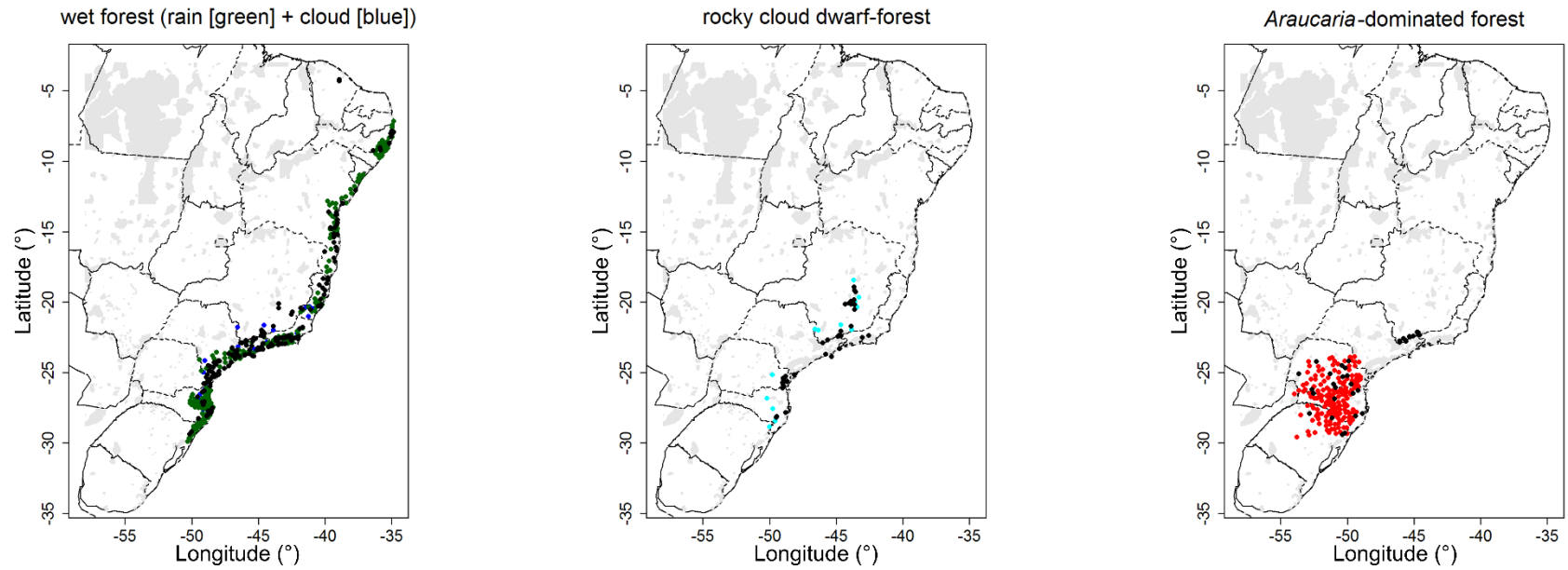




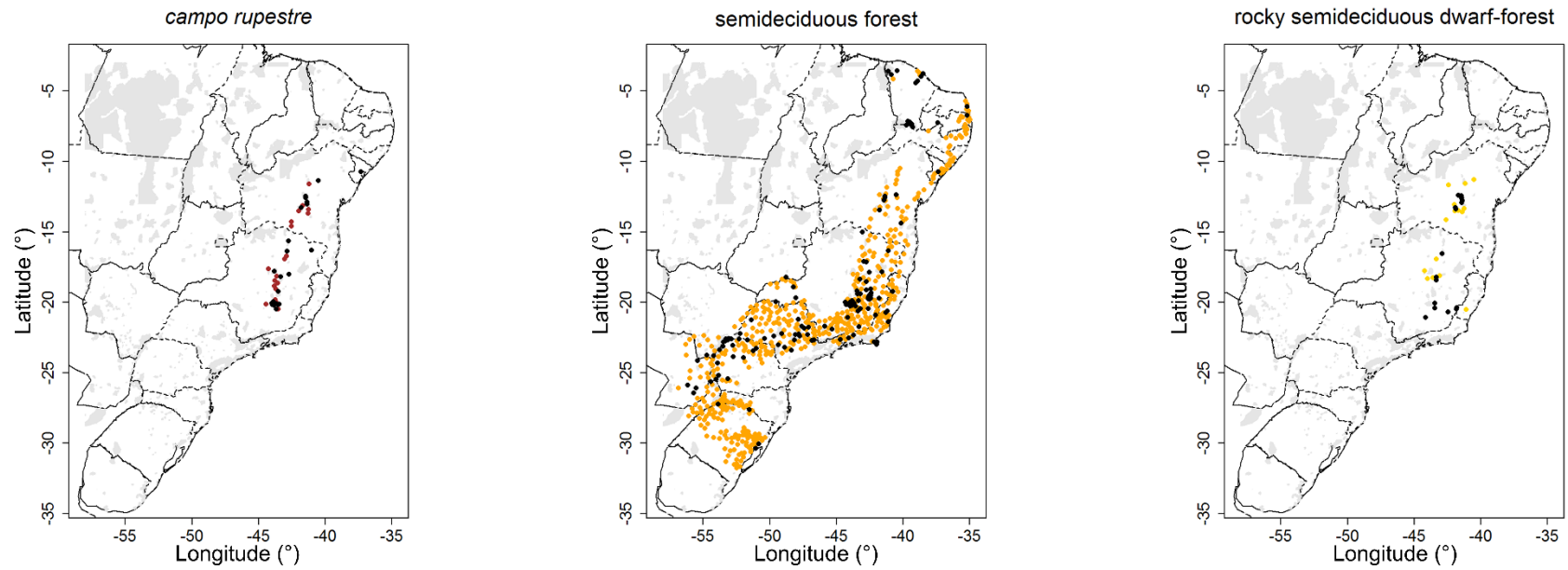
**Figure 3** Ordination of 1,753 Atlantic Domain sites yielded by non-metric multidimensional scaling (NMDS) of their tree species composition with their a priori classification into vegetation types (symbols). Diagrams are provided for axes 1 x 2 (a) and 1 x 3 (b). Arrows in each diagram represent the 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.



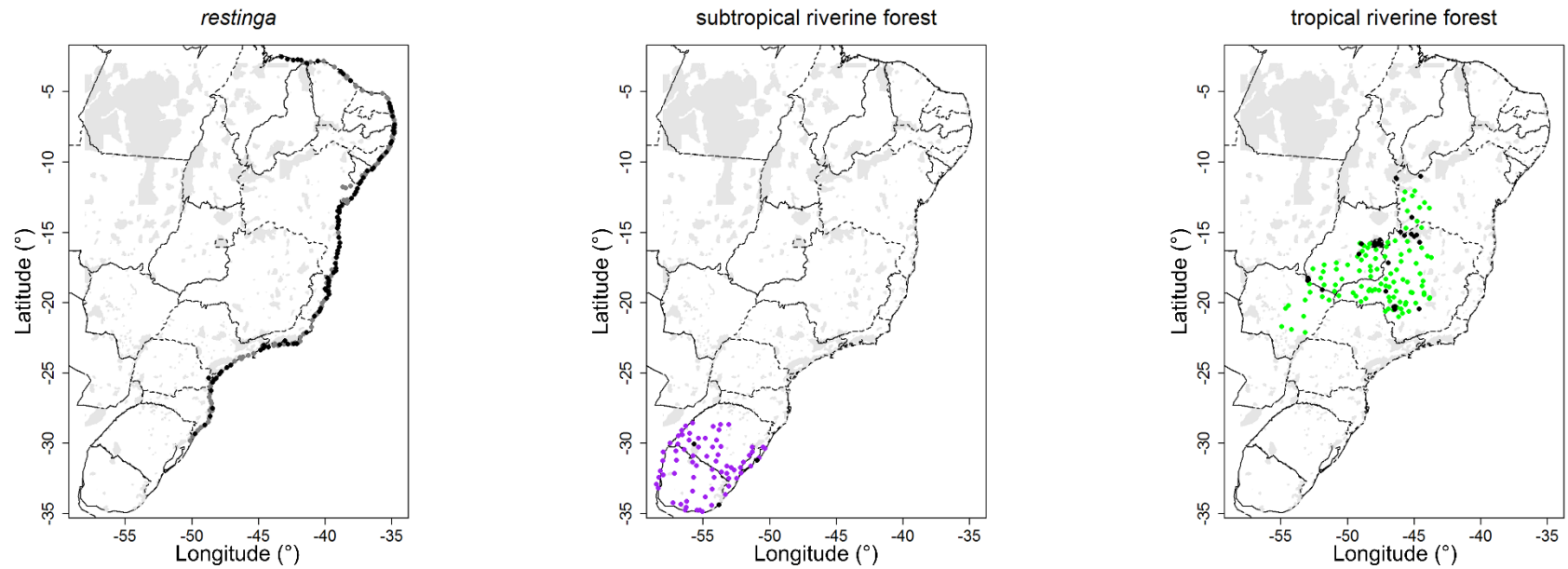
**Figure 4** Decomposition of the pairwise floristic dissimilarity between marginal and rain forest sites of the South American Atlantic Domain (e.g. bullets in the *Araucaria*-dominated triangle represent pairwise dissimilarities between each of the 193 *Araucaria*-dominated forest sites and all the 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.



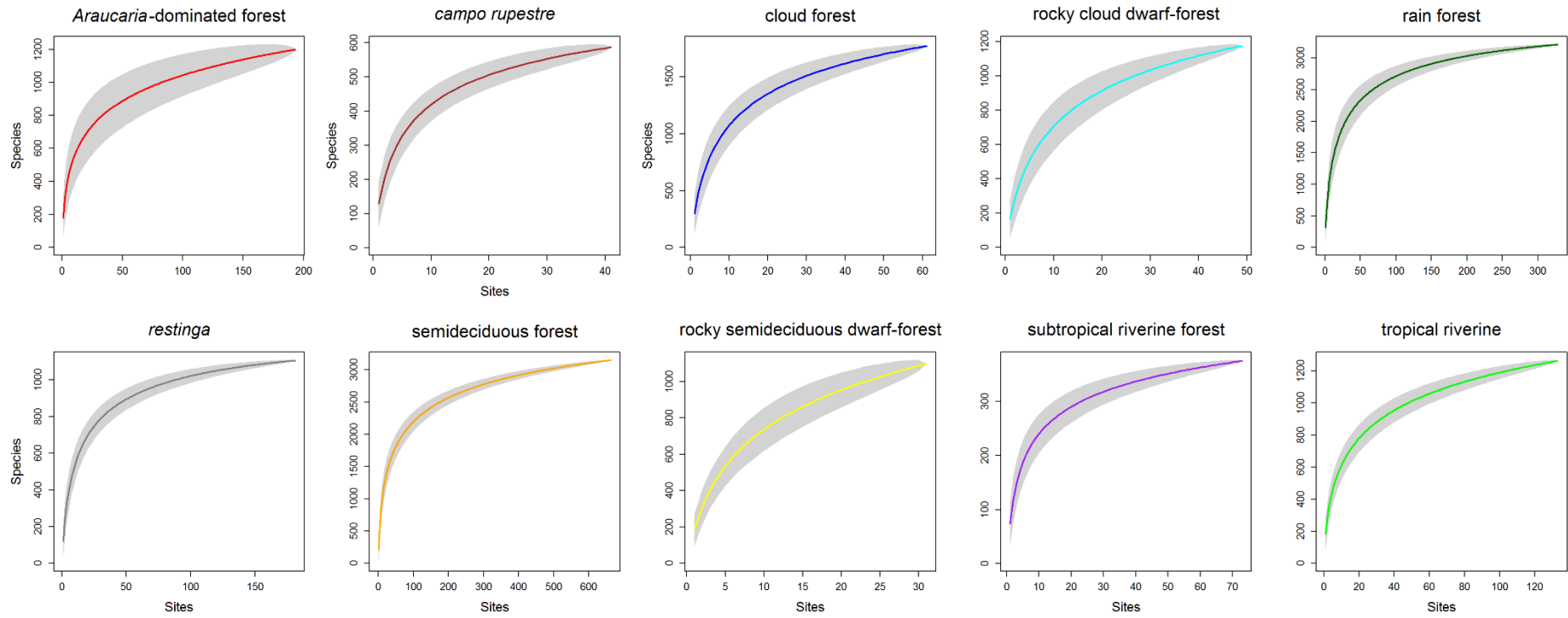
**Figure 5** Conservation assessment of wet forests (rain + cloud), rocky cloud dwarf-forests and *Araucaria*-dominated forests of the South American Atlantic Domain. Black bullets represent woody plant communities occurring within protected areas. Grey areas represent the current network of protected 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.



**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.



**Figure S1** Species accumulation curve per vegetation type, using a sample-based rarefaction method. Grey shadow shows confidence intervals from standard deviation.

**Table S1** Relationship between habitat quality and variation in tree community composition across the Atlantic Domain of South America. 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 forests and marginal habitats. Goodness-of-fit of the predictor variables were assessed through adjusted coefficients of determination, Akaike Information Criterion (AIC), F-values and significance tests ( $P < 0.01$  in all cases). adj.  $R^2$  cum. = cumulative adjusted coefficient of correlation.

	adj. $R^2$	$\Delta$ AIC	F
Patch area	0.003	-316.83	5.183
Edge perimeter	0.005	-317.83	3.003
Core area index	0.005	-317.86	2.019
Fractal dimension index	0.006	-317.78	1.917

**Table S2** Top 50 diagnostic species of the five marginal and stressing habitats of the Atlantic Domain defined by the main explanatory environmental emerging from the community turnover models. The top 50 diagnostic species of the non-stressed habitat (i.e. rain forests) of the Atlantic Forest Domain are also given.

---

**Stressed marginal habitat: seasonally dry**

---

Families	Species
Anacardiaceae	<i>Astronium fraxinifolium</i> Schott
Anacardiaceae	<i>Myracrodruon urundeuva</i> Allemão
Apocynaceae	<i>Aspidosperma cuspa</i> (Kunth) S.F.Blake ex Pittier
Apocynaceae	<i>Aspidosperma cylindrocarpon</i> Müll.Arg.
Apocynaceae	<i>Aspidosperma subincanum</i> Mart. ex A.DC.
Arecaceae	<i>Acrocomia aculeata</i> (Jacq.) Lodd. ex Mart.
Bignoniaceae	<i>Handroanthus impetiginosus</i> Mattos
Bignoniaceae	<i>Jacaranda cuspidifolia</i> Mart. ex A.DC.
Bignoniaceae	<i>Tabebuia roseoalba</i> (Ridl.) Sandwith
Bignoniaceae	<i>Zeyheria tuberculosa</i> (Vell.) Bureau
Combretaceae	<i>Terminalia argentea</i> Mart.
Combretaceae	<i>Terminalia fagifolia</i> Mart.
Ebenaceae	<i>Diospyros hispida</i> A.DC.
Euphorbiaceae	<i>Manihot carthagenensis</i> (Jacq.) Müll.Arg.
Icacinaceae	<i>Emmotum nitens</i> (Benth.) Miers
Leguminosae	<i>Albizia niopoides</i> (Spruce ex Benth.) Burkart
Leguminosae	<i>Anadenanthera peregrina</i> (L.) Speg.
Leguminosae	<i>Apuleia leiocarpa</i> (Vogel) J.F.Macbr.
Leguminosae	<i>Bowdichia virgilioides</i> Kunth
Leguminosae	<i>Chloroleucon acacioides</i> (Ducke) Barneby & J.W.Grimes
Leguminosae	<i>Dipteryx alata</i> Vogel
Leguminosae	<i>Enterolobium contortisiliquum</i> (Vell.) Morong
Leguminosae	<i>Hymenaea martiana</i> Hayne
Leguminosae	<i>Machaerium acutifolium</i> Vogel
Leguminosae	<i>Machaerium hirtum</i> (Vell.) Stellfeld
Leguminosae	<i>Pityrocarpa moniliformis</i> (Benth.) Luckow & R.W.Jobson
Leguminosae	<i>Plathymeria reticulata</i> Benth.
Leguminosae	<i>Platypodium elegans</i> Vogel
Leguminosae	<i>Pterodon emarginatus</i> Vogel
Leguminosae	<i>Pterogyne nitens</i> Tul.
Leguminosae	<i>Senna velutina</i> (Vogel) H.S.Irwin & Barneby
Leguminosae	<i>Sweetia fruticosa</i> Spreng.
Malpighiaceae	<i>Heteropterys byrsonimifolia</i> A.Juss.
Malvaceae	<i>Guazuma ulmifolia</i> Lam.
Malvaceae	<i>Luehea grandiflora</i> Mart. & Zucc.



Malvaceae	<i>Sterculia striata</i> A.St.-Hill. & Naudin
Moraceae	<i>Maclura tinctoria</i> (L.) D.Don ex Steud.
Myrtaceae	<i>Campomanesia velutina</i> (Cambess.) O.Berg
Myrtaceae	<i>Eugenia stictopetala</i> DC.
Myrtaceae	<i>Myrcia tomentosa</i> (Aubl.) DC.
Myrtaceae	<i>Psidium guineense</i> Sw.
Nyctaginaceae	<i>Guapira graciliflora</i> (Mart. ex J.A.Schmidt) Lundell
Opiliaceae	<i>Agonandra brasiliensis</i> Miers ex Benth. & Hook.f.
Phyllanthaceae	<i>Phyllanthus acuminatus</i> Vahl
Proteaceae	<i>Euplassa inaequalis</i> (Pohl) Engl.
Rhamnaceae	<i>Rhamnidium elaeocarpum</i> Reissek
Rubiaceae	<i>Simira corumbensis</i> (Standl.) Steyerl.
Rutaceae	<i>Zanthoxylum riedelianum</i> Engl.
Salicaceae	<i>Casearia gossypiosperma</i> Briq.
Sapindaceae	<i>Talisia esculenta</i> (A.St.-Hil.) Radlk.
Verbenaceae	<i>Aloysia virgata</i> (Ruiz & Pav.) Juss.

---

**Stressed marginal habitat: low temperature extremes**

---

Families	Species
Anacardiaceae	<i>Lithrea brasiliensis</i> Marchand
Anacardiaceae	<i>Schinus engleri</i> F.A.Barkley
Annonaceae	<i>Annona rugulosa</i> (Schltdl.) H.Rainer
Aquifoliaceae	<i>Ilex brevicuspis</i> Reissek
Aquifoliaceae	<i>Ilex microdonta</i> Reissek
Aquifoliaceae	<i>Ilex paraguariensis</i> A.St.-Hil.
Araucariaceae	<i>Araucaria angustifolia</i> (Bertol.) Kuntze
Asparagaceae	<i>Cordyline spectabilis</i> Kunth & Bouché
Asteraceae	<i>Baccharis semiserrata</i> DC.
Asteraceae	<i>Piptocarpha angustifolia</i> Dusén ex Malme
Asteraceae	<i>Vernonanthura discolor</i> (Spreng.) H.Rob.
Bignoniaceae	<i>Handroanthus albus</i> (Cham.) Mattos
Canellaceae	<i>Cinnamodendron dinisii</i> Schwacke
Celastraceae	<i>Maytenus ilicifolia</i> Mart. ex Reissek
Cyatheaceae	<i>Alsophila setosa</i> Kaulf.
Dicksoniaceae	<i>Dicksonia sellowiana</i> Hook.
Euphorbiaceae	<i>Gymnanthes klotzschiana</i> Müll.Arg.
Euphorbiaceae	<i>Manihot grahamii</i> Hook.
Euphorbiaceae	<i>Sebastiania brasiliensis</i> Spreng.
Lamiaceae	<i>Vitex megapotamica</i> (Spreng.) Moldenke
Lauraceae	<i>Cinnamomum amoenum</i> (Nees & Mart.) Kosterm.
Lauraceae	<i>Nectandra lanceolata</i> Nees
Lauraceae	<i>Nectandra megapotamica</i> (Spreng.) Mez
Lauraceae	<i>Ocotea porosa</i> (Nees & Mart.) Barroso
Lauraceae	<i>Ocotea puberula</i> (Rich.) Nees
Lauraceae	<i>Ocotea pulchella</i> (Nees & Mart.) Mez
Leguminosae	<i>Mimosa scabrella</i> Benth.
Melastomataceae	<i>Leandra regnellii</i> (Triana) Cogn.

Melastomataceae	<i>Miconia cinerascens</i> Miq.
Monimiaceae	<i>Hennecartia omphalandra</i> J.Poiss.
Myrtaceae	<i>Acca sellowiana</i> (O.Berg) Burret
Myrtaceae	<i>Calypttranthes concinna</i> DC.
Myrtaceae	<i>Campomanesia xanthocarpa</i> (Mart.) O.Berg
Myrtaceae	<i>Eugenia uruguayensis</i> Cambess.
Myrtaceae	<i>Myrceugenia euosma</i> (O.Berg) D.Legrand
Myrtaceae	<i>Myrceugenia glaucescens</i> (Cambess.) D.Legrand & Kausel
Myrtaceae	<i>Myrcianthes gigantea</i> (D.Legrand) D.Legrand
Myrtaceae	<i>Myrrhinium atropurpureum</i> Schott
Rutaceae	<i>Zanthoxylum fagara</i> (L.) Sarg.
Salicaceae	<i>Banara tomentosa</i> Clos
Salicaceae	<i>Xylosma tweediana</i> (Clos) Eichler
Sapindaceae	<i>Allophylus guaraniticus</i> (A.St.-Hil.) Radlk.
Sapindaceae	<i>Cupania vernalis</i> Cambess.
Sapindaceae	<i>Matayba elaeagnoides</i> Radlk.
Solanaceae	<i>Solanum mauritianum</i> Scop.
Solanaceae	<i>Solanum pseudo-quina</i> A.St.-Hil.
Solanaceae	<i>Solanum sanctae-catharinae</i> Dunal
Solanaceae	<i>Solanum variabile</i> Mart.
Styracaceae	<i>Styrax leprosus</i> Hook. & Arn.
Symplocaceae	<i>Symplocos uniflora</i> (Pohl) Benth.

---

**Stressed marginal habitat: high salinity**

---

Families	Species
Anacardiaceae	<i>Anacardium occidentale</i> L.
Annonaceae	<i>Annona acutiflora</i> Mart.
Apocynaceae	<i>Aspidosperma pyricollum</i> Müll.Arg.
Aquifoliaceae	<i>Ilex integerrima</i> (Vell.) Reissek
Aquifoliaceae	<i>Ilex psammophila</i> Reissek
Arecaceae	<i>Syagrus schizophylla</i> (Mart.) Glassman
Bignoniaceae	<i>Jacaranda bracteata</i> Bureau & K.Schum
Boraginaceae	<i>Cordia restingae</i> M.Stapf
Cactaceae	<i>Cereus fernambucensis</i> Lem.
Calophyllaceae	<i>Kielmeyera neglecta</i> Saddi
Celastraceae	<i>Maytenus distichophylla</i> Mart. ex Reissek
Celastraceae	<i>Maytenus littoralis</i> Car.-Okano
Chrysobalanaceae	<i>Chrysobalanus icaco</i> L.
Chrysobalanaceae	<i>Couepia schottii</i> Fritsch
Clusiaceae	<i>Clusia fluminensis</i> Planch. & Triana
Combretaceae	<i>Combretum glaucocarpum</i> Mart.
Ebenaceae	<i>Diospyros gaultheriifolia</i> Mart.
Euphorbiaceae	<i>Croton sphaerogynus</i> Baill.
Humiriaceae	<i>Humiriastrum spiritu-sancti</i> Cuatrec.
Lauraceae	<i>Ocotea arenicola</i> L.C.S.Assis & Mello-Silva
Leguminosae	<i>Abarema filamentosa</i> (Benth.) Pittier
Leguminosae	<i>Brodriguesia santosii</i> R.S.Cowan

Leguminosae	<i>Copaifera arenicola</i> (Ducke) J.Costa & L.P.Queiroz
Leguminosae	<i>Inga maritima</i> Benth.
Leguminosae	<i>Macrobium rigidum</i> R.S.Cowan
Leguminosae	<i>Moldenhawera blanchetiana</i> Tul.
Melastomataceae	<i>Miconia francavillana</i> Cogn.
Melastomataceae	<i>Mouriri cearensis</i> Huber
Melastomataceae	<i>Tibouchina francavillana</i> Cogn.
Myrtaceae	<i>Calycolpus legrandii</i> Mattos
Myrtaceae	<i>Calyptanthes restingae</i> Sobral
Myrtaceae	<i>Eugenia azeda</i> Sobral
Myrtaceae	<i>Eugenia ilhensis</i> O.Berg
Myrtaceae	<i>Myrcia hirtiflora</i> DC.
Myrtaceae	<i>Myrcia insularis</i> Gardner
Myrtaceae	<i>Myrcia littoralis</i> DC.
Myrtaceae	<i>Myrcia lundiana</i> Kiaersk.
Myrtaceae	<i>Myrcia ovata</i> Cambess.
Myrtaceae	<i>Myrcia rotundifolia</i> (O.Berg) Kiaersk.
Nyctaginaceae	<i>Guapira pernambucensis</i> (Casar.) Lundell
Olacaceae	<i>Dulacia papillosa</i> (Rangel) Sleumer
Primulaceae	<i>Jacquinia armillaris</i> Jacq.
Primulaceae	<i>Myrsine parvifolia</i> DC.
Rhamnaceae	<i>Scutia arenicola</i> (Casar.) Reissek
Rubiaceae	<i>Melanopsidium nigrum</i> Colla
Rubiaceae	<i>Tocoyena bullata</i> (Vell.) Mart.
Sapindaceae	<i>Matayba livescens</i> (Radlk.) R.L.G.Coelho, Souza & Ferrucci
Sapotaceae	<i>Manilkara triflora</i> (Allemão) Monach.
Ximeniaceae	<i>Ximenia americana</i> L.

---

**Stressed marginal habitat: high grass coverage**

---

Families	Species
Araliaceae	<i>Schefflera macrocarpa</i> (Cham. & Schltdl.) Frodin
Asteraceae	<i>Baccharis retusa</i> DC.
Asteraceae	<i>Eremanthus capitatus</i> (Spreng.) MacLeish
Asteraceae	<i>Eremanthus glomerulatus</i> Less.
Asteraceae	<i>Eremanthus incanus</i> (Less.) Less.
Asteraceae	<i>Eremanthus polycephalus</i> (DC.) MacLeish
Asteraceae	<i>Lychnophora ericoides</i> Mart.
Asteraceae	<i>Lychnophora pinaster</i> Mart.
Asteraceae	<i>Lychnophora salicifolia</i> Mart.
Asteraceae	<i>Moquinia racemosa</i> (Spreng.) DC.
Asteraceae	<i>Moquiniastrum paniculatum</i> (Less.) G.Sancho
Asteraceae	<i>Paralychnophora bicolor</i> (DC.) MacLeish
Asteraceae	<i>Wunderlichia mirabilis</i> Riedel ex Baker
Bignoniaceae	<i>Handroanthus ochraceus</i> (Cham.) Mattos
Calophyllaceae	<i>Kielmeyera petiolaris</i> Mart.
Celastraceae	<i>Plenckia populnea</i> Reissek
Clusiaceae	<i>Clusia nemorosa</i> G.Mey.

Ericaceae	<i>Agarista coriifolia</i> (Thunb.) Hook.f. ex Nied.
Ericaceae	<i>Agarista glaberrima</i> (Sleumer) Judd
Ericaceae	<i>Gaylussacia brasiliensis</i> (Spreng.) Meisn.
Ericaceae	<i>Gaylussacia montana</i> (Pohl) Sleumer
Euphorbiaceae	<i>Stillingia saxatilis</i> Müll.Arg.
Lamiaceae	<i>Aegiphila verticillata</i> Vell.
Lauraceae	<i>Ocotea percoriacea</i> Kosterm.
Lauraceae	<i>Ocotea pomaderroides</i> (Meisn.) Mez
Leguminosae	<i>Calliandra asplenioides</i> (Nees) Renvoize
Leguminosae	<i>Chamaecrista brachystachya</i> (Benth.) Conc., L.P. Queiroz & G.P. Lewis
Leguminosae	<i>Chamaecrista cytisoides</i> (DC. ex Collad.) H.S. Irwin & Barneby
Leguminosae	<i>Dalbergia miscolobium</i> Benth.
Leguminosae	<i>Stryphnodendron adstringens</i> (Mart.) Coville
Malpighiaceae	<i>Byrsonima variabilis</i> A. Juss.
Melastomataceae	<i>Miconia albicans</i> (Sw.) Triana
Melastomataceae	<i>Miconia theizans</i> (Bonpl.) Cogn.
Melastomataceae	<i>Trembleya parviflora</i> (D. Don) Cogn.
Myrtaceae	<i>Calypttranthes brasiliensis</i> Spreng.
Myrtaceae	<i>Eugenia puniceifolia</i> (Kunth) DC.
Myrtaceae	<i>Eugenia vetula</i> DC.
Myrtaceae	<i>Myrcia mischophylla</i> Kiaersk.
Myrtaceae	<i>Myrcia mutabilis</i> (O. Berg) N. Silveira
Primulaceae	<i>Myrsine emarginella</i> Miq.
Primulaceae	<i>Myrsine guianensis</i> (Aubl.) Kuntze
Rubiaceae	<i>Cordia elliptica</i> (Cham.) Kuntze
Rubiaceae	<i>Cordia vinosa</i> (Cham.) Kuntze
Salicaceae	<i>Casearia eichleriana</i> Sleumer
Styracaceae	<i>Styrax aureus</i> Mart.
Symplocaceae	<i>Symplocos oblongifolia</i> Casar.
Vochysiaceae	<i>Qualea cordata</i> (Mart.) Spreng.
Vochysiaceae	<i>Vochysia elliptica</i> Mart.
Vochysiaceae	<i>Vochysia emarginata</i> (Vahl) Poir.
Vochysiaceae	<i>Vochysia thyrsoidea</i> Pohl

---

**Stressed marginal habitat: waterlogged riverine**

---

Families	Species
Annonaceae	<i>Cardiopetalum calophyllum</i> Schlttdl.
Annonaceae	<i>Guatteria sellowiana</i> Schlttdl.
Annonaceae	<i>Unonopsis guatterioides</i> (A. DC.) R. E. Fr.
Annonaceae	<i>Xylopia emarginata</i> Mart.
Aquifoliaceae	<i>Ilex integerrima</i> (Vell.) Reissek
Arecaceae	<i>Butia yatay</i> (Mart.) Becc.
Arecaceae	<i>Mauritia flexuosa</i> L. f.
Bignoniaceae	<i>Jacaranda brasiliana</i> (Lam.) Pers.
Burseraceae	<i>Protium spruceanum</i> (Benth.) Engl.
Calophyllaceae	<i>Calophyllum brasiliense</i> Cambess.
Cannabaceae	<i>Celtis chichape</i> (Wedd.) Miq.

Celastraceae	<i>Cheiloclinium cognatum</i> (Miers) A.C.Sm.
Celastraceae	<i>Maytenus floribunda</i> Reissek
Chrysobalanaceae	<i>Hirtella glandulosa</i> Spreng.
Chrysobalanaceae	<i>Licania apetala</i> (E.Mey.) Fritsch
Erythrolalaceae	<i>Heisteria ovata</i> Benth.
Euphorbiaceae	<i>Gymnanthes schottiana</i> Müll.Arg.
Euphorbiaceae	<i>Maprounea guianensis</i> Aubl.
Lauraceae	<i>Aniba heringeri</i> Vattimo-Gil
Lauraceae	<i>Nectandra cissiflora</i> Nees
Lauraceae	<i>Nectandra warmingii</i> Meisn.
Lauraceae	<i>Ocotea spixiana</i> (Nees) Mez
Leguminosae	<i>Albizia inundata</i> (Mart.) Barneby & J.W.Grimes
Leguminosae	<i>Hymenolobium heringeranum</i> Rizzini
Leguminosae	<i>Inga alba</i> (Sw.) Willd.
Leguminosae	<i>Inga laurina</i> (Sw.) Willd.
Leguminosae	<i>Inga nobilis</i> Willd.
Leguminosae	<i>Tachigali rubiginosa</i> (Mart. ex Tul.) Oliveira-Filho
Melastomataceae	<i>Miconia cuspidata</i> Mart. ex Naudin
Melastomataceae	<i>Miconia elegans</i> Cogn.
Melastomataceae	<i>Tococa guianensis</i> Aubl.
Moraceae	<i>Ficus obtusifolia</i> Kunth
Moraceae	<i>Ficus obtusiuscula</i> (Miq.) Miq.
Moraceae	<i>Pseudolmedia laevigata</i> Trécul
Myristicaceae	<i>Viola sebifera</i> Aubl.
Myrtaceae	<i>Eugenia uruguayensis</i> Cambess.
Myrtaceae	<i>Myrcia fenziiana</i> O.Berg
Myrtaceae	<i>Myrcianthes cisplatensis</i> (Cambess.) O.Berg
Oleaceae	<i>Chionanthus trichotomus</i> (Vell.) P.S.Green
Phyllanthaceae	<i>Richeria grandis</i> Vahl
Picramniaceae	<i>Picramnia sellowii</i> Planch.
Primulaceae	<i>Myrsine leuconeura</i> Mart.
Primulaceae	<i>Myrsine parvifolia</i> DC.
Rubiaceae	<i>Faramea latifolia</i> (Cham. & Schltdl.) DC.
Rubiaceae	<i>Ferdinandusa speciosa</i> Pohl
Rubiaceae	<i>Ixora brevifolia</i> Benth.
Salicaceae	<i>Salix humboldtiana</i> Willd.
Sapotaceae	<i>Micropholis venulosa</i> (Mart. & Eichler) Pierre
Verbenaceae	<i>Citharexylum montevidense</i> (Spreng.) Moldenke
Vochysiaceae	<i>Callisthene major</i> Mart.

---

**Atlantic Forest non-marginal habitats: stressed essentially by light**

---

Families	Species
Annonaceae	<i>Annona neosericea</i> H.Rainer
Aquifoliaceae	<i>Ilex paraguariensis</i> A.St.-Hil.
Aquifoliaceae	<i>Ilex theezans</i> Mart. ex Reissek
Arecaceae	<i>Geonoma schottiana</i> Mart.
Asteraceae	<i>Vernonanthura discolor</i> (Spreng.) H.Rob.

Asteraceae	<i>Vernonanthura puberula</i> (Less.) H.Rob.
Bignoniaceae	<i>Jacaranda micrantha</i> Cham.
Bignoniaceae	<i>Jacaranda puberula</i> Cham.
Cyatheaceae	<i>Alsophila setosa</i> Kaulf.
Dicksoniaceae	<i>Dicksonia sellowiana</i> Hook.
Euphorbiaceae	<i>Alchornea sidifolia</i> Müll.Arg.
Lamiaceae	<i>Vitex megapotamica</i> (Spreng.) Moldenke
Lauraceae	<i>Aniba firmula</i> (Nees & Mart.) Mez
Lauraceae	<i>Cryptocarya aschersoniana</i> Mez
Lauraceae	<i>Nectandra grandiflora</i> Nees
Lauraceae	<i>Nectandra megapotamica</i> (Spreng.) Mez
Lauraceae	<i>Nectandra membranacea</i> (Sw.) Griseb.
Lauraceae	<i>Nectandra oppositifolia</i> Nees
Lauraceae	<i>Nectandra puberula</i> (Schott) Nees
Lauraceae	<i>Ocotea bicolor</i> Vattimo-Gil
Lauraceae	<i>Ocotea odorifera</i> (Vell.) Rohwer
Lauraceae	<i>Ocotea porosa</i> (Nees & Mart.) Barroso
Lauraceae	<i>Ocotea puberula</i> (Rich.) Nees
Lauraceae	<i>Persea willdenovii</i> Kosterm.
Leguminosae	<i>Inga sessilis</i> (Vell.) Mart.
Leguminosae	<i>Tachigali denudata</i> (Vogel) Oliveira-Filho
Malpighiaceae	<i>Byrsonima ligustrifolia</i> A.Juss.
Melastomataceae	<i>Miconia cabucu</i> Hoehne
Melastomataceae	<i>Miconia cinerascens</i> Miq.
Melastomataceae	<i>Miconia pusilliflora</i> (DC.) Naudin
Melastomataceae	<i>Tibouchina pulchra</i> Cogn.
Melastomataceae	<i>Tibouchina sellowiana</i> Cogn.
Monimiaceae	<i>Mollinedia schottiana</i> (Spreng.) Perkins
Myrtaceae	<i>Calyptranthes concinna</i> DC.
Myrtaceae	<i>Campomanesia guaviroba</i> (DC.) Kiaersk.
Myrtaceae	<i>Eugenia brasiliensis</i> Lam.
Myrtaceae	<i>Myrceugenia myrcioides</i> (Cambess.) O.Berg
Myrtaceae	<i>Myrcia anacardiifolia</i> Gardner
Myrtaceae	<i>Myrcia brasiliensis</i> Kiaersk.
Myrtaceae	<i>Myrcia palustris</i> DC.
Myrtaceae	<i>Myrcia pubipetala</i> Miq.
Myrtaceae	<i>Myrcia racemosa</i> (O.Berg) Kiaersk.
Ochnaceae	<i>Quiina glaziovii</i> Engl.
Rubiaceae	<i>Psychotria suterella</i> Müll.Arg.
Sabiaceae	<i>Meliosma sellowii</i> Urb.
Salicaceae	<i>Casearia obliqua</i> Spreng.
Sapotaceae	<i>Chrysophyllum inornatum</i> Mart.
Solanaceae	<i>Solanum diploconos</i> (Mart.) Bohs
Symplocaceae	<i>Symplocos uniflora</i> (Pohl) Benth.
Urticaceae	<i>Coussapoa microcarpa</i> (Schott) Rizzini

---