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1 Brazilian montane rainforest expansion induced by Heinrich Stadial 1 event

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35 Abstract

36 The origin of modern disjunct plant distributions in the Brazilian Highlands with strong floristic

37 affinities to distant montane rainforests of isolated mountaintops in the northeast and northern

38 Amazonia and the Guyana Shield remains unknown. We tested the hypothesis that these

- 39 unexplained biogeographical patterns reflect former ecosystem rearrangements sustained by
- 40 widespread plant migrations possibly due to climatic patterns that are very dissimilar from
- 41 present-day conditions. To address this issue, we mapped the presence of the montane arboreal
- 42 taxa Araucaria, Podocarpus, Drimys, Hedyosmum, Ilex, Myrsine, Symplocos, and Weinmannia,

43 and cool-adapted plants in the families Myrtaceae, Ericaceae, and Arecaceae (palms) in 29 44 palynological records during Heinrich Stadial 1 Event, encompassing a latitudinal range of 30°S 45 to 0° S. In addition, Principal Component Analysis and Species Distribution Modelling were used 46 to represent past and modern habitat suitability for *Podocarpus* and *Araucaria*. The data reveals 47 two long-distance patterns of plant migration connecting south/southeast to northeastern Brazil 48 and Amazonia with a third short route extending from one of them. Their paleofloristic 49 compositions suggest a climatic scenario of abundant rainfall and relative lower continental 50 surface temperatures, possibly intensified by the effects of polar air incursions forming cold 51 fronts into the Brazilian Highlands. Although these taxa are sensitive to changes in temperature, 52 the combined pollen and speleothems proxy data indicate that this montane rainforest expansion 53 during Heinrich Stadial 1 Event was triggered mainly by a less seasonal rainfall regime from the 54 subtropics to the equatorial region.

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56 Keywords: Heinrich Stadial 1 event (HS1), pollen, Atlantic Forest, *Podocarpus, Araucaria*,

57 Migration, Polar Air Masses, Cold Fronts, Brazilian Highlands

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The origin of disjunct vegetation types in mountain landscapes of southeastern and central Brazil that display a strong affinity to wet montane floras of northern South America remains unknown. Earlier hypotheses^{1,2} suggested cold and wet migration corridors possibly in the Eocene or Miocene, later affected by the Quaternary climatic change, might have allowed ancient contact between plant populations now isolated on distant mountaintops.

In this study we investigate the impact on tropical montane vegetation of an enhanced South American Summer Monsoon (SASM) regime between 18.1 and 14.7 kcal yr BP in synchrony with glacial episodic iceberg discharge in the North Atlantic, known as Heinrich Stadial 1 (HS1), as indicated by speleothem isotope records^{3–7}. Oxygen isotopes in the Botuverá cave speleothems have indicated that wet phases prevailed during the last glacial cycle in southern Brazil⁸. Additional support for this scenario comes from calcite deposits at lake margins within caves and expansion of wet forests in the HS1 of northern Bahia, currently covered by semi-arid vegetation (caatinga), suggested by abundant plant megafossils in calcareous tufas, belonging to arboreal and herbaceous
 taxa presently found in the Atlantic and Amazon rainforests⁹.

73 We hypothesize that the intensified precipitation within the area climatologically affected by 74 the South Atlantic Convergence Zone (SACZ) and the Intertropical Convergence Zone (ITCZ) 75 promoted conditions suitable for the establishment of north-south migration corridors for the 76 expansion of montane forest. These possible former connections between southeast and central Brazil, from 31° to 22° S lat. and southeastern Amazonia could, therefore, explain much of the 77 78 modern occurrence of disjunct humid and cold-adapted taxa in elevated areas of cerrado and semi-79 arid caating reaching 4°S, with counterparts in the tepuis of the Guyana Shield, including those in 80 Roraima (northern Brazilian Amazonia) and in Venezuela.

81

82 Methods

83 We infer vegetational and correlated climatic changes during the HS1 event by analyzing 84 selected arboreal pollen taxa, in most cases with abundance higher than 5%, in Brazilian Late 85 Quaternary pollen records, with morphological features that allow identification to genus level and in some cases only to family¹⁰, the exception of which is genus Araucaria Juss., represented in Brazil 86 87 only by A. angustifolia (Bert.) O. Kuntze. The selected cold/mild and cold-humid adapted genera are 88 Araucaria Juss., Podocarpus L'Hér. ex Pers., Drimys J.R. Forst. & G. Forst., Hedyosmum Sw., Ilex 89 L., Myrsine L., Symplocos Jacq., and Weinmannia L., as well as the families Myrtaceae Juss., 90 Ericaceae Juss. and Arecaceae Bercht. & J. Presl (sin. Palmae Juss., palms), chosen based on their frequent presence in glacial pollen signals of tropical America $^{12-15}$. It is noteworthy that in southern 91 92 and southeastern Brazil, *Podocarpus* is represented by two species in the highlands, *i.e. P. lambertii* 93 Klotzsch ex Endl. and *P. sellowii* Klotzsch ex Endl.. Pollen rain analyses in this area¹¹ indicate that 94 its pollen counts can be as low as 0.8% to indicate significant presence in native coastal rainforests. 95 These taxa are stenopalynous; although some of them may contain thousands of members,

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96 their pollen is represented only by one morphological type, and thus does not permit separation of 97 species i.e., Myrtaceae Juss.. Although palm pollen can be assigned to different genera, it frequently 98 appears in pollen records simply as Arecaceae or Palmae.

99 Montane species of the families Myrtaceae, Ericaceae and Arecaceae were verified in 100 herbarium collections of The Field Museum of Natural History and the Department of Botany of the 101 Institute of Biological Sciences of the University of Sao Paulo and in the Flora do Brasil 2020¹⁶. 102 Myrtaceae is represented by a total of 17 genera and 53 species. Ericaceae, an almost exclusive 103 montane family of shrubs and trees comprised of 12 genera, 99 species and 27 varieties, commonly 104 found in high altitude montane ecosystems of Brazil where they are subjected to sub-zero temperatures at certain periods of the year². The palm family Arecaceae is represented on montane 105 106 with subtropical humid climate by 5 genera and 19 species. A list of montane species for these three 107 families are given in Supplementary Information.

108 A detailed survey of the Late Pleistocene palynological literature in Brazil reveals a total of 29 109 pollen profiles from continental sedimentary records containing HS1 age sediments: 1. Cambará do Sul¹⁷; 2. São Francisco de Assis¹⁸; 3. Serra da Boa Vista¹⁹; 4. Serra do Tabuleiro²⁰; 5. Pato Branco 110 ²¹; 6. Volta Velha ²²; 7. Curucutu ²³; 8. Colônia Crater ¹⁵; 9. Serra de Botucatu ²⁴; 10. Monte Verde 111 ²⁵; 11. Lagoa de Itaipu ²⁶; 12. Morro do Itapeva ¹¹; 13. Lagoa dos Olhos ^{26, 27}; 14. Salitre ¹⁴; 15. Serra 112 Negra¹³; 16. Brejo do Louro²⁸; 17. Serra do Espinhaço²⁹; 18. Buritizeiro³⁰; 19. and 20. Crominia³¹; 113 21. Turfa de Inhumas³²; 22. Lagoa Bonita³³; 23. Águas Emendadas³⁴; 24. Chapada dos Veadeiros 114 ³⁵; 25. and 26. Serra dos Carajas ^{36,37}; 27. Lago Cacó ³⁸; 28. and 29. Lagoa da Pata ^{12,39}. 115

Four of these records are from the lowlands of equatorial regions of eastern³⁷ and western Amazonia^{39,40} and one study is from Lagoa do Caçó⁴¹, at the easternmost Amazonian forest/savanna transition in the State of Maranhão, close to the Atlantic coast in northern Brazil. The remaining pollen records are distributed in montane forests of the Brazilian highlands, a patch of remaining humid vegetation within the modern Cerrado (Brazilian Savanna) domain of southeastern 122

123 Since the physiognomy of montane forests, specially in southern and southeastern Brazil are 124 characterized in general by an 30-40 m high emergent layer containing Araucaria underlain by a 125 sub-canopy containing *Podocarpus*, we mapped their potential distribution during the late glacial 126 phase and under current conditions. Species Distribution Model (SDM) were generated with MaxEnt^{85,86} version 3.3.3k, for the HS1 phase in the Brazilian Highlands, correlating pollen records 127 128 with monthly mean convective precipitation rate (PRECC), large-scale precipitation rate (PRECL), surface (TS) and minimum surface temperature (TSMIN) from CCSM3 Trace21k dataset⁸⁷, at a 129 130 resolution finer than the $3.5^{\circ} \times 3.5^{\circ}$ grid. Potential distribution maps of *Podocarpus* (20 training and 131 4 test samples, 0.965 average training AUC for the replicate run and 0.012 standard deviation) and 132 Araucaria (9 training and 2 test samples, 0.976 average training AUC for the replicate runs and 133 0.006 standard deviation).

134 Modern Species Distribution models (SDM) for Araucaria (represented only by A. angustifolia) and Podocarpus (represented by P. lambertii and P. sellowii) were generated with 135 MaxEnt^{85,86} version 3.3.3k with bootstrap resampling of 20 replicates, using 19 bioclimatic 136 137 variables, obtained from worldclim version 2.0, at a resolution finer than the 1 km \times 1 km grid, and 138 modern occurrence points of SpeciesLink and SiBBr / GBIF: Araucaria angustifolia (124 training 139 and 13 test samples, 0.987 average training AUC for the replicate runs and 0.001 standard deviation), 140 Podocarpus lambertii (157 training and 17 test samples, 0.984 average training AUC for the 141 replicate runs and 0.001standard deviation) and Podocarpus sellowii (124 training and 13 test 142 samples, 0.987 average training AUC for the replicate run and 0.001standard deviation).

To illustrate the distribution of fossil pollen data from the Brazilian Highlands during HS1 we made shaded relief images (Figures 1-3, 6 and supplementary figures) of the ETOPO1 Global Digital Elevation Model⁴² with 01-minute spatial resolution, draped by a custom hypsometric color scale. For the continental area, shaded relief illumination is from 060°N, 30° above horizon, with 40 times
vertical exaggeration. In the oceanic area, illumination is from 060°N, 20° above horizon, with 5
times vertical exaggeration. Raster shading and color scale creation⁴³ were performed in GRASSGIS 7.4, map composition in QGIS 3.2 and final artwork in Inkscape 0.92.
Of all 89 pollen records examined in our survey, only 29 encompassed large time sections of
the last glacial cycle as shown in Figure 1 (and in supplementary materials), which highlight the two
gymospermous taxa of the Brazilian Flora, *Podocarpus* and *Araucaria*, conspicuous elements of

southern/southeastern vegetation, during HS1 and indicative of subtropical climates^{14, 19, 25, 26}.

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Figure 1. Presence (red circles) and absence (white circles) of *Podocarpus* (a) and *Araucaria* (b) pollen in HS1 records of Brazil. Areas above 610 m elevation are highlighted in red. Dashed line is the border of Brazil. Base layer: Shaded relief image of ETOPO1 Global DEM (continental area: shaded relief illumination from 060°N, 30° above horizon, 40 times vertical exaggeration; oceanic area: illumination from 060°N, 20° above horizon, 5 times vertical exaggeration).

160

161 Northward migration during HS1 conditions

162 The fossil pollen data reveal constant presence of humid forest elements in montane corridors 163 following three major routes during the HS1 event: a northward expansion linking southern-164 southeastern Brazil to southern Amazonia, via Serra do Mar/Mantiqueira, central Brazil, Serra Geral, 165 Serra de Carajás, hereafter Southern-southeastern Brazil to southern Amazonia (route SSA) and a 166 northward expansion linking southern-southeastern Brazil to northeastern Brazil, via Serra do 167 Mar/Mantiqueira, Serra do Espinhaço, Chapada Diamantina, Serra de Ipiabapa, hereafter Southern-168 southeastern Brazil to northeastern Brazil (route SSN) and a more restricted distribution connecting 169 southern/southeastern to central Brazil, extending from 30°S to 18°S, hereafter Southern-170 Southeastern Brazil (route SSB; see Figure 2, lower right). The SSA and SSN pattern are evident for 171 *Podocarpus, Ilex, Myrsine, Hedyosmum, Myrtaceae and Arecaceae, describing an arch-like direction.* 172 Some of these taxa extended from the southern/southeastern coast at latitudes as low as 30°S, to the 173 central elevated regions of the Brazilian subtropics, thus reaching southeastern Amazonia at 5° S 174 (Podocarpus, Hedyosmum and Arecaceae) and 4°S within the modern Cerrado/Amazon rainforest 175 ecotone of northern Maranhão State (Myrtaceae, Myrsine) (routes SSA and SSN, respectively; 176 Figure 2). It is noteworthy that although most species participate in these different pathways, their 177 environmental characteristics are fundamentally different. SSA is associated with the humid and 178 warm Amazonian lowlands, while SSN is associated with xeric environments such as the semi-arid 179 caatinga of the northeast, and SSB is restricted to humid and cool habitats of the southern high-180 elevation mountains.

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182 Figure 2: SSA, SSN and SSB migration routes for montane taxa during HS1 and pollen record 183 locations in Brazil (open circles). Route SSA extends from southern/southeastern Brazil to southern 184 Amazonia in the State of Pará. Route SSN extends from Southern-Southeastern to Northeastern 185 Brazil lacks palynological support but is supported by modern distributions of montane taxa and 186 Lagoa do Cacó (sedimentary record 28). SSB route connects coastal southern and southeastern sites 187 up to 18°S synchronous with polar air mass incursions and lowered temperatures as supported by 188 pollen evidence. Areas above 610 m elevation are highlighted in red. Dashed line is the border of 189 Brazil. Base layer: Shaded relief image of ETOPO1 Global DEM (continental area: shaded relief 190 illumination from 060°N, 30° above horizon, 40 times vertical exaggeration; oceanic area: 191 illumination from 060°N, 20° above horizon, 5 times vertical exaggeration).

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193 We hypothesize that modern plant distributions on isolated mountaintops of northeastern Brazil indicate that various rainforest arboreal taxa^{2,44} possibly reached these regions through a 194 195 secondary fork-like branch emerging at 22°S and extending until 18°S into the Brazilian highlands, 196 very likely to have been maintained by orographic rains and/or adiabatic cooling. In addition, from 197 18°S northwards, the SSN route could have reached latitudes within the present-day domain of semi-198 arid caatinga. Although this additional route during HS1 cannot be confirmed by palynological 199 analyses due to the lack of study sites in that region, macrobotanical evidence in calcareous tufas deposited at ca. 17 kcal yr BP⁴⁵ indicate the presence of Atlantic/Amazonian rainforest elements 200 201 such as Aparisthmium Endl., Annonaceae Juss., Chrysobalanaceae R. Br., Drymonia coccinea 202 (Aubl.) Wiehler, *Luehea grandiflora* Mart., *Prunus sellowii* Koehne, *Sloanea* L., *Tetrastylidium*203 Endl. at 10°S lat. during Heinrich Stadial events in Northeastern Brazil.

Route SSB, utilized by *Araucaria*, *Drimys*, *Symplocos*, *Weinmannia* and Ericaceae, appeared to have had a more restricted distribution in Southeastern Brazil limited within a latitudinal band between 30°S and 18°S. This pathway appears to have two different latitudinal components: a coastal distribution at low elevation from 30°S to 22°S (*Araucaria*, *Drimys*, *Symplocos*, *Weinmannia*, and Ericaceae) and a high montane component from 22°S to 18°S (*Araucaria* and *Drimys*).

209 All migration pathways suggest that during HS1 a long chain of mountains, starting at the 210 Serra do Mar, followed by the Serra da Mantiqueira and deriving into the Serra do Espinhaco and the 211 Brazilian Central Plateau, functioned as an efficient corridor for the migration of montane elements as proposed by earlier biogeographers⁴⁶, possibly under an enhanced humid phase in the SACZ and 212 ITCZ climate domains^{5–7}. Also, the occurrence of cold-adapted trees such as *Araucaria* beyond their 213 214 present-day northern limit suggests the possibility that intensified polar air incursions into the 215 interior of South America might have dropped the temperatures during the HS1 period as has been inferred for the last glacial period^{37,47}. During that time, the tilt of the Earth's axis, the eccentricity of 216 217 the orbit and the longitude of the perihelion may have affected the solar radiation at the top of the 218 atmosphere. Therefore, it is possible that under a scenario of less intensified solar radiation during 219 HS1 polar circulation became somewhat stronger while the Hadley circulation was weakened and 220 this mechanism is likely to have generated a larger displacement of polar air towards northern South America⁴⁸. 221

Under these conditions of enhanced humidity and lowered temperatures, the maintenance of both routes appears to be controlled by different pollen and seed dispersal abilities. Most taxa that migrated further along the SSA route have wind-dispersed pollen and are dioecious, two evolutionary traits directly linked to high dispersal potential⁴⁹, in addition to seed dispersal by birds (Table 1), all of which may have granted them increased ecological amplitude and greater colonization ability. Moreover, these taxa can occur in both late and early successional stages, whichcan be interpreted as highly adapted to these vegetational changes.

229 Taxa displaying the SSN route, in general, are characterized by slightly less efficient 230 dispersal of pollen in terms of distance by entomophily as well as zoochory, other than bird-231 dispersed, seeds. We hypothesize that these these main routes were actually transects of high 232 montane microrefugia alignments during the humid and cold phase of HS1 and probably in earlier 233 glacial phases. Therefore, the small nuclei of montane vegetation acted as sources of immigrants to 234 other microrefugia along theses routes, where all dispersal syndromes were highly efficient, thus 235 permitting geneflow between these populations. Support for this hypothesis comes from a modernal relictual *Podocarpus* microrefuge in semi-arid vegetation at Morro do Chapeu, Bahia at 11°S^{50,51}. 236 237 There, rocky otucrops reduce mean annual temperature by 5°C and augment humidity by 12%. 238 Under this scenario, final coalescence of these microrefugia may have formed rather contiguous 239 humid forested corridors. Testing these hypotheses requires more pollen records especially at lower 240 latitudes of southern Amazonia and northeastern Brazil. This paleoclimatic scenario is supported by a marine pollen record off the coast of northeastern Brazil⁵², containing continental sediments 241 242 generated in the region of modern semi-arid vegetation. This record shows an HS1 pollen zone, 243 characteristic of humid climate, with significant percentages of SSA route taxa such as Hedyosmum, 244 Ilex, and Myrtaceae, together with Symplocos and Cyathea Sm. It is clear that entomophilous 245 pollination and animal-dispersed seeds did not hinder the very long dispersal ability of Drimys 246 possibly due to the beneficial effects of nearby microrefugia and therefore shorter dispersal distances 247 needed for population expansion. The data suggest that the SSN route could have extended well into 248 northeastern Brazil, where Drimys, Hedyosmum, Symplocos, Ericaceae, Podocarpus, Myrsine, Ilex, 249 Weinmannia and others are all found at the modern altitude of 1500 m in the Chapada Diamantina range, in northeastern Brazil. 250

251 The main feature of route SSB is the northward expansion of Araucaria, a major element in 252 ombrophilous rainforest of high elevations of southern/southeastern Brazil in consortium with 253 Podocarpus. It can be considered a good proxy for relatively low temperature and high humidity^{13,14,27,53,54}. Our hypothesis suggests that its migration pattern reaching 18°S was likely to be 254 255 controlled by low temperature regimes and low precipitation variability throughout the year during 256 HS1. Although low modern temperature regimes at the Serra do Espinhaço (site 17) are conducive 257 to sustaining gymnosperm forests as they did during HS1, the site no longer has adequate humidity 258 due to irregular distribution of precipitation during the long dry season.

Hereafter represented by *Podocarpus*, demonstrate wider latitudinal expansion abilities, ranging from 30°S to 0°S, than those displayed by SSB, hereafter represented by *Araucaria* (Supplementary Figures 1-11), where taxa were restricted to latitudes between 30°S and 18°S.

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Table 1. Reproductive characters of montane arboreal taxa displaying SSA, SSN and SSB migrationroutes.

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| Routes | Succession | Pollen dispersal | Seed dispersal | Reproduction |
|---------|---|--|---|---|
| SSN-SSA | Late secondary but resistant to disturbance ⁵⁵ | Anemophilous ⁵⁶ (wind) | Zoochory (Birds, mammals) ^{57,58} | Dioecious |
| SSN-SSA | Early and Late 59,60 | Entomophilous ^{61,62} , Anemophilous ⁶³ | Autochory ⁶⁶ , Zoochory ⁶⁶ (Birds) | Dioecious |
| SSN-SSA | Early and Late ⁶⁴ Intermediate ⁶⁵ | Anemophilous Entomophilous | Zoochory ^{66,67} (Birds) | Monoecious |
| SSN-SSA | Late ⁶⁸ | Anemophilous ⁶⁹ | Zoochory (Birds) ^{69,70} | Dioecious |
| SSN-SSA | Late and early ⁶⁰ | Entomophilous, Ornithophilous ⁷² | Zoochory ^{67,71} (Bat, bird, small and medium mammals) ^{72,73} | Monoecious |
| SSN-SSA | Early, intermediate or late ⁷⁴ | Entomophilous, Anemophilous ⁷⁵ | Zoochory (Bird, small mammals) ⁷² , Autochory | Monoecious |
| SSB | Early ⁷⁶ | Anemophilous | Zoochory ⁷⁶ (Birds, mammals) | Dioecious |
| SSN | Late secondary 77 | Entomophilous ⁷⁸ | Zoochory (Birds, small mammals) ⁷⁸ | Dioecious |
| SSN | Late secondary ⁶⁰ | Entomophilous ⁷⁹ Ornithophilous | Zoochory ⁶⁷ | Monoecious |
| SSN | Early and secondary 77 | Entomophilous ^{73,80} | | Monoecious |
| | SSN-SSA SSN-SSA SSN-SSA SSN-SSA SSN-SSA SSN-SSA SSN SSN SSN | SSN-SSALate secondary but resistant to disturbance55SSN-SSAEarly and Late 59,60SSN-SSAEarly and Late 64 Intermediate 65SSN-SSALate 68SSN-SSALate and early60SSN-SSAEarly, intermediate or late74SSBEarly76SSNLate secondary 77 Late secondary60 | SSN-SSALate secondary but resistant to disturbance55Anemophilous56 (wind)SSN-SSAEarly and Late 59,60Entomophilous 63 AnemophilousSSN-SSAEarly and Late 59,60Entomophilous 63 AnemophilousSSN-SSAEarly and Late 64 Intermediate 65AnemophilousSSN-SSALate 68AnemophilousSSN-SSALate and early60Entomophilous, OrnithophilousSSN-SSAEarly, intermediate or late74Entomophilous, OrnithophilousSSBEarly76AnemophilousSSNLate secondary77EntomophilousSSNLate secondary60EntomophilousSSNLate secondary60Entomophilous | SSN-SSALate secondary but resistant to disturbance55Anemophilous56 (wind)Zoochory (Birds, mammals)57,58SSN-SSAEarly and Late 59,60Entomophilous 61,62 Anemophilous 63 EntomophilousAutochory66 Zoochory66 (Birds) Zoochory66 (Birds) Zoochory66 (Birds)SSN-SSAEarly and Late 64 Intermediate 65Anemophilous EntomophilousAutochory66, Zoochory66 (Birds) Zoochory66 (Birds)SSN-SSALate 68Anemophilous EntomophilousZoochory 66,67 (Birds) Zoochory66 (Birds)SSN-SSALate 68Anemophilous EntomophilousZoochory 67,71 (Bat, bird, small and medium mammals)72,73SSN-SSALate and early60Entomophilous, Ornithophilous 72Zoochory (Bird, small mammals)72,73SSBEarly, intermediate or late74Entomophilous AnemophilousZoochory (Bird, small mammals)72,73SSNLate secondary 77Entomophilous AnemophilousZoochory (Birds, small mammals)78 Zoochory67 |

Ericaceae

SSN

Early⁸¹ and Late⁸²

Gaylussacia – Entomophilous ⁸⁰ Agarista Ornitophilous ⁸⁰

Zoochory, Autochory, Anemochory⁷⁰

Monoecious

- 266
- 267

268 Climatic changes and montane vegetation expansion during HS1

269 Pollen histories of arboreal taxa common in humid and cold forests of glacial age in Brazil^{13,14,23,37,40} support the hypothesis of intensification of transient climatic systems under glacial 270 271 regime during HS1. We suggest that continental surface temperatures lowered by the effects of polar 272 air incursions in South America had a significant forcing effect on modern plant biogeographical 273 patterns by fostering long-distance migration of currently montane elements. One of the best-known 274 lines of indirect evidence for this hypothesis is given by the vegetation of the Pico das Almas (13° 275 34'S), in the Chapada Diamantina mountain range, northeastern Brazil. This vegetation is floristically more related to that of the Andean paramo and subparamo forests² with genera like 276 277 Podocarpus, Drimys, Symplocos, Weinmannia, and Hedyosmum (SSA pattern), and to the flora of 278 the tepuis of Venezuela. The second line of indirect evidence is the pollen record of the Icatu site at 279 10° S, currently under semi-arid vegetation in northeastern Brazil, which shows during the Pleistocene/Holocene transition⁸³ at c. 11 kcal yr BP abundant cold and humid-adapted taxa such as 280 281 Podocarpus, Ilex, Myrtaceae and Hedyosmum coexisting with Humiria Aubl., a taxon of shrubs to 282 large trees of the Guyanas and Guyana-influenced Amazon and currently present at Serra do Espinhaço range above 1000 m altitude⁸⁴. 283

Although alternative and viable hypotheses for such biogeographical patterns may suggest that connections could have been established during the cold phases of the Oligocene^{1,2}, following the tropical decline of the Eocene, Late Pleistocene pollen data points to a powerful reorganization of ecosystems in South America during the terminal phases of the last glacial cycle. To test this Late Quaternary expansion of cold and humid forests, *i.e.* augmentation of the potential distribution of the fundamental niche of our selected montane taxa into northern Brazil, we generated a Species Distribution Model (SDM) for *Podocarpus* and *Araucaria* for the HS1 phase in the Brazilian Highlands, by correlating observations of taxa occurrences in palynological records, representatives of the SSA, SSN and SSB routes, with monthly mean of precipitation and surface temperature from climatic layers from the CCSM3 Trace21k dataset⁸⁷ (Figure 3).

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295 Figure 3. Montane forest potential distribution during HS1 represented by *Podocarpus* (a) and Araucaria (b), where black and white circles indicate presence and absence, respectively, in pollen 296 297 records. White areas show SDM maps generated in MaxEnt version 3.3.3k for prediction of montane forests, using presence in pollen records during HS1 correlated with climatic layers from CCSM3 298 Trace21k dataset. Areas above 610 m elevation are highlighted in red. Dashed line is the border of 299 300 Brazil. Base layer: Shaded relief image of ETOPO1 Global DEM (continental area: shaded relief 301 illumination from 060°N, 30° above horizon, 40 times vertical exaggeration; oceanic area: 302 illumination from 060°N, 20° above horizon, 5 times vertical exaggeration).

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306 The resulting maps highlight areas of habitat suitability over large sections of the SSA and SSB routes especially those between 30°S and 14°S, a region where the South American Monsoonal 307 System was intensified during HS1^{6,7,88}. The disjunct high suitability for *Podocarpus* for the Carajás 308 lakes region (site 25) and very low suitability for Lagoa do Caçó⁴¹ (site 27) might be due to the 309 310 absence of continental pollen records in these equatorial and subequatorial regions in Brazil during HS1. On the other hand, a marine pollen record off the coast of Ceará⁵⁹, showing expansion of cold-311 312 adapted montane arboreal elements during HS1, provide strong evidence for high humidity levels brought about by the southward displacement of the ITCZ⁶. This scenario is confirmed by CCSM3 313 Trace21k dataset⁸⁷ simulation data analyses for current semi-arid Apodi region (<250 m elevation, 314 315 mean annual temperature 28.5°C), nearby Cacó lake, indicating average annual accumulation of 316 2650 mm associated with high precipitation levels of monthly mean Convective Precipitation Rate 317 (PRECC) and mean annual surface temperatures (TS) of around 22.6°C, of c. during HS1 and (Figure 4). Therefore, we estimate a temperature depression of c. 5°C, which is supported by similar 318

cooling between ca. 14 – 17 Krs BP, revealed by noble gases paleotemperature record in groundwater in northeastern Brazil⁸⁹. In addition to conducive temperature, precipitation values are also well above the ecological requirements for sustaining a cold and humid forest vegetation with *Podocarpus* at Caco Lake, currently under mean annual precipitation of 1400-1500 mm and mean annual temperature of $25^{\circ}C^{38}$.

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Figure 4. Boxplot of monthly averages of convective precipitation rate (PRECC) in mm/month (a) and mean monthly surface temperature TS °C (b) at Chapada do Apodi, next to Caçó Lake, derived from Simulation of the Transient Climate of the Last 21000 Years (TraCE-21k) during HS1. Rscripts were generated to produce boxplots.

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332 The frequency of *Podocarpus* in pollen records analyzed depict a strong latitudinal control. In 333 the southernmost range of its distribution (30°S-22°S) it could be found in elevations ranging from 334 sea level to 1157 m, followed by an intermediate range from north of 22° S to 10° S where it was 335 restricted to elevations higher than 610 m (Figure 5a). In its northernmost limit, lying between 6° S 336 and 3°S, *Podocarpus* eventually reached the Amazonian lowlands, thus descending from 540 m to 80 337 m elevation (Figure 5a, lower right), next to Caçó Lake. Araucaria, on the other hand, a good 338 representative of the SSB route, shows a dissimilar distribution pattern in the HS1 pollen records 339 ranging from 30°S at sea level to 750 m at 26°S with its northern limit during the glacial times at 340 18°S in 1246 m elevation, with maximum elevation reached at 1820 m at 22°S. The separating line 341 between sites north and south of 18°S (Figure 5b) suggests the northernmost limit for incursion of 342 polar air masses during HS1, a fact that possibly imprinted a biogeographical boundary still observed in the modern southeastern Atlantic rainforest with a higher plant species turnover⁹⁰ north of 18°S. 343 344 Molecular genetic data from three common species of tree frogs widely distributed along the Atlantic rainforest⁹¹ support forest stability in the central core area of this vegetation type in the late 345 346 Pleistocene. Combining these with our results, it becomes clear that stability of forest physiognomic 347 persisted during the Late Pleistocene concurrent with migration of cold-adapted plant species

348 northwards propelled by H1 events, which in turn might have contributed to the establishment of

349 biogeographical compartmentalization of the montane coastal vegetation specially north of 18°S.

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Figure 5. Scatter plot of altitude (m) vs. latitude (°S) for *Podocarpus* (a) and *Araucaria* (b) as indicated by presence (filled circles) and absence (clear circles) in pollen records during HS1. Rscripts were generated to produce the scatter plot.

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357 Modern parameters and the climate of HS1 for the Brazilian Highlands

358 Podocarpus L' Her. ex Pers. and Araucaria (Bertol.) Kuntze stand out for beeing more 359 ecologically informative in terms of precipitation and temperature requirements in southern and 360 southeastern Brazil. Species Distribution Model (SDM) maps for A. angustifolia, P. lambertii and P. 361 sellowii, shown in Figure 6, confirm a geographical restriction of Araucaria in southern/southeastern 362 Brazil as opposed to a large distribution of *Podocarpus*, ranging rom 30°S to ca 5°S. Data cleaning methods was used to check the quality of data of modern distribution⁸⁵, i.e. validation of the 363 364 taxonomic identification in relation to the available literature with its corresponded latitude and 365 longitude coordinates was performed. Georeferencing errors were evaluated and discarded from the 366 database and a filter was applied to select only occurrences within the Brazilian territory. 367

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369 Figure 6. Modern Potential Distribution maps for *Podocarpus* (a) and *Araucaria angustifolia* (b) where occurrences of taxa are shown by yellow and blue dots, respectively. White areas show SDM 370 371 maps generated by MaxEnt version 3.3.3k for prediction of montane forest, using presence from SpeciesLink and SiBBr / GBIF database and 19 bioclimatic data layers from WorldClim dataset 372 373 version 2.0. Areas above 610 m elevation are highlighted in red. Dashed line is the border of Brazil. 374 Base layer: Shaded relief image of ETOPO1 Global DEM (continental area: shaded relief 375 illumination from 060°N, 30° above horizon, 40 times vertical exaggeration; oceanic area: illumination from 060°N, 20° above horizon, 5 times vertical exaggeration). 376

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At the northernmost edge of this distribution range, *Podocarpus* is found in relictual

populations in orographically controlled humid "islands" within semi-arid climates^{50,51}, isolated in the Pleistocene, as indicated by genetic data⁹². Anotherline of evidence for expanded montane forest in this region is the discovery^{9,45} of fossilized leaves of rainforest taxa found in the late glacial calcareous tufas in a modern Caatinga region adds more support for this climatic mechanism during Heinrich Stadial events throughout the last glacial period. However, the mode that humid adapted plants migrated to present-day semi-arid regions in South America is still unknown.

The current distribution of *Araucaria angustifolia* reaches its northern limit at 21°S in any elevation, at altitudes of about 400 to 1750 m above sea level (asl) under less than three months dry season, whereas from 24° to 31°S this taxon occurs as low as at sea level up to ca. 1200 m, under year-round high humidity levels.

In order to investigate the factors controlling its modern distribution as well as *Podocarpus lambertii* occurrences, we used a 15-year long data set of rainfall data CPC Morphing technique (CMORPH)⁹³, corrected by the Brazilian meteorological station network data^{94,95}, between 2000 and 2015. Afterwards, R-scripts were written to generate descriptive statistics for the occurrence of each taxon. Box plots and histograms were generated based on values of 1° x 1° latitude grid of total daily accumulated precipitation data. These analyses yielded mean values of precipitation for 6 months periods, for the seasons, months and annual precipitation for that historic series.

397 Finally, a Principal Component Analysis (PCA) was carried out for both Podocarpus and 398 Araucaria in order to discriminate the roles of precipitation and temperature in relation to the 399 following variables: cumulative annual precipitation in mm, total precipitation in Winter, Spring, 400 Summer and Autunm, wet and dry periods. Modern occurrence of Araucaria angustifolia and 401 *Podocarpus lambertii* in Brazil are controlled mainly by mean total annual precipitation of 1680+180 402 mm and 1520+220 mm based on a 15-year climatic series (2000-2015), whereas optimum mean 403 annual temperature for both taxa are ca. 17.5°C as indicated by Species Distribution Model and 404 WorldClim dataset.

405 PCA biplots shown on Figure 7 indicate that annual and summer variables are the main 406 loading values for the PC1 (84.11%) and PC2 (15.15%) components, respectively. The simultaneous 407 occurrence of Araucaria angustifolia and Podocarpus lambertii is discernibed as a main central 408 cluster (Figure 7a) for 1750 mm annual precipitation. Outside this range, only Podocarpus can 409 survive as it tolerates higher precipitation variability (Figure 7b). The latitudinal control for 410 Araucaria is significantly stronger when compared to *Podocarpus* that can thrive in microrefugia in 411 latitudes outside the Araucaria-Podocarpus associations typical of south/southeastern Brazil (Figure 412 7d and 7e). The PCA diagram of the combined distribution, with overlapping clusters, of both taxa 413 shows that the modern occurrences of Araucaria angustifolia and Podocarpus lambertii in Brazil are 414 controlled mainly by mean total annual precipitation of 1680 \pm 180 mm and 1520 \pm 220 mm 415 respectively based on a 15-year climatic series (2000-2015). These values range well within the 416 classical precipitation values used in the literature for both taxa for the Brazilian highlands.

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419 Figure 7. PCA biplot for the modern distribution of Podocarpus lambertii and Araucaria 420 angustifolia in relation to mean values of total annual precipitation, performed by PAST 3.21 (a). 421 Boxplots of each annual total precipitation value representing number of years (2000-2015) for 422 *Podocarpus lambertii* (1520 \pm 220 mm) (b) and *Araucaria angustifolia* (1680 \pm 180 mm) (c). Scatter plot of Total Annual Precipitation (mm) vs. Latitude (°) of modern distribution for Podocarpus 423 424 lambertii and Araucaria angustifolia, respectively (d) and (e). Precipitation data were based on 425 hourly rainfall estimates with CMORPH between 2000 and 2015, corrected by the Brazilian 426 meteorological station network. R-scripts were generated to produce boxplots and the scatter plot. 427

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PCA biplots for *Araucaria* (Figure 8a) reveals annual and summer variables are the main loading values for the PC1 (71.47%) and PC2 (27.07%) component. PCA loadings indicate that the distribution of *Araucaria angustifolia* is primarily influenced by anual acumulated precipitation and well distributed precipitation long the year, both in dry and wet seasons, respectively. Figures 8b and 8c indicates low precipitation variability as a significant parameter for explaining *Araucaria* distribution (Figure 8d) under modern conditions. Therefore, it's clear that this taxon does not 436 tolerate dry conditions even during the dry months, showing an optimum value of precipitation

437 around 500 mm for the period of March to August.

438 We suggest that individualistic species reshuffling in the three migration routes during HS1

439 was constrained by their physiological responses within these temperature and precipitation ranges.

440 Morevorer, the climatic confinment in terms of humidity stability possibly explains why Araucaria

did not migrate further than lat 18°S in route SSB during HS1.

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Figure 8. PCA biplot (a) for modern distribution of *Araucaria angustifolia* in relation to mean values of total annual precipitation, performed by PAST 3.21. Annual (b), wet (c) and dry (d) season histograms for total precipitation values representing number of years (2000-2015), in relation to mean values of total monthly precipitation. Precipitation data were based on hourly rainfall estimates with CMORPH between 2000 and 2015, corrected by the Brazilian meteorological station network. R-scripts were generated to produce boxplots and the scatter plot.

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454 Conclusions

455 Our analyses provide strong evidence for the establishment of migration corridors of montane 456 forest taxa, facialtitated by the presence of microrefugia, connecting different ecosystems in a 457 continental scale, during humid and cold conditions related to Heinrich Stadial 1, from 18.1 to 14.7 458 kcal yr BP. Analysis of published Brazilian fossil pollen records corroborate with a climatological 459 scenario of high humidity sustained by the South American Monsoonal System under lowered 460 temperatures resulting in more regular polar air mass incursions, reaching 18°S latitude, thus forming 461 frequent cold fronts advancing northwards, into Amazonia and northeastern Brazil. Consequently, 462 the two main migration routes, here coined SSA and SSN, respectively, were established. On those 463 montane pathways, different plant taxa were able to disperse taking full advantage of certain 464 reproductive traits, especially anemophilous pollen and bird dispersed seeds. It's possible, that 465 effective migration along these routes were facilitated by the presence of previous montane forests

466 microrefuges, which might have expanded downslope towards the lowlands during HS1, thus 467 forming coalesced vegetated corridors. The proximity bwtween these established microrefugia 468 permitted a series of local population expansions along the three montane routes during these cold 469 and humid events.

It becomes clear that mean annual temperature depression played a major role during the wet and cold HS1 phase in Brazil of at least 5°C, as indicated by temperature estimation based on noble gas paleotemperature records not for Last Glacial Maximum but also for HS1⁸⁹. In addition, the presence of modern humid microrefuge containing montate taxa such as *Poducarpus*⁵⁰ within hyperxerophylous caatinga is indicating a previous wetter climate conditions that took place during the establishment of SSN route.

476 The Brazilian highlands latitudinal range of 30°S to 18°S, conducive to expansion of 477 montane vegetation with Araucaria during HS1, has probable ecological limits controlled by 478 temperature. However, in its northern boundary of the range, intense monsoon rainfall caused shorter 479 seasonality in comparison to its current limit at 21 °S while mean annual temperatures are today 480 approximately similar. Currently, at 18°S latitude, long dry seasons of 5 to 6 months inhibit the 481 growth of Araucaria angustifolia. In comparison, its fossil pollen occurrence during HS1 implies in a 482 well-distributed precipitation throughout the year. By integrating the pollen data with speleothem isotope records^{3,5,7}, we can assume that South American Monsoon regime during HS1 was longer 483 484 with higher annual precipitation rates.

Unlike *Araucaria* and other taxa that followed the SSB migration route, *Podocarpus* and others were able to migrate further north and beyond the highland domain, thus reaching distant lowlands regions due to their ability to disperse pollen and seeds more efficiently, and to germinate and grow in understory and dark forests. Their enlarged biogeographical range during HS1 primarily reflects a close approximation of their fundamental niches in opposition to their realized niche after

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the onset of Holocene warm climates. This significant habitat reduction is likely to have established
 modern disjunct distribution patterns between southern/southeastern and northeastern Brazil.

We, therefore, conclude that, although we do not devalue a possible scenario of early migration corridors during the Eocene/Miocene^{1,2} of Brazil, a significant imprint of the HS1 in

- 494 delineating modern disjunct distributions there is unquestionable.
- 495 One of the major implications of this study deals with possible impact of rising temperature

496 predicted for future climatic scenarios on a substantial loss of tropical montane biodiversity. Our

- 497 investigation suggests that the change in rainfall distribution may potentially enhance this process.
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508 **Contributions**

509 J.L.D.P., F.W.C., G.C.T.C., P.L.P.C., N.P., R.C., M.B., A-J. H., L.F., A.H., F.B., M.C., E.C., F.F., 510 K.H., A.M.L., M.N., A.R., P.T., F.S., D.A-S., F.A-S, Z.Z. and P.E.O. contributed to the analysis 511 and discussion of migration routes. J.L.D.P. and P.E.O. performed the select of taxa, analysis of 512 presence and absence of taxa in pollen records. G.C.T.C and P.E.O. performed to analysis of 513 reproductive characters of taxa. J.L.D.P., P.L.P.C., A.J.H., L.F., A.H., M.D.C.S.L., A.J.P.F., C.H.G. 514 and P.E.O. contributed to data cleaning, species distribution modeling method and analysed the data. J.L.D.P., F.W.C., G.C.T.C., N.M.S., A.J.H., L.F., A.H., W.H.L.P., F.V., M.D.C.S.L., A.J.P.F. 515 516 and P.E.O. contributed to analysis of variability of precipitation / CMORPH, climate and 517 paleoclimate. J.L.D.P., F.W.C., C.M.C., N.M.S, C.H.G., P.L.P.C. and P.E.O. contributed to analysis and discussion of data of CCSM3 TraCE-21k simulation. J.L.D.P., I.H-T., V.B.M., R.A.S., T.K.A., 518 519 M.A.S. and P.E.O. performed the survey of pollen records. J.L.D.P., F.W.C., G.C.T.C., C.H.G. and P.E.O. performed the analysis of altitude vs. latitude. J.L.D.P., P.L.P.C., F.W.C., G.C.T.C., 520 521 M.D.C.S.L., A.J.P.F, C.H.G. and P.E.O. contributed to design of figures and maps. J.L.D.P. and 522 P.E.O. wrote the manuscript.

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524 Competing interests

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- 526 The authors declare no competing interests.

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754 **Figures Captions**

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Figure 1. Presence (red circles) and absence (white circles) of *Podocarpus* (a) and *Araucaria* (b) pollen in HS1 records of Brazil. Areas above 610 m elevation are highlighted in red. Dashed line is the border of Brazil. Base layer: Shaded relief image of ETOPO1 Global DEM (continental area: shaded relief illumination from 060°N, 30° above horizon, 40 times vertical exaggeration; oceanic area: illumination from 060°N, 20° above horizon, 5 times vertical exaggeration).

761 Figure 2: SSA, SSN and SSB migration routes for montane taxa during HS1 and pollen record locations in Brazil (open circles). Route SSA extends from southern/southeastern Brazil to southern 762 763 Amazonia in the State of Pará. Route SSN extends from Southern-Southeastern to Northeastern 764 Brazil lacks palynological support but is supported by modern distributions of montane taxa and 765 Lagoa do Caçó (sedimentary record 28). SSB route connects coastal southern and southeastern sites 766 up to 18°S synchronous with polar air mass incursions and lowered temperatures as supported by 767 pollen evidence. Areas above 610 m elevation are highlighted in red. Dashed line is the border of Brazil. Base layer: Shaded relief image of ETOPO1 Global DEM (continental area: shaded relief 768 769 illumination from 060°N, 30° above horizon, 40 times vertical exaggeration; oceanic area: 770 illumination from 060°N, 20° above horizon, 5 times vertical exaggeration).

771 Figure 3. Montane forest potential distribution during HS1 represented by *Podocarpus* (a) and 772 Araucaria (b), where black and white circles indicate presence and absence, respectively, in pollen 773 records. White areas show SDM maps generated in MaxEnt version 3.3.3k for prediction of montane 774 forests, using presence in pollen records during HS1 correlated with climatic layers from CCSM3 775 Trace21k dataset. Areas above 610 m elevation are highlighted in red. Dashed line is the border of 776 Brazil. Base layer: Shaded relief image of ETOPO1 Global DEM (continental area: shaded relief 777 illumination from 060°N, 30° above horizon, 40 times vertical exaggeration; oceanic area: 778 illumination from 060°N, 20° above horizon, 5 times vertical exaggeration).

Figure 4. Boxplot of monthly averages of convective precipitation rate (PRECC) in mm/month (a) and mean monthly surface temperature TS °C (b) at Chapada do Apodi, next to Caçó Lake, derived from Simulation of the Transient Climate of the Last 21000 Years (TraCE-21k) during HS1. Rscripts were generated to produce boxplots.

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Figure 5. Scatter plot of altitude (m) vs. latitude (°S) for *Podocarpus* (a) and *Araucaria* (b) as indicated by presence (filled circles) and absence (clear circles) in pollen records during HS1. Rscripts were generated to produce the scatter plot.

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788 Figure 6. Modern Potential Distribution maps for *Podocarpus* (a) and *Araucaria angustifolia* (b) 789 where occurrences of taxa are shown by yellow and blue dots, respectively. White areas show SDM 790 maps generated by MaxEnt version 3.3.3k for prediction of montane forest, using presence from 791 SpeciesLink and SiBBr / GBIF database and 19 bioclimatic data layers from WorldClim dataset 792 version 2.0. Areas above 610 m elevation are highlighted in red. Dashed line is the border of Brazil. 793 Base layer: Shaded relief image of ETOPO1 Global DEM (continental area: shaded relief 794 illumination from 060°N, 30° above horizon, 40 times vertical exaggeration; oceanic area; 795 illumination from 060°N, 20° above horizon, 5 times vertical exaggeration).

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797 Figure 7. PCA biplot for the modern distribution of Podocarpus lambertii and Araucaria

- 798angustifolia in relation to mean values of total annual precipitation, performed by PAST 3.21 (a).799Boxplots of each annual total precipitation value representing number of years (2000-2015) for800Podocarpus lambertii (1520 \pm 220 mm) (b) and Araucaria angustifolia (1680 \pm 180 mm) (c). Scatter801plot of Total Annual Precipitation (mm) vs. Latitude (°) of modern distribution for Podocarpus802lambertii and Araucaria angustifolia, respectively (d) and (e). Precipitation data were based on803hourly rainfall estimates with CMORPH between 2000 and 2015, corrected by the Brazilian804meteorological station network. R-scripts were generated to produce boxplots and the scatter plot.
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Figure 8. PCA biplot (a) for modern distribution of *Araucaria angustifolia* in relation to mean values of total annual precipitation, performed by PAST 3.21. Annual (b), wet (c) and dry (d) season histograms for total precipitation values representing number of years (2000-2015), in relation to mean values of total monthly precipitation. Precipitation data were based on hourly rainfall estimates with CMORPH between 2000 and 2015, corrected by the Brazilian meteorological station network. R-scripts were generated to produce boxplots and the scatter plot.


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Table 1. Reproductive characters of montane arboreal taxa displaying SSA, SSN and SSB migration

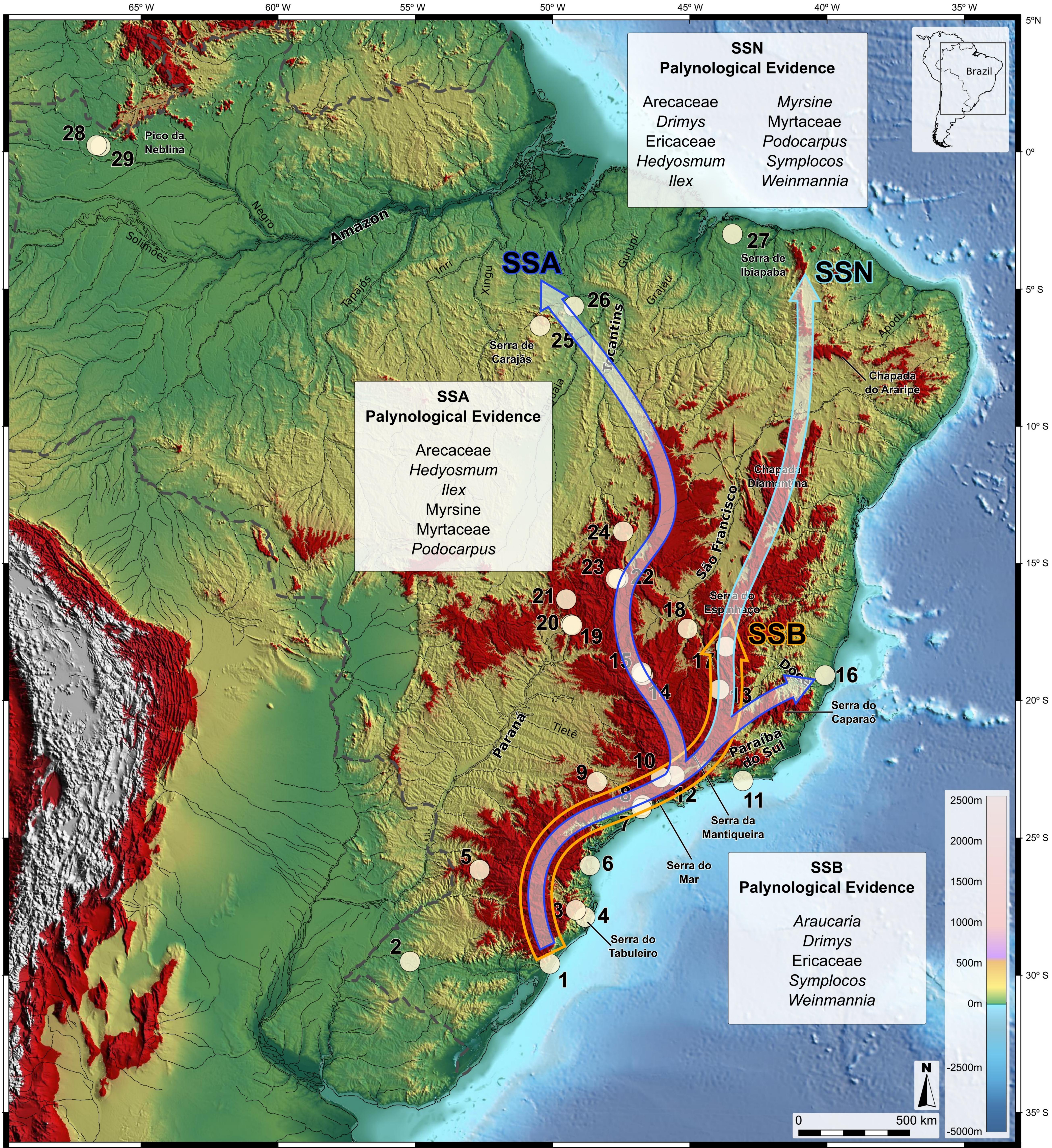


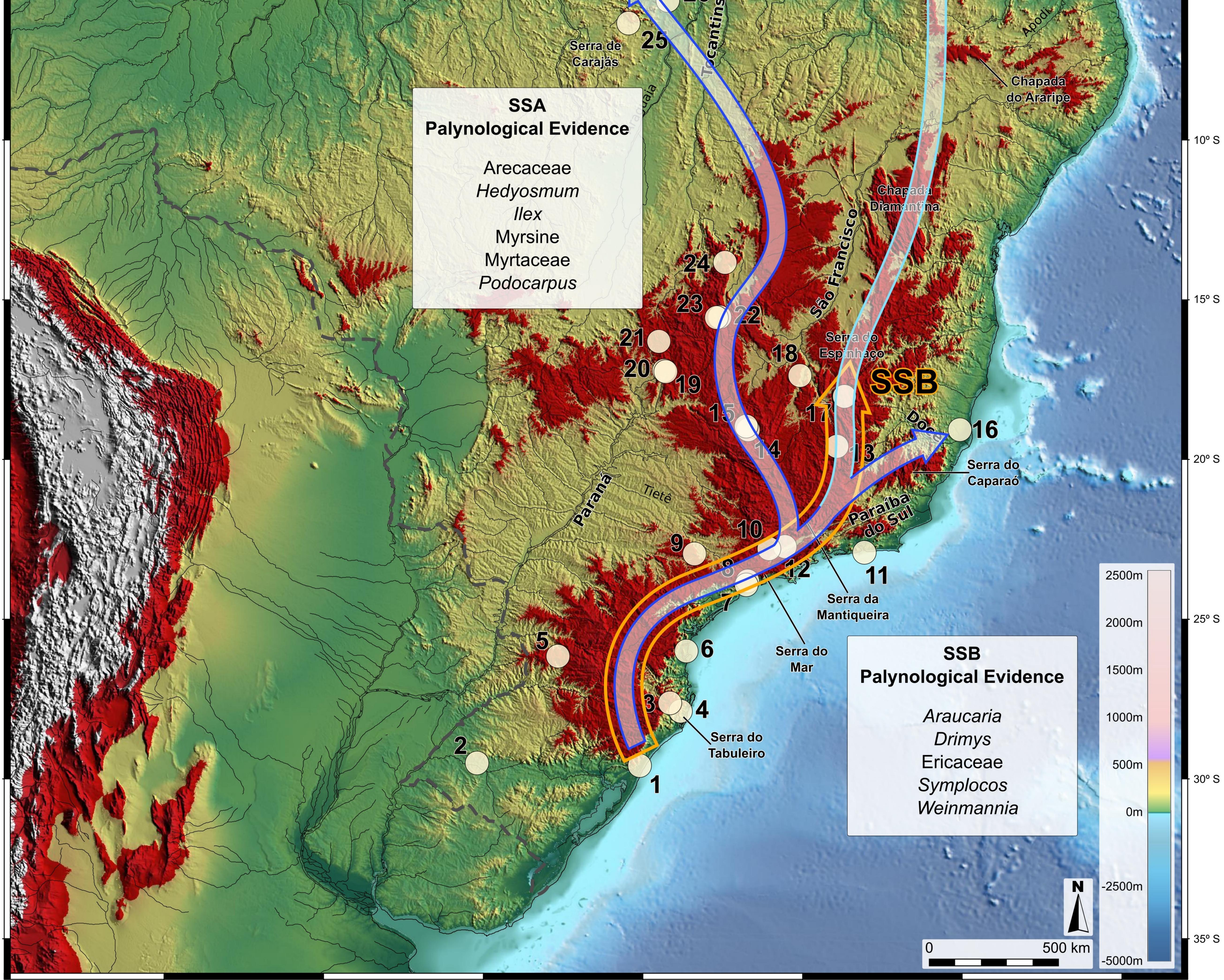
Podocarpus





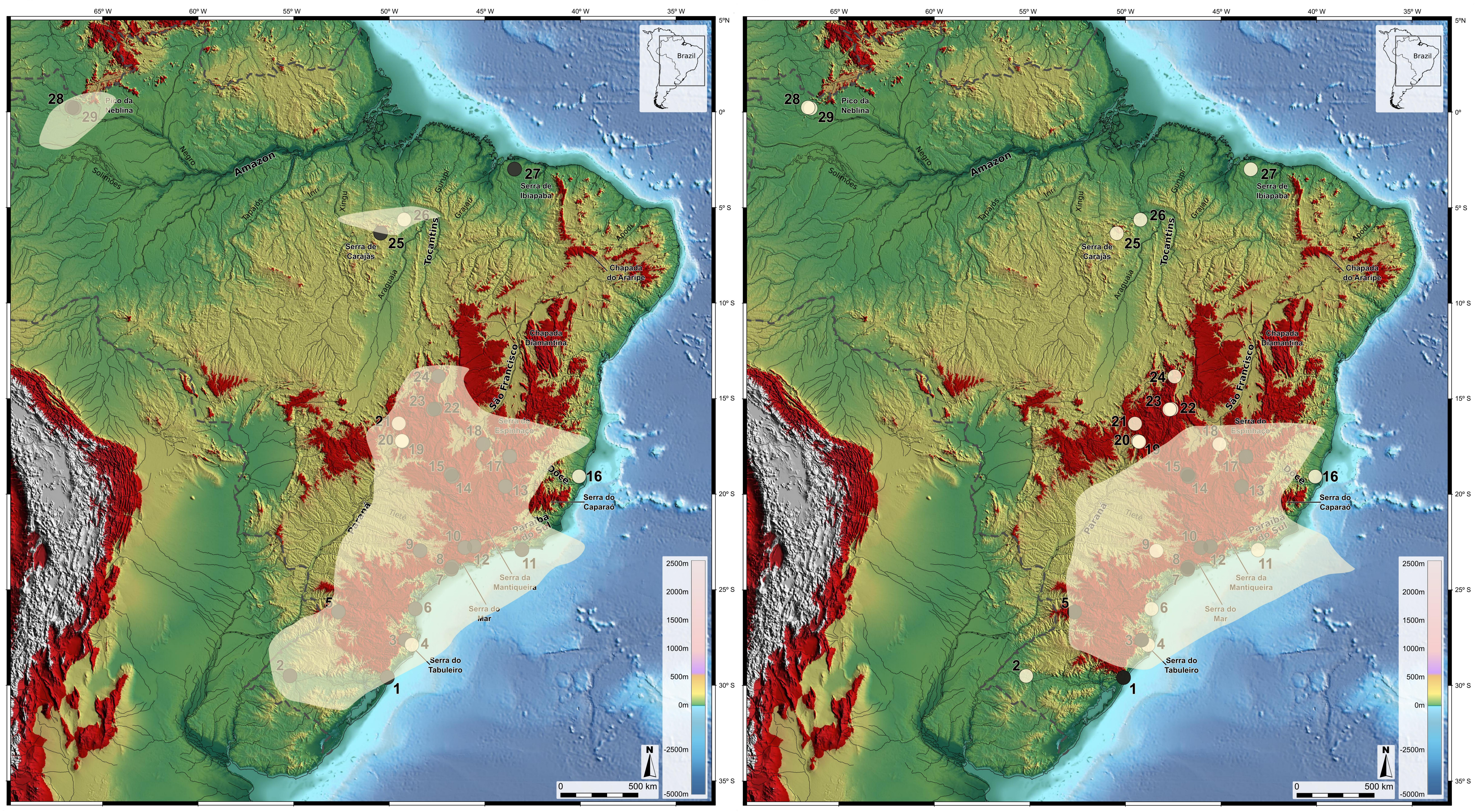
Araucaria











Podocarpus



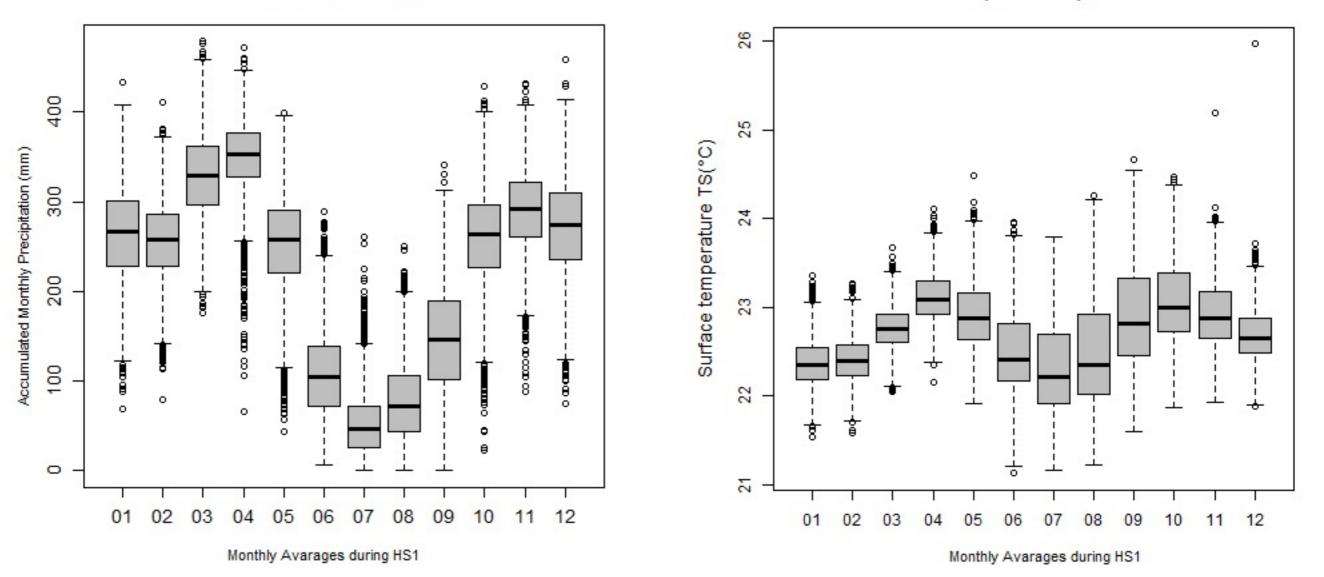


Araucaria

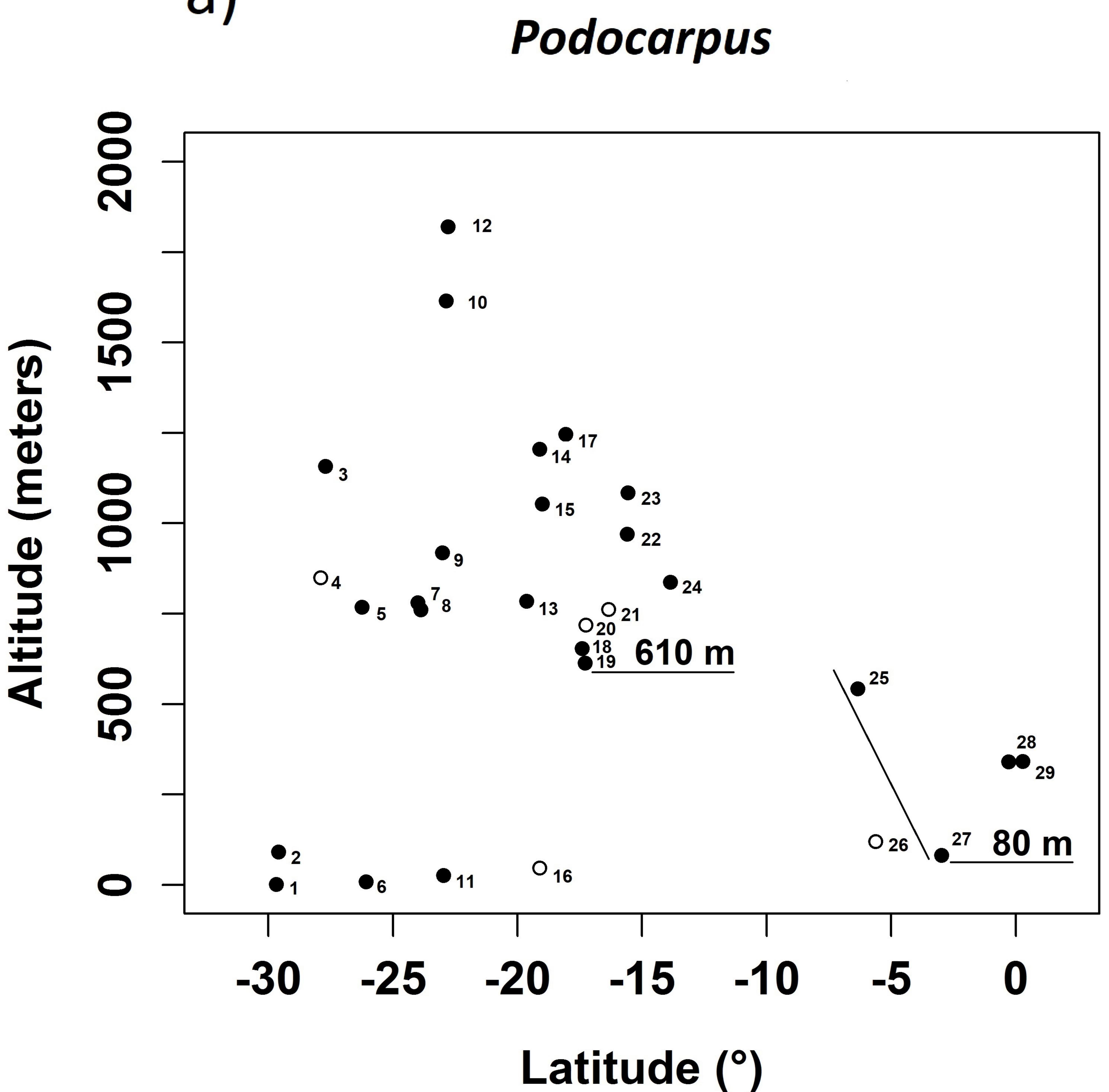
a)

Chapada do Apodi

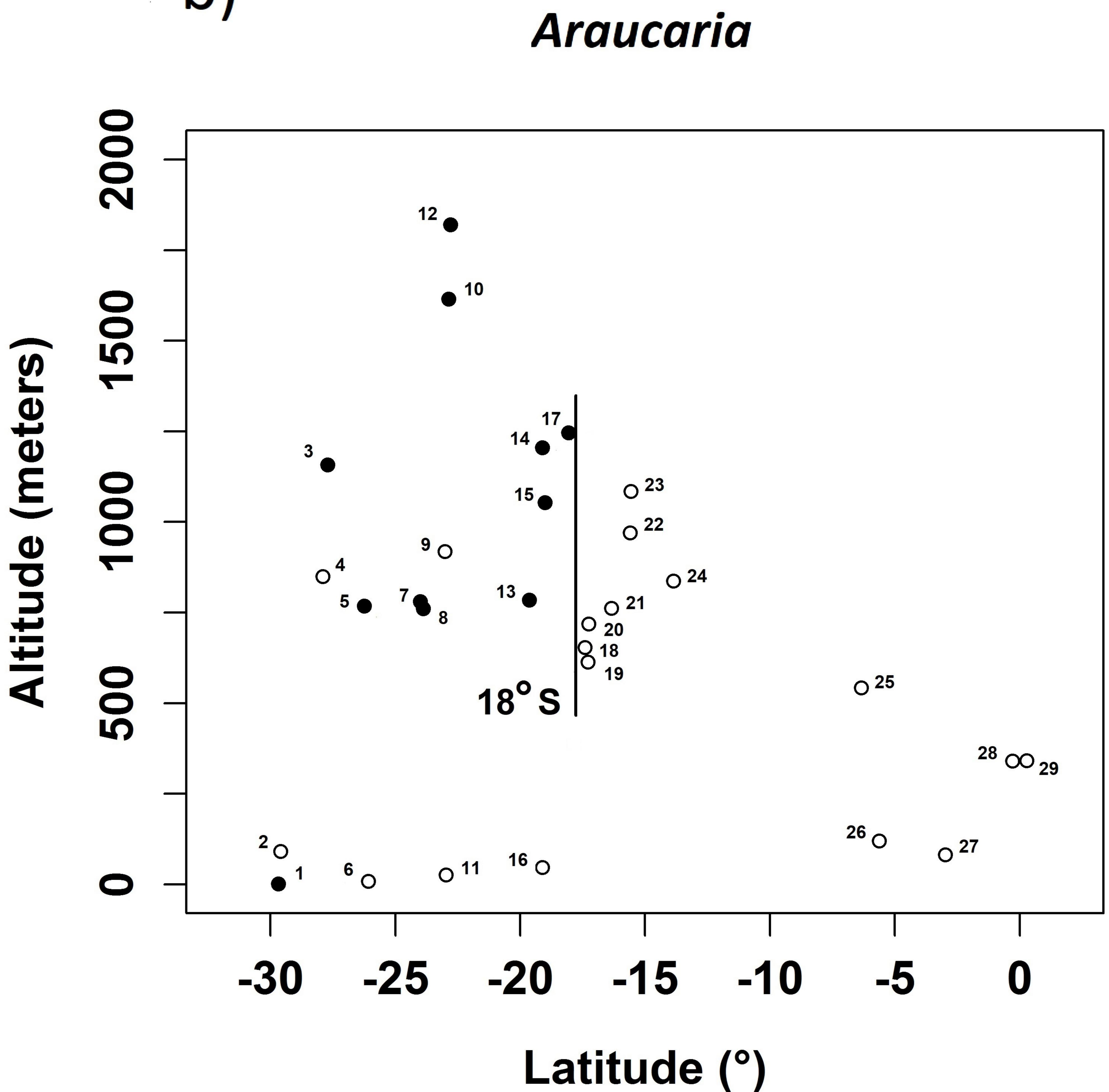
Chapada do Apodi



b

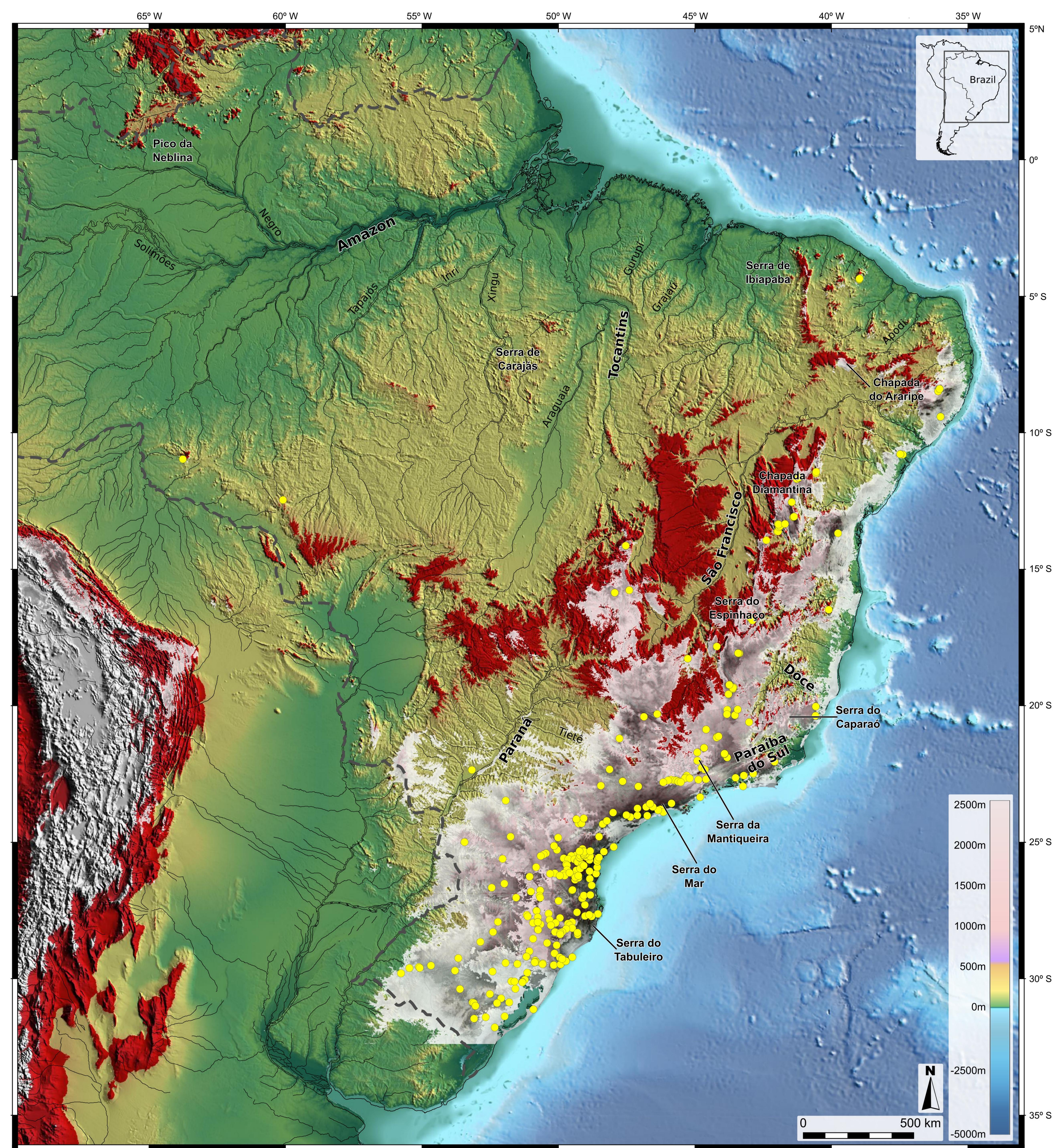


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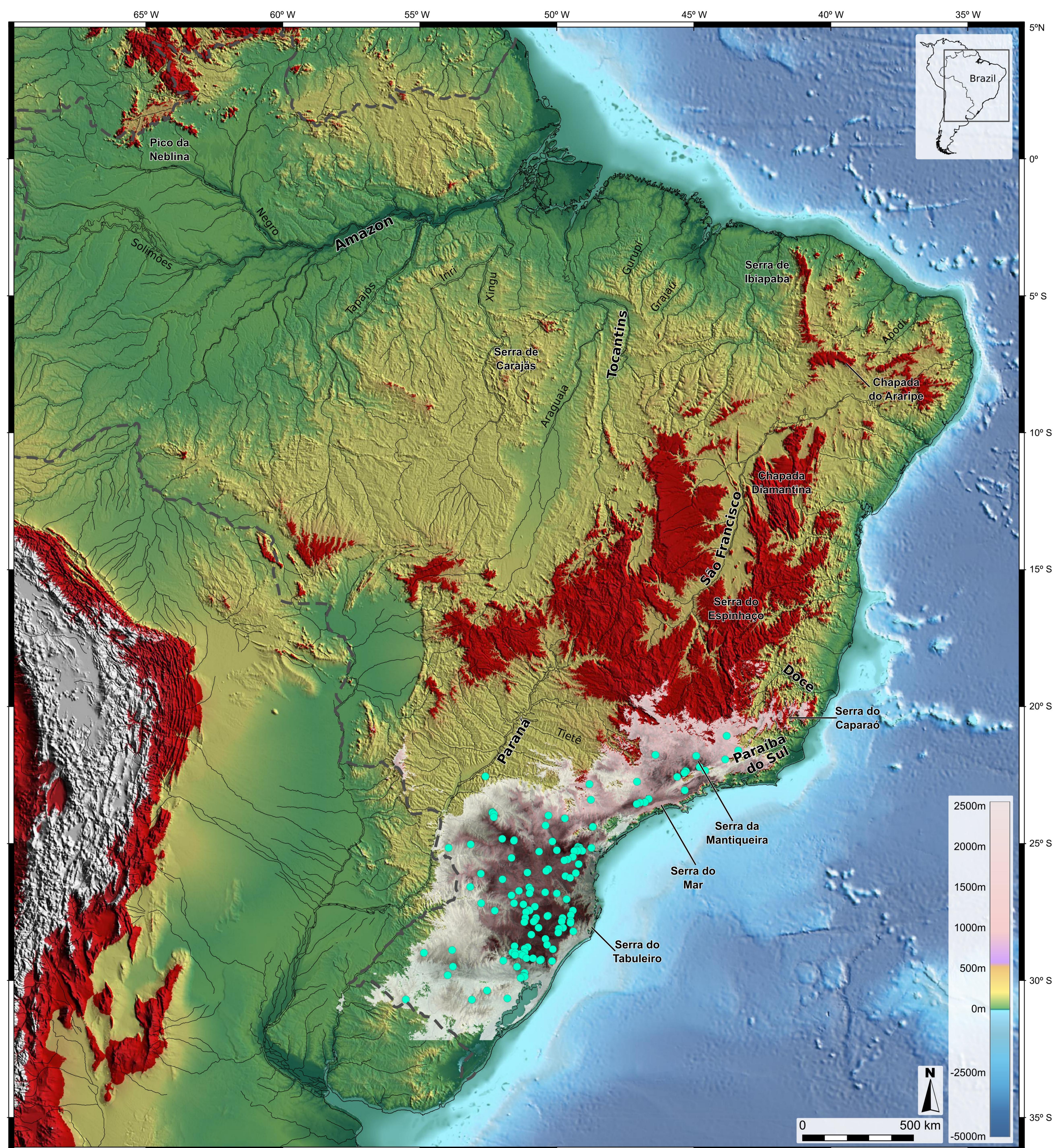
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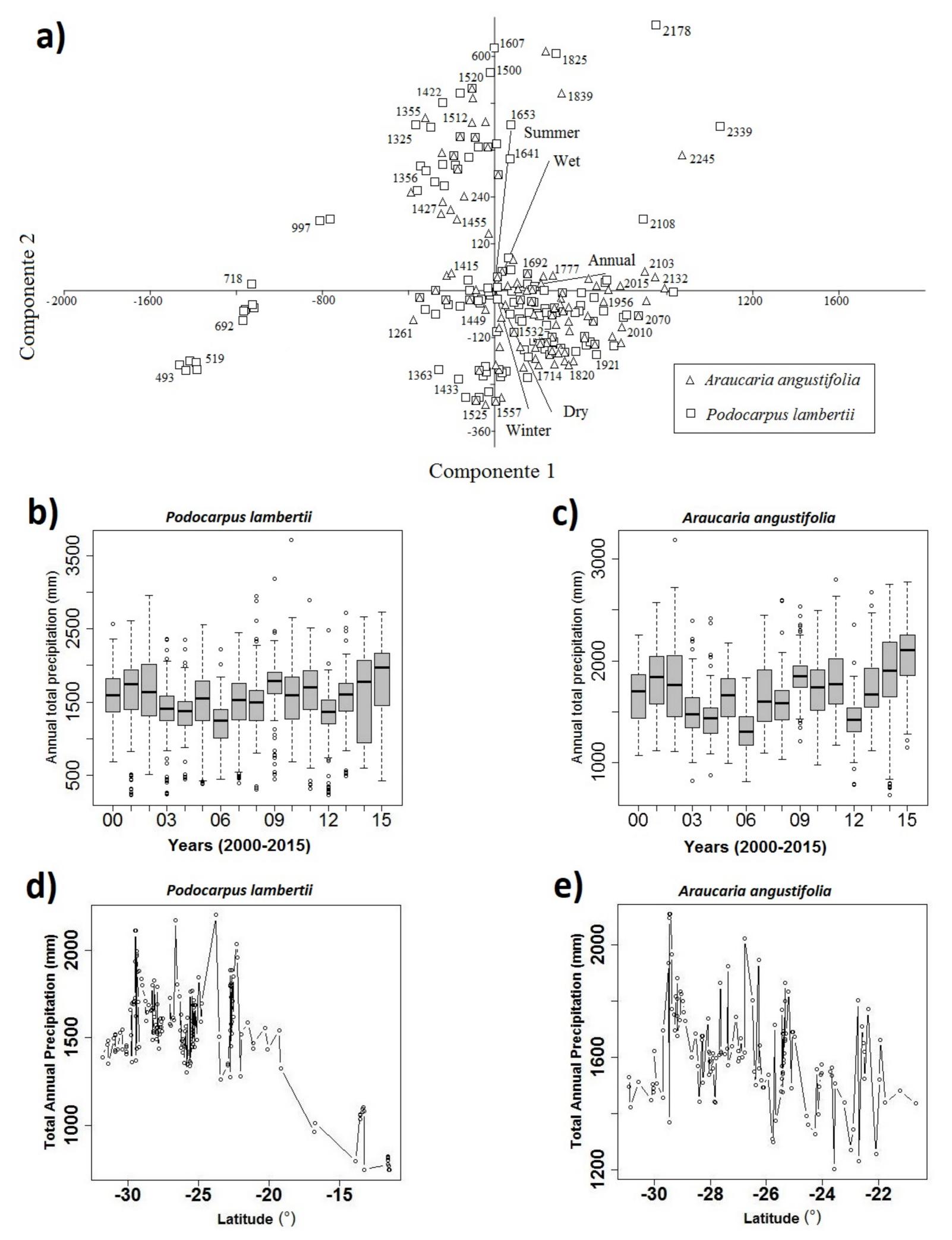


Podocarpus

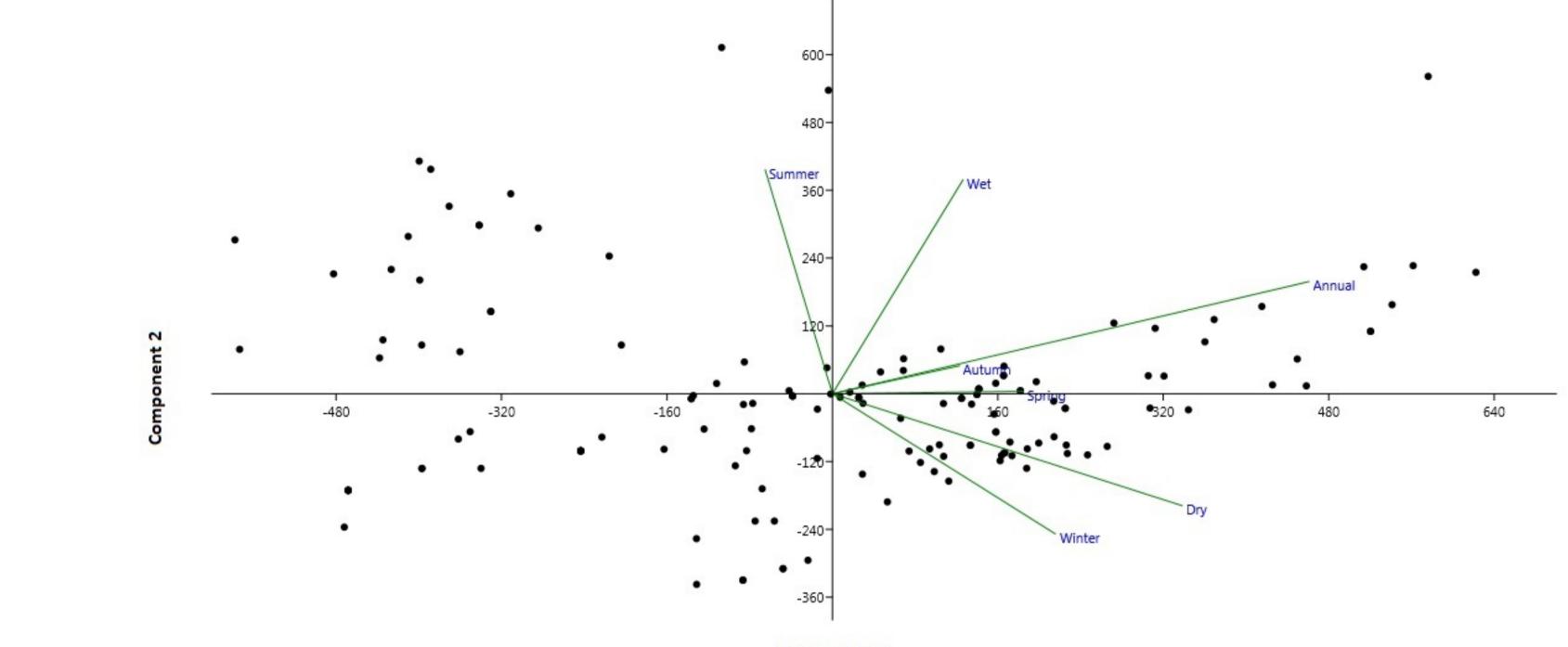




Araucaria angustifolia



a



Component 1

