Title: Current climate, isolation and history drive global patterns of tree phylogenetic endemism

Authors: B. Sandel[1], P. Weigelt[2], H. Kreft[2], G. Keppel[2,3,4], M. T. van der Sande[5,6,7], S. Levin[8,9], S. Smith[10], D. Craven[2,8,11], T.M. Knight[8,9,11]

Corresponding author: Brody Sandel (bsandel@scu.edu)

Present addresses:

[1] Department of Biology, Santa Clara University, 500 El Camino Real, Santa Clara CA 95053

[2] Biodiversity, Macroecology and Biogeography, University of Goettingen, Büsgenweg 1, 37077 Göttingen, Germany

[3] Natural and Built Environments Research Centre, School of Natural and Built Environments, University of South Australia, GPO Box 2471, Adelaide, South Australia 5001, Australia

[4] Future Industries Institute, University of South Australia, Mawson Lakes Campus, GPO Box 2471, Adelaide, South Australia 5001, Australia

[5] Institute for Global Ecology, Florida Institute of Technology, Melbourne, FL, USA

[6] Institute for Biodiversity & Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands

[7] Forest Ecology and Forest Management Group, Wageningen University and Research, P.O. Box 47, 6700 AH Wageningen, the Netherlands

[8] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany.

[9] Institute of Biology, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany

[10] Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan

[11] Department of Community Ecology, Helmholtz Centre for Environmental Research- UFZ, Theodor-Lieser Strasse 4, 06120 Halle (Salle), Germany

Data Accessibility: All data at the country level are available as a GIS shapefile at datadryad.org.

Biosketch: We are a group of researchers interested in obtaining a global understanding of tree distributions and identifying hotspots of conservation priorities. We hope that this will provide useful input to global policies to support effective conservation efforts.

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2   DR. BRODY SANDEL (Orcid ID : 0000-0003-2162-6902)

3   DR MASHA VAN DER SANDE (Orcid ID : 0000-0002-6845-2308)

4   DR. DYLAN CRAVEN (Orcid ID : 0000-0003-3940-833X)

5

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10   **Title:** Current climate, isolation and history drive global patterns of tree phylogenetic endemism

11   **Running title:** Global patterns of tree phylogenetic endemism

12   **Abstract**

13   *Aim*: We mapped global patterns of tree phylogenetic endemism (PE) to identify hotspots and test

14   hypotheses about possible drivers. Specifically, we tested hypotheses related to current climate,

15   geographical characteristics and historical conditions, and assessed their relative importance in shaping

16   PE patterns.

17   *Location*: Global

18   *Time period:* We used the present distribution of trees, and predictors covering conditions from the mid-

19   Miocene to present.

20   *Major taxa studied*: All seed-bearing trees.

21   *Methods*: We compiled distributions for 58,542 tree species across 463 regions worldwide, matched

22   these to a recent phylogeny of seed plants, and calculated PE for each region. We used a suite of

23   predictor variables describing current climate (e.g. mean annual temperature), geographical

24   characteristics (e.g. isolation) and historical conditions (e.g. tree cover at the last glacial maximum) in a

25   spatial regression model to explain variation in PE.

26   *Results*: Tree PE was highest on islands, and was higher closer to the equator. All three groups of

27   predictor variables contributed substantially to the PE pattern. Isolation and topographic heterogeneity

28   promoted high PE, as did high current tree cover. Among mainland regions, temperature seasonality

29   was strongly negatively related to PE, while mean annual temperature was positively related to PE on

30   islands. Some relationships differed among the major floristic regions. For example, tree cover at the

31   last glacial maximum was a positive predictor of PE in the Paleotropics, while tree cover at the Miocene

32   was a negative predictor of PE in the Neotropics.

33   *Main conclusions*: Globally, PE can be explained by a combination of geographic, historical, and current

34   factors. Some geographic variables appear to be key predictors of PE. However, the impact of historic

35   and current climate variables differs considerably among the major floristic regions, reflecting their

36   unique histories. Hence, the current distribution of trees is the result of globally relevant geographic

37   drivers and regional climatic histories.

38   **Key words:** Trees, Phylogenetic endemism, Biogeography, Isolation, Climate stability, Islands, Historical

39   contingency

40   **Introduction**

41   The remarkable disparity in the distribution of terrestrial biodiversity has fascinated biologists for more

42   than two centuries (von Humboldt and Bonpland, 1807; Kier et al., 2009; Harrison and Noss, 2017).

43   Thirty-six recognized biodiversity hotspots, which cover 2.4% of the Earth's land surface, contain an

44   estimated 50% of all endemic plant species and 42% of all endemic terrestrial vertebrate species (Myers

45   et al. 2000, Hrdina and Romportl 2017). Endemism lies at the core of understanding the variation of

46   biodiversity across space, revealing how speciation, extinction, dispersal and biophysical barriers

47   influence species distributions (Lomolino et al., 2010). Traditionally, studies of endemism have focused

48   on taxonomic measures of endemism, which only account for the number of endemic or range-

49   restricted species in a particular area (Kier et al., 2009, Williams et al., 1996) and do not capture the rich

50   history of how clades have diversified over evolutionary time (Rosauer et al., 2009; Mishler et al., 2014).

51   Phylogenetic endemism (PE) addresses this shortcoming by integrating evolutionary history (i.e.

52   phylogenetic uniqueness) with the range sizes of clades, weighting each branch in a phylogenetic tree by

53   the inverse of the descendent clade's total range size (Rosauer et al., 2009). Hence, geographic regions

54   with high PE contain clades that are narrowly distributed and phylogenetically unique, and whose loss

55   would lead to a large decline in evolutionary history. As such, PE can play a central role in conservation

56   planning (Mishler et al. 2014). Further, spatial patterns of PE can unveil the roles played by speciation

57   and extinction events in determining large-scale biodiversity patterns, such as the latitudinal diversity

58   gradient (Schluter and Pennell 2017). For example, they can shed light on the long-standing question of

59   whether the tropics are species-rich because of high speciation rates (a cradle of diversity, producing

60   clusters of closely related species and relatively low PE) or because of low extinction rates (a museum of

61   diversity, with many endemic species separated by long branches from their closest relatives; Stebbins

62   1974). Thus, understanding the spatial pattern of PE and its historical and environmental drivers can

63   help reveal the mechanisms underlying biogeographic patterns (Mishler et al. 2014).

64   While drivers of large-scale patterns of species diversity for multiple taxa, including plants, mammals,

65   amphibians, birds, and ants, are well known (Hawkins et al. 2003, Field et al. 2009, Stein et al. 2014),

66   how these drivers shape patterns of PE is uncertain. Areas with high species richness also tend to have

67   high endemism, though this is not always the case (Daru et al. 2015). Mismatches between species

68   diversity, and endemism and PE are informative, as they can reveal mechanisms that promote one but

69   not the other. For example, islands often have high endemism but moderate species richness, indicating

70   that geographic isolation might play an important role in promoting endemism, but *in situ* diversification

71   is not rapid enough to produce high species richness (Cronk 1997, Kier et al. 2009).

72   Three main categories of drivers influence patterns of species diversity and may similarly determine the

73   distribution of (phylogenetic) endemism. First, current climatic conditions, such as mean annual

74   precipitation, mean annual temperature and seasonality are typically important correlates of diversity

75   (e.g., Currie 1991; Hawkins et al. 2003). In general, more plant species are found in regions with warm,

76   humid and aseasonal climates (e.g. Kreft and Jetz, 2007). Second, geographic characteristics such as

77   greater area and environmental heterogeneity, or lower geographic isolation, also increase species

78   diversity (Stein et al., 2014). Principle among these is topographic heterogeneity (Jetz and Rahbek 2002,

79   Keppel et al. 2016). Environmental heterogeneity is assumed to drive species diversity via coexistence,

80   promoting species persistence during unfavorable times and may increase speciation rates (Stein and

81   Kreft 2015). At the same time, heterogeneity often creates dispersal barriers that may decrease species

82   diversity but may increase speciation rates (Quintero and Jetz, 2018). Third, historic climatic conditions

83   including long-term climate stability and the availability of suitable habitat through time, have been

84   found to positively affect taxonomic endemism or phylogenetic diversity (Dynesius and Jansson 2000;

85   Jansson, 2004, Sandel et al. 2011, Kissling et al. 2012). There are reasons to expect a region with a long

86   history of high tree cover to have high or low PE. On one hand, areas with higher tree cover might be

87 associated with larger range sizes per species, leading to low endemism. On the other hand, high tree

88 cover and climatic stability over time may support higher tree species richness, providing increased

89 opportunities for allopatric speciation and promoting the coexistence of more small-ranged species

90 (Losos and Schluter 2000).

91 Here, we examine drivers of PE among ~60,000 tree species on Earth (Beech et al., 2017). Trees may

92 show different patterns than other taxa, such as mammals (Rosauer and Jetz, 2014) and grasses (Sandel

93 et al. 2016), due to their long lifespans, long dispersal distances, and the tolerances to frost and drought

94 present in many tree species (Nathan, 2006; Choat et al., 2012; Zanne et al., 2014). Further, unlike

95 mammals or grasses, trees are not a monophyletic group, but rather a growth form that has evolved and

96 been lost numerous times (Smith and Donoghue 2008). Trees also provide vital ecosystem services (e.g.,

97 Gamfeldt et al., 2013) and support the biodiversity of many other taxa (e.g., Staab et al., 2014; Barnes et

98 al., 2017). Thus, describing patterns of PE and understanding their covariation with past and present

99 environmental and geographical conditions is essential for efforts to protect existing diversity and to

100 determine the likely importance of future threats, such as climate change.

101 It is difficult to predict whether historical climate, current climate or geography will be most important

102 for explaining modern PE patterns of trees. On one hand, the long lifespans and generation times of

103 trees slow down evolutionary processes (Smith and Donoghue 2008) and the dispersal of species as

104 climate changes (Svenning and Skov 2004), implying that historical factors may play a large role in

105 explaining modern patterns of PE (Zanne et al. 2014; Ma et al., 2016; e.g., Feng et al., 2017). On the

106 other hand, the abilities of many tree species to disperse long distances might allow them to track their

107 optimal environmental conditions (Zanne et al. 2014; Kremer et al., 2012), and may result in current

108 rather than past climate conditions better predicting patterns of tree PE (Ma et al., 2016). Finally, the

109 ability of tree species to occur across vast temperature and precipitation gradients could result in a high

110 importance of geographic characteristics, such as the range of elevations present in an area or access to

111 glacial refugia, as an important predictor of PE (Ma et al., 2016; Hazzi et al., 2018).

112 **Methods**

113 *Species data and distribution data*

114 The GlobalTreeSearch database (BGCI 2017) served as the main source of tree distributions, offering

115 country-level distribution data for 58,762 tree species. To obtain finer-grained distribution information

116 for some large countries (USA, Canada, Mexico, Brazil, China and Australia), we replaced country-level

117   information with sub-national tree checklists from the Global Inventory of Floras and Traits (GIFT)

118   database (Weigelt et al. 2019, data from Baker and Duretto 2011, Barker et al. 2005, Queensland

119   Government 2014, Short et al. 2011, VicFlora 2016, Western Australian Herbarium 2017, Royal Botanic

120   Gardens and Domain Trust 2017, USDA NRCS 2015, Chinese Virtual Herbarium 2016, Jardim Botânico do

121   Rio de Janeiro 2016, CONABIO 2016) leading to a global dataset of tree checklists for 463 geographic

122   regions worldwide. GIFT includes regional plant checklists from published Floras and checklists as well as

123   information on functional traits like growth form extracted from the included floras as well as large

124   global trait databases. For combining the GlobalTreeSearch and GIFT data, we processed species names

125   from the GlobalTreeSearch with the same taxonomic standardization procedure as applied for all

126   species in GIFT (see Weigelt et al. 2019) which led to a set of 58,258 taxonomically standardized species

127   names in the GlobalTreeSearch data. Replacing large countries from the GlobalTreeSearch database

128   with smaller entities from GIFT resulted in a loss of 663 species that were not covered by the small-scale

129   checklists from GIFT. At the same time, the checklists from GIFT included 947 tree species not covered

130   by the GlobalTreeSearch, leading to a final dataset with 58,542 tree species. To apply a definition of

131   trees as similar as possible among the two datasets, we removed tree species from GIFT that were not

132   included in the GlobalTreeSearch data if other trait data in GIFT included conflicting trait information

133   (non-woody tissue, obligate epiphytic or climbing habit, or plant height below 2 m) if less than 70% of

134   the resources in GIFT agreed on the growth form being tree, and if no members of the given plant family

135   were included in the GlobalTreeSearch (e.g. cycads, tree ferns, grass trees or bamboos).

136   Trees are a relatively well-studied group and the GlobalTreeSearch data represent the most

137   comprehensive attempt to date to compile their distribution information. Nevertheless, some regions

138   and taxa may be undersampled. Some areas with high species richness, such as southeast Asia, have not

139   been extensively surveyed and are therefore probably still somewhat undersampled. Other biodiverse

140   countries including Colombia, Brazil and China have more up-to-date species lists that are likely to be

141   more complete (Beech et al. 2017). Any estimate of the numbers of missing species in less-sampled

142   countries would be very imprecise, and it is still more difficult to know how these missing species would

143   change the PE of a region (because it is unknown where on the phylogeny these species would occur).

144   We explored a possible role of sampling bias by mapping the residuals of models predicting species

145   richness and PE from a set of climate variables (see below for variables and model details), and assessing

146   whether the residuals were associated with regions of suspected undersampling.

147   *Phylogeny*

148 We used a large, dated phylogeny of seed plants with 353,185 tips from Smith and Brown (2018) as a

149 backbone to build a phylogeny of all species in the dataset. We conservatively bound species into the

150 backbone using dating information from congeners in the tree using '*congeneric.merge'* in the R package

151 '*pez*' (Pearse et al. 2015).

Phylogenetic endemism

153 We used a variant of Rosauer et al.'s (2009) phylogenetic endemism (PE; myr/km^2), by modifying the R

154 function phyloendemism(), written by D. Nipperess, and contained in the package PDcalc (currently on

155 GitHub; https://github.com/davidnipperess/PDcalc). The PE of a region is the total phylogenetic branch

156 length encompassed by species in that region, where the phylogeny is modified such that each branch

157 length divided is by the global range size of its descendent clade. The original function computes range

158 size for each species as the number of regions where it occurs. We updated it to estimate range size as

159 the total area of all regions where a species occurs, to account for widely varying region size in our data

160 set. For comparison, we also computed PE values based on counts of regions occupied, which was fairly

161 well correlated with our measure of area-based PE (r = 0.71).

162 Our implementation also differs in being an unrooted measure of PE. This means that the measure of PE

163 includes the branch length to the root of the tree only if the root node lies on the path between two tips

164 in the sample. We prefer this unrooted version, since it is insensitive to arbitrarily making the tree

165 deeper via the inclusion of an outgroup.

Ancillary metrics of diversity and endemism

167 Patterns of PE are ultimately driven by a combination of both taxonomic endemism and phylogenetic

168 uniqueness. To improve our ability to interpret PE, we therefore computed measures of phylogenetic

169 and non-phylogenetic diversity and endemism that relate to these two components. The diversity

170 metrics were species richness (S) and the rarified Phylogenetic Diversity Index (*rarPDI*, Sandel 2018).

171 *rarPDI* is derived from Faith's (1992) unrooted phylogenetic diversity (PD) and its richness-standardized

172 variant, the Phylogenetic Diversity Index (PDI, Tsirogiannis and Sandel 2016). PDI is calculated as the

173 standardized effect size of the PD, relative to the expectation and variance of PD for a random draw of S

174 species from the tree, where S is the species richness of the assemblage. PDI is dependent on species

175 richness in the presence of a phylogenetic selection process (such as environmental filtering, Sandel

176 2018). Therefore, we also calculated *rarPDI* by rarefying the region-by-species matrix to 100 species per

177 region and computing PDI on this matrix. We repeated this rarefaction 100 times, and used the mean

178 across replicates. We calculated *rarPDI* using the R package PhyloMeasures (Tsirogiannis and Sandel

179 2016). Positive *rarPDI* values indicate higher phylogenetic diversity than is expected under a null model

180 (i.e. phylogenetic overdispersion), while negative values indicate lower than expected phylogenetic

181 diversity (i.e. phylogenetic clustering).

182 For taxonomic endemism, we calculated range size rarity (RSR, sum(1/range size) for all species in a

183 region). In the special case of a star phylogeny (i.e. all species form a single polytomy), RSR is equivalent

184 to PE. PE and RSR were highly correlated (r = 0.95), so we also calculated the residuals of an ordinary

185 regression of PE against RSR to identify the regions that have unusual PE values given their RSR. We call

186 this the PE Index, or PEI.

187 *Predictor variables*

188 For each region, we considered a range of candidate variables that have been shown or hypothesized to

189 relate to tree diversity and/or endemism. Broadly, these can be classified into three groups. The first

190 group (*Geographic variables*) described the geographical context. This group included the area of the

191 region (AREA; in km²), the maximum range of elevations found within the region (ELEV_RANGE; in m),

192 and the proportion of landmass relative to open water surrounding each region summed up for buffer

193 distances of 100, 1000 and 10,000 km around the focal region (SLMP; unitless; Weigelt and Kreft 2013).

194 SLMP serves as a measure of potential source areas for colonization. It is highest for regions located in

195 the center of large continents and lowest for isolated islands. The second group (*Climatic variables*)

196 described modern climate. We used four variables to describe the mean and seasonality of temperature

197 and precipitation (annual mean temperature; TEMP; °C, annual precipitation; PREC; mm/yr, standard

198 deviation of mean monthly temperatures; VAR_TEMP; °C, coefficient of variation in monthly

199 precipitation; VAR_PREC; unitless; Karger et al. 2017). These variables were calculated as described by

200 Weigelt et al. (2013). Finally, we used four variables (*Historical variables*) to describe historical climate

201 and vegetation dynamics. These were the velocity of temperature change since the Last Glacial

202 Maximum (VELOCITY; m/yr, following Sandel et al. 2011 but based on 1 km² resolution input rasters)

203 and estimates of cover of woody vegetation types at present (Olson et al. 2001), the Last Glacial

204 Maximum (Ray and Adams 2001), Pliocene (PRISM4 Paleoenvironmental Reconstruction 2016) and

205 Middle Miocene (Henrot et al. 2010) (CURR_TREES, LGM_TREES, PLIO_TREES, MIO_TREES; proportion

206 tree cover). These estimates are based on paleoclimate reconstructions combined with paleovegetation

207 records. These four time points describe the expansion and contraction of woody vegetation types over

208 time.

209 *Regions*

210 We performed separate analyses for mainland and island regions. Two factors motivated this decision:

211 first, the factors that drive diversity and endemism may differ between islands and mainlands (Kier et al.

212 2009) and second, estimates of past tree cover were generally not available for islands, requiring us to

213 omit those variables from all models including islands.

214 To examine how the effects of geographic, climatic, and historical variables on PE varied among regions

215 with different biogeographic histories, we further divided mainland regions into the four major floristic

216 kingdoms (Australis, Holarktis, Neotropis, Paleotropis), following Good (1947), as updated by Takhtajan

217 (1986). We excluded the kingdoms of Antarktis (no tree species) and merged the Capensis with the

218 Paleotropis because this kingdom is much smaller than the other kingdoms and smaller than the country

219 of South Africa for which we have tree distribution data. All analyses were repeated within these

220 kingdoms.

221 *Analysis*

222 We fit ordinary linear regression models to explain variation in the response variables (mainly PE, see SI

223 for S, RSR, PD, PDI, rarPDI and PEI) using all predictor variables, with regions as replicates (total N=463).

224 In most cases, there was little residual spatial autocorrelation. However, some autocorrelation remained

225 in certain cases, so we also fit error simultaneous autoregressive models (Kissling and Carl 2008) with a

226 neighborhood of 1000 km, which successfully removed autocorrelation over the smallest distance

227 classes. In all cases, we report standardize d regression coefficients. Multicollinearity was not a major

228 issue in our analyses as predictor variables were not strongly collinear and all variance inflation factors

229 (VIF) were <5, sample sizes were large (N = 335 for mainlands, N = 93 for islands), and the residual

230 variances for most models were relatively low (Morrisey and Ruxton 2018).

231 We then repeated this process within the four floristic kingdoms. Within these kingdoms, the predictor

232 variables sometimes exhibited high multicollinearity. In particular, VIF was greater than 10 for TEMP in

233 the Australis, and >5 for PREC, VAR_TEMP, VAR_PREC and SLMP in the Australis, PREC in the Neotropis

234 and PREC and CURRENT_TREES in Paleotropis. Thus, these regression coefficients are expected to have

235 higher uncertainty, though neither their estimates nor their standard errors are biased as a result

236 (Morrissey and Ruxton 2018).

237 Finally, we used variance partitioning to ascribe the explanatory power of the linear models to each of

238 the three groups of variables or to their overlaps. We did not do variance partitioning for islands, since

239 most historical variables had to be omitted from models for islands.

240 Prior to regression analyses, we transformed our variables to meet normality assumptions as follows: S,

241 PD, RSR and PE were log-transformed. PREC and VAR_TEMP were square root-transformed, and

242 VELOCITY, AREA and ELEV_RANGE were log-transformed.

243 All analyses were conducted in R (R Core Team 2017), using the raster (Hijmans 2017), sp (Pebesma and

244 Bivand 2005) and spdep (Bivand and Piras 2015) packages.

245

246 **Results**

247 Phylogenetic endemism (PE) was highest in tropical regions and on islands (Figure 1). Among mainland

248 regions, there was a notable asymmetry between the northern and the southern hemisphere, with

249 more modest declines in PE with increasing latitude in the south, and more marked decreases in the

250 north. Among all mainland regions, Costa Rica had the highest PE, while Lord Howe Island had the

251 highest PE among islands (Table 1, 2).

252 Two geographic variables, connectivity (Surrounding landmass proportion, SLMP) and elevational range

253 (ELEV_RANGE), were the only consistently significant predictors of PE for both island and mainland

254 regions (Figure 2). Surrounding landmass had the most consistent influence, with a negative effect on PE

255 (Figure 2), i.e. higher PE in more isolated regions. Among all mainland regions, all islands and within

256 three of the four mainland kingdoms (all except Holarctis), increasing connectivity decreased PE. PE

257 increased with elevational range (ELEV_RANGE) among all mainlands and especially among island

258 regions. In addition, area had a negative and mean annual temperature a positive relationship with PE

259 on islands, while for mainland regions temperature seasonality was a negative predictor.

260 Floristic kingdoms differed in historic and current climate explanatory variables that were significant

261 predictors of PE (Fig. 2). Historical cover by forests had modest but significant influences on PE among

262 mainland areas in tropical regions only. The influence of historical forest cover depended on the time

263 period. Regions with high current tree cover generally had higher PE, but this relationship was only

264 significant for the Neotropis. High tree cover deeper in history (Miocene) was associated with lower PE

265   for Neotropis, and high tree cover during LGM was related to higher PE for Paleotropis. The velocity of

266   temperature change from the LGM to present had no significant association with PE.

267   Current climate also exerted strong controls on PE (Figure 2). Among mainlands, low temperature

268   seasonality (VAR_TEMP) was the main predictor of high PE for Holarctis and Neotropis, while low

269   precipitation seasonality was an important predictor in Paleotropis. In three of the four mainland

270   kingdoms (all but Neotropis), higher annual precipitation was associated with higher PE.

271   Variance partitioning revealed that nearly equal proportions of variance was explained among the three

272   predictor variable groups. Each group uniquely explained between 8-10% of the variance in PE. Climate

273   and historical predictors shared the largest fraction of variance explained (12%) and a further 12% of the

274   variance explained was shared across all three predictor variable groups. In total, 65% of the variance in

275   PE was explained by these predictor variables.

276   We considered a range of other biogeographic patterns in trees, including species richness, taxonomic

277   endemism and phylogenetic diversity (Figures S1-S8). Overall, geographical patterns of PE and range size

278   rarity were nearly indistinguishable (RSR) (r = 0.99, Figure 3, Figure S1, S6). PE was also highest in areas

279   with high species richness (r = 0.39), high PD (r = 0.41) and high rarPDI (r = 0.35, all P < 0.001), but these

280   correlations were only moderate. To attempt to isolate the effect of phylogenetic uniqueness on PE

281   from the strong effect of species range size, we calculated the residuals of the regression of PE on RSR,

282   hereafter called the phylogenetic endemism index (PEI). PEI showed little variation across latitudes, but

283   revealed high PE for a given RSR (i.e. demonstrating high phylogenetic uniqueness) in some regions

284   including southern South America, East and Southern Asia, eastern and southwestern Australia and

285   western Africa (Fig. 3, Table 1). Across mainland regions, PEI was highest in large regions with high tree

286   cover during the LGM, and low climate change velocities (Figure S8). Among islands, PEI decreased with

287   increasing elevational range. Historical variables explained the largest unique fraction of the variance in

288   PEI, with nearly no overlapping explanations from the three variable groups (Figure S8).

289   Maps of residuals of species richness and PE identified regions that are known biodiversity hotspot

290   anomalies, including South Africa and Madagascar, but did not suggest dramatic undersampling in

291   Southeast Asia or Sub-Saharan Africa (Figure S9). Thus, while the GlobalTreeSearch data are certainly

292   incomplete, we do not see evidence for strong spatial biases in the tree inventory completeness.

293   **Discussion**

294 Our analysis of the world's trees reveals that phylogenetic endemism (PE) varies by orders of magnitude,

295 is higher on islands than mainlands, is explained almost equally by geographic, historical, and current

296 factors and is highly correlated with taxonomic endemism. While some geographic variables (especially

297 connectivity and elevational range) appear to consistently predict PE, the effect of historic and current

298 climate variables differs considerably among the floristic kingdoms. PE is highly correlated with RSR,

299 showing that it is driven primarily by variation in range size rather than evolutionary uniqueness.

300 As expected, geographic factors strongly influence PE, with isolation and topographic heterogeneity

301 promoting endemism. Being isolated from regions with similar climatic conditions likely promotes

302 endemism by supporting a diversity of species with small range sizes and preventing biotic exchange.

303 Hence, isolation results in high observed PE of trees on islands relative to mainland regions and also

304 higher PE in mainland regions that are less strongly embedded in continental landmass (e.g. coastal

305 regions or peninsulas, Taylor and Regal 1978). Similarly, topographic heterogeneity creates a diverse

306 array of small habitat patches that simultaneously support high species richness and small range sizes

307 (McFadden et al. 2019). These results are consistent with previous results for plants and animals that

308 have focused on taxonomic endemism (Ohlemüller et al. 2008, Kier et al. 2009, Sandel et al. 2011).

309 In mainland regions, PE is highest near the equator and declines steeply away from the equator in the

310 Northern Hemisphere but mildly in the Southern Hemisphere. The strong decline in PE to the north

311 could reflect the increasing land area and correspondingly larger range sizes of tree species. Land area in

312 the Southern Hemisphere declines toward the pole, producing smaller ranges and higher endemism.

313 This is consistent with results from birds, in which range sizes are strongly correlated with the

314 availability of land in latitudinal bands (Orme et al. 2006). At any given latitude, the PE of islands is

315 higher than on mainlands most likely because of strong effects of geographical isolation. This supports

316 previous results for taxonomic endemism of vascular plants by Kier et al. (2009).

317 We expected that habitat availability through time could positively or negatively relate to PE, with high

318 habitat area possibly leading to larger range sizes, but also greater potential for allopatric speciation. We

319 found that PE is positively associated with current tree cover, suggesting that the net effect of tree cover

320 might be higher tree endemism. However, intriguingly, historic tree cover during the Miocene, Pliocene,

321 and last glacial maximum (LGM) usually did not have a significant positive influence on endemism

322 (except a positive influence of LGM tree cover on PE within the Paleotropics). Instead, Miocene tree

323 cover had a negative influence on both RSR and PE, globally and especially within the Neotropics. This

324   suggests that long periods of high tree cover might have promoted species range extensions, thus

325   overwhelming the positive influence of recent tree cover.

326   The negative effect of Miocene tree cover on PE was particularly important in Neotropis. This could

327   reflect the fact that the Miocene was a geologically dynamic period for Neotropis, with substantial uplift

328   of the Andes and associated rearrangement of the major river networks (Hoorn et al. 1995). These

329   events likely promoted diversification in South America (Hughes et al. 2012). North and Central America

330   were separated from South America throughout the Miocene and had relatively low tree cover. Since

331   the Miocene, Central America has developed high tree cover and endemism, but many plant lineages in

332   modern Central America have their origins in South America (e.g. members of Malpighiaceae (Willis et

333   al. 2014)).

334   Tree cover during the LGM emerged as a particularly important predictor in Paleotropis. Because of the

335   cold global climate during the LGM most regions in Africa experienced a substantial decrease in tree

336   cover (Couvreur 2014). This contraction may be linked to higher extinction rates of palms in that region

337   (Kissling et al. 2012). On the other hand, Southeast Asia experienced a relatively stable climate,

338   maintaining high tree cover through the LGM and promoting high endemism (Feng et al. 2016). Perhaps

339   because of this historical idiosyncrasy, tree PE today is unevenly distributed across Paleotropis, being

340   much higher in southeast Asia than Africa.

341   Climate change velocity since the LGM did not significantly explain current tree PE for any region or

342   floristic kingdom. However, more unstable climates (higher velocities) harbor less PE than expected

343   given their taxonomic endemism (i.e., climate velocity was negatively associated with PEI on mainlands).

344   This suggests that environmental filtering is occurring in areas with rapidly changing climate, such that

345   only certain clades can migrate fast enough to keep pace with the change (Svenning et al. 2015, Ma et

346   al. 2016, Qian and Sandel 2017). Historical factors explained more of the variance of PEI than geographic

347   and current climate factors, supporting the idea that historical variables play an important role in driving

348   variation in phylogenetic distinctiveness.

349   Current climate influenced global patterns of PE as expected, with high temperature and precipitation

350   and low seasonal variation in temperature and precipitation promoting endemism. Australia is an

351   interesting case, in which current precipitation was an overwhelmingly strong predictor of PE. This may

352   reflect the fact that arid conditions in Australia have developed fairly recently, with wet and warm

353   conditions dominating until the mid-Miocene. Aridification became particularly severe about 4 mya

354 (Byrne et al. 2008). Thus, most Australian lineages are ancestrally adapted to wetter conditions (Byrne et

355 al. 2011), and, as evolutionary transitions from wet to dry conditions are rare (Crisp et al. 2009), these

356 older lineages are now primarily restricted to the wet portions of the country. This would suggest that

357 arid regions are unusually species-poor in Australis compared to wetter regions, which is indeed the

358 case. The two distinct hotspots in Australia– one in the arid southwest and one on the wet east coast -

359 include many phylogenetically distinct and small-ranged species, supporting the finding that modern

360 climatic conditions act as a strong filter on species' capacity to escape or tolerate drought conditions

361 (Choat et al. 2012).

362

363 The PE pattern observed for trees is similar in many respects to that of mammals (Rosauer and Jetz

364 2015). Both groups show latitudinal gradients with particular declines in PE toward the north.

365 Furthermore, mammal PE appears to be influenced by a combination of current climate, historical

366 conditions and geographic context (especially isolation), just as we found for trees. In part, this likely

367 reflects shared biogeographic histories and ecological factors that similarly shape patterns in these two

368 groups. On the other hand, it might also reflect a functional reliance of many mammal species on trees,

369 whereby the biogeographic patterns of trees to drive parallel patterns in other groups, likely also

370 including other groups as well, such as insects (Novotny et al. 2006) and amphibians (Vie et al. 2009).

371 The relationship between taxonomic endemism and phylogenetic endemism was stronger for trees than

372 for mammals, perhaps because mammals, unlike trees, are a phylogenetic clade.

373

374 Our set of tree species included both angiosperms and gymnosperms, and it is possible that the patterns

375 of PE would be strongly driven by the presence or absence of a few gymnosperm species, which are

376 deeply divergent from the angiosperms. However, gymnosperms made up only ~1% of the tree species,

377 and the nature of PE as a PD-like measure means that it is weighted towards the most speciose groups.

378 We calculated PE for just angiosperms and just gymnosperms (Figure S10), and found that angiosperm

379 PE was very well correlated with that for all trees (r = 0.995) and reasonably well correlated with that of

380 gymnosperms (r = 0.543).

381

382 Our findings have important implications for conservation. We need to prioritize conservation efforts

383 on the current hotspots that support high PE, due to historic, geographic and current climate factors.

384 Endemic species of trees, as well as other taxonomic groups, tend to be associated with small habitat

385 patches that support high species richness and small range sizes (e.g., islands, mainland peninsulas), and

386   conservation of these small areas of land would disproportionately benefit global tree conservation. We

387   find that PE is positively associated with proximity to the equator and current tree cover, and thus, our

388   results reinforce the conservation urgency for the vast Neotropical forests of central and south America.

389   In regions such as Australis, where tree species is highly associated with current climate, climate change

390   is an acute threat, and unique species within rapidly changing regions should be prioritized for *ex situ*

391   conservation.

392

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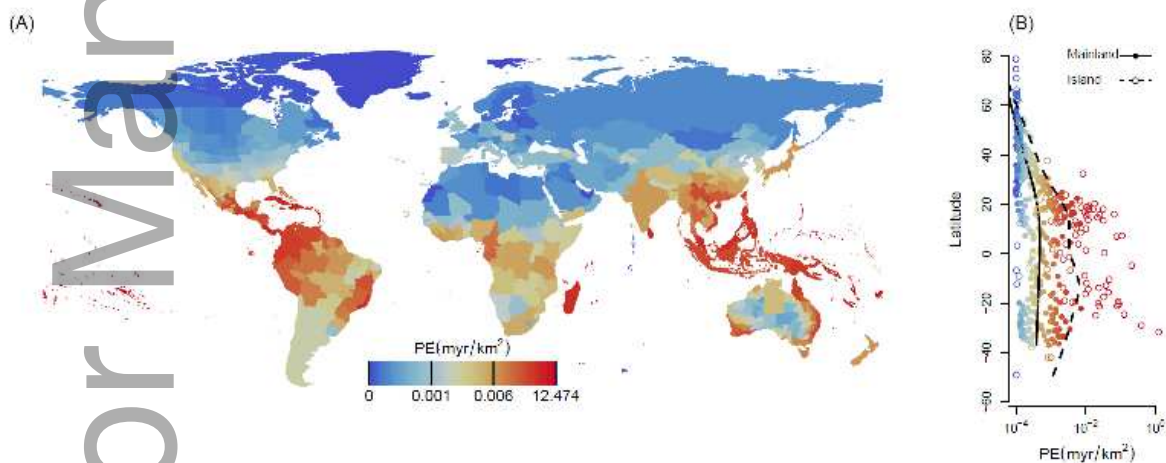
584

585   Figure 1: Global patterns of phylogenetic endemism (myr/km²) of trees (n=58,542 tree species) across

586   463 countries and other administrative units. The map (A) color scale is based on percentile-transformed

587   values. In (B), the fitted lines are lowess regressions, separately fitted for island and mainland regions.

588
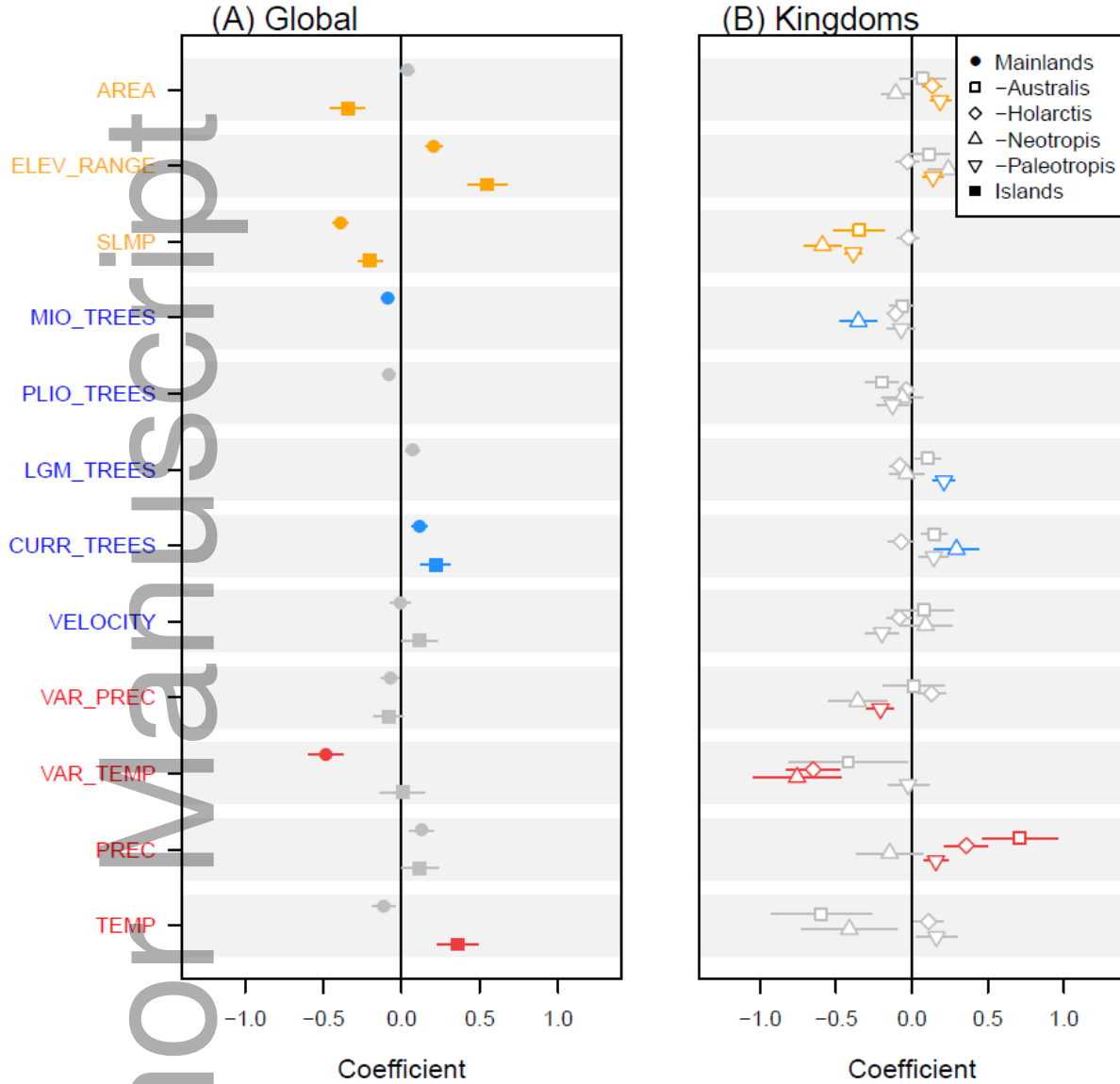
Figure 2: Standardized regression coefficients from multiple simultaneous autoregressive models for
phylogenetic endemism of trees for A) global mainland and island regions and B) the four major floristic
kingdoms excluding islands. Bars around each point show the standard error of the coefficient estimate.
Significant geographic, historical and climate variables are indicated in orange, blue and red,
respectively. Non-significant explanatory variables (P > 0.05) are indicated in grey.

A) Range size rarity (RSR)

B) Phylogenetic endemism index (PEI)

C) RSR-PE relationship
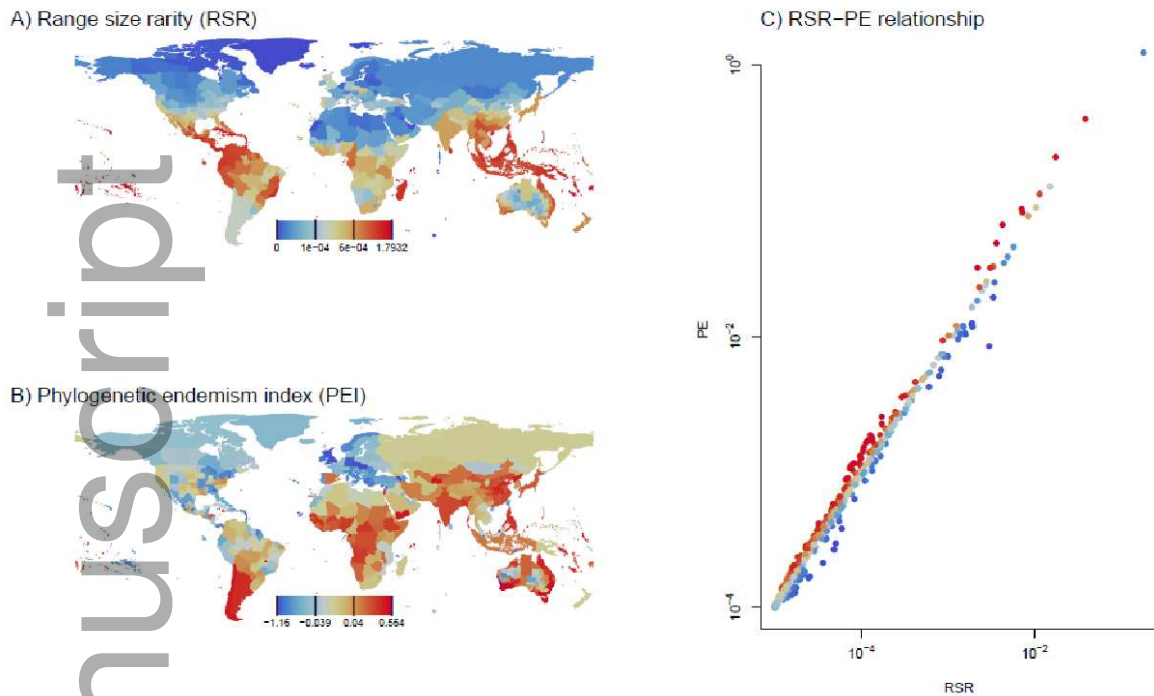
594

595 Figure 3: Global patterns of taxonomic endemism measured as range-size rarity (RSR (km^{-2}), A), the

596 relationship between RSR and phylogenetic endemism (PE; C), and the phylogenetic endemism index

597 (PEI, B) derived from the residuals of RSR-PE relationship.

598

599 **Table 1: The top 10 mainland regions for tree species richness, phylogenetic endemism (PE) and**

600 **phylogenetic endemism index (PEI)**

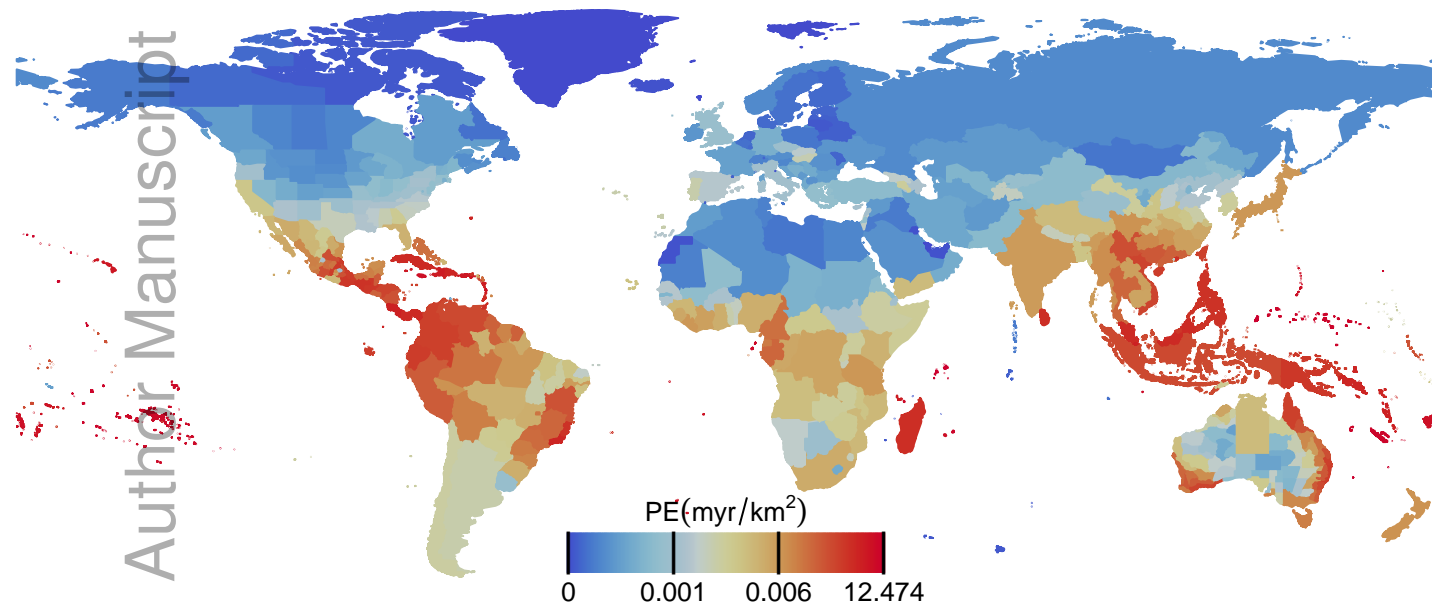| Region	Species	Region	PE	Region	PEI
Colombia	5750	Costa Rica	0.100	Esperance Plains, Australia	0.423
Malaysia	4946	Rio de Janeiro, Brazil	0.073	Warren, Australia	0.395
Venezuela	4652	Panama	0.070	Mallee, Australia	0.393
Peru	4456	Malaysia	0.061	Jarrah Forest, Australia	0.365
Amazonas	4132	Hong Kong (State)	0.056	Distrito Federal, Brazil	0.356
Ecuador	3590	Chiapas, Mexico	0.047	Swan Coastal Plain, Australia	0.349
Yunnan	3016	Espirito Santo, Brazil	0.040	Geraldton Sandplains, Australia	0.319
Bolivia	2986	Oaxaca, Mexico	0.040	Southern Tablelands, Australia	0.314
Pará, Brazil	2737	Guerrero, Mexico	0.039	Northern Tablelands, Australia	0.310
Panama	2663	Guatemala	0.037	Central Tablelands, Australia	0.304

601

602

603 **Table 2: The top 10 island regions for S, PE and PEI**

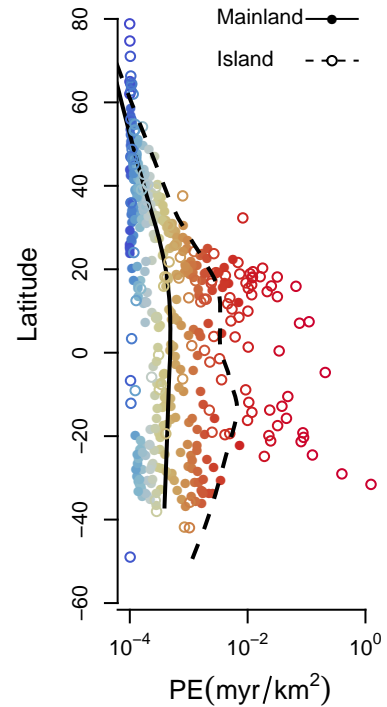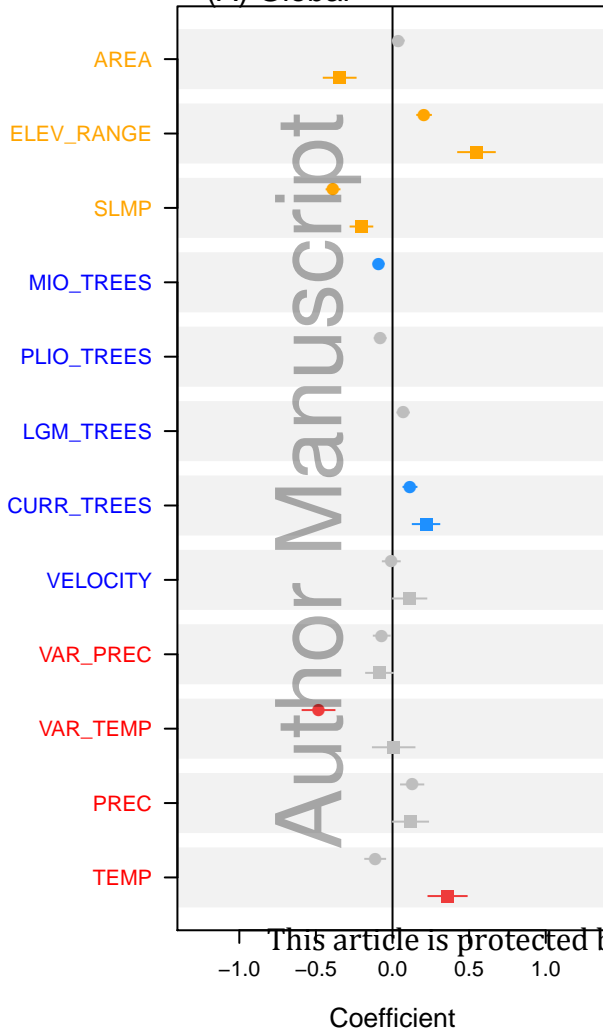| Region	Species	Region	PE	Region	PEI
Indonesia	5181	Lord Howe Island	12.474	United States Minor Outlying Islands	0.564
Madagascar	3215	Norfolk Island	3.998	Guam	0.479
Papua New Guinea	2586	Seychelles	2.084	Kiribati	0.404
Philippines	2197	Pitcairn Islands	1.262	Christmas Island	0.404
New Caledonia	1467	Palau	1.107	Kangaroo Island	0.364
Hainan	1326	Mauritius	0.893	Cook Islands	0.343
Cuba	1317	Cook Islands	0.870	Seychelles	0.329
Haiti	1046	New Caledonia	0.811	Tasmania	0.280
Dominican Republic	1027	Micronesia	0.763	New Caledonia	0.250
Sri Lanka	855	United States Minor Outlying Islands	0.663	Norfolk Island	0.209

604

(A)

(B)

PE(myr/km^2)

0   0.001   0.006   12.474

Mainland ●——
Island   ○----

Latitude

PE(myr/km^2)

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(A) Global

(B) Kingdoms

Legend:
- Mainlands
- −Australis
- −Holarctis
- −Neotropis
- −Paleotropis
- Islands

Y-axis categories (top to bottom): AREA, ELEV_RANGE, SLMP, MIO_TREES, PLIO_TREES, LGM_TREES, CURR_TREES, VELOCITY, VAR_PREC, VAR_TEMP, PREC, TEMP

X-axis: Coefficient (−1.0, −0.5, 0.0, 0.5, 1.0)

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A) Range size rarity (RSR)

B) Phylogenetic endemism index (PEI)

C) RSR−PE relationship