

Community dissimilarity of angiosperm trees reveals deep-time diversification across tropical and temperate forests

Kusumoto, Buntarou; Kubota, Yasuhiro; Baselga, Andrés; Gómez-Rodríguez, Carola; Matthews, Tom; Murphy, Daniel J.; Shiono, Takayuki

DOI:
[10.1111/jvs.13017](https://doi.org/10.1111/jvs.13017)

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Document Version
Peer reviewed version

Citation for published version (Harvard):
Kusumoto, B, Kubota, Y, Baselga, A, Gómez-Rodríguez, C, Matthews, T, Murphy, DJ & Shiono, T 2021, 'Community dissimilarity of angiosperm trees reveals deep-time diversification across tropical and temperate forests', *Journal of Vegetation Science*, vol. 32, no. 2, e13017. <https://doi.org/10.1111/jvs.13017>

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1 Journal: Journal of Vegetation Science

2 Type: Special issue

3

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5 **Community dissimilarity of angiosperm trees reveals deep-time diversification**
6 **across tropical and temperate forests**

7

8 Running head: Regional patterns of community dissimilarity

9

10 Buntarou, Kusumoto^{1,2}

11 Yasuhiro, Kubota³

12 Andrés Baselga⁴

13 Carola Gómez-Rodríguez⁵

14 Thomas J. Matthews^{6,7}

15 Daniel J. Murphy⁸

16 Takayuki, Shiono³

17

18 1. University Museum, University of the Ryukyus, 1 Sembaru, Nishihara, Okinawa, 903-
19 0213 Japan

20 2. Kasuya Research Forest, Faculty of Agriculture, Kyushu University, 394 Tsubakuro,
21 Sasaguri, Fukuoka, 811-2415 Japan (current affiliation)

22 3. Faculty of Science, University of the Ryukyus, 1 Sembaru, Nishihara, Okinawa, 903-
23 0213 Japan

24 4. CRETUS Institute. Department of Zoology, Universidade de Santiago de Compostela,

- 25 c/ Lope Gómez de Marzoa s/n, 15782 Santiago de Compostela, Spain
- 26 5. CRETUS Institute. Department of Functional Biology, Universidade de Santiago de
27 Compostela, c/ Lope Gómez de Marzoa s/n, 15782 Santiago de Compostela, Spain
- 28 6. GEES (School of Geography, Earth and Environmental Sciences) and Birmingham
29 Institute of Forest Research, University of Birmingham, Birmingham, B15 2TT
- 30 7. CE3C – Centre for Ecology, Evolution and Environmental Changes/Azorean
31 Biodiversity Group and Universidade. dos Açores – Depto de Ciências Agrárias e
32 Engenharia do Ambiente, PT-9700-042, Angra do Heroísmo, Açores, Portugal.
- 33 8. Royal Botanic Gardens Victoria, Melbourne 3004, Australia

34

35 Correspondence

36 Buntarou, Kusumoto, University Museum, University of the Ryukyus, 1 Sembaru,
37 Nishihara, Okinawa, 903-0213 Japan

38 Email: kusumoto.buntarou@gmail.com

39

40 **Funding information**

41 Financial support was provided by the Japan Society for the Promotion of Science
42 (no20H03328), Program for Advancing Strategic International Networks to Accelerate
43 the Circulation of Talented Researchers by the Japan Society for the Promotion of Science
44 and the Environment Research and Technology Development fund

45 (JPMEERF20184002) of the Ministry of the Environment, Japan.

46

47 **Abstract**

48 **Question:** To better understand the influence of deep-time diversification on extant plant
49 communities, we assessed how community dissimilarity increases with spatial and
50 climatic distances at multiple taxonomic ranks (species, genus, family, and order) in
51 angiosperm trees. We tested the prediction that the dissimilarity-to-distance relationship
52 should change across taxonomic ranks depending on the deep-time diversification in
53 different biogeographic regions reflecting geohistories and geographical settings.

54 **Location:** Global

55 **Methods:** Using a dataset of plot-based surveys across the globe (861 plots), we compiled
56 a community composition matrix comprising 21,455 species, 2,741 genera, 240 families,
57 and 57 orders. We then calculated Sørensen's pairwise dissimilarity (β_{sor}), and its turnover
58 (β_{sim}) and nestedness (β_{sne}) components, among plots within seven biogeographical
59 regions. Finally, we modelled the relationships between the biotic dissimilarities and the
60 spatial/climatic distances at each taxonomic rank, and compared them among regions.

61 **Results:** β_{sor} and β_{sim} increased with increasing spatial and climatic distance in all
62 biogeographical regions: β_{sim} was dominant in all biogeographical regions in general,
63 while β_{sne} showed relatively high contributions to total dissimilarity in the temperate
64 regions with historically unstable climatic conditions. The β_{sim} -distance curve was more
65 saturated at smaller spatial scales in the tropics than in the temperate regions. In general,
66 the curves became flatter at higher taxonomic ranks (order or family), with exception of
67 Africa, North America, and Australia pointing to region-specific geographical constraints.

68 **Conclusions:** Compositional dissimilarity was generally shaped through the abrupt
69 turnover of species along spatial/climatic gradients. The relatively high importance of the
70 nestedness component in the temperate regions suggests that historical dispersal filters

71 related to extinction/colonization may play important roles. Region-specific changes in
72 the turnover and nestedness components across taxonomic ranks suggest differential
73 imprints of historical diversification over deep evolutionary time in shaping extant
74 diversity patterns in each biogeographical region.

75

76 **Keywords:** angiosperm trees; biogeographical regions; beta diversity; dissimilarity
77 decomposition; dispersal limitation; distance decay; environmental filtering; taxonomic
78 diversity

79

80 **Introduction**

81 The similarity in species composition between local biological communities decreases
82 with spatial/environmental distance. This pattern, known as distance decay of similarity
83 or simply distance-decay, is ubiquitous across organisms and biological systems (Nekola
84 & White 1999; Soininen et al. 2007). The decrease of similarity with distance is
85 mechanistically driven by dispersal limitation (Hubbell 2001) and niche constraints
86 (Gilbert & Lechowicz 2004), mediated through contemporary environmental gradients
87 and evolutionary diversification. Indeed, there are a number of empirical studies that have
88 applied a distance-decay approach to answer different questions related to community
89 assembly processes: niche partitioning along current environmental gradients (Bellier et
90 al. 2014; Trujillo et al. 2019; Cacciatori et al. 2020), historical species sorting through
91 dispersal of organisms (Qian 2009; Saito et al. 2015), dispersal barriers related to
92 geographical constraints (Stuart et al. 2012), differences in dispersal ability among taxa
93 (Gómez-Rodríguez & Baselga 2018; Gómez-Rodríguez et al. 2020) and historical habitat
94 stability (Fitzpatrick et al. 2013). A common theme linking these studies is their use of

95 the shape of distance decay curves as a measure to infer the role of historical and
96 contemporary factors in generating diversity patterns under study (Morlon et al. 2008;
97 Réjou-Méchain & Hardy 2011; Gómez-Rodríguez & Baselga 2018). Rooted in this
98 approach, we here propose that assessing distance decay patterns at multiple taxonomic
99 ranks (species, genus, family, and order) will allow inferring the influence of deep-time
100 diversification on extant plant communities, and its contrasting relevance in tropical and
101 temperate biogeographic regions.

102

103 Angiosperm tree floras in tropical and temperate regions are regarded as evolutionary
104 source and sink, respectively. Many clades that now comprise the tropical flora have been
105 hypothesized to have originated in western Gondwana, which was part of the
106 supercontinent that contained South America and Africa (Fine & Ree 2006; Christenhusz
107 & Chase 2012), and subsequently diversified, after crossing long-standing geographic
108 barriers, among the continents through the Eocene, Oligocene, and Miocene (Hardy et al.
109 2012). In temperate areas, many extant lineages are thought to have originated from the
110 Asian tropical flora (Wen 1999; Donoghue 2008) and afterward have regionally
111 diversified in East Asia, Northern America, and Europe in response to the Plio-
112 Pleistocene global cooling (Fine & Ree 2006). Macroscale diversity patterns of
113 angiosperm trees are characterized by evolutionary radiations within disjunct
114 families/genera in tropical and temperate forests (Gentry 1988; Donoghue & Smith 2004)
115 and taxon-specific selective dispersal/extinction related to paleoclimate changes in
116 temperate regions (Svenning 2003; Eiserhardt et al. 2015).

117

118 The aforementioned studies suggest that the study of taxonomic diversity across lower

119 (species) to higher taxonomic ranks (genus, family, and order) could provide a
120 fundamental basis for better understanding deep-time diversification related to geohistory
121 including paleoclimates. Indeed, correlations of species richness within a higher
122 taxonomic group (family or order) among continents have been shown to represent a
123 consistent biogeographical pattern resulting from diversification at different evolutionary
124 time scales and related to family-specific niche conservatism and global-scale dispersal
125 (Ricklefs & Renner 2012; Munoz et al. 2012; Chen et al. 2012). Therefore, we propose
126 that assessing the distance decay curves of tree angiosperm communities at a range of
127 taxonomic ranks, which provide a surrogate for a macroevolutionary hierarchy (Graham
128 et al. 2016), should reveal any historical imprint on current spatial diversity patterns
129 (Munoz et al. 2014; Yeh et al. 2019). Specifically, regional differences in deep-time
130 diversification should be reflected in the geographical distribution of higher-rank taxa,
131 such as genera, families or orders, through processes such as niche conservatism and
132 dispersal limitation (Kerckhoff et al. 2014; Weiser et al. 2018).

133

134 While similarity indices are commonly used in distance decay studies (Nekola & White
135 1999), compositional dissimilarity (i.e. 1 - similarity) metrics can describe the equivalent
136 patterns and some of these metrics can be partitioned into turnover and nestedness-
137 resultant components (Baselga 2010; Legendre 2014; Soininen et al. 2017). The turnover
138 component represents taxonomic replacement that may be caused by species sorting
139 associated with niche differentiation, evolutionary processes such as radiation and
140 allopatric speciation, and/or dispersal limitation (Leibold et al. 2004; Leprieur et al. 2011).
141 The nestedness component reflects changes in species richness caused by selective
142 species loss or gain that may be associated with recent vicariant events, e.g. insular

143 changes by sea-level rise (Rijsdijk et al. 2014), or a colonization lag after drastic
144 environmental changes such as ice age disturbances (Hortal et al. 2011). Therefore, each
145 component is expected to have an independent relationship with geographical and
146 environmental distance (Antão et al. 2019; Bevilacqua & Terlizzi 2020), and their relative
147 importance may change depending on historical habitat stability (Baselga et al. 2012).
148 The turnover component can be expected to have a steep slope and an asymptotic
149 relationship with spatial distance under strong dispersal limitation, while a flatter
150 relationship would be observed when dispersal limitation is weak or absent (Gómez-
151 Rodríguez et al. 2020). The nestedness component is expected to linearly decrease with
152 increasing spatial/environmental distance under strong dispersal limitation, but to be
153 independent of distance under no dispersal limitation (Gianuca et al. 2016; Antão et al.
154 2019).

155

156 Using a global dataset of forest plots (861 plots), we quantified pairwise compositional
157 dissimilarity of angiosperm tree communities at different taxonomic ranks (species, genus,
158 family, and order) in seven biogeographical regions (South American, African, Indo-
159 Pacific, Australian, North American, West Eurasian, and East Eurasian). We compared
160 the relationship between compositional dissimilarity and spatial/climatic distance (i.e.
161 dissimilarity-to-distance relationship) between the biogeographical regions and between
162 the taxonomic ranks in order to explore the effect of deep-time diversification on the
163 spatial patterns of extant tree communities. Based on the aforementioned reasoning, we
164 tested the following predictions: i) taxonomic turnover will be the dominant component
165 of dissimilarity in historically stable regions (Baselga et al. 2012), such as regions that
166 contain tropical areas; ii) in contrast, the nestedness component will be predominant in

167 historically unstable regions (e.g. temperate areas in higher latitudes) that have
168 experienced extinction and colonization events in response to the expansion/retreat of ice
169 sheets due to paleo-climate changes (Baselga et al. 2012; Soininen et al. 2017); iii) the
170 relationship between the turnover component and spatial/climatic distance will be very
171 steep at short distances, quickly saturating at maximum dissimilarity at the species level
172 due to strong dispersal limitation, while the relationship will become flatter at higher
173 taxonomic ranks. This flattening should be more marked in the regions containing tropical
174 areas because of the older evolutionary age of tropical areas, which should have allowed
175 higher-level taxa to spread across wider areas (i.e. lower dispersal limitation); iv) however,
176 the steep relationship between the turnover component and spatial/climatic distances
177 should remain asymptotic even at higher taxonomic ranks (Cowling et al. 2015) if
178 climatic gradients and/or vicariance have been maintained over large time periods; and v)
179 the nestedness component should show a negative linear relationship with spatial/climatic
180 distance at the species level in historically unstable regions, but be independent from the
181 distances at higher taxonomic ranks due to less dispersal limitation.

182

183 **Materials and Methods**

184 *Angiosperm tree community data*

185 Community composition data of angiosperm tree species were collated from a series of
186 plot-based surveys across the globe (Ulrich et al. 2016; Kubota et al. 2018). The data were
187 compiled from a literature census using various search engines, including Web-Of-
188 Science (Thomson-Reuters, New York, NY, USA) and Google Scholar
189 (<http://scholar.google.com/>), and web-based forest plot databases (e.g. Gentry's data;
190 www.wlbcntr.org/gentry_data.htm). Our dataset only includes plots where the absolute

191 number of individuals was recorded for all tree species at a given census threshold in
192 individual size (i.e. diameter at breast height). The taxonomic classification (species,
193 genus, family, and order) was standardized following The Plant List
194 (<http://www.theplantlist.org/>). Unnamed species and morphospecies identified only to
195 genus were treated as individual species (we confirmed that excluding these species did
196 not meaningfully affect the results of the dissimilarity-to-distance analyses). We excluded
197 naturally/artificially disturbed plots and plots with less than two angiosperm tree species.
198 We also excluded gymnosperms (163 species) from the data. The final dataset comprised
199 861 plots (range = 100–520,000 m²; Fig. 1). Using all plots, we created community
200 composition matrices for four taxonomic ranks: species (21,455 species), genus (2741
201 genera), family (240 families), and order (57 orders). We then subdivided each matrix
202 into seven biogeographical regions. We defined the biogeographical regions using a
203 modified version of Cox et al.'s floral Kingdoms (South American, African, Indo-Pacific,
204 Australian, and Holarctic; Cox et al. 2001): we subdivided the Holarctic Kingdom into
205 North American, West Eurasian and East Eurasian (Fig. 1) because of their differences in
206 geohistory and paleoclimatic conditions. South American, African, Indo-Pacific,
207 Australian regions include tropical areas, while North American, West Eurasian and East
208 Eurasian are temperate areas. In this study, we avoided a more detailed regionalization
209 (e.g. ecoregions) because of the limited number of plots and their spatially
210 inhomogeneous distribution (Fig. 1). More details of the data compilation process are
211 provided in Ulrich et al. (2016) and Kubota et al. (2018).

212

213 Community under-sampling is a potential problem in dissimilarity analyses (Beck et al.
214 2013), especially in cases such as ours where data are taken from multiple sources that

215 have used different census schemes (e.g. plot area and the size criterion for measuring
216 individuals). Therefore, the plots were screened based on sampling completeness: we
217 estimated sample coverage (SC) based on relative species abundance, which is an
218 unbiased estimate represented by the proportion of all detected individuals (Chao et al.
219 2020): SC values are in the range 0 to 1. We filtered the plots at $SC \geq 0.9$ ($n = 661$; Fig.
220 2) and also examined other criteria (≥ 0.7 , 0.8, and 0.85) to test the potential influence of
221 arbitrary choices of SC thresholds. SCs filtered out the incompletely sampled plots which
222 cannot be distinguished by plot-areas or census thresholds, allowing us to include the
223 local communities which were equivalently well sampled (Fig. S1 in Appendix S1).
224 Differences in plot areas and census thresholds are particularly likely to influence
225 absolute abundance differences among the plots (Baselga 2013). Therefore, we used
226 presence/absence information in the dissimilarity analyses.

227

228 *Dissimilarity calculation*

229 Using the subset of equivalently well-sampled plots ($SC \geq 0.7$, 0.8, 0.85, or 0.9), we
230 calculated pairwise dissimilarity between plots within the same biogeographic region (Fig.
231 1) for each taxonomic rank (species, genus, family, and order). We followed Baselga's
232 (2010) beta diversity partitioning framework based on Sørensen dissimilarity (β_{sor}), which
233 was decomposed into turnover (β_{sim}) and nestedness-resultant dissimilarity (β_{sne})
234 components. The compositional dissimilarity of lower taxonomic ranks is inevitably
235 influenced by the dissimilarity of higher taxonomic ranks due to the ranks being
236 hierarchically structured: β_{sne} should be higher at higher taxonomic rank, although β_{sim} is
237 predominant at lower (e.g. species) taxonomic rank. Before analyzing dissimilarity-to-
238 distance relationships, we assessed whether the influence of deep-time diversification on

239 beta diversity is region-specific or not by evaluating correlations between the
240 dissimilarity matrices at different taxonomic ranks for each dissimilarity component (β_{sor} ,
241 β_{sim} , and β_{sne}) in each biogeographical region.

242

243 *Spatial and climatic distances*

244 The spatial distance was defined by the great-circular distance between each pair of plots.
245 We downloaded climatic (Bio-1–19) and elevation data at 30-arc second resolution from
246 the WorldClim ver. 2.1 database (Fick and Hijmans 2017; <http://www.worldclim.org>),
247 overlapped them with the plot coordinates, and assigned the information to each plot. To
248 analyze the effect of climatic distance, we calculated the Euclidean distance in the 20-
249 dimensional space between plots using the variables after standardization (i.e. mean = 0
250 and variance = 1).

251

252 *Statistical analysis*

253 We modeled the relationship between pairwise compositional dissimilarity (β_{sor} , β_{sim} , and
254 β_{sne}) and spatial/climatic distance (i.e. the dissimilarity-distance curve) in each region and
255 for each taxonomic rank using both negative exponential and power-law functions
256 (Nekola & McGill 2014); these functions were fitted using a generalized linear modelling
257 approach with a Gaussian distribution and a log-link function (Millar et al. 2011). Model
258 fit was evaluated using pseudo- r^2 defined as $1 - (\text{model deviance}/\text{null deviance})$
259 (McFadden 1973). The two functions provided similar fits to the data according to
260 Akaike's Information Criterion (Table S1 in Appendix S1), and thus we only present
261 results for the negative exponential model in the main text (see Fig. S2 in Appendix S1
262 for the results using the power-law model). In the negative exponential model, the

263 intercept and slope can be interpreted as the initial dissimilarity (inherent compositional
264 variation among the closest local communities) and the speed of compositional change
265 (or rate of decay), respectively. We tested for differences in the intercepts and slopes of
266 the negative exponential model between biogeographical regions by bootstrapping
267 (multiple comparisons among each pair of regions): we computed 1,000 bootstrap
268 samples for each parameter, calculated the difference in parameter values between two
269 regions, calculated the proportion of positive and negative differences respectively, and
270 used the smaller of these (i.e. upper or lower tails) proportions as a p-value. We also
271 assessed the influence of SC thresholds (SC = 0.7~0.9) on the parameter estimation by
272 evaluating the inter-regional rank correlations for the effect size of parameters between
273 the different SC thresholds. In addition, we fitted a locally estimated scatterplot
274 smoothing curve to visualize changes in the relative importance of the turnover
275 component to overall dissimilarity (β_{sim}/β_{sor}) along the spatial/climatic distance gradients.

276

277 All statistical analyses and graphical works were undertaken using R ver. 3.6.1 (R Core
278 Team 2019) and the following packages: ‘betapart’ (Baselga & Orme 2012) to calculate
279 and decompose pairwise compositional dissimilarity, ‘geosphere’ (Hijmans 2019) to
280 calculate spatial distance, ‘iNEXT’ (Hsieh et al. 2016) for calculating the sampling
281 completeness of each plot, and ‘multcompView’ (Graves et al. 2019) for multiple
282 comparisons.

283

284 **Results**

285 The parameters (especially slopes) of the negative exponential models at lower SC
286 thresholds (0.7–0.85) differed from those estimated using $SC \geq 0.9$, particularly for the

287 climatic distance model (Fig. S3 in Appendix S1). The inter-regional ranking of effect
288 size was consistent for the spatial distance models (i.e. Spearman's rank correlation $\rho =$
289 1), whereas change in the order was observed in the climatic distance model ($\rho = 0.75 \sim$
290 1.00). Therefore, we only show the results using the most strict criteria ($SC \geq 0.9$) for all
291 subsequent analyses.

292

293 Total dissimilarity (β_{sor}), the turnover component (β_{sim}), and the nestedness component
294 (β_{sne}) showed strong correlations between the taxonomic ranks, but with substantial
295 variation in its degree between the regions (Table S2 in Appendix S1), indicating the
296 influence of region-specific deep-time diversification on shaping turnover/nestedness-
297 resultant beta diversity.

298

299 *Total dissimilarity and spatial distance*

300 β_{sor} increased with increasing spatial distance between sites, and this finding was
301 consistent within all biogeographical regions (Fig. 3). The negative exponential model
302 provided a relatively good fit to the dissimilarity-distance pattern at the species level (r^2
303 = 0.34–0.74), but the amount of explained variance generally decreased along taxonomic
304 ranks from genus to order (Fig. 4; $r^2 = 0.08$ –0.66 for genera; $r^2 = 0.01$ –0.55 for families;
305 $r^2 = <0.01$ –0.43 for orders). The intercept and slope of the negative exponential model
306 became smaller at higher taxonomic ranks (Fig. S4 and S5 in Appendix S1).

307

308 *Relationships between turnover and nestedness-resultant components and spatial* 309 *distance*

310 The spatial patterns of β_{sim} were well characterized by the negative exponential model,

311 especially at the species level (Fig. 3a), and exhibited an asymptotic increase with spatial
312 distance (Fig. 4). β_{sim} was the predominant component of β_{sor} in all geographical regions
313 except for sites near to each other in the West Eurasian region (Fig. 5), but the relative
314 importance of β_{sim} decreased along the taxonomic ranks from genus to order. The intercept
315 and slope of the β_{sim} -distance curve were smaller in the temperate regions (North
316 American, West Eurasian, and East Eurasian) where the β_{sim} at species level slowly
317 saturated over the entire geographical extent at the species level (Fig. S4 and S5). In
318 contrast, the intercept and/or slope of the β_{sim} -distance curve was larger in the regions
319 containing tropical areas (South American, African, and Indo-Pacific) where the β_{sim} at
320 species level saturated at a smaller geographical extent (Fig. 4). The β_{sim} values became
321 lower, and the shape of the curve became flatter, at higher taxonomic ranks in the South
322 American and Indo-Pacific regions (Fig. 4). In contrast, the slope of the curve was
323 relatively steep even at the family and order levels in the African, Australian, and North
324 American regions (Fig. 4 and S5).

325

326 β_{sne} was poorly explained by the negative exponential model (Fig. 3a); the relationship
327 between β_{sne} and spatial distance was mostly flat, while a negative linear relationship was
328 found at the species level in the Holarctic regions, especially in West Eurasian (Fig. 4 and
329 S5). At the species level, β_{sne} accounted for a major proportion of β_{sor} only within sites
330 near to each other in the Holarctic regions (Fig. 5). However, the relative importance of
331 β_{sne} increased at higher taxonomic ranks even in the regions containing tropical areas,
332 especially in South American (Fig. S4).

333

334 *Relationships between taxonomic dissimilarity and climatic distance*

335 In general, the increase in pairwise taxonomic dissimilarity (β_{sor} , β_{sim} , and β_{sne}) with
336 climatic distance was similar to that observed with spatial distance (Fig. S6-S8 in
337 Appendix S1). The negative exponential models fitted using climatic distance had slightly
338 better explanatory power than the models fitted using spatial distance for most regions
339 and ranks, but provided worse fits at the species and genus levels in the Indo-Pacific,
340 African, West Eurasian , and Australian regions (Fig. 3). β_{sor} and β_{sim} exhibited steep
341 slopes and quick asymptotic saturation in all regions at the species level, while the
342 saturation was relatively slower in Australian and the temperate regions compared to the
343 South American, African and Indo-Pacific regions (all containing tropical areas) (Fig. S6).
344 The slope of the β_{sim} -distance curve was smaller at higher taxonomic ranks, but it
345 remained relatively high even at the family and order levels in the African and North
346 American regions (Fig. S6 and S8). The relative importance of β_{sim} to β_{sor} increased with
347 the climatic distance, especially in the West Eurasian at the species level, while the pattern
348 was less clear at the family and order levels (Fig. 5).

349

350 **Discussion**

351 Our results reveal substantial differences in patterns of variation in local angiosperm tree
352 communities across different biogeographic regions, with contrasting effects of deep time
353 processes of diversification between the biogeographical regions with and without
354 tropical areas. The overall dissimilarity of angiosperm communities between forest plots
355 was found to increase with spatial and climatic distance (a distance decay pattern) in all
356 biogeographical regions, and was mainly driven by the turnover component at lower
357 taxonomic ranks (species and genus), although its relative contribution decreased at
358 higher taxonomic ranks (family and order). However, these patterns showed region-

359 specific variations. The regions containing tropical areas (South American, African, and
360 Indo-Pacific) showed steeper increases in total dissimilarity and the turnover component
361 with spatial/climatic distances compared with the temperate regions (North American,
362 West Eurasian, and East Eurasian), while Australian region showed intermediate trends
363 Fig. 4, S5, S6, and S8).

364

365 The fast increase in dissimilarity in regions with tropical areas was mostly associated with
366 the turnover component, indicating a fast compositional replacement along spatial and
367 climatic distance gradients, especially at the species level. This is in line with previous
368 studies of tropical forests (Condit et al. 2002; Tuomisto et al. 2003; Pennington et al.
369 2009; Trujillo et al. 2019) that found an important role of environmental filtering and
370 dispersal limitation in generating species turnover. The decreasing compositional
371 dissimilarity with increasing taxonomic rank (from species, genus, family to order) and
372 the flattening of the dissimilarity-distance curves may reflect the deeper evolutionary
373 history of tropical forests (Munoz et al. 2014). Specifically, orders and families of
374 angiosperm trees probably radiated globally across phylogenetic niche space (Hubbell
375 2001) under warmer climates through the Cretaceous to the Paleogene, and then
376 subsequently species and genera within those regions diversified in response to different
377 drivers, including geographical isolation and tropical-specific historical habitat stability
378 through the Cenozoic (Fine & Ree 2006). Indeed, our results showed the highest species
379 turnover rates in South American region (Fig. 4), providing a support for the view of the
380 region as an evolutionary “engine” of plant diversity (Antonelli et al. 2015). Moreover,
381 the turnover–distance relationships were flatter at the higher taxonomic ranks, suggesting
382 that the persistence or accumulation (dispersal) of old lineages (Coronado et al. 2015)

383 plays a role in generating the high degrees of overall dissimilarity across the taxonomic
384 ranks (Pennington et al. 2009). This interpretation is also supported by the higher
385 contribution of the nestedness component at the family and order levels in South
386 American region than in the other regions (Fig. 4 and 5). Meanwhile, some regions (e.g.
387 African, Australian, and North American regions), regardless of whether they include
388 tropical areas, exhibited a persistent steep dissimilarity-distance curve in regard to the
389 turnover component (Fig. S5), at both the family and order levels. This suggests
390 taxonomic diversification at deeper time scales (Prinzing et al. 2001) and/or the
391 persistence of different and older lineages in isolated sites (Tiffney & Manchester 2001;
392 Tolley et al. 2011) as a result of geohistorically related biogeographical constraints, e.g.
393 elevational gradients in the tropics (Qian & Ricklefs 2016) or climatic refugia (Tiffney &
394 Manchester 2001; Byrne 2008; Tolley et al. 2011).

395

396 In contrast, North American and both West and East Eurasian regions, comprising
397 temperate floras, showed a slower saturation in total dissimilarity and the turnover
398 component with spatial and climatic distances, and a relatively higher contribution of the
399 nestedness component in shaping the dissimilarity patterns of angiosperm tree
400 communities than in the remaining regions, all of them containing tropical areas (Figs. 3,
401 S4 and S5). In addition, the nestedness component was less dependent on either spatial
402 or climatic distance in these regions. These findings are consistent with the findings of
403 previous studies of the temperate biota (Keil et al. 2012; Lenoir et al. 2012; Fitzpatrick et
404 al. 2013; Soininen et al. 2017; Antão et al. 2019), which suggest that the nestedness
405 component reflects the signal of historical processes that become more evident under
406 unstable and harsh environmental conditions in higher latitudes (Baselga et al. 2012).

407 Indeed, temperate angiosperm tree assemblages have been shown to have experienced
408 genus-level local extinction in response to Quaternary glaciations and/or global cooling
409 in the Holarctic regions (Svenning 2003; Eiserhardt et al. 2015; Shiono et al. 2018),
410 supporting the role of historical dispersal filters in shaping the nestedness-resultant
411 dissimilarity of angiosperm tree communities in temperate forests.

412

413 In general, the negative exponential models fitted using spatial- and climatic-distance had
414 comparable explanatory power and were similar in terms of the shape of the dissimilarity-
415 distance curves (Fig. 3, 4, and S6), suggesting that environmental filtering and/or
416 dispersal limitation have important roles in driving compositional turnover (Trujillo et al.
417 2019). However, a relatively lower explanatory power for the climatic distance model (i.e.
418 it explained 11% less variance than the spatial distance model) was observed in the Indo-
419 Pacific at the species level (Fig. 3). This suggests that taxonomic turnover in this region
420 is likely to be driven by dispersal limitation and/or other geographical factors, such as the
421 spatial separation between islands and continental landmasses, and variation in island
422 sizes (Ibanez et al. 2018). Moreover, the Indo-Pacific tropical forests are phylogenetically
423 similar to the East Eurasian temperate forests (Kubota et al. 2018), suggesting the regional
424 divergence of the temperate flora originating from the Asian tropics (out-of-Asia
425 hypothesis; Donoghue 2008). Therefore, in the East Eurasian region, the highest
426 contribution of the turnover component compared with the other Holarctic regions (Fig.
427 4-5, S4-S5) may also be promoted by *in situ* diversification of angiosperm trees through
428 geographical vicariance related to high insularity and highly dissected topography (Xiang
429 et al. 2004; Kubota et al. 2014).

430

431 One potential caveat of analyzing assemblage dissimilarity between local plots is that
432 species occurrence data obtained in vegetation plots might potentially suffer from
433 sampling incompleteness (Beck et al. 2013). To deal with sampling bias, we computed
434 sampling completeness using species relative abundance in individual plots (Chao et al.
435 2020) and assessed the spatial patterns of taxonomic dissimilarity by only analyzing
436 nearly completely sampled plots (sampling completeness $\geq 90\%$). Loosening of the SC
437 threshold down to 70% did not alter the general dissimilarity trends (Fig. S3), but it did
438 cause a slight reduction in the slope of the dissimilarity-spatial distance curve in some
439 regions. This suggests that including incomplete plots in which common species are likely
440 to be well sampled but rare species are likely to be missed may overestimate similarity
441 among local communities. Another potential bias is related to the shortfall of taxonomic
442 knowledge, especially at higher taxonomic levels (family or order). Indeed, the taxonomic
443 resolution of lineages differs among clades and regions, and in particular, is poorly
444 resolved for the tropics (Laffan 2018). For example, in Malesia, it is estimated that only
445 29% (of approximately 45,000) vascular plant species have been comprehensively treated
446 taxonomically in the Flora Malesiana, and while there are additional taxonomic
447 publications and treatments for this region, these are fragmented and overall the flora very
448 much remains incompletely known and described (Middleton et al 2019). From the
449 viewpoint of filling gaps in our knowledge of plant biodiversity, further taxonomic and
450 systematic studies are needed to better understand the relative role of evolutionary events
451 at different time scales in shaping the taxonomic dissimilarity of woody angiosperms
452 globally.

453

454 **Concluding remarks**

455 As with many macroecological patterns, the increase in dissimilarity with distance can be
456 studied at multiple spatial scales (Nekola & White 1999; Wang et al. 2011; Fitzpatrick et
457 al. 2013; Olivier & van Aarde 2014; Kasel et al. 2017; Chun & Lee 2017; Trujillo et al.
458 2019). There have been many studies focused on the dissimilarity-distance pattern of
459 vegetation that measure beta diversity at different spatial extents, from local scales
460 (Morlon et al. 2008; Wang et al. 2011; Wang et al. 2018) through to regional (Condit et
461 al. 2002; Tuomisto et al. 2003) and global-scales (Fitzpatrick et al. 2013; König et al.
462 2017). Despite these previous studies of beta diversity at local, regional and global scales,
463 there are few examples of studies that use local community data to analyze large-scale
464 dissimilarity patterns (but see Myers et al. 2013; Kubota et al. 2018). In addition, beta
465 diversity patterns at multiple taxonomic scales were unexplored though it is potentially
466 informative to understand the imprints of deep-time diversification in extant diversity
467 patterns. The present study contributes to filling this knowledge gap by showing how
468 pairwise taxonomic dissimilarity and its components (calculated within biogeographical
469 regions) at different taxonomic ranks change across biogeographical regions through the
470 analysis of local tree communities across the globe. Our findings of taxonomic
471 dissimilarity among angiosperm tree communities, which showed region-specific
472 variations in the dissimilarity-to-distance relationships across taxonomic ranks, reveal the
473 geographical pattern of diversification that is mechanistically driven by niche assembly
474 at higher taxonomic ranks (Ricklefs & Renner 2012), and global/regional-scale dispersal
475 limitation (Hubbell 2001).

476

477 To conclude, our results generally supported our five predictions. First, taxonomic
478 turnover increased faster with spatial/climatic distance in those biogeographical regions

479 encompassing the tropics, i.e., in those areas where climatic conditions have been more
480 stable historically, compared to the temperate regions. Second, in general, the turnover
481 component decreased and its relationship with spatial/climatic distance became flatter at
482 higher taxonomic ranks (order or family); this may reflect the evolutionary histories of
483 angiosperm trees associated with region-specific geohistories in the tropics and
484 extratropics. However, and third, we also found relatively steep turnover patterns with
485 spatial/climatic distances in African, North American, and Australian regions at family
486 and/or order levels, which may be related to region-specific geographical constraints.
487 Fourth, the nestedness component was generally smaller than the turnover component
488 and almost independent from spatial/climatic distance in the regions containing tropical
489 areas at the species level. However, and fifth, the nestedness component comprised a
490 relatively larger proportion of overall dissimilarity in the Holarctic regions, which are
491 often more historically unstable regions. In sum, the relationship between pairwise
492 dissimilarity and distance for angiosperm tree communities at species, genus, family, and
493 order levels illustrates the importance of geographical filters associated with historical
494 and contemporary factors, in shaping regional beta diversity patterns of angiosperm trees.

495

496 **Acknowledgements**

497 We are grateful to members of the data management team of the Kubota-lab, the
498 University of the Ryukyus, for their support with data compilation. We thank Dr. Meelis
499 Pärtel for inviting us to contribute to the Special Feature.

500

501 **Data availability statement**

502 The relevant data used in this study is available from Zenodo (doi:
503 10.5281/zenodo.4572404).

504

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770

771 **Supporting information**

772 **Appendix S1.** Supplementary tables and figures

773

774

775 **Figure legends**

776 **Fig. 1** The global distribution of forest plots across seven biogeographical regions: South
777 American, African, Indo-Pacific, Australian, North American, West Eurasian, and East
778 Eurasian. Plots were colored by sampling completeness (SC).

779

780 **Fig. 2** Histograms for sampling completeness evaluated as sampling coverage (SC) per
781 community in seven biogeographical regions (South American, African, Indo-Pacific,
782 Australian, North American, West Eurasian, and East Eurasian). The equivalently well-
783 sampled plots ($SC \geq 0.9$) were used in the dissimilarity-distance analyses.

784

785 **Fig. 3** Pseudo r^2 of negative exponential models for the relationships between taxonomic
786 dissimilarity and (a) geographical and (b) climatic distance per taxonomic rank [species
787 (SP), genus (GN), family (FM) and order (OR)] in each biogeographical region: South
788 American (SA), African (AF), Indo-Pacific (IP), Australian (AU), North American (NA),
789 West Eurasian (WE) and East Eurasian (EE). Total dissimilarity matrices (β_{sor}) were
790 decomposed into turnover (β_{sim}) and nestedness (β_{sne}) components. Dashed line represents
791 5% for a visual guide.

792

793 **Fig. 4** The relationship between pairwise dissimilarity and spatial distance (dissimilarity
794 -to-distance relationship) as fitted by a negative exponential model from presence-
795 absence composition data at the species, genus, family and order levels, in each
796 biogeographical region: South American (SA), African (AF), Indo-Pacific (IP),
797 Australian (AU), North American (NA), West Eurasian (WE) and East Eurasian (EE).

798 Total dissimilarity matrices (β_{sor}) were decomposed into the turnover (β_{sim}) and
799 nestedness-resultant (β_{sne}) components.

800

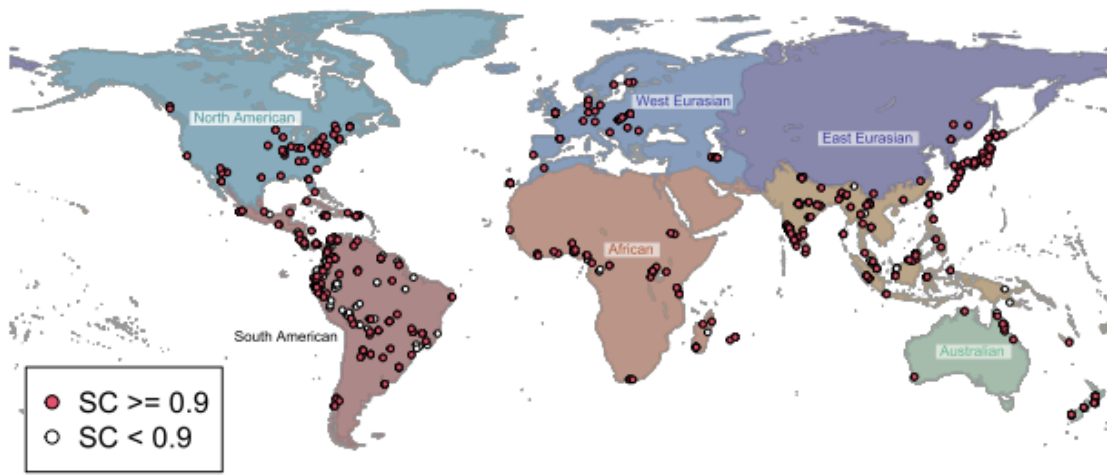
801 **Fig. 5** Changes in the relative importance of the turnover component to total dissimilarity
802 ($\beta_{\text{sim}}/\beta_{\text{sor}}$) along geographical (left) and climatic (right) distance per taxonomic rank
803 [species (SP), genus (GN), family (FM) and order (OR)] in each biogeographical region:
804 South American (SA), African (AF), Indo-Pacific (IP), Australian (AU), North American
805 (NA), West Eurasian (WE) and East Eurasian (EE). Climatic distance is calculated as the
806 Euclidian distance between sites based on 19 bioclim variables and elevation. Locally
807 estimated scatterplot smoothing curves (LOESS) are shown.

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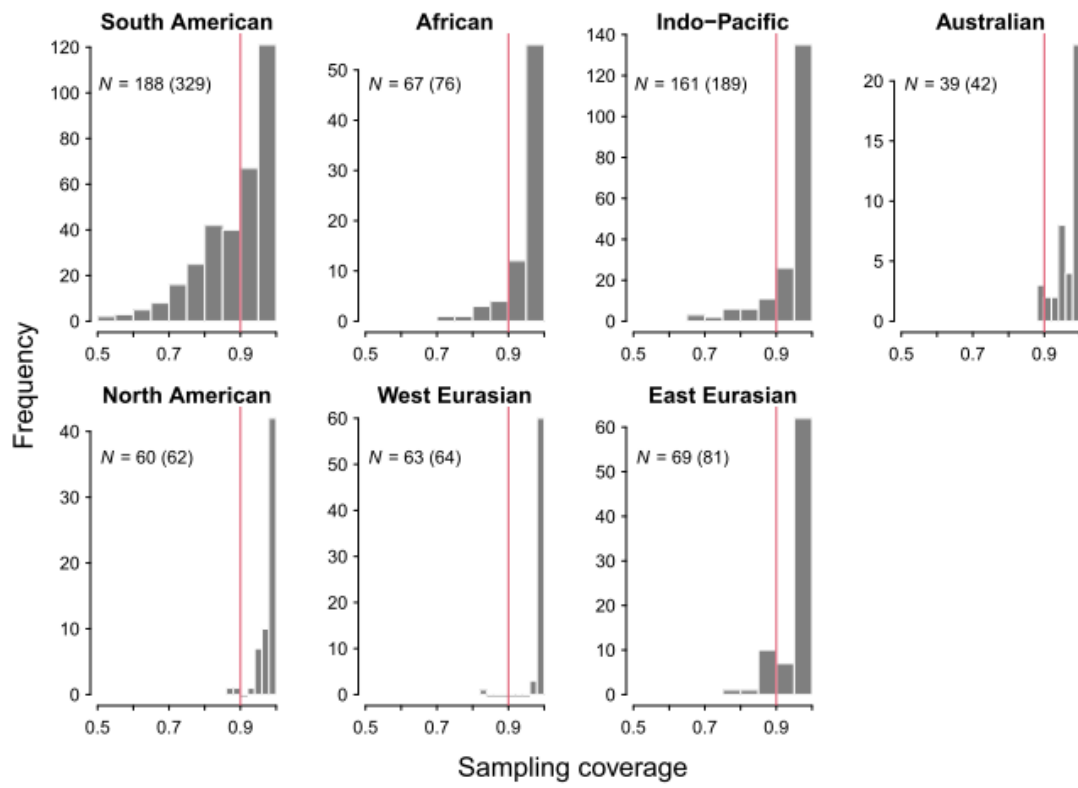
811 **Fig. 1**



812

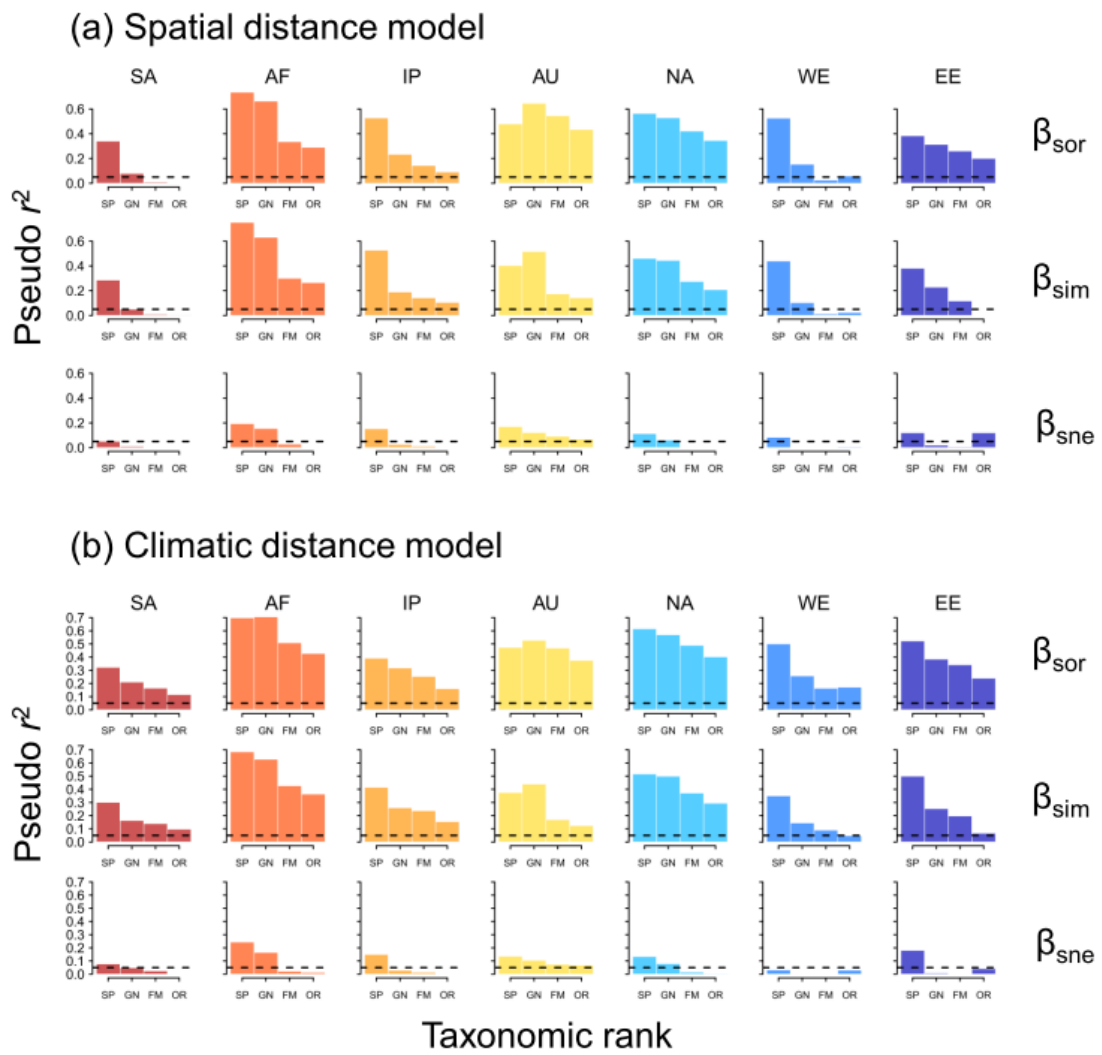
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814 **Fig. 2**

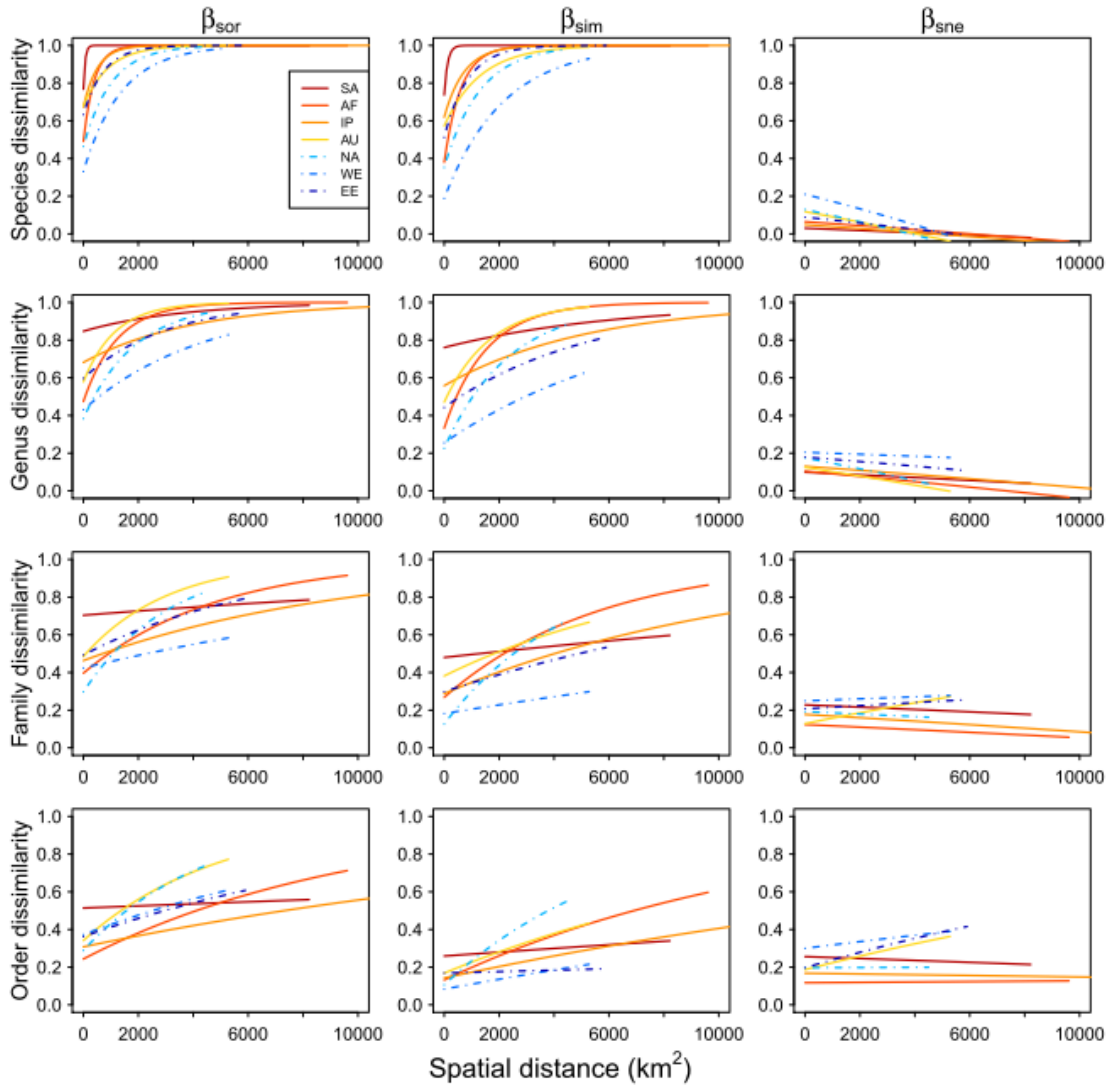


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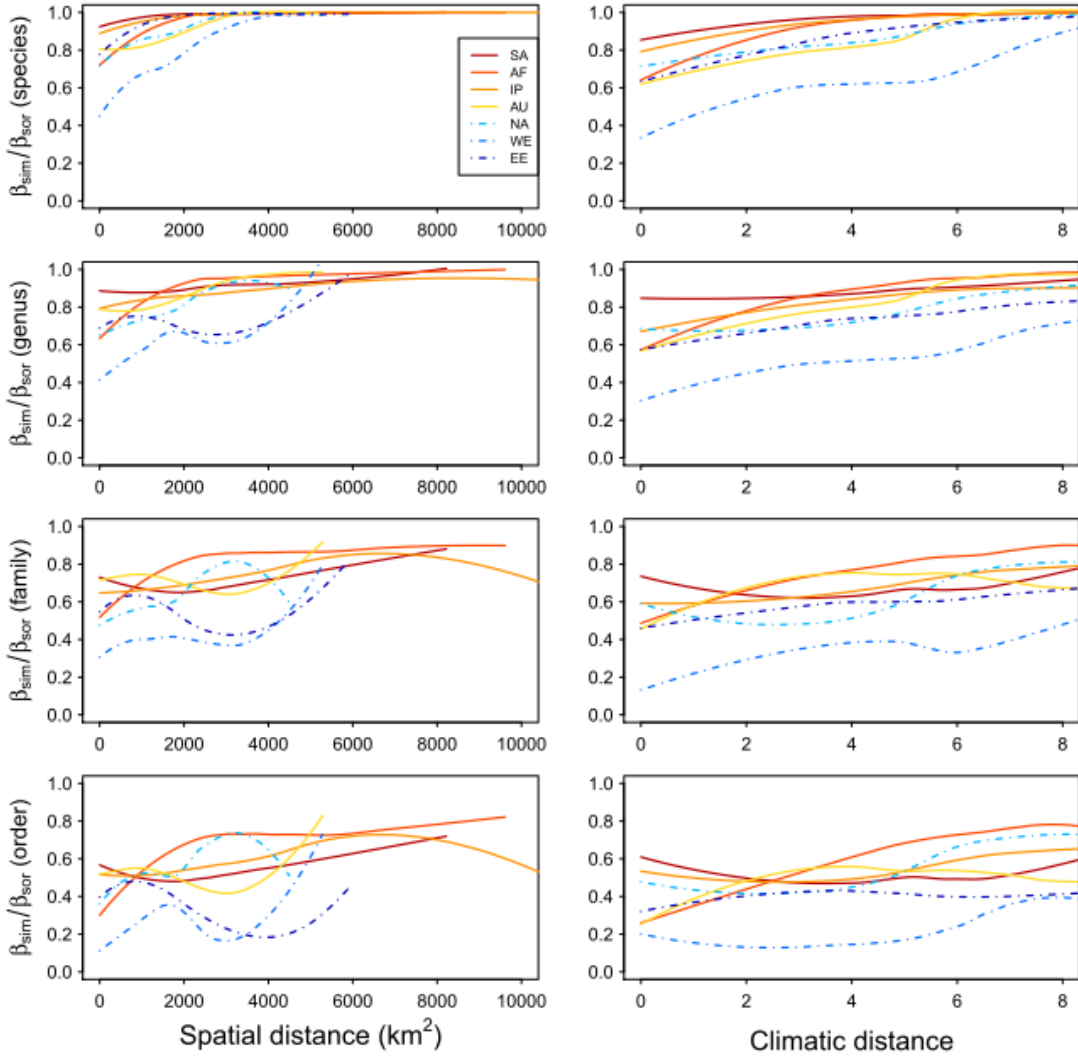


820 **Fig. 4**



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