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Citation for published version:

Leite Rezende, V, Pontara, V, Bueno, ML, van den Berg, E, Silva de Miranda, PL, Oliveira-filho, ATD & Dexter, K 2020, 'Phylogenetic regionalization of tree assemblages reveals novel patterns of evolutionary affinities in the Atlantic Forest', *Journal of biogeography*. <https://doi.org/10.1111/jbi.14038>

Digital Object Identifier (DOI):

[10.1111/jbi.14038](https://doi.org/10.1111/jbi.14038)

Link:

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

Document Version:

Peer reviewed version

Published In:

Journal of biogeography

Publisher Rights Statement:

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1 **Phylogenetic regionalization of tree assemblages reveals novel patterns of**
2 **evolutionary affinities in the Atlantic Forest**

3 **Short running title: Phylogenetic regionalization of the Atlantic Forest**

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8 **ACKNOWLEDGEMENTS**

9 V.L.R. and V.P. thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brazil (CAPES)
10 for the Postdoctoral scholarship. E.v.d.B had the support of the Conselho Nacional de Desenvolvimento
11 Científico e Tecnológico (CNPq).

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17 **Abstract**

18 **Aim** We used a phylogenetic approach to group assemblages of woody plant into major vegetation units
19 in the Atlantic Forest, thus for the first time incorporating information on species evolutionary
20 relationships into a bioregionalization of this critical hotspot. A phylogenetic regionalization will provide
21 a spatially explicit framework for answering many basic and applied questions in biogeography, ecology
22 and conservation

23
24 **Location** Atlantic Forest

25
26 **Methods** Our data set comprises 614 genera and 116 families, spread over 1755 assemblages. To place
27 assemblages in a multivariate evolutionary composition space, we used a phylogenetically-informed
28 ordination analysis, and to determine what the main phylogenetic groups of assemblages were, we used
29 K-means clustering based on phylogenetic dissimilarity of assemblages. To quantify how well
30 environmental variables distinguish the phylogenetic groups found we implemented classification tree
31 approaches. Then, to explore the evolutionary turnover between the phylogenetic groups, we calculated
32 phylogenetic beta diversity. Finally, we determined the lineages that are most strongly associated with
33 individual phylogenetic groups using an indicator analysis for lineages.

34
35 **Results** Our analyses suggest that there are seven principal groups, in terms of evolutionary lineage
36 composition, in the Atlantic Forest. The greatest turnover of phylogenetic lineage composition separates
37 tropical evergreen rain forest and semideciduous assemblages from subtropical and highland assemblages.
38 The mixed subtropical forest showed the lowest phylogenetic compositional similarity values with other
39 groups. Tropical rain forest had the highest number of significant indicator lineages, and the highest values
40 of the indicator statistic for lineages.

41
42 **Main conclusions** We found that the most pronounced evolutionary division separates southern and
43 highland tree assemblages from those occurring under more tropical climates and at lower elevations. Our
44 phylogenetic analyses point to an environmentally driven compositional division, likely based on the
45 regular occurrence of freezing versus non-freezing temperatures. Precipitation and edaphic regimes that
46 assemblages experience had less definitive effects on their evolutionary lineage composition.

47
48 **Keywords:** South America, rainforest, NeoTropTree, phyloregions, mixed forest, lineage diversity,
49 latitudinal gradient, subtropical forests

50
51

52 Introduction

53 The substitution of phylogenetic clades in space is a fundamental pattern of biodiversity (Eiserhardt
54 *et al.*, 2013), and an essential goal of biogeography and conservation biology is to identify regions that are
55 significantly different from each other in their composition (Williams, 1996; Magnusson, 2004). The niche
56 conservatism hypothesis assumes that closely related species should be more ecologically similar, and thus
57 overlap more in their ecological niche, than those that are more distantly related (Connolly *et al.*, 2011;
58 Gerhold *et al.*, 2015). This can lead closely related species to be “filtered” into environmentally similar
59 areas (Cavender-Bares *et al.*, 2004; Cavender-Bares *et al.*, 2009; Graham *et al.*, 2009; Vamosi *et al.*, 2009).
60 Therefore, phylogenetic relationships and other mechanisms (e.g. dispersal limitation and biotic
61 interactions) can help to explain why all groups of organisms do not appear in all geographic regions (Crisp
62 & Cook, 2012).

63 The association of species assemblages into distinct phylogenetically delimited biogeographic
64 units can capture historical processes, such as diversification, niche conservatism, dispersal and extinction
65 that have operated over millions of years (Daru *et al.*, 2017; Crisp & Cook, 2012; Guo *et al.*, 2012; Wu *et al.*,
66 2016). Recently, phylogenetic information for plants has begun to be incorporated into regionalization
67 schemes, which has shown how such evolutionary data can provide new insights into the spatial structure
68 of biodiversity, and reveal hidden evolutionary affinities between vegetation types (Daru *et al.*, 2017; Daru
69 *et al.*, 2016; Segovia *et al.*, 2020). The means by which vegetation types are grouped into compositional
70 units has major implications for conservation, landscape management, and projected ecosystem change,
71 and the implementation of a phylogenetic perspective may provide additional information beyond
72 traditional hotspot approaches. As suggested by Daru *et al.* (2017), more evolutionarily distinct
73 phyloregions, or phylogenetically-delimited groups of assemblages, might deserve greater conservation
74 priority since they may encompass more rare and distinct biodiversity. Thus, by grouping species
75 assemblages into biogeographic units using information on their shared evolutionary histories (Holt *et al.*,
76 2013), we can gain insight into the evolutionary and ecological processes shaping species geographical
77 distributions, which can in turn serve as a tool to help guide conservation projects on the basis of
78 evolutionary heritage.

79 The Atlantic Forest is one of the most endangered ecological regions on earth, being considered
80 one of the 35 hotspots for biodiversity conservation in a global context (Mittermeier *et al.*, 2004).
81 Angiosperms represent approximately 94% of all vascular plants in the Atlantic Forest, and are distributed
82 in 208 plant families (Werneck *et al.*, 2011). There are approximately 15,510 angiosperm species from the
83 Atlantic Forest, the majority of which are endemic at the species level (8,710), and some even at the genus
84 (210) or family level (14) (Flora do Brasil 2020). Amongst the angiosperms of the Atlantic Forest, woody
85 species represent a highly diverse group (>7,000 species) (Flora do Brasil 2020). Dissecting this
86 biodiversity hotspot, Neves *et al.* (2017) classified the Atlantic Forest into 10 main vegetation types with

87 various environmental characteristics operating as filters determining the distribution of the non-rain forest
88 vegetation types (marginal habitats). The high woody plant diversity is therefore attributable, at least in
89 part, to the successful utilization of the diversified habitats and microhabitats present in this region, which
90 are generated by temperature, rainfall and soil variation resulting from the latitudinal breadth and
91 elevational complexity of the region (Scarano, 2009; Neves *et al.*, 2017, Canditio & Souza 2019). In a
92 recent study, Canditio & Souza (2019) suggested that woody plant ecoregions in the Atlantic Forest reflect
93 (at least partially) historical events, quantified via a variable representing the historical climatic stability
94 of the Atlantic Forest over the last 120 kyr. Climatic (in)stability on this timescale very well may have
95 shaped the distribution of individual species, and ecoregions that are delimited based on species
96 composition. Phylogenetically-delimited compositional units could also be shaped by climatic instability,
97 but phylogenetic lineages in angiosperms are millions of years old and other processes operating on deeper
98 timescales (e.g., niche conservatism, diversification) likely have a larger influence on where units fall in
99 geographic and environmental space. No study to date has taken an explicitly phylogenetic perspective,
100 which can account for deeper-time evolutionary processes, in delimiting vegetation units of the Atlantic
101 Forest.

102 In the present study we use a phylogenetic approach to group assemblages of woody angiosperm
103 species into major compositional units in the Atlantic Forest, thus for the first time incorporating
104 information on species evolutionary relationships into a bioregionalization of this critical hotspot. We
105 opted to work with woody species because data for tree assemblages vastly exceeds that available for
106 any other group of plants (Eisenlohr & Oliveira-Filho, 2015), and because trees represent the largest and
107 longest lived of plant species, providing the foundation for terrestrial ecosystems (O'Brien *et al.*, 2000).
108 A phylogenetic regionalization of the Atlantic Forest will provide a spatially explicit framework for
109 answering many basic and applied questions in historical and ecological biogeography and conservation
110 for this exceptionally biodiverse region. While ecoregions based on species composition may reflect
111 processes of dispersal limitation unrelated to environmental factors (e.g. biogeographic barriers such as
112 rivers), we expect that phylogenetically-delimited biogeographic regions will reflect deeper evolutionary
113 processes, particularly the evolutionarily conserved environmental associations of phylogenetic lineages
114 (Segovia *et al.*, 2020). Specifically, given that the Atlantic Forest spans areas that experience freezing
115 temperatures and areas that do not and that adaptation to freezing conditions is a major ecophysiological
116 barrier for angiosperm lineages (Zanne *et al.*, 2014), we predict that phylogenetically-delimited
117 compositional groups will align with temperature regime (Duarte *et al.*, 2014). In addition, we expect
118 clades with a southern temperate origin, referred to as 'Gondwanan clades' (*sensu* Segovia & Armesto
119 2015), will be affiliated with southern phylogenetic groups that experience freezing temperatures.
120 Neotropical angiosperm lineages also show clear affiliations with water availability (Neves *et al.*, 2020),
121 which leads us to additionally predict that phylogenetic groups of assemblages will secondarily align
122 with precipitation regime. Thus overall, we expect habitats, such as highland or semideciduous forests,
123 that have been classified as marginal because they occur under extremes of temperature or water

124 availability (Scarano 2009, Neves *et al.*, 2017), to represent distinct phylogenetic groups. Finally, as
125 edaphic specialization may be more variable within angiosperm lineages (Fine *et al.*, 2005, Nascimento
126 *et al.*, 2020), we expect that edaphically marginal formations, such as coastal vegetation mosaics (i.e.
127 *restingas*) and forests associated with rock outcrops, to not form distinct phylogenetic groups.
128

129 **Material and Methods**

130 *Study area*

131 Our study area comprises the entire extension of the Atlantic Forest (*sensu latissimo*), which
132 stretches for over 3,500 km across equatorial, tropical and subtropical latitudes in South America and is
133 renowned world-wide for being one of the most diverse of 35 biodiversity hotspots for conservation
134 prioritization (Myers *et al.*, 2000). The *sensu latissimo* concept of the Atlantic Forest includes rain forests,
135 semideciduous forests, *Araucaria*-dominated ‘mixed’ forests, coastal vegetation (*restinga*), rock-outcrop
136 associated forests, cloud forests and riverine forests, the latter nested within other major vegetation
137 formations or domains such as the Cerrado and Pampas (see Appendix 1 for further details, including
138 associated environmental parameters; see also Oliveira-Filho *et al.*, 2006 and Neves *et al.*, 2017).

139 *Data base*

140 Floristic data were obtained from the NeoTropTree database (<http://www.neotropree.info/>;
141 Oliveira-Filho, 2015), which consists of a compilation of tree species lists and occurrence records collected
142 from the literature and herbarium specimens. Each sampling assemblage has a radius of 5 km and contains
143 records of occurrence of tree species that can be found in that area and within a single, given vegetation
144 type. Where two or more vegetation types co-occur in one 10 km diameter area, these were treated as
145 spatially overlapping assemblages but assigned to different vegetation types (see description, history and
146 protocol of NeoTropTree at http://www.neotropree.info). Major heterogeneity in vegetation type within
147 10 km diameter areas was common in eastern South America (Silva de Miranda *et al.*, 2018). In addition
148 to the presence and absence data for tree species, each assemblage is characterized by numerous
149 descriptive and environmental data, such as altitude, geo-edaphic and climatic variables. We built a
150 presence/absence matrix of genera for all 1,755 assemblages to use in downstream analyses. As found by
151 Cantidio & Souza (2019), we might expect that abundance data will reveal more than presence–absence
152 data. However, we are not aware of the public availability of large-scale abundance data for the entire
153 domain, including all of its (micro)habitats (although see de Lima *et al.*, 2015 for the largest-scale effort
154 to date).

155 Our data set focuses on angiosperms and comprises 614 genera, and 116 families, spread over 1755
156 assemblages. The inclusion of ferns and gymnosperms has a very strong effect on phylogenetic diversity

157 metrics, yet they are exceedingly rare over most of the Atlantic Forest, so they were excluded from analyses
158 (*sensu* Kembel & Hubbell, 2006, Honorio-Coronado *et al.*, 2015). For phylogenetic analysis we use a
159 temporally-calibrated, genus-level phylogenetic tree constructed using maximum likelihood phylogenetic
160 analyses of the *rbcL* and *matK* plastid regions by Neves *et al.* (2020). This molecular phylogeny
161 encompasses 1,100 tree genera from South America and includes 89% of the angiosperm tree genera in
162 our study area. We excluded 68 angiosperm genera from the distribution dataset that were not found in this
163 genus-level phylogenetic tree. Together they represented 1.55% of the occurrence records in the dataset.

164 *Data analysis*

165 To place assemblages in a multivariate evolutionary composition space, we used an approach
166 developed by Pavoine (2016). Specifically, we conducted a principal component analysis of a Hellinger
167 transformed compositional matrix that not only includes the occurrence of genera in assemblages, but also
168 the occurrence of phylogenetic nodes. This approach is recommended for having high discriminatory
169 power to detect changes in evolutionary lineage composition over gradients, while also being connected
170 to an ordination that can serve to place lineages and assemblages in the same compositional space. We
171 implemented this approach using the `evoPCAHellinger()` function in the `adiv` package (Pavoine 2016). To
172 determine what the main groups of assemblages were in terms of evolutionary composition, we used K-
173 means clustering based on Euclidean distance between assemblages in the compositional ordination space.
174 We chose this approach because large differences in richness (here phylogenetic diversity) between sites
175 may affect analyses based on the Sørensen, or similar indices, and their phylogenetic equivalents (e.g.,
176 *Phylosor*), while the placement of assemblages in ordination space should be less affected by richness
177 differences. Thus, the Euclidean distance between assemblages in ordination space should largely reflect
178 compositional differences (Fayolle *et al.*, 2014). For calculating the distance between assemblages in
179 ordination space, we used the first five axes of the evolutionary ordination, as a scree plot showed a large
180 decrease in variation explained by subsequent axes. To understand the environmental correlates of these
181 ordination axes, we used general linear models. For determining the optimal number of groups in the
182 clustering analysis, we used an analysis of gap statistics, average silhouette widths and an elbow plot (see
183 Appendix S2 in Supporting Information).

184 We used a random forest classification tree approach (Breiman, 2001), to assess whether the
185 phylogenetic groups identified could be distinguished using environmental data. The random forest
186 classification consists of many individual decision trees that operate as an ensemble; it aggregates the votes
187 from different decision trees to decide the final class of the test object. For this, we used altitude and 27
188 environmental variables available for each site (at 30 arc-second resolution) in the NeoTropTree database
189 (description, history and NeoTropTree protocol at <http://www.neotropree.info>) (Table 1).

190 In order to evaluate the success rate of the classification tree approach in assigning sites to
191 phylogenetic groups and to determine which assemblages were incorrectly classified using environmental
192 variables, we generated confusion matrices. We also estimated the importance of each variable for
193 distinguishing phylogenetic groups of assemblages using Breiman's measure of importance (Breiman,
194 2001), specifically the mean decrease in the Gini coefficient when a variable is chosen to split a node.

195 To explore phylogenetic turnover between the seven phylogenetic groups, we calculated
196 phylogenetic beta diversity (PBD), using the Phylosor metric. This metric calculates the proportion of
197 phylogenetic branch length shared between two phylogenetic groups relative to the total branch length of
198 all taxa in the two groups. We also determined the lineages that are most strongly associated with individual
199 phylogenetic groups using an indicator analysis for lineages (Dufrene & Legendre, 1997), which was based
200 on the presence versus absence in assemblages of the genera descended from each phylogenetic node
201 (*sensu* Segovia *et al.*, 2020). We also included terminal nodes, i.e. individual genera, in the indicator
202 analysis.

203 All analyses were conducted in the R 3.2.3 Statistical Environment (R Core Team, 2017) using the
204 following packages: 'picante' (Kembel *et al.*, 2015), 'vegan' (Oksanen *et al.*, 2016), 'adiv' (Pavoine, 2016),
205 'cluster' (Maechler, 2018), 'factoextra' (Kassambara, 2016), ape (Paradis *et al.*, 2019), 'labdsv' (Roberts,
206 2016) and randomForest package in the R statistical software (Liaw & Wiener, 2002).

207 208 **Results**

209
210 The optimal number of groups in our phylogenetically-informed compositional classification of
211 assemblages varied from seven to nine, with all methods giving good support for seven clusters (Appendix
212 S3). We therefore subsequently focused on seven phylogenetic groups (Fig. 1), which we have named based
213 on their dominant vegetation types: (1) Tropical and subtropical coastal vegetation mosaic (including
214 *restinga* and mangrove); (2) Tropical rain forest; found along the Atlantic coast extending from northeast
215 to southeast Brazil; the southern limit was found to occur in Rio de Janeiro state at the latitude of 23° 33'
216 S (almost exactly coinciding with the Tropic of Capricorn), in the Paraty municipality; (3) Tropical
217 semideciduous forest, in which 30 to 60% of the leaf mass is deciduous in the dry season, and which also
218 extends southwards to near the Tropic of Capricorn; (4) Tropical and subtropical highland forests, which
219 have a frequently more open vegetation, usually found above 1000 m.a.l.s. with a low canopy, between 3
220 and 5 m in height, including some cloud dwarf-forest; scattered taller trees may emerge from the canopy;
221 (5) Subtropical rain forest; rain forest found on the southern portion of the Atlantic coast and also including
222 most cloud forests from north of the Tropic of Capricorn); (6) Subtropical semi-deciduous forest, in which
223 30 to 60% of the leaf mass is deciduous in the cold season;; (7) Mixed angiosperm and gymnosperm
224 subtropical forest; *Araucaria angustifolia* often makes up more than 50% of canopy crowns, and may
225 reach 30 m in height. The other tree species in mixed forest are angiosperms, except for *Podocarpus*

226 *lambertii*, which may be locally abundant (Oliveira-Filho, 2015). We provide maps in the supplementary
 227 materials showing the distribution of phylogenetic groups when an alternative number of groups was
 228 selected (Appendix S3).
 229

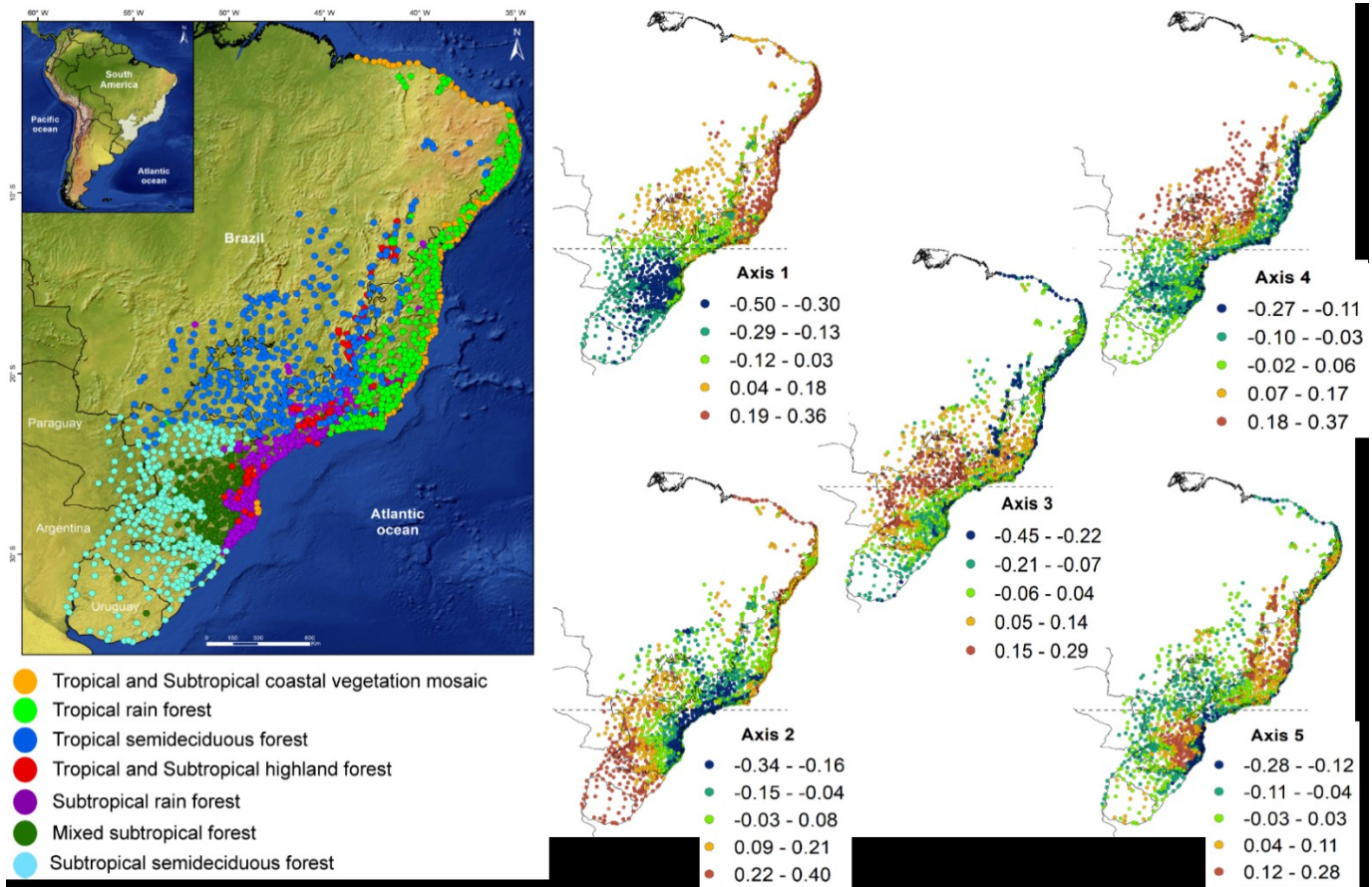


Figure 1. Map showing the geographical distribution of the seven phylogenetic groups of tree assemblages found in the Atlantic Forest as well as the distribution of values for the first five axes from an evolutionary ordination of sites based on their phylogenetic composition.

Temperature variables seem to be more important than precipitation and edaphic variables (as quantified) for distinguishing phylogenetic groups in the Atlantic Forest. The five most important environmental variables for classification were related to temperature: (1) temperature seasonality, (2) altitude, (3) minimum annual temperature, (4) temperature annual range and (5) mean annual temperature (Table 1).

Table 1. The mean variable importance value for all environmental variables included in the random forest analysis.

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Environmental variables	Mean Decrease in Gini Coefficient	Source
Temperature seasonality	121.55	WorldClim 2005
Altitude	113.66	CGIAR, 2006
Minimum temperature	113.19	WorldClim 2005
Temperature annual range	87.65	WorldClim 2005
Mean annual temperature	81.22	WorldClim 2005
Soil water storage	75.15	EMBRAPA's protocol
Grassy cover	71.92	Google Earth© images
Maximum temperature	69.40	WorldClim 2005
Precipitation in the dry period	66.56	WorldClim 2005
Temperature daily range	64.71	WorldClim 2005
Precipitation seasonality	56.02	WorldClim 2005
Isothermality	50.88	WorldClim 2005
Potential evapotranspiration	50.10	Zomer <i>et al.</i> , 2008
Ranked soil sand percentage	45.67	Harmonized World Soil Database v 1.2
Water deficit severity	39.35	Water's Climate Diagram
Ranked soil drainage	36.63	EMBRAPA's protocol
Precipitation in the wet period	35.75	WorldClim 2005
Aridity index	35.07	Zomer <i>et al.</i> , 2008
Water deficit duration	33.45	Water's Climate Diagram

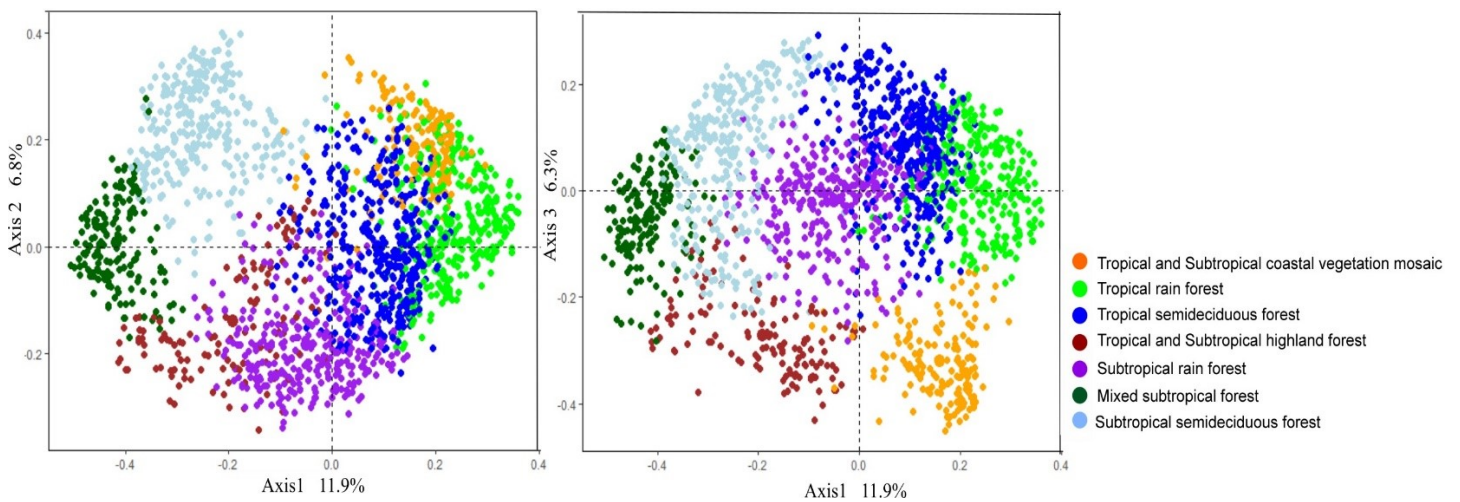
Hyper seasonality	31.49	interpolating known values*
Water excess duration	28.95	Water's Climate Diagram
Number of days of frost	27.18	interpolating known values*
Ranked rockiness of soil	26.77	Harmonized World Soil Database v 1.2
Ranked salinity of soil	25.07	Harmonized World Soil Database v 1.2
Cloudiness (light interception)	24.83	interpolating known values*
Mean annual precipitation	24.31	WorldClim 2005
Water excess severity	23.98	Water's Climate Diagram
Ranked total base saturation in soil	10.89	Harmonized World Soil Database v 1.2

243 *Obtained from interpolating known values as response variables with elevation, latitude and the WorldClim layers as
244 predicting variables

245 In the evolutionary composition ordination (Fig. 2), the first axis explained ~12% of the variation
246 in the phylogenetic compositional data, and largely split the assemblages located north of the Tropic of
247 Capricorn (tropical zone) from those located south of this line (subtropical zone). Exceptions were
248 subtropical rain forests and highland forests which group with other assemblages below the Tropic of
249 Capricorn along this axis, but can be found to the north of the Tropic of Capricorn at higher elevations.
250 The coastal vegetation mosaic group also had a few assemblages found south of the Tropic of Capricorn.
251 Minimum temperature and temperature seasonality were the most strongly correlated variables with this
252 axis (Appendix S4). The tropical and subtropical areas in our study do not differ substantially in
253 precipitation regime, but have markedly different temperature regimes (Fig.3). Along this axis, the nodes
254 *Tapirira*, *Detarioideae*, *Burseraceae*, *Papilionoideae*, *Chrysobalanaceae*, *Humiriaceae* and
255 *Dichapetalaceae* were associated with tropical assemblages, while *Myrceugenia*, *Clethra*, *Laplacea*,
256 *Cunoniaceae*, *Canellales*, *Prunus*, *Symplocos*, *Lauraceae* (*Cinnamomum* + *Persea*) and *Piptocarpha* were
257 associated with subtropical assemblages (Appendix S5). In our dataset 83% of *Tapirira* occurrence records
258 are found above the Tropic of Capricorn and 92% of *Myrceugenia* occurrence are found in the subtropical
259 portion or in high altitude sites. The second axis (6.8%) showed a gradient mainly linked to maximum

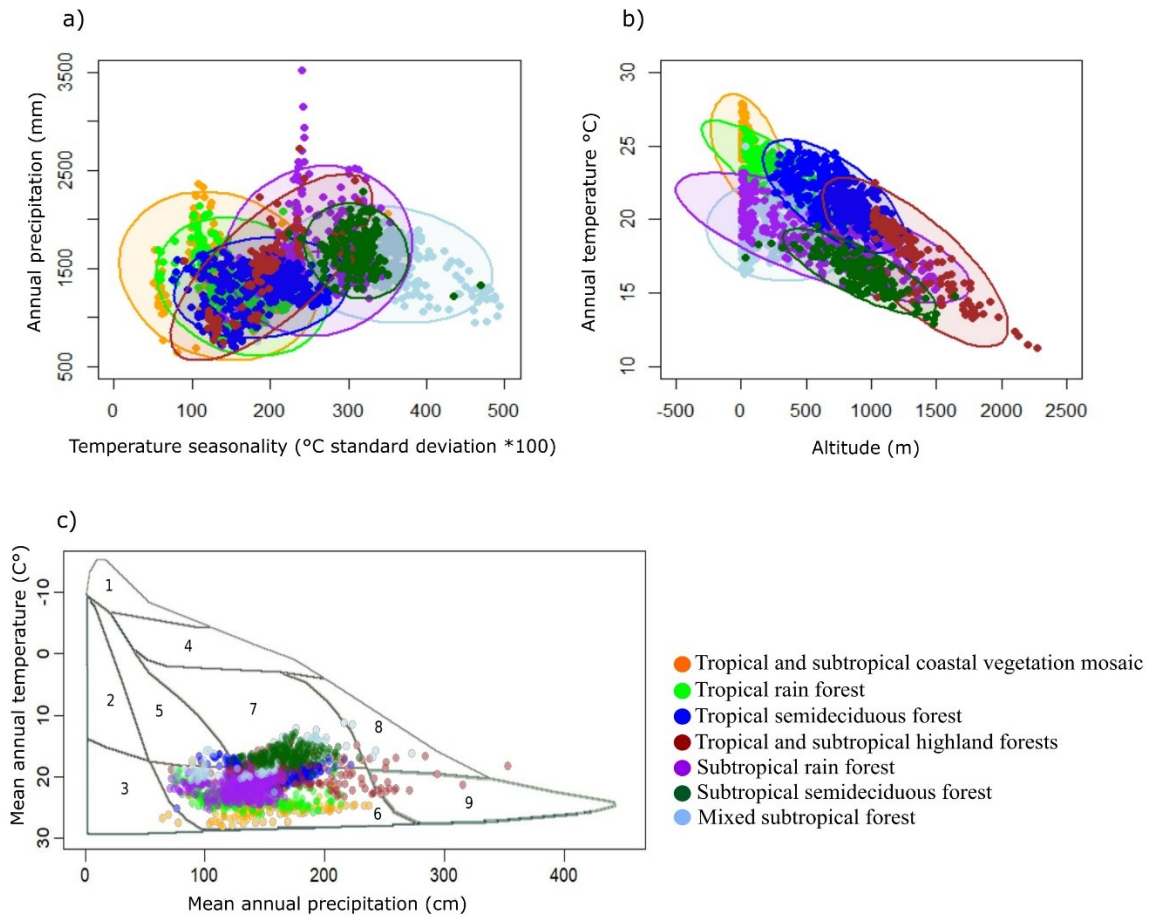
260 temperature and isothermality (Appendix S4). The tropical and subtropical coastal vegetation mosaic and
261 the subtropical semideciduous forest, the phylogenetic groups occurring at the lowest altitudes and
262 experiencing the highest maximum temperatures (30 and 31°C, respectively; Fig.3; Table 2), showed
263 positive values for Axis 2 (with only three Subtropical Semideciduous sites found with negative values for
264 Axis 2). The tropical and subtropical highland forest group (25°C mean maximum temperature) and
265 subtropical rain group forest (including cloud forest assemblages at high altitude; with 27°C mean
266 maximum temperature) have the great majority of sites with negative values for Axis 2. Negative values
267 for this axis are mainly associated with the Melastomataceae genera *Macairea* and *Trembleyia* (Appendix
268 S5). For axis 3, grassy cover and soil salinity were the most important variables, with Tropical and
269 Subtropical highland forest and Tropical and Subtropical coastal vegetation mosaics having negative
270 values for the axis. Positive values for this axis are associated mainly with *Cedrela* (Meliaceae) (Appendix
271 S5).

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Figure 2. First three axes from an evolutionary principal component analysis showing the distribution of assemblages according to their phylogenetic composition. Symbols represent the phylogenetic groups found in the Atlantic Forest.



282

283 **Figure 3.** Distribution of assemblages with respect to (A) mean annual precipitation and temperature
 284 seasonality; (B) mean annual temperature and altitude. The ellipses encompass the points of a given group.
 285 (C) Distribution of sites in climatic space across the nine biomes proposed by Whittaker, R. H. (1975),
 286 considering mean annual precipitation (in centimetres) and mean annual temperature (in degrees Celsius).
 287 1- Tundra; 2- Subtropical desert; 3- Temperate grassland desert; 4- Boreal forest; 5- Woodland shrubland;
 288 6- Tropical dry forest and savanna; 7- Temperate forest; 8- Temperate rain forest; 9- Tropical rain forest.

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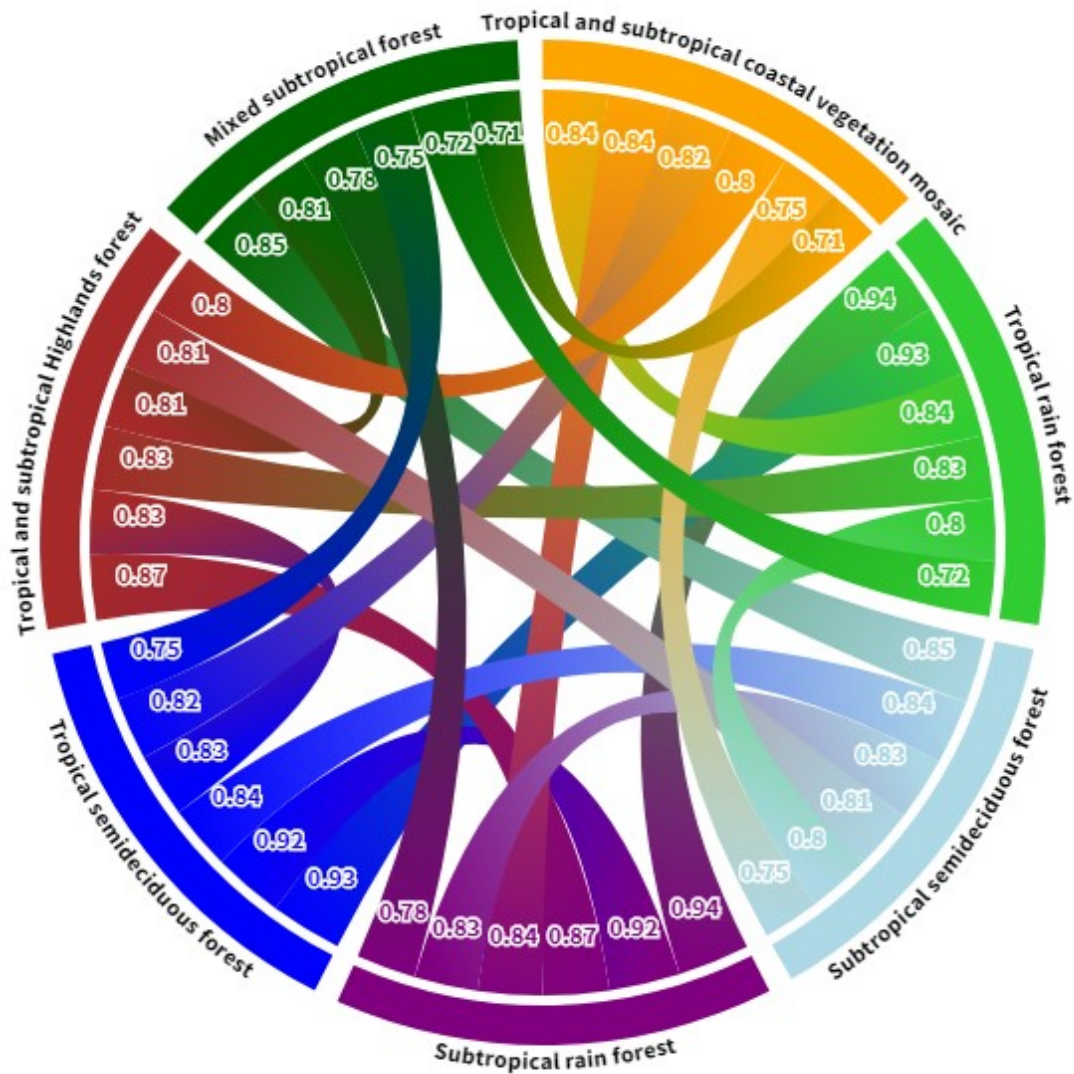
299 **Table 2.** Geographical and climatic characterization of the seven phylogenetic groups of tree assemblages
 300 found in the Atlantic Forest in terms of evolutionary lineage composition.
 301

Phylogenetic group	Number of assemblages	Vegetation type (% match)	Latitude (upper and lower 95% quantiles of distribution)	Mean distance from the ocean (km; range in brackets)	Mean altitude (m; range in brackets)
Tropical and subtropical coastal vegetation mosaic	167	90% <i>Restinga</i> ; 7% Semideciduous and 3% Rain Forest	2° 46' S 25° 16' S	6 (1-87)	33 (3-395)
Tropical rain forest	308	46% Rain and 54% Semideciduous Forest	4° 40' S; 23° 01' S	79 (1-310)	356 (15-1122)
Tropical semideciduous forest	383	66% Semideciduous and 33% Tropical Riverine; 1% Rock-outcrop Forest	9° 17' S; 23° 12' S	455 (41-952)	717 (265-1300)
Tropical and subtropical highland forest	131	49% Rock-outcrop; 44% Cloud; 5% Araucaria-dominated, 2% Tropical Riverine Semideciduous Forest	12° 05' S; 27° 00' S	236 (4-1017)	1322 (820-2278)
Subtropical rain forest	307	58% Rain, 13% Cloud; 12% Semideciduous; 10% <i>Restinga</i> ; 4% Araucaria-dominated; 2% Rock-outcrop; 1% Tropical Riverine Forest	17° 02' S; 29° 16' S	61 (1-323)	621 (2-1533)

Subtropical semideciduous forest	300	65% Semideciduous; 24% Subtropical Riverine; 11% Araucaria-dominated Forest	22°41' S; 34° 09' S	372 (1-853)	306 (3- 853)
Mixed subtropical forest	159	92% Araucaria-dominated; 4% Subtropical Riverine; 3% Cloud; 1% Semideciduous Forest	24° 05' S; 30° 21' S	195 (1-1017)	747 (4-498)

302

303 The mixed angiosperm and gymnosperm subtropical forest showed the lowest phylogenetic
304 compositional similarity values with the others groups, despite that gymnosperms were not included in the
305 analysis (four similarity values of the six pairwise comparisons are below 80%; Mean value ~ 77%; Fig.
306 4). Among all phylogenetic groups, just the subtropical semideciduous forest and the tropical and
307 subtropical highland forest showed similarity values higher than 80% with the mixed subtropical forest.
308 Interestingly, the tropical semideciduous forest was more similar to rain forest (tropical and subtropical)
309 than to subtropical semideciduous forest. The similarity values among any of these three phylogenetic
310 groups (tropical and subtropical rain forest, tropical semideciduous forest) was always above 90%. The
311 lowest value of similarity was found between the mixed subtropical forest and the tropical and subtropical
312 coastal vegetation mosaic (71%; Fig.4). While similarity values overall seem high (particularly compared
313 to taxonomic presence/absence analyses), it is worth noting that they are based on the presence versus
314 absence of genera in the entirety of each phylogenetic group of assemblages. The values thus represent an
315 upper estimate of similarity, but should be comparable among different pairwise comparisons.



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319 **Figure 4.** Phylogenetic similarity among the different phylogenetic groups found in the Atlantic Forest.
320 Numbers represent the pairwise Phylogenetic Sorensen's Similarity Index (PhyloSor), with higher values
321 indicating higher similarity in evolutionary lineage composition.

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323 The tropical rain forest phylogenetic group showed the highest number of significant indicator
324 lineages (206), and the highest values of the indicator statistic (Table 3; Appendix S6). The lineage with
325 the highest indicator value (0.56) for tropical rain forest was a subclade of the Malpighiales, which includes
326 the genera *Rinorea*, *Paypayrola*, *Amphirrhox*, *Kuhlmanniodendron* and *Carpotroche* (Table 3).

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328 **Table 3.** Indicator analysis for lineages of the seven phylogenetic groups found in Atlantic Forest. Numbers
329 in parentheses represent indicator values for the node.

Phylogenetic group	No. Species	No. Genera	No. of significant indicator lineages (p<0.005)	Lineage with highest indicator statistic and genera in lineage (indicator value in brackets).
Tropical and subtropical coastal vegetation mosaic	1328	387	40	Capparaceae subclade <i>Neocalyptrocalyx</i> , <i>Cynophalla</i> (0.45)
Tropical rain forest	3156	533	206	Malpighiales subclade (Violaceae and Achariaceae): <i>Rinorea</i> , <i>Paypayrola</i> , <i>Amphirrhox</i> , <i>Kuhlmanniodendron</i> , <i>Carpotroche</i> (0.56)
Tropical semideciduous forest	2263	493	90	Papilionoideae subclade: <i>Grazilodendron</i> , <i>Platypodium</i> (0.5)
Tropical and subtropical highland forest	2030	387	33	Ericaceae subclade: <i>Agarista</i> , <i>Gaultheria</i> (0.42)
Subtropical rain forest	2632	478	104	Lauraceae subclade: <i>Aniba</i> , <i>Licaria</i> (0.35)
Subtropical semideciduous forest	1202	374	38	Polygonaceae subclade: <i>Triplaris</i> , <i>Ruprechtia</i> (0.36)
Mixed subtropical forest	1025	287	46	Canellales (Canellaceae and Winteraceae)

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Discussion

We found that the most pronounced evolutionary division in tree assemblages of the Atlantic Forest occurs at the Tropic of Capricorn which seems to represent a southern latitudinal limit for phylogenetically-delimited groups of tree assemblages associated with the tropics. Subtropical groups do make it north of the Tropic of Capricorn, but only at higher elevations. Previous studies have found a north versus south division in species composition in the Atlantic Forest (Carnaval *et al.*, 2014 for vertebrates, mainly reptiles and amphibians; Canditio & Souza, 2019 for shrubs and trees), which has been attributed to biogeographic effects (i.e. vicariance, dispersal limitation) centered on the Rio Doce. However, evolutionary analyses point to an environmentally driven division, likely based on the regular occurrence of freezing versus non-freezing temperatures (Segovia *et al.*, 2020). We found that phylogenetic conservatism for a tropical versus extratropical niche may be the most important factor in shaping the broadscale evolutionary biogeography of the Atlantic Forest. However, any vegetation formation might be thought of as a snapshot of multiple interacting factors (environmental, evolutionary and historical process) that determine the distribution of taxa (Duarte *et al.*, 2014). The northward migration of Gondwanan lineages from subtropical areas and the current relictual distribution of these lineages at high elevations in tropical areas represent an example of the importance of these interacting factors (Segovia & Armesto, 2015).

Overall, our results are in accordance with our hypothesis that phylogenetic groups would most strongly align with temperature regime. Our hypothesis that precipitation regime would be of secondary importance, particularly in the tropics, received less evidence. While evergreen rain forests and semideciduous forests are more clearly segregated in subtropical areas, there is substantial mixing of rain forest and semideciduous forest within the tropical rain forest group (Table 2, Fig. 4). As pointed out by Oliveira-Filho & Fontes (2000) and also observed by Neves *et al.* (2017), the tree flora of tropical semideciduous forests is largely a subset of the tropical evergreen rain Atlantic forests. Therefore, though semideciduous forests have endemic lineages, most of its plant lineage diversity can also be found in rain forests. In our database, 92,8% of the genera that occur in the Tropical semideciduous forest also occur in the Tropical rainforest. Thus, the *a priori* division of these forests into two categories is based on physiognomic differences, especially leaf deciduousness, and may be driven by either facultative deciduousness or variation in the abundance of deciduous genera, which our presence/absence data cannot assess. Lastly, our hypothesis that edaphically-driven vegetation types would not form distinct phylogenetic groups received partial support. For example, coastal vegetation mosaics (a.k.a. *restinga*),

365 which are most environmentally distinct in terms of soils, did form a clear phylogenetic group (Appendix
366 S1). In contrast, forests associated with rock outcrops were combined with cloud forests in a single high
367 elevation group, despite having divergent edaphic environments (Appendix S1).

368 The geographical pattern of differentiation found between Tropical and Subtropical phylogenetic
369 groups can be further explained by the fact that the extratropical portion of South America went through
370 different historical biogeographical processes such as natural fragmentation and gradual extinction of
371 woody lineages, mainly due to the contraction of temperate forest, and the uplift of the Andes, which
372 drastically altered precipitation and temperature regimes (Rezende *et al.*, 2018; Hinojosa & Villagrán,
373 2005; Ortiz-Jaureguizar & Cladera, 2006). Relicts of these extratropical forests would have remained at
374 specific locations along the southern Pacific coast of South America (Hinojosa & Villagrán, 2005), on the
375 Brazilian plateau (Rezende *et al.*, 2015) and on the slopes of the tropical Andean Range (Villagran &
376 Hinojosa, 1997; Segovia & Armesto, 2015). These relicts of extratropical forest are consistent with our
377 phylogenetic analyses, where tropical areas at higher elevations (above 1300m) were found to be more
378 evolutionarily linked to subtropical forests than to tropical forests, even though they occur in a matrix of
379 tropical forest. Analyses using species composition have found finer-scale compositional distinctions
380 among high altitude vegetation types (Neves *et al.*, 2017), including splitting them into five different
381 groups (evergreen cloud dwarf-forest; evergreen cloud forest; rocky highland seasonal savanna; rocky
382 highland seasonal dwarf-forest and mixed Araucaria forest), but our analyses suggest that these vegetation
383 types are broadly occupied by the same phylogenetic lineages of angiosperms. These high altitude areas,
384 which are formally within the tropics ($< 23^\circ$ S latitude), offer climatic conditions similar to those found in
385 subtropical areas, favoring the occurrence of extratropical tree lineages at tropical latitudes. Altitudinal
386 migrations were also caused by glacial cycles through the spread, contraction and fragmentation of the
387 ranges of cool-and warm-adapted species (Collevatti *et al.*, 2012; Turchetto-Zolet *et al.*, 2013; Leopold *et*
388 *al.*, 2015). Some examples of these extratropical lineages are members of the Cunoniaceae and
389 Winteraceae (Hooghiemstra, 1984; Segovia & Armesto 2015), found here associated with subtropical and
390 highland forests.

391 The influence of phylogenetic conservatism for precipitation regime in shaping the evolutionary
392 structure of the Atlantic Forest was not as clear when examining how semideciduous and rain forest
393 assemblages fell into phylogenetic groups. This may reflect a complex interplay of deciduousness driven
394 by temperature and precipitation regimes. In contrast with the results found by Neves *et al.* (2017) with
395 taxonomic composition data, we found relatively high phylogenetic similarities between tropical
396 semideciduous forest and tropical and subtropical rain forests, with subtropical semideciduous forests
397 being phylogenetically diverged from those other three groups. The similarities between tropical
398 semideciduous and rain forests suggest that the divergent precipitation regime that semideciduous forests
399 experience, with mean annual precipitation below 1,600 mm and water stress in five to six months of each
400 year, is not causing a major phylogenetic turnover of tree assemblages, even if it is sufficient to cause
401 markedly divergent phenology. Meanwhile, in the subtropical portion of Atlantic Forest, rainfall is
402 relatively high and constant across the year, and temperature is reported to be a more important variable

403 in explaining phenology and species composition across forest types (Alvares *et al.*, 2013; Giehl &
404 Jarenkov 2012, Neves *et al.*, 2017; Oliveira-Filho *et al.*, 2006; Oliveira -Filho *et al.*, 2015; Rezende *et al.*,
405 2015). Thus, the phylogenetic divergence between semideciduous and rain forests in the subtropical
406 portion of the Atlantic Forest reinforces the predominance of temperature regime in shaping the
407 distribution of phylogenetic groups of tree assemblages. In addition, we found that the semideciduous
408 forest phylogenetic group was more restricted to inland areas than Neves *et al.* (2017), with tropical rain
409 forest occupying a much larger area (not restricted to a narrow band along the coast). This can be especially
410 important from a conservation perspective, since wet forests have twice as much protection as marginal
411 habitats (Neves *et al.*, 2017), and according to our phylogenetic results many protected areas allocated to
412 preserve the marginal habitats of Atlantic Forest can actually be protecting more wet forest.

413 The importance of climatic niche conservatism for shaping biogeography may be lower for some
414 vegetation types, such as coastal vegetation (e.g. *restinga*; Hesp, 2008), in which temperatures are more
415 constant throughout the year, even in subtropical areas. For this specific vegetation type, soil variables (e.g.
416 salinity, texture and fertility) are suggested to be key in driving its floristic distinctness (Marques *et al.*,
417 2011; Silva & Souza, 2018; Canditio & Souza, 2019). When analyzing floristic composition data, Neves
418 *et al.* (2017) found the *restinga* to be strikingly distinct from the other Atlantic vegetation types, both
419 floristically and environmentally, and we found a similar pattern with our phylogenetic approach. As an
420 example, the genus *Cedrela* (Meliaceae) has a wide distribution (from Mexico to Argentina) and occurs in
421 different climatic regimes. However the genus does not develop properly in poorly drained or shallow soils
422 (IPEF, 2005), which can justify the association of *Cedrela* with the third axis of our evolutionary ordination
423 (in the opposite direction of the *restinga* sites).

424 The Atlantic tropical rain forest is thought to be an old climatically stable vegetation formation
425 (Carnaval & Moritz 2008; Carnaval *et al.*, 2014, Costa *et al.*, 2018, Canditio & Souza 2019), which may
426 explain why it has the highest number of indicator lineages among the seven phylogenetic groups. Overall,
427 our lineage indicator results are consistent with the distributional occurrence of Atlantic Forest species
428 according to Flora do Brasil (2020). As an example, *Kuhlmanniodendron* (Achariaceae) (indicator of
429 tropical rain forest) is restricted to the Atlantic Rain Forests of Bahia and Espírito-Santo states (Flora do
430 Brasil, 2020). Another endemic genus of Atlantic Forest is *Grazilodendron* (Fabaceae), that we found to
431 be an indicator of tropical semideciduous forest. This genus is monotypic, with just one species
432 (*Grazilodendron riocenssis*), which shows a restricted distribution in the states of Bahia, Espírito Santo
433 and Rio de Janeiro, in southeastern Brazil (de Lima, 2012), and with a predominant occurrence in the
434 seasonal lowland forests in the Região dos Lagos, Rio de Janeiro state (Ribeiro & Lima, 2009). For
435 tropical and subtropical highland forest, we found two Ericaceae genera (*Agarista* and *Gaultheria*) to be
436 indicators of this evolutionary group. In the Neotropical region, the Ericaceae family finds its center of
437 diversity and endemism (Luteyn, 2002) at altitudes between 1000 and 3000 m, in cold, open and humid
438 mountainous environments (Luteyn, 1989). We found *Drimys* (Winteraceae) and *Cinnamodendron*
439 (Canellaceae) to be the most important genera for subtropical mixed forest. These lineages show a broad
440 distribution throughout the Southern Hemisphere, and are often suggested to have a Gondwanan origin,

441 which reached higher elevation areas in southeast Brazil via a northward migration route (Segovia &
442 Armesto, 2015).

443 Our study showed that genera and higher-level lineages of trees in the Atlantic Forest largely
444 segregate into southern and highland tree assemblages versus those occurring under more tropical climates
445 at lower elevations. In lowland areas, the highest phylogenetic turnover was found to occur at the Tropic
446 of Capricorn line separating tropical from subtropical assemblages. Mixed forests (with angiosperms and
447 gymnosperms), the phylogenetic assemblage group that is exposed to the highest amount of frost, were
448 the most distinct phylogenetically from the other groups, notwithstanding that gymnosperms were not
449 included in the analysis. This result is driven by the high number of Gondwanan lineages found in mixed
450 forests, demonstrating that the different Atlantic Forest vegetation types are composed of lineages of
451 diverse evolutionary origins. The high variability in tree phylogenetic composition among the
452 phylogenetic groups found here reinforces the great floristic wealth of the Atlantic Forest, where many
453 distinct phyloregions can be found. It is worth noting that the tropical rain forest vegetation type is often
454 considered the main core of the Atlantic Forest, while other vegetation types are considered floristically
455 poor marginal habitats. The phylogenetic turnover found here underpins the importance of improving
456 conservation efforts for the entire domain, aiming to preserve the distinct lineages found in each vegetation
457 type.

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462 DATA AVAILABILITY STATEMENT

463 The NeoTropTree database are available at: <http://www.neotropree.info/>

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466 BIOESKETCH

467 Vanessa L. Rezende is a Research Fellow at the Federal University of Lavras, Brazil. She is interested in
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469 South America.

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472 Author contributions: V.L.R., V.P., M.L.B., A.O.F. and K.G.D designed the paper; V.L.R. and A.O.F.
473 assembled the database; V.L.R., P.L.S-M and K.G.D. analysed the data; V.L.R., V.P., M.L.B., A.O.F. and
474 K.G.D. led the writing. All authors read and approved the final work.

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477 SUPPORTING INFORMATION

478 Additional Supporting Information may be found in the online version of this article:

479 Appendix S1. Soil and climatic characterization of the seven vegetation types found in the Atlantic
480 Forest in terms of species composition, further information can be found in Neves *et al.* (2017).
481 Appendix S2. Results obtained by different methods used to determining the optimal number of clusters.
482 The gap statistic method (compares the total within intra-cluster variation for different values of k with
483 their expected values under null reference distribution of the data); The average silhouette method
484 (computes the average silhouette of observations for different values of k) and the elbow method (define
485 clusters such that the total intra-cluster variation [or total within-cluster sum of square (WSS)] is
486 minimized).
487 Appendix S3. Maps showing the geographical distribution of the different phylogenetic groups of tree
488 assemblages found in the Atlantic Forest. Each map represents the suggested groups for different values
489 of k. A) k=1; B) k=2; C) k=3; D) k=4; E) k=5; F) k= 6; G) k=7; H) k=8; I) k=9; J) k=10.
490 Appendix S4. Adjusted r^2 values found between each axis of the evoPCA and environmental and soil
491 variables. * represent significant values.
492 Appendix S5. Principal component analysis of a Hellinger transformed compositional matrix (EvoPCA)
493 showing the phylogenetic nodes contribution.
494 Appendix S6 Indicator analysis for lineages of the seven phylogenetic groups found in Atlantic Forest.
495 Genera names were extracted from each indicator node. Numbers indicates different subclades. Clade
496 names and numbers as the same as the annotated phylogeny (Supplementary Material).

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499 **References**

500

501 Alvares, C. A., Stape, J.L., Sentelhas, P.C., de Moras Gonçalves, J.L., Sparovek, G. (2013). Köppen's
502 climate classification map for Brazil. *Meteorologische Zeitschrift*, 22, 711–728.

503

504 Andresen E., Arroyo-Rodríguez V., Escobar F. (2018) Tropical Biodiversity: The Importance of Biotic
505 Interactions for Its Origin, Maintenance, Function, and Conservation. In: W. Dáttilo & V. Rico-Gray (Eds.),
506 *Ecological Networks in the Tropics* (pp 1-13). Cham, Springer.

507

508 Breiman, L. (2001). Random forests. *Machine Learning*, 45, 5–32.

509

510 Canditio, L. S., & Souza, A. F. (2019). Aridity, soil and biome stability influence plant ecoregions in the
511 Atlantic Forest, a biodiversity hotspot in South America. *Ecography*, 42, 1887-1898.

512 <https://doi.org/10.1111/ecog.04564>

513

- 514 Carnaval, A. C., & Moritz, C. (2008). Historical climate modelling predicts patterns of current biodiversity
515 in the Brazilian Atlantic forest. *Journal of Biogeography*, 35, 1187–1201. <https://doi.org/10.1111/j.1365-2699.2007.01870.x>
- 517 Carnaval, A. C., Waltari, E., Rodrigues, M. T., Rosauer, D., VanDerWal, J., Damasceno, R., Prates, I.,
518 Strangas, M., Spanos, Z., Rivera, D., Pie, M. R., Firkowski, C. R., Bornschein, M. R., Ribeiro, L. F.,
519 Moritz, C. (2014). Prediction of phylogeographic endemism in an environmentally complex biome.
520 *Proceedings of the Royal Society B: Biological Sciences*. 281, 20141461–20141461.
521 <https://doi.org/10.1098/rspb.2014.1461>
- 522 Cavender-Bares J., Ackerly D. D., Baum D. A., Bazzaz F. A. (2004). Phylogenetic overdispersion in
523 Floridian oak communities. *The American Naturalist*, 163, 823–843. <https://doi.org/10.1086/386375>
- 524 Cavender-Bares, J., Kozak, K.H., Fine, P.V.A., Kembel, S.W. (2009). The merging of community
525 ecology and phylogenetic biology. *Ecology Letters*, 12, 693–715.
- 526 Collevatti, R., Terribile, L. C., Lima-Ribeiro, M. S., Nabout, J., Oliveira, G., Rangel, T. F., Rabelo, S. G.,
527 Diniz-Filho, J. (2012). A coupled phylogeographical and species distribution modelling approach recovers
528 the demographical history of a Neotropical seasonally dry forest tree species. *Molecular Ecology*. 21,
529 5845–5863. <https://doi.org/10.1111/mec.12071>
- 530 Connolly, J., Cadotte, M.W., Brophy, C., Dooley, A., Finn, J., Kirwan, L., Rocher, R., Weigelt, A. (2011).
531 Phylogenetically diverse grasslands are associated with pairwise interspecific processes that increase
532 biomass. *Ecology*, 92, 1385–1392.
- 533 Costa, G.C., Hampe, A., Ledru, M.-P., Martinez, P.A., Mazzochini, G.G., Shepard, D.B., Werneck, F.P.,
534 Moritz, C., Carnaval, A.C. (2018). Biome stability in South America over the last 30 kyr: Inferences from
535 long-term vegetation dynamics and habitat modelling. *Global Ecology and Biogeography*, 27, 285–297.
536 <https://doi.org/10.1111/geb.12694>
- 537 Crisp, M. D., & Cook, L. G. (2012). Phylogenetic niche conservatism: What are the underlying
538 evolutionary and ecological causes? *New Phytologist*, 196, 681–94. <https://doi.org/10.1111/j.1469-8137.2012.04298.x>
- 540 Daru, B.H., Elliott, T.L., Park, D.S., Davies, T.J. (2017). Understanding the processes underpinning
541 patterns of phylogenetic regionalization. *Trends in Ecology and Evolution*, 32, 845–860.
542 <https://doi.org/10.1016/j.tree.2017.08.013>

- 543 Daru, B.H., van der Bank, M., Maurin, O., Yessoufou, K., Schaefer, H., Slingsby, J., Davies, T.J. (2016).
544 A novel phylogenetic regionalization of phytogeographical zones of southern Africa reveals their hidden
545 evolutionary affinities. *Journal of Biogeography*, 43, 155–166. <https://doi.org/10.1111/jbi.12619>
- 546 de Lima, H.C (2102). *Grazilodendron* in Lista de Espécies da Flora do Brasil, Jardim Botânico do Rio
547 de Janeiro. Jardim Botânico do Rio de Janeiro. Available at:
548 <<http://floradobrasil.jbrj.gov.br/2012/FB079073>>.
- 549 de Lima, R. A., Mori, D. P., Pitta, G., Melito, M. O., Bello, C., Magnago, L. F., Zwiener, V. P., Saraiva,
550 D. D., Marques, M. C., de Oliveira, A. A., Prado, P. I. (2015). How much do we know about the
551 endangered Atlantic Forest? Reviewing nearly 70 years of information on tree community surveys.
552 *Biodiversity and Conservation*, 24, 2135-2148. <https://doi.org/10.1007/s10531-015-0953-1>
- 553 Duarte, L.D.S., Bergamin, R.S., Marcilio-Silva, V., Seger, G.D.D.S., Marques, M.C.M. (2014).
554 Phylobetadiversity among forest types in the Brazilian Atlantic Forest complex. *PLoS ONE*, 9, e105043.
- 555 Dufrene, M., & Legendre, P. (1997). Species Assemblages and Indicator Species: The Need for a Flexible
556 Asymmetrical Approach. *Ecological Monographs*, 67, 345-366. <http://dx.doi.org/10.2307/2963459>
- 557 Eisenlohr, P.V., & Oliveira-Filho, A.T. (2015). Revisiting patterns of tree species composition and their
558 driving forces in the Atlantic forests of southeastern Brazil. *Biotropica*, 47, 689–701.
- 559 Eiserhardt, W. L., Svenning, J. C., Baker, W. J., Couvreur, T. L. P., Balslev, H. (2013). Dispersal and
560 niche evolution jointly shape the geographic turnover of phylogenetic clades across continents. *Scientific*
561 *Reports*, 3, 1164.
- 562 Fayolle, A., Swaine, M.D., Bastin, J.F., Bourland, N., Comiskey, J.A., Dauby, G., Doucet, J.L., Gillet,
563 J.F., Gourlet-Fleury, S., Hardy, O.J., Kirunda, B. (2014). Patterns of tree species composition across
564 tropical African forests. *Journal of Biogeography*, 41, 2320-2331.
- 565 Fine, P.A., Daly, D.C., Cameron, K.M. (2005). The contribution of edaphic heterogeneity to the evolution
566 and diversity of burseracear trees in the western Amazon. *Evolution*, 59, 1464-1478.
- 567 Flora do Brasil 2020, em construção. Jardim Botânico do Rio de Janeiro. Available at:
568 <http://floradobrasil.jbrj.gov.br>.
- 569 Gerhold, P., Cahill, J.F. Jr, Winter, M., Bartish, I.V., Prinzing, A. (2015). Phylogenetic patterns are not
570 proxies of community assembly mechanisms (they are far better). *Functional Ecology*, 29, 600– 614.

- 571 Giehl, E. L. H., & Jarenkow, J. A. (2012). Niche conservatism and the differences in species richness at
572 the transition of tropical and subtropical climates in South America. *Ecography*, 35, 933–943.
- 573 Graham, C. H., Parra, J. L., Rahbek, C., McGuire, J. A. (2009). Phylogenetic structure in tropical
574 hummingbird communities. *Proceedings of the National Academy of Sciences of the United States of*
575 *America*, 107(1):514. <https://doi.org/10.1073/pnas.0901649106>
- 576 Guo, Y. Y., Luo, Y. B., Liu, Z. J., Wang, X. Q. (2012). Evolution and biogeography of the Slipper Orchids:
577 Eocene vicariance of the Conduplicate genera in the Old and New World tropics. *Plos One*, 7, e38788.
578 <https://doi.org/10.1371/journal.pone.0038788>
- 579 Hesp, P.A. (2008). Coastal dunes in the tropics and temperate regions: location, formation, morphology
580 and vegetation processes. In: M.L., Martínez, & N.P., Psuty (Eds.), *Coastal Dunes. Ecology and*
581 *Conservation*. Ecological Studies (Vol. 171, pp. 29-52). Berlin: Springer.
- 582 Hinojosa, L. F. & Villagrán, C. (2005). Did South American mixed paleofloras evolve under thermal
583 equability or in the absence of an effective Andean barrier during the Cenozoic? *Palaeogeography,*
584 *Palaeoclimatology and Palaeoecology*, 217, 1–23. <https://doi.org/10.1016/j.palaeo.2004.11.013>
- 585 Holt, B. G., Lessard, J. P., Borregaard, M. K., Fritz, S. A., Araujo, M. B., Dimitrov, D., Fabre, P. H.,
586 Graham, C. H., Graves, G. R., Jønsson, K. A., Nogues-Bravo, D., Wang, Z., Whittaker, R. J., Fjeldsa, J.,
587 Rahbek, C. (2013). An update of Wallace’s zoogeographic regions of the world. *Science*. 339, 74–78.
588 <https://doi.org/10.1126/science.1228282>
- 589 Honorio-Coronado, E. N., Dexter, K., Pennington, R.T., Chave, J., Lewis, S. L., ... Phillips, O. L. (2015).
590 Phylogenetic diversity of Amazonian tree communities. *Diversity and Distribution*, 21, 1295-1307.
591 <https://doi.org/10.1111/ddi.12357>
- 592 Hooghiemstra, H. (1984). Vegetational and climatic history of the high plain of Bogotá, Colombia: a
593 continuous record of the last 3,5 million years. *Dissertationes Botanicae*, J. Cramer, Vaduz 79, 368.
- 594 Instituto de Pesquisas e Estudos Florestais (IPEF). (2005). *Cedrella fissilis* (Cedro). Available at:
595 <https://www2.ipef.br/identificacao/cedrella.fissilis.asp>.
- 596 Kassambara, A. & Mundt, F. (2016). factoextra: Extract and Visualize the Results of Multivariate Data
597 Analyses. Retrieved from <https://CRAN.R-project.org/package=factoextra>, r package version 1.0.3.
- 598 Kembel, S. W. & Hubbell, S. P. (2006). The phylogenetic structure of a neotropical forest tree community.
599 *Ecology*. 87, 86-99. [https://doi.org/10.1890/0012-9658\(2006\)87\[86:TPSOAN\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[86:TPSOAN]2.0.CO;2)

600 Kembel, S.W., Ackerly, D.D., Blomberg, S.P., Cornwell, W.K., Cowan, P.D., Helmus, M.R., Morlon, H.,
601 Webb, C.O. (2015). Package “picante”. R tools for integrating phylogenies and ecology. R package
602 version 1.6-2.

603 Leopold, D.R., Tanentzap, A.J., Lee, W.G., Heenan, P.B., Fukami, T. (2015). Evolutionary priority effects
604 in New Zealand alpine plants across environmental gradients. *Journal of Biogeography*, 42, 729–737.
605 <https://doi.org/10.1111/jbi.12441>

606 Luteyn, J. L. (1989). The genus *Gaultheria* in Brazil. *Boletim do Mus Emilio Goeldi*. 11, 623-627.

607 Luteyn, J. L. (2002). Diversity, adaptation and endemism in Neotropical Ericaceae: biogeographical
608 patterns in the Vaccinieae. *Lancaster*, 68, 55-87.

609 Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R News*, 2, 18 –22.

610 Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K. (2018). cluster: Cluster Analysis Basics
611 and Extensions. R package version 2.0.7-1.

612 Magnusson, W. E. (2004). Ecoregion as a pragmatic tool. *Conservation Biology*, 18, 4–6.
613 <https://doi.org/10.1111/j.1523-1739.2004.t01-1-00L13.x>.

614 Marques, M.C.M., Swaine, M.D., Liebsch, D. (2011). Diversity distribution and floristic differentiation of
615 the coastal lowland vegetation: implications for the conservation of the Brazilian Atlantic Forest.
616 *Biodiversity and Conservation*, 20, 153–168. <https://doi.org/10.1007/s10531-010-9952-4>

617 Mittermeier, R. A., P. R. Gil, M. Hoffmann, J. Pilgrim, J. Brooks, C. G. Mittermeier, J. Lamourux, G. B.
618 Fonseca. (2004). *Hotspots Revisited: Earth’s Biologically Richest and Most Endangered Terrestrial*
619 *Ecoregions*. Washington, DC, Cemex.

620 Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B., Kent, J. (2000). Biodiversity hotspots
621 for conservation priorities. *Nature*, 403, 853–858.

622 Nascimento, A.A.D., Silva Carvalho, L.C.D., Vega, M.R., Villela, D.M., Nascimento, M.T. (2020).
623 Environment, not phylogeny, drives herbivory and leaf attributes in trees from two contrasting forest
624 formations of the Brazilian Atlantic Forest. *Plant Ecology & Diversity*, 13, 147-158.

625 Neves, D.M., Dexter, K.G., Baker, T.R., de Souza, F.C., Oliveira-Filho, A.T., Queiroz, L.P., Lima, H.C.,
626 Simon, M.F., Lewis, G.P., Segovia, R.A., Arroyo, L. (2020). Evolutionary diversity in tropical tree
627 communities peaks at intermediate precipitation. *Scientific Reports*, 24, 1-7.
628 <https://doi.org/10.5061/dryad.gflvhhmk0>

- 629 Neves, D.M.; Dexter, K.G; Pennington, R.T.; Valente, A.S.M.; Bueno, M.L.; Eisenlohr, P.V.; Fontes,
630 M.A.L.; Miranda, P.L.S.; Moreira, S.N.; Rezende, V.L.; Saiter, F.Z.; Oliveira-Filho, A.T. (2017).
631 Dissecting a biodiversity hotspot: The importance of environmentally marginal habitats in the Atlantic
632 Forest Domain of South America. *Diversity and Distributiion*, 23: 898-909.
633 <https://doi.org/10.1111/ddi.12581>
- 634 O'Brien, K.L. & Leichenko, R.M. (2000). Double exposure: assessing the impacts of climate change
635 within the context of economic globalization. *Global Environmental Change*, 10, 221–232.
636 [https://doi.org/10.1016/S0959-3780\(00\)00021-2](https://doi.org/10.1016/S0959-3780(00)00021-2)
- 637 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L.,
638 Solymos, P., Stevens, M.H.H., Wagner, H. (2016). vegan: community ecology package. R package version
639 2.0–3. [http:// www.CRAN.R-project.org/package=vegan](http://www.CRAN.R-project.org/package=vegan)
- 640 Oliveira-Filho, A.T. (2015). Um Sistema de classificação fisionomico-ecológica da vegetação
641 Neotropical. In P.V. Eisenlohr, J.M. Felfili, M.M.R.F. Melo, L.A. Andrade, J.A.A. Meira-Neto (Eds.),
642 *Fitossociologia no Brasil: Métodos e estudos de casos* (Vol.2, pp. 452–473). Viçosa, Editora UFV.
- 643 Oliveira-Filho, A.T., Budke, J.C., Jarenkow, J.A., Eisenlohr, P.V., Neves, D.R.M. (2015). Delving into
644 the variations in tree species composition and richness across South American subtropical Atlantic and
645 Pampean forests. *Journal of Plant Ecology*, 8, 242-260. [https:// doi.org/10.1093/jpe/rtt058](https://doi.org/10.1093/jpe/rtt058)
- 646 Oliveira-Filho, A. T., Jarenkow, J. A., Rodal, M. J. N. (2006). Floristic relationships of seasonally dry
647 forests of eastern South America based on tree species distribution patterns. In R. T. Pennington, J. A.
648 Ratter, G. P. Lewis (Eds.), *Neotropical savannas and dry forests: Plant diversity, biogeography and*
649 *conservation* (pp. 151–184). Boca Raton, USA: CRC Press.
- 650 Ortiz-Jaureguizar, E., & Cladera, G.A. (2006). Paleoenvironmental evolution of southern South America
651 during the Cenozoic. *Journal of Arid Environments*, 66, 498–532. [https://doi.org/](https://doi.org/10.1016/j.jaridenv.2006.01.007)
652 [10.1016/j.jaridenv.2006.01.007](https://doi.org/10.1016/j.jaridenv.2006.01.007)
- 653 Paradis E, Blomberg S, Bolker B, Brown J, Claude J, Cuong HS, Desper R. 2019. Package 'ape'. Analyses
654 of phylogenetics and evolution , v.2-4.
- 655 Pavoine, S. (2016). A guide through a family of phylogenetic dissimilarity measures among sites. *Oikos*,
656 **125**, 1719–1732. <https://doi.org/10.1111/oik.03262>
- 657
- 658 Rezende, V.L., Bueno, M.L., Eisenlohr, P.V., Oliveira-Filho, A.T. (2018). Patterns of tree species variation
659 across southern South America are shaped by environmental factors and historical process. *Perspective in*

- 660 *Plant Ecology Evolution and Systematic*, 34, 10–16. <https://doi.org/10.1016/j.ppees.2018.07.002>
- 661 Rezende, V.L., Eisenlohr, P.V., Vibrans, A.C., Oliveira-Filho, A.T. (2015). Humidity, low temperature
662 extremes, and space influence floristic variation across an insightful gradient in the Subtropical Atlantic
663 Forest. *Plant Ecology*, 216, 759–774. <https://doi.org/10.1007/s11258-015-0465-9>
- 664 Ribeiro, R. D. & Lima, H. C. (2009). Riqueza e distribuição geográfica de espécies arbóreas da família
665 Leguminosae e implicações para a conservação no Centro de Diversidade Vegetal de Cabo Frio, Rio de
666 Janeiro, Brasil. *Rodriguésia*, 60, 111-117. <http://dx.doi.org/10.1590/2175-7860200960106>.
- 667 Roberts, D. W. (2019). labdsv: Ordination and multivariate analysis for ecology. R package version 2.0-
668 1. <https://CRAN.R-project.org/package=labdsv>
- 669 Scarano, F. R. (2009). Plant communities at the periphery of the Atlantic rain forest: Rare-species bias
670 and its risks for conservation. *Biological Conservation*, 142, 1201–1208.
- 671 Segovia, R.A. & Armesto, J.J. (2015). The Gondwanan legacy in South American biogeography. *Journal*
672 *of Biogeography*, 42, 209–217. <https://doi.org/10.1111/jbi.12459>.
- 673
- 674 Segovia, R.A., Pennigton, R.T., Baker, T.R., Souza, F.C., Neves, M. N., Davis, C.D., Armesto, J.J.,
675 Oliveira-Filho, A. T., Dexter, K.G. (2020). Freezing and water availability structure the evolutionary
676 diversity of trees across the Americas. *Science Advances*, 6, eaaz5373.
677 <https://doi.org/10.1126/sciadv.aaz5373>
- 678 Silva, A.C. & Souza, A.F. (2018). Aridity drives plant biogeographical sub regions in the Caatinga, the
679 largest tropical dry forest and woodland block in South America. *Plos One*, 13, e0196130.
680 <https://doi.org/10.1371/journal.pone.0196130>
- 681 Turchetto-Zolet, A.C., Pinheiro, F., Salgueiro, F., Palma-Silva, C. (2013) Phylogeographical patterns shed
682 light on evolutionary process in South America. *Molecular Ecology*, 22, 1193–1213.
683 <http://doi.org/10.1111/mec.12164>
- 684 Vamosi, S.M., Heard, S.B., Vamosi, J.C., Webb, C.O. (2009). Emerging patterns in the comparative
685 analysis of phylogenetic community structure. *Molecular Ecology*, 18, 572-592.
- 686 Villagran, C. & Hinojosa, L.F. (1997). Historia de los bosques del sur de Sudamerica, II: Analisis
687 fitogeografico. *Revista Chilena de Historia Natural*, 70, 241–267.
- 688 Werneck, M.D.S.; Sobral, M.E.G.; Rocha, C.T.V.; Landau, E.C., Stehmann, J.R. (2011). Distribution and
689 Endemism of Angiosperms in the Atlantic Forest. *Natureza & Conservação*, 9, 188-193.

690 Williams, P.H. (1996) Mapping Variations in the Strength and Breadth of Biogeographic Transition Zones
691 Using Species Turnover. *Proceedings of the Royal Society of London. Series B*, 263, 579-588.
692 <https://doi.org/10.1098/rspb.1996.0087>.

693 Whittaker, R.H. (1975). *Communities and Ecosystems*. MacMillan, New York

694 Wu, K., Chen, C.-N. N., Soong, K. (2016). Long distance dispersal potential of two seagrasses *Thalassia*
695 *hemprichii* and *Halophila ovalis*. *PLoS One*, 11, e0156585. <https://doi.org/10.1371/journal.pone.0156585>

696 Zanne, A. E., Tank, D. C., Cornwell, W. K., Eastman, J. M., Smith, S. A., FitzJohn, R. G., ... Beaulieu, J.
697 M. (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature*, 506, 89– 92.