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Phylogenetic linkages between composition and structure of tree communities shed light on historical processes influencing tropical rainforest diversity

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| Abstract: | The separation of the Neotropics, Afrotropics and Madagascar has subjected their biotas to different histories. Based on current knowledge of these histories, we developed the following predictions about the |

phylogenetic structure and composition of rainforest tree communities: (Hypothesis 1) isolation of Gondwanan biotas generated differences in phylogenetic composition among biogeographical regions; (H2) major Cenozoic extinction events led to lack of phylogenetic structure in Afrotropical and Malagasy communities; (H3) greater angiosperm diversification in the Neotropics led to greater phylogenetic clustering there than elsewhere; (H4) phylogenetic overdispersion is expected near the Andes due to the co-occurrence of magnoliids tracking conserved habitat preferences and recently diversified eudicot lineages. Using abundance data of tropical rainforest tree species from 94 communities in the Neotropics, Afrotropics and Madagascar, we computed net relatedness index (NRI) to assess local phylogenetic structure, i.e. phylogenetic clustering vs. overdispersion relative to regional species pools, and principal coordinates of phylogenetic structure (PCPS) to assess variation in phylogenetic composition across communities. We observed significant differences in phylogenetic composition among biogeographical regions (agreement with H1). Overall phylogenetic structure did not differ among biogeographical regions, but results indicated variation from Andes to Amazon. We found widespread phylogenetic randomness in most Afrotropical and all Malagasy communities (agreement with H2). Most of Central Amazonian communities were phylogenetically random, although some communities presented phylogenetic clustering (partial agreement with H3). We observed phylogenetic overdispersion near the Andes (agreement with H4). We identified lineages linked to shifts in local phylogenetic structure among communities. We were able to identify how differences in lineage composition are related to local phylogenetic co-occurrences across biogeographical regions that have been undergoing different climatic and orographic histories during the past 100 Myr. We observed imprints of history following Gondwana breakup on phylobetadiversity and local phylogenetic structure of rainforest tree communities in the Neotropics, Afrotropics and Madagascar.

1 Original research

2

3 **Phylogenetic linkages between composition and structure of tree**
4 **communities shed light on historical processes influencing tropical**
5 **rainforest diversity**

6

7 Marcos B. Carlucci^{1,2*}, Guilherme D. S. Seger¹, Douglas Sheil^{3,4,5}, Iêda L. Amaral⁶, George
8 B. Chuyong⁷, Leandro V. Ferreira⁸, Ulisses Galatti⁸, Johanna Hurtado⁹, David Kenfack¹⁰,
9 Darley C. Leal⁸, Simon L. Lewis^{11,12}, Jon C. Lovett¹¹, Andrew R. Marshall¹³, Emanuel
10 Martin¹⁴, Badru Mugerwa⁴, Pantaleo Munishi¹⁵, Átila Cristina A. Oliveira⁶, Jean Claude
11 Razafimahaimodison¹⁶, Francesco Rovero^{14,17}, Moses N. Sainge¹⁸, Duncan Thomas¹⁹, Valério
12 D. Pillar¹ & Leandro D. S. Duarte¹

13

14 ¹ Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio Grande do Sul, Av Bento
15 Gonçalves 9500, CP 15007, Porto Alegre, RS 91501-970, Brazil. ² Programa de Pós-Graduação em
16 Ecologia e Evolução, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Goiânia, GO
17 74690-900, Brazil. ³ Center for International Forestry Research, PO Box 0113 BOCBD, Bogor
18 16000, Indonesia; ⁴ Institute of Tropical Forest Conservation, Mbarara University of Science and
19 Technology, PO Box, 44, Kabale, Uganda; ⁵ School of Environmental Science and Management,
20 Southern Cross University, PO Box 157, Lismore, NSW 2480, Australia; ⁶ Instituto Nacional de
21 Pesquisas da Amazônia (INPA), Av André Araújo 2936, CP 478, Manaus, AM 69060-011, Brazil; ⁷
22 Department of Botany and Plant Physiology, University of Buea, PO Box 63 Buea, SWP Cameroon; ⁸
23 Museu Paraense Emílio Goeldi, Av Perimetral 1901, Belém, PA 66077-530, Brazil; ⁹ Organization for

24 *Tropical Studies, La Selva Biological Station, Sarapiquí, Costa Rica;* ¹⁰ *Center for Tropical Forest*
25 *Science, Smithsonian Institution Global Earth Observatory, Smithsonian National Museum of Natural*
26 *History, West Loading Dock, 10th and Constitution Ave, NW Washington, DC 20560-0166, USA;* ¹¹
27 *School of Geography, University of Leeds, Leeds, LS2 9JT , UK;* ¹² *Department of Geography,*
28 *University College London, London, WC 1E 6BT, UK;* ¹³ *Environment Department, University of*
29 *York, Heslington, York, YO10 5DD, UK;* ¹⁴ *College of African Wildlife Management Mweka,*
30 *Department of Wildlife Management, P.O. Box 3031 Moshi, Tanzania;* ¹⁵ *Sokoine University of*
31 *Agriculture (SUA), Faculty of Forestry and Nature Conservation, Department of Forest Biology, PO*
32 *Box 3010, Morogoro, Tanzania;* ¹⁶ *Centre ValBio, BP 33 Ranomafana Ifanadiana, 312 Fianarantsoa,*
33 *Madagascar;* ¹⁷ *Tropical Biodiversity Section, MUSE - Museo delle Scienze, Corso del Lavoro e della*
34 *Scienza 3, 38123, Trento, Italy;* ¹⁸ *WWF-CFP Cameroon/Korup Forest Dynamics Plot (KFDP),*
35 *Tropical Plant Exploration Group (TroPEG), P.O. Box 18 Mundemba, Ndian, South West Region,*
36 *Cameroon;* ¹⁹ *Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon*
37 *97331, USA;*

38

39

40 * E-mail: marcos.carlucci@gmail.com

41 **Abstract**

42 The separation of the Neotropics, Afrotropics and Madagascar has subjected their biotas to
43 different histories. Based on current knowledge of these histories, we developed the following
44 predictions about the phylogenetic structure and composition of rainforest tree communities:

45 (Hypothesis 1) isolation of Gondwanan biotas generated differences in phylogenetic
46 composition among biogeographical regions; (H2) major Cenozoic extinction events led to
47 lack of phylogenetic structure in Afrotropical and Malagasy communities; (H3) greater
48 angiosperm diversification in the Neotropics led to greater phylogenetic clustering there than
49 elsewhere; (H4) phylogenetic overdispersion is expected near the Andes due to the co-
50 occurrence of magnoliids tracking conserved habitat preferences and recently diversified
51 eudicot lineages. Using abundance data of tropical rainforest tree species from 94
52 communities in the Neotropics, Afrotropics and Madagascar, we computed net relatedness
53 index (NRI) to assess local phylogenetic structure, i.e. phylogenetic clustering vs.
54 overdispersion relative to regional species pools, and principal coordinates of phylogenetic
55 structure (PCPS) to assess variation in phylogenetic composition across communities. We
56 observed significant differences in phylogenetic composition among biogeographical regions
57 (agreement with H1). Overall phylogenetic structure did not differ among biogeographical
58 regions, but results indicated variation from Andes to Amazon. We found widespread
59 phylogenetic randomness in most Afrotropical and all Malagasy communities (agreement
60 with H2). Most of Central Amazonian communities were phylogenetically random, although
61 some communities presented phylogenetic clustering (partial agreement with H3). We
62 observed phylogenetic overdispersion near the Andes (agreement with H4). We identified
63 lineages linked to shifts in local phylogenetic structure among communities. We were able to
64 identify how differences in lineage composition are related to local phylogenetic co-

65 occurrences across biogeographical regions that have been undergoing different climatic and
66 orographic histories during the past 100 Myr. We observed imprints of history following
67 Gondwana breakup on phylobetadiversity and local phylogenetic structure of rainforest tree
68 communities in the Neotropics, Afrotropics and Madagascar.

For Review Only

69 Introduction

70 Historical factors influence the formation of regional species pools (MacArthur 1972,
71 Ricklefs 1987, Cracraft 1994), and, consequently, the structure of the local communities
72 assembled from them (Parmentier and Hardy 2009, Leibold et al. 2010, Lessard et al. 2012a,
73 Gerhold et al. 2015). Studies have inferred macroevolutionary processes structuring local
74 communities by evaluating how phylogenetic patterns differ across biogeographical barriers
75 and habitats (Graham et al. 2009, Kooyman et al. 2011, Fine and Kembel 2011, Kissling et al.
76 2012, Lessard et al. 2012b, Eiserhardt et al. 2013, Hawkins et al. 2014). Although these
77 studies demonstrated that historical processes likely determine community structure,
78 understanding the linkages between local phylogenetic structure and the variation in
79 phylogenetic composition among regions remains a challenge. Commonly used measures of
80 community phylogenetic structure enable the assessment of local phylogenetic clustering and
81 overdispersion relative to a regional species pool (Webb et al. 2002), but give no information
82 on which lineages are associated with phylogenetic clustering or overdispersion (Duarte
83 2011). For instance, two communities with the same phylogenetic structure measured using a
84 given metric may have very different species composition (Graham et al. 2009). Hence,
85 studies usually infer historical processes affecting phylogenetic structure by evaluating both
86 taxonomic beta diversity (differences in species composition among communities) and
87 phylobetadiversity (differences in lineage composition among communities), which links
88 current phylogenetic structure and macroevolutionary processes for certain lineages (Graham
89 and Fine 2008, Graham et al. 2009). One way to link phylogenetic structure and composition
90 is to use both the net relatedness index (NRI; Webb et al. 2002) as a measure of local
91 phylogenetic structure and PCPS analysis (phylogenetic coordinates of phylogenetic
92 structure; Duarte 2011, Duarte et al. 2012) to measure phylobetadiversity and identify the

93 most common lineages in sets of communities. PCPS analysis synthesises phylobetadiversity
94 into ordination vectors (PCPS) representing variation in phylogenetic composition across
95 communities. Thus, by using PCPS, it is possible to identify the lineages linked to shifts in
96 phylogenetic structure values (NRI) across biogeographical barriers, as those created by
97 vicariance (see the methods for more information on this approach). Observing how lineage
98 composition differences among communities relate to phylogenetic co-occurrences may
99 improve the inference of major macroevolutionary influences on current species co-
100 occurrences (Gerhold et al. 2015).

101 In this study, we compute NRI and PCPS values across the Neotropics, Afrotropics
102 and Madagascar and integrate them to test biogeographical hypotheses related to the
103 fragmentation of Gondwana and onward history. The Gondwanan vicariance started during
104 the Cretaceous, ca. 112-106 Ma (Wilf et al. 2013), separating the Neotropical, Afrotropical,
105 and Malagasy biotas. South America remained connected to Antarctica and Australia through
106 the Early-Middle Eocene (Wilf et al. 2013). The Gondwanan breakup coincided with the early
107 evolution of many extant lineages of angiosperms, and with the first appearance of the
108 arboreal habit among angiosperms (Feild and Arens 2007). The major lineages of
109 angiosperms, namely magnoliids, eudicots and monocots, appeared over a period of ca. 15
110 Ma (Aptian-Albian) from ca. 125 to 110 Ma (Feild and Arens 2007), so that the ancestors of
111 these lineages should have been present in the early flora of the two newly developing
112 continents.

113 Among angiosperms, magnoliids form a major clade that diverged before monocots
114 and eudicots (APG 2009). Magnoliids are considered “southern wet forest survivors” because
115 they currently co-occur with other “ancient” clades (e.g. Proteaceae) in forests that are similar
116 in composition to the Gondwanan rainforests they were part of during the Cretaceous

117 (Kooyman et al. 2014). Today, these Gondwana-like rainforests are found in the South
118 American highlands (Segovia and Armesto 2015). Magnoliid species usually bear conserved
119 traits of early angiosperms (from ca. 120 Ma) that limit water usage, which led to overall
120 lower photosynthetic capacity compared to eudicots (Feild et al. 2002, Boyce et al. 2009,
121 Brodribb and Feild 2010). Habitat (and biome) tracking (sensu Ackerly 2003) is a major
122 tendency among plants due to phylogenetic niche conservatism (Crisp et al. 2009), because,
123 under major changes of regional conditions, plants more often move to other places with
124 similar conditions than quickly adapt to the changing environment (Donoghue 2008). Thus
125 magnoliids today are mostly associated with tropical upland, shady and wet forests (Feild and
126 Arens 2007), which suggests these plants track habitats across space and time (Duarte 2011,
127 Debastiani et al. 2015).

128 The Gondwanan vicariance led to increasingly isolated biotas, subject to different
129 climatic and orographic histories, which likely led to differences in net diversification
130 (speciation minus extinction) of angiosperm clades between the Neotropics, Afrotropics and
131 Madagascar (Gentry 1982, Parmentier et al. 2007, Vences et al. 2009, Ghazoul and Sheil
132 2010, Morley 2011). The separation of Gondwanan landmasses and their biotas increased
133 during the Cenozoic (Morley 2011), when South America, Africa and Madagascar became
134 totally separated from Antarctica and Australia (Wilf et al. 2013). A recent phylogeny based
135 on molecular and fossil data implies a major diversification of angiosperm lineages after the
136 Cretaceous-Paleogene (KPB) boundary (Silvestro et al. 2015). In the Neotropics, the
137 persistence of a wet climate has maintained large areas of continuous rainforest across time,
138 which promoted high speciation (and low extinction) rates, especially of monocots and
139 eudicots (Gentry 1982, Colinvaux et al. 2000, Maslin et al. 2005, Morley 2011, Kissling et al.
140 2012, ter Steege et al. 2013). The accumulation of species in the Neotropics is consistent with

141 the time-integrated species area effect (Fine and Ree 2006). By contrast, the role of major dry
142 periods affecting floristic composition during the glacial ages of the late Cenozoic was much
143 greater in the Afrotropics than in the Neotropics (Colinvaux et al. 2000, Parmentier et al.
144 2007, Ghazoul and Sheil 2010). These dry periods led to rainforest retraction, which caused
145 major extinctions during the Cenozoic across the Afrotropics (Parmentier et al. 2007, Morley
146 2011). These climatic fluctuations reduced habitat availability across time, which reduced
147 speciation rates in the Afrotropics compared to the Neotropics (Kissling et al. 2012).
148 Similarly, major climatic fluctuations affected the diversification of the insular Malagasy flora
149 (Vences et al. 2009), where time-integrated species-area effect might have been even more
150 intense than in the Afrotropics considering the even smaller availability of rainforest area
151 through time.

152 Within the Neotropics, the uplift of the Andes during the Cenozoic (from ca. 40 Ma)
153 influenced the recent diversification of many taxa (e.g. hummingbirds; Graham et al. 2009),
154 including the rapid diversification of many angiosperm lineages (Gentry 1982, Richardson et
155 al. 2001, Hughes and Eastwood 2006) by creating a spatial configuration of habitats that
156 promoted speciation, such as island-like habitats isolated by valleys of different
157 environmental conditions (Hughes and Eastwood 2006). Furthermore, given the preference of
158 magnoliids for tropical upland forests (Feild and Arens 2007), mountain ranges such as the
159 Andes are also likely to serve as refugia for magnoliid species tracking habitat preferences,
160 thus reducing extinction rates. The net result of the effect of historical climatic and orographic
161 differences between the Neotropics, Afrotropics and Madagascar was higher net
162 diversification of angiosperms in the Neotropics (Gentry 1982, Parmentier et al. 2007).

163 Considering the higher angiosperm diversification rates in the Neotropics compared
164 to the Afrotropics and Madagascar and their distinct biogeographical histories, we expect to

165 find major differences in phylogenetic composition among these regions (Hypothesis 1, Table
166 1). Because of Cenozoic major extinction events likely have decreased net diversification in
167 the Afrotropics and Madagascar, there should be widespread random phylogenetic structure in
168 Afrotropical and Malagasy rainforest communities (Hypothesis 2, Table 1). Considering the
169 higher climatic stability and habitat availability during the Cenozoic and subsequent higher
170 angiosperm diversification in the Neotropics, we expect to observe widespread phylogenetic
171 clustering in the Central Amazon (Hypothesis 3, Table 1). The co-occurrence of species
172 belonging to recently-diversified lineages with species belonging to early-diversified lineages
173 tracking ancestral habitats (i.e. magnoliids) have likely led to phylogenetic overdispersion in
174 communities near the Andes (Hypothesis 4, Table 1).

175

176 **Methods**

177 *Study sites*

178 We compiled tree inventories for 115 sites from Neotropical (not including Atlantic
179 rainforests), Afrotropical and Malagasy rainforests, i.e. Central American, Amazonian,
180 Andean, Guineo-Congolian and Malagasy rainforests: seven sites of the Tropical Ecology,
181 Assessment and Monitoring Network (TEAM) (data sets available at
182 <http://www.teamnetwork.org>), 74 Alwyn Gentry's forest sites (available at
183 http://www.wlbcenter.org/gentry_data.htm), and 34 sites from surveys published in the
184 literature. TEAM's sites consisted in five to nine 1-ha plots per site. Alwyn Gentry's sites
185 consisted of one 0.1 ha transect per site. The surveys obtained from the literature had variable
186 sampling efforts. We compiled data from a total of 89 sites for the Neotropics, 23 sites for the
187 Afrotropics, and three sites for Madagascar. We used data from these 115 sites to build the

188 pool of species of each biogeographic region (See Supplementary material Appendix 1 for the
189 list of sites).

190 The inclusion criterion of species was diameter at breast height (DBH) ≥ 5 cm in
191 Gentry's surveys and DBH ≥ 10 cm in most remaining surveys (Table A1 in Supplementary
192 material Appendix 1). We selected only the data for trees with DBH ≥ 5 cm from Gentry's
193 transects, because Gentry's sites had the smallest sampling sizes and DBH ≥ 5 cm is more
194 inclusive than greater stem diameters. We standardised the data by removing non-arboreal
195 species, conifers and ferns from the surveys.

196 In this study, data on the identity and abundance of angiosperm tree species were
197 pooled for each site. Among the 115 sites used for building the regional species pool, we
198 obtained abundance data for 94 sites (76 in the Neotropics, 15 in the Afrotropics, and three in
199 Madagascar). Each of these 94 sites was used as a sampling unit in data analyses, and we will
200 refer to them as "communities" throughout the article. The majority of species (95.5%) were
201 identified at least to the genus level, which enabled us to use them in the phylogenetic
202 analyses. Each individual identified to the genus level at a given community was regarded as
203 a species specific to that community. Species not identified at least to the genus level (4.5%)
204 were excluded from the data matrix. We corrected species identities for nomenclatural
205 synonyms using the online tool Taxonomic Name Resolution Service v3.2 (Boyle et al. 2013).

206 Given that the different sources (TEAM Network, Gentry forest transects and
207 surveys from the literature) had different sampling sizes and inclusion criteria of tree
208 individuals (DBH), we tested for the effect of data source on the variation of NRI (see
209 analyses in Supplementary material Appendix 2). NRI did not significantly differ among data
210 sources (Supplementary material Appendix 2).

211

212 *Phylogenetic tree*

213 We built a phylogenetic tree from the megatree R20120829 (available at
214 <https://github.com/camwebb/tree-of-trees/blob/master/megatrees/R20120829.new>), which is
215 based on the phylogenetic backbone (well resolved for deep phylogenetic relationships such
216 as orders) proposed by APG III (APG 2009) and on relationships among families according to
217 Stevens (2001). Considering that we were interested in deep relationships in the phylogenetic
218 tree, we did not need to build a high-resolution tree. Then, we standardised the resolution of
219 the megatree by removing infra-family phylogenetic relationships, keeping the resolution at
220 the “family level” for the whole tree, with polytomies linking species within genus and genera
221 within family. The tree branch lengths were adjusted through the BLADJ algorithm in
222 Phylocom 4.2 software (Webb et al. 2008) following clade age estimates by Bell et al. (2010).
223 Undated clades were evenly interpolated between dated clades. We used the module
224 *Phylomatic 2* in the software Phylocom 4.2 (Webb et al. 2008) to build a phylogeny with all
225 the species present in our global species pool (6,056 tree species from the 115 compiled forest
226 surveys), i.e. including the Neotropics, Afrotropics, and Madagascar (Supplementary material
227 Appendix 3, Fig. A4). Finally, we calculated a matrix of phylogenetic distances, in millions of
228 years, between pairs of terminal taxa for the entire phylogeny.

229 We removed conifer species from our data set because we were interested in
230 angiosperm tree phylogenetic patterns. Moreover, only four out of the 6,059 species were
231 gymnosperms. These four species comprised 224 individuals in four out of the 94
232 communities with species abundance, or 0.19% of the total of individuals recorded in the 94
233 communities. In terms of proportion these plants would not be important for revealing alpha
234 and beta phylogenetic patterns across rainforest tree communities. Nonetheless, given the age

235 of the deep node separating gymnosperms from angiosperms, their inclusion would likely be
236 sufficient for obscuring most of the patterns we discuss here.

237 In regard to non-arboreal species, such as herbs and lianas, most of the studies used
238 did not record them. Therefore, although it would be interesting to include such plants in the
239 analyses, we were not able to do so. Moreover, the inclusion of herbaceous and other non-
240 woody species are unlikely to affect local phylogenetic structure and phylobetadiversity
241 results, because these life forms evolved multiple times in different lineages of the major
242 angiosperm clades, i.e. magnoliids, monocots and eudicots (Fitzjohn et al. 2014). Therefore,
243 these plants would be likely represented in many of the lineages that are already represented
244 in our data set, thereby not changing major observed patterns.

245

246 *Linking shifts in local phylogenetic structure to changes in phylogenetic composition*
247 *across communities*

248 For testing our hypotheses, we used two approaches. One approach is the net relatedness
249 index (NRI), which measures phylogenetic structure in values representing clustering vs.
250 overdispersion relative to a species pool (Webb et al. 2002). The other approach is the
251 phylogenetic coordinates of phylogenetic structure (PCPS), which synthesises
252 phylobetadiversity into ordination vectors representing changes in phylogenetic composition
253 across communities (Pillar and Duarte 2010, Duarte 2011). Using PCPS, we identified
254 lineages linked to shifts in phylogenetic structure values (NRI) across biogeographical
255 regions. Both methods are briefly explained next.

256 We evaluated phylogenetic structure (clustering vs. overdispersion) of local
257 communities relative to regional species pool using the net relatedness index (NRI; Webb et

258 al. 2002), which is the standardised effect size of mean pairwise phylogenetic distances
259 among co-occurring taxa in a community. Significant positive values of NRI indicate that taxa
260 are more related than expected by chance (phylogenetic clustering), while significant negative
261 values indicate that taxa are less related than expected by chance (phylogenetic
262 overdispersion) given a regional species pool. Communities presenting NRI values that do not
263 differ from the null expectation of phylogenetic structure are interpreted as being
264 phylogenetically random relative to the regional species pool. We used the null model
265 *phylogeny.pool*, which controls for species richness and draws species without replacement
266 from the phylogeny with equal probability of being included in the null communities (Kembel
267 et al. 2010). We computed NRI values for each community using species pools defined by
268 biogeographical region (Neotropics, Afrotropics or Madagascar). We calculated NRI values
269 by weighting species abundances. We computed NRI as $-1 \times ses.mpd$ using the package
270 Picante v. 1.6.2 (Kembel et al. 2010) in the statistical software R (R Core Team 2015).

271 We did not use a global species pool comprising all the communities across all the
272 three biogeographical regions for two reasons. First, the Neotropics had tree species richness
273 three to five times higher than the Afrotropics or Madagascar. Second, our compilation was
274 asymmetric, with more communities in the Neotropics (89) than in the Afrotropics (23) and
275 Madagascar (3). This precluded us from properly interpreting differences among
276 biogeographical regions regarding changes in NRI values when the size of the species pool
277 increased from a regional to a global scale.

278 PCPS are ordination vectors expressing orthogonal gradients in phylogenetic
279 composition across communities (Duarte 2011, Duarte et al. 2012, 2014a) and can be used to
280 identify lineages that better represent different parts of environmental or biogeographical
281 gradients (Brum et al. 2013, Duarte et al. 2014a). PCPS vectors were extracted by principal

282 coordinates analysis (PCoA) on matrix **P** of phylogeny-weighted species composition (Pillar
283 and Duarte 2010, Duarte 2011) for each community. In PCPS, lineage commonness across
284 communities is evaluated using correlation of species with PCPS vectors (Duarte 2011).
285 Labelling species according to their clades enables identification of the lineages better
286 representing different communities. Shifts in local phylogenetic structure likely reflect the
287 variation in phylogenetic composition across communities. Then, subsequently correlating
288 PCPS scores with NRI values enable identification of the lineages related to phylogenetic
289 clustering or phylogenetic overdispersion. The PCPS with the highest eigenvalue describes
290 major changes in phylogenetic composition among communities related to the split of deep
291 tree nodes (e.g. nodes splitting magnoliids from eudicots and monocots from eudicots); as the
292 eigenvalues of other PCPS vectors decrease, changes in phylogenetic composition related to
293 splits of shallower nodes appear (Duarte et al. 2014a).

294 We opted to use species abundances rather than species occurrences in the matrix of
295 species per community, because the latter generated a strong arch effect (Legendre and
296 Legendre 2012) on PCPS ordination, which would limit inferences about phylogenetic
297 composition across communities and regions. Moreover, abundances are better descriptors of
298 species performance at the local scale than mere occurrence. Our sampling units describe
299 local communities of a particular habitat where species co-occur, differently from lists of
300 species at coarser spatial grains such as 110 km x 110 km cells, for which occurrences would
301 maybe be more appropriate. We computed PCPS using the package PCPS v. 1.0.1 (Debastiani
302 and Duarte 2014) in the software R. For details on the calculation of matrix **P** of phylogeny-
303 weighted species composition see Pillar and Duarte (2010). See Duarte et al. (2014) for a flow
304 chart of the phylogenetic fuzzy-weighting method, and Duarte et al. (2012) for a flow chart of
305 the PCPS analysis.

306 We used a coarse-resolution phylogenetic tree because our historical hypotheses deal
307 with deep relationships in the phylogenetic tree. NRI is little affected by loss of resolution
308 terminally in the phylogeny, especially in phylogenies with a great number of species
309 (Swenson 2009), as ours. Moreover, the lack of phylogenetic resolution is more likely to
310 generate false negative than false positive results in phylogenetic dispersion analyses
311 (Swenson 2009). The PCPS vectors used (PCPS I and II) captured the deep relationships in
312 the phylogenetic tree, which deals with a temporal scale consistent with our historical
313 hypotheses. Furthermore, a recent study has shown that terminal lack of resolution in the
314 phylogeny did not affect the first and second PCPS vectors (Maestri et al. 2016).

315 In order to test whether the phylogenetic structure and composition of rainforest tree
316 communities differed between the Neotropics, Afrotropics and Madagascar, we compared
317 NRI values among biogeographical regions and PCPS scores among biogeographical regions,
318 respectively. We used ANOVA to test for the significance of these comparisons. Pearson's
319 correlation was used to test for the relationship between shifts in local phylogenetic structure
320 (NRI values) and the variation in phylogenetic composition (PCPS scores) across
321 communities, and Dutilleul's correction (Dutilleul 1993) was used to account for the
322 influence of spatial autocorrelation on the number of degrees of freedom. Spatial analyses
323 were performed using SAM (Rangel et al. 2010).

324

325 **Results**

326 The 115 sites across the Neotropics, Afrotropics, and Madagascar contained 6,056 species.
327 The Neotropics had the highest species richness (4,668), followed by the Afrotropics (1,095)
328 and Madagascar (347). Considering the 94 communities with species abundances separately,

329 [these contained 5,506 species – 4,346 species for the Neotropics, 857 species for the](#)
330 [Afrotropics, and 347 for Madagascar.](#) The actual species pool of the Amazon rainforest
331 harbours between 16,000 and 25,000 tree species [>10 cm diameter](#) (ter Steege et al. 2013,
332 Slik et al. 2015), [while](#) the Afrotropical rainforest has between 4,500 and 6,000 tree species
333 (Slik et al. 2015). [Then,](#) our [global](#) species pool would represent approximately [19-30%](#) of the
334 actual pool of tree species of the rainforests of the [Neotropics, Afrotropics and Madagascar](#)
335 (not considering the Brazilian Atlantic forest). This sample [is likely](#) a good representation of
336 the phylogenetic composition of trees in [these biogeographical regions.](#)

337 We identified [major changes in](#) phylogenetic composition correlated to shifts in
338 phylogenetic structure across communities in different biogeographical regions (Fig. 1).
339 Figure 2 provides maps of PCPS eigenvalues and NRI values to aid in the spatial
340 interpretation of phylogenetic composition and structure patterns. The first PCPS eigenvector
341 synthesised a gradient in phylogenetic composition across communities represented by major
342 angiosperm lineages: magnoliids, monocots, and eudicots (see Supplementary material
343 Appendix [3](#), Fig. [A4](#) to locate clades in angiosperm phylogeny). Monocots were better
344 represented in Andean and Western Amazonian communities (Fig. 1, 2a, c). Magnoliids were
345 better represented in [some of the Andean](#) communities (Fig. 1, 2a, c). The second PCPS
346 eigenvector described a [gradient in phylogenetic composition](#) characterised mostly by
347 monocots being more represented in the Neotropics, while magnoliids and eudicots being
348 well represented in the three biogeographic regions (Fig. 1, 2c). The phylogenetic
349 composition differed between [Neotropics and Afrotropics](#) for both PCPS I and II (Fig. 2a-d).

350 Phylogenetic structure (NRI) values did not differ [among the three](#) biogeographical
351 regions (Fig. 2f). Rather, phylogenetic structure varied within the Neotropics, with
352 communities near the Andes showing phylogenetic overdispersion [and Central Amazonian](#)

353 communities showing phylogenetic randomness or clustering (Fig. 2e). Phylogenetic
354 overdispersion was associated with communities near the Andes with high representation of
355 magnoliids or monocots (Fig. 1). Eleven out of 32 Andean communities presented significant
356 phylogenetic overdispersion. Mathematically this means that there were more pairwise
357 phylogenetic distances (for NRI calculation) being computed down to basal nodes when
358 comparing eudicots to magnoliids or to monocots (see Supplementary material Appendix 3,
359 Fig. A4 for angiosperm phylogeny).

360 Values of NRI were significantly correlated with PCPS I ($r = 0.791$, $F_{30.2} = 50.35$, P
361 $<.001$; see Supplementary material Appendix 4, Fig. A5). Negative PCPS I scores were
362 associated with negative NRI values (Fig 1, Fig. A5), which means that high representation of
363 magnoliids or monocots, especially in the Andes, was related to phylogenetic overdispersion.
364 The relationship between NRI values and PCPS II was also significant ($r = 0.28$, $F_{52.1} = 4.42$, P
365 $= 0.04$; Fig. A5), although their relationship was not linear. Negative PCPS II scores were
366 associated with negative NRI values (Fig 1, Fig. A5), which means that high representation of
367 monocots near the Andes was related to phylogenetic overdispersion. Positive PCPS II scores
368 in turn were associated with both negative and positive NRI values (Fig 1, Fig. A5), which
369 means that high representation of magnoliids near the Andes was related to phylogenetic
370 overdispersion, while high representation of eudicots in some Central Amazonian_ and some
371 Afrotropical_ communities was related to phylogenetic clustering. Six out of 44 Central
372 Amazonian communities and two out of 15 Afrotropical communities presented significant
373 phylogenetic clustering. Phylogenetic randomness predominated in Afrotropical and
374 Malagasy communities, and in most Central Amazonian communities (Fig. 2e).

375 In summary, we observed (i) major changes in phylogenetic composition correlated
376 to shifts in phylogenetic structure across communities in different biogeographical regions

377 (agreement with H1), (ii) widespread phylogenetic randomness in Afrotropical and Malagasy
378 communities (agreement with H2), (iii) phylogenetic clustering in some Central Amazonian
379 communities related to high representation of eudicots (partial agreement with H3), and (iv)
380 widespread phylogenetic overdispersion near the Andes associated with the co-occurrence of
381 eudicots with magnoliids (agreement with H4) or monocots.

382

383 Discussion

384 *Linkages between phylogenetic structure and regional composition in Neotropical and* 385 *Afrotropical rainforest tree communities*

386 By evaluating the linkages between phylogenetic structure and phylobetadiversity in light of
387 the Gondwanan biogeographical history, we were able to test our four hypotheses. As
388 predicted, we identified major differences in phylogenetic composition with magnoliids better
389 represented near mountain ranges (Andes). The variation in phylogenetic composition was
390 accompanied by shifts in phylogenetic structure across biogeographical regions. Phylogenetic
391 overdispersion was related to the high representation of magnoliids and monocots in
392 communities near the Andes. The nodes that separate magnoliids and eudicots and monocots
393 and eudicots are deep in the phylogeny, which increase phylogenetic diversity in places where
394 magnoliids or monocots co-occur with eudicots (or the three lineages co-occur).

395 Extant magnoliids are usually associated with upland, shady and wet habitats (Feild
396 and Arens 2007), which suggest magnoliids such as Lauraceae, Winteraceae and Annonaceae
397 track this kind of habitats across space and time (Duarte 2011, Debastiani et al. 2015). Indeed,
398 magnoliids bear conserved traits that limit their establishment in open and drier habitats other
399 than forest understoreys (Feild and Arens 2007). In addition, magnoliids appear to track

400 ancestral-like habitats in Andean highlands (e.g. *Drimys* spp. that today occur in high
401 elevations of the Andes; Colinvaux et al. 2000), which is consistent with the information that
402 early-diverged lineages show conserved austral Gondwanan niches in high latitudes and
403 elevations of the Andes (Segovia and Armesto 2015). Besides providing refugia for lineages
404 with conserved habitat preferences (e.g. magnoliids), the Andes appears to have promoted the
405 recent diversification of many angiosperm lineages, especially of eudicots and monocots
406 (Richardson et al. 2001, Kissling et al. 2012). Therefore, phylogenetic overdispersion in some
407 of the Andean communities is consistent with the co-occurrence of magnoliid species tracking
408 conserved habitat preferences with eudicot species of lineages that diversified recently in the
409 Andes. In a similar line, Diniz-Filho et al. (2007) argued that bird species accumulation in the
410 Neotropics was the combined result of conservatism of ancestral tropical niches and recent
411 diversification of lineages composed of small-ranged species in the Andes. The co-occurrence
412 of eudicots and monocots is another plausible explanation for the phylogenetic overdispersion
413 near the Andes, because monocots, similarly to magnoliids, would increase phylogenetic
414 diversity in presence of eudicots due to the deep node splitting these clades in the phylogeny.
415 This result is consistent with recent finding that Western Amazonian tree communities tend to
416 be phylogenetically overdispersed (Honorio Coronado et al. 2015).

417 Although most of the communities in the Central Amazon presented phylogenetic
418 random values (38 out of 44 communities), we found support for our hypothesis of
419 phylogenetic clustering in Central Amazon for six communities. This clustering is related to
420 the dominance of eudicots in these communities, as elucidated by PCPS analysis. Dominance
421 of eudicot species in local communities likely reflects the Amazonian pool of species, which
422 is dominated by species of this clade. Eudicots underwent high diversification in the Amazon
423 (Gentry 1982), which may have been promoted by the time-integrated species-area effect

424 (Fine and Ree 2006). Eudicot-dominated communities tend to be clustered because they are
425 composed of many closely-related species, i.e. these communities have high phylogenetic
426 redundancy. The Amazonian species pool is also well represented by monocot species,
427 especially palms (Arecaceae) (Kissling et al. 2012). Previous studies observed phylogenetic
428 clustering in Amazonian palm assemblages (Kissling et al. 2012, Eiserhardt et al. 2013). The
429 likely reason why we did not find phylogenetic clustering associated with monocots is that we
430 considered communities composed by not only monocots, but also by eudicots and
431 magnoliids.

432 As hypothesised, we found phylogenetic randomness in Afrotropical and Malagasy
433 communities, which is consistent with what was previously found for Afrotropical monocot
434 communities (Kissling et al. 2012). Phylogenetic randomness in the Afrotropics and
435 Madagascar might be a result of major extinctions that occurred during the Cenozoic (Vences
436 et al. 2009, Kissling et al. 2012). Although we presented results for just three Malagasy
437 communities, our results for Madagascar are probably unbiased. NRI is a measure of local
438 phylogenetic structure relative to regional species pool. We built a species pool for
439 Madagascar with species from three communities. Swenson (2009) showed that small pool
440 sizes are likely to bias results towards phylogenetic clustering or overdispersion rather than
441 towards randomness. Therefore, the results of phylogenetic randomness in Madagascar are
442 likely reliable.

443

444 *Linking alpha phylogenetic structure with phylobetadiversity; what do we gain by*
445 *identifying lineages responsible for observed patterns?*

446 While many studies have assessed patterns of local phylogenetic structure, phylobetadiversity
447 and/or taxonomic beta diversity, this has not been enough to identify the lineages responsible
448 for shifts in local phylogenetic structure across regions or habitats (Kooyman et al. 2011, Fine
449 and Kembel 2011, Kissling et al. 2012, Eiserhardt et al. 2013, Hawkins et al. 2014). If
450 historical biogeography inferences deeply rely on the information of how lineages evolved
451 across space and time, it is essential to identify which lineages are responsible for differences
452 in local phylogenetic structure across biogeographical barriers to clarify the historical
453 processes influencing current community structure. While species composition at the local
454 scale may be ephemeral, lineage composition in regional species pools is likely to persist for
455 millions of years (Gerhold et al. 2015). The knowledge on which lineage is linked to a given
456 phylogenetic structure provides insight on the historical processes that were important for the
457 formation of the regional species pool and, consequently, the structuring of local
458 communities.

459 For instance, we were able to relate the observed phylogenetic overdispersion near
460 the Andes (as shown by NRI) to high representation of monocot and magnoliid species in the
461 region (as shown by PCPS), which caused phylogenetic overdispersion when species of these
462 clades co-occurred with eudicots. By knowing that magnoliids tracked conserved habitat
463 preferences, and that there was recent diversification of eudicot and monocot lineages during
464 the uplift of the Andes, we were able to discuss the historical processes influencing
465 phylogenetic structure of communities of the region. Therefore, integrating PCPS and NRI
466 unifies local phylogenetic structure and phylobetadiversity in a relatively straightforward
467 framework.

468

469 **Conclusions**

470 By linking local phylogenetic structure with regional phylogenetic composition, we were able
471 to identify how differences in lineage composition are related to phylogenetic co-occurrences
472 at the local scale across communities in biogeographical regions that have been undergoing a
473 major vicariance process during the past 100 Myr. By doing so, we were able to infer how
474 macroevolutionary processes influenced current species co-occurrences. We observed
475 historical imprints on the phylobetadiversity and local phylogenetic structure of rainforest tree
476 communities in the Neotropics and Afrotropics. Our results suggest that Gondwanan
477 vicariance, uplift of mountain ranges and their subsequent effect on angiosperm
478 diversification and habitat tracking explain current variation in phylogenetic composition and
479 structure of rainforest tree communities across regions. By identifying the linkages between
480 lineage composition and phylogenetic structure across communities in the Neotropics,
481 Afrotropics and Madagascar, we hope to contribute to the discussion on the historical and
482 ecological processes that shaped the structure of rainforest tree communities in these regions
483 with different biogeographical histories.

484

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508

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646

647

648 Supplementary material (Appendix EXXXXX at <www.oikosoffice.lu.se/appendix>).

649 | Appendix 1–4.

For Review Only

650 **Table 1.** Hypotheses of the study, showing the predictions about the influence of historical factors on
 651 the structuring of rainforest tree communities in the Neotropics, Afrotropics, and Madagascar.

| | Historical processes | Predictions about phylogenetic composition and structure | References |
|--------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------|
| Hypothesis 1 | <u>The breakup of Gondwana led to increasing isolation of biotas. The biogeographic regions were completely separated in the Cenozoic, when great differences in diversification rates between regions occurred due to different climatic and orographic histories.</u> | <u>Major differences</u> in phylogenetic composition between biogeographical regions, with eudicots well represented throughout study <u>communities</u> and magnoliids better represented near mountain ranges. | Ghazoul and Sheil 2010, Morley 2011, Wilf et al. 2013, Duarte et al. 2014b, Silvestro et al. 2015 |
| Hypothesis 2 | <u>Major extinction events during the Cenozoic resulted in regional lineage pools with low redundancy of recently-diverged lineages in the Afrotropics and Madagascar.</u> | <u>The low number of recently-diverged lineages and a more balanced regional species pool would lead to random phylogenetic structure in Afrotropical and Malagasy communities.</u> | Parmentier et al. 2007, Vences et al. 2009, Kisling et al. 2012 |
| Hypothesis 3 | <u>High speciation and low extinction rates of eudicots due to persistence of large areas of rainforest through the Cenozoic</u> led to a regional species pool dominated by this clade in the Neotropics, especially for Central Amazonian communities. | <u>Species from rich recently-diversified eudicot lineages</u> would be more likely to be drawn from the regional species pool during community assembly, leading to widespread phylogenetic clustering in Central Amazonian communities. | Gentry 1982, Fine and Ree 2006 |
| Hypothesis 4 | At a regional scale the uplift of the Andes promoted recent diversification of eudicots, as well as gave rise to montane, moist and shady habitats, <u>similar to those that existed in Gondwana. Magnoliids generally show conserved preferences for these Gondwana-like habitats, and seem to have tracked them northwards coming from southern Andes and Patagonia. Today magnoliids tracking conserved habitat preferences co-occur with eudicot lineages that diversified during the Cenozoic in northern Andes.</u> | The node splitting magnoliids <u>from</u> other angiosperms, including eudicots, is deep in the phylogeny. Thus, the <u>co-occurrence</u> of magnoliids tracking conserved habitat preferences with recently-diverged eudicots <u>increase phylogenetic diversity</u> , leading to phylogenetic overdispersion in <u>northern Andean</u> communities. | Feild and Arens 2007, Graham 2009, Wilf et al. 2013, Segovia and Armesto 2015 |

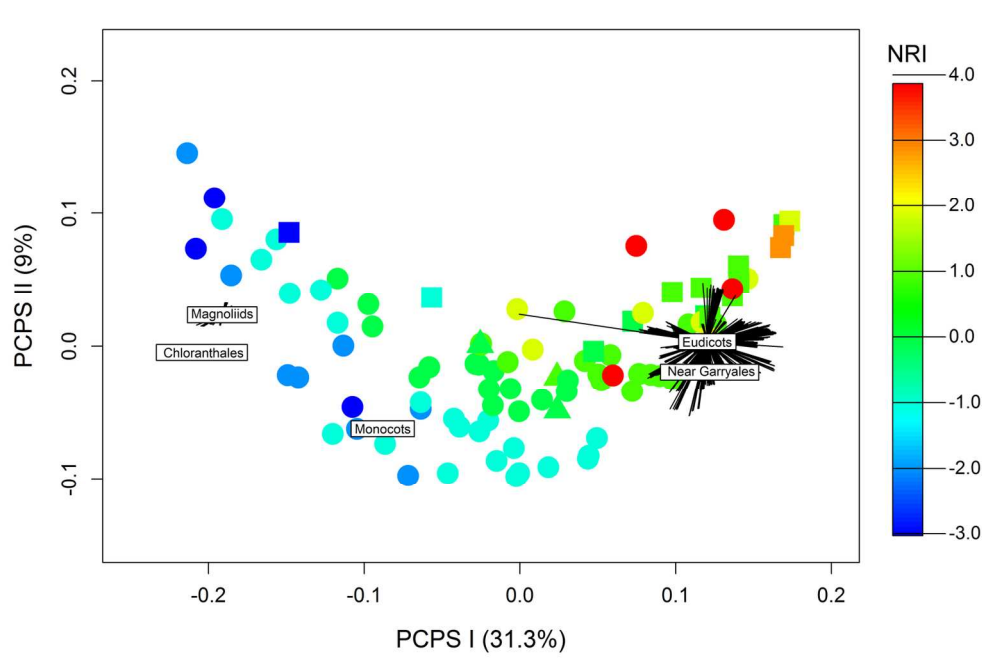


Figure 1. Scatter diagram of the two main ordination vectors representing variation in phylogenetic composition of angiosperm trees across Neotropical, Afrotropical and Malagasy rainforest communities. Ordination vectors were computed using principal coordinates of phylogenetic structure (PCPS) approach (Duarte 2011). Phylogenetic structure was assessed using net relatedness index (NRI; Webb et al. 2002) computed according to regional species pools (Afrotropics, square; Neotropics, circle; and Madagascar, triangle). High positive values indicate phylogenetic clustering (reddish colours), values near zero indicate random phylogenetic structure (greenish colours) and high negative values indicate phylogenetic overdispersion (bluish colours). For the geographical location of sites, see Fig. 2.

152x101mm (300 x 300 DPI)

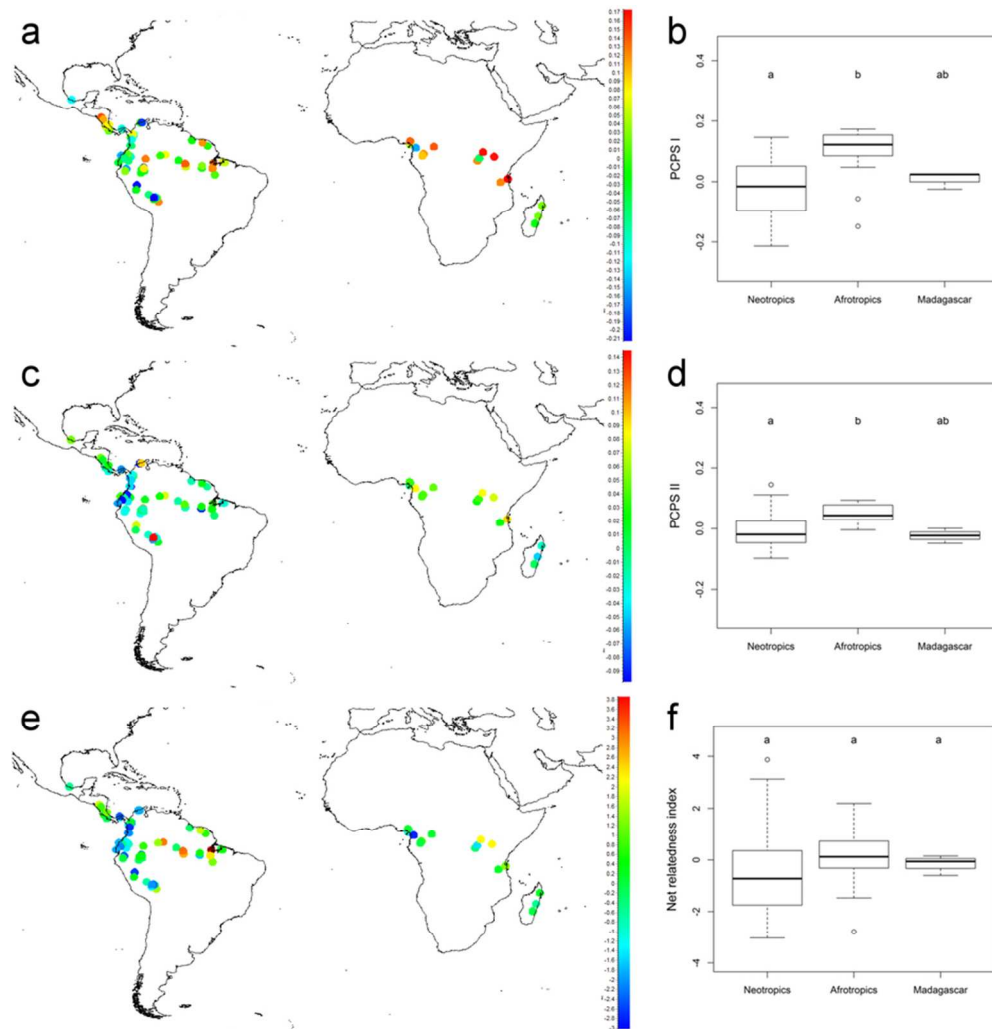


Figure 2. Spatial variation in phylogenetic composition (a, c) and structure (e) of angiosperm trees across Neotropical, Afrotropical and Malagasy rainforest communities. Phylogenetic composition and structure were assessed using principal coordinates of phylogenetic structure (PCPS) and net relatedness index, respectively. Phylogenetic composition differed between Neotropics and Afrotropics for the two main PCPS vectors (b, d). Local phylogenetic structure did not differ among biogeographical regions (f), but varied from Andes to Amazon in the Neotropics. Different letters over the boxplots represent significant comparisons under $P < 0.001$ for ANOVA and Tukey tests. The variation in phylogenetic structure (NRI) values (e) is represented by the same colours used in Fig. 1.

80x82mm (300 x 300 DPI)

1 Supplementary material for

2 **“Phylogenetic linkages between composition and structure of tree communities shed**
3 **light on historical processes influencing tropical rainforest diversity”**

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5

6 **Appendix 1.** Lists of TEAM Network’s sites (7), Gentry’s sites (74), published studies (34
7 sites from 32 studies) used to compile rainforest tree species pools for Neotropics, Afrotropics
8 and Madagascar. TEAM data sets are available at <http://www.teamnetwork.org>. Gentry’s
9 transect data is available at <http://www.mobot.org/mobot/research/gentry/welcome.shtml>.

10

11 **(a) TEAM’s sites used:** NEOTROPICS - Volcán Barva (La Selva Biological Station and
12 Braulio Carrillo National Park, Costa Rica), Manaus (three different field stations near the
13 city of Manaus, Brazil) and Caxiuanã (Caxiuanã National Forest, Brazil); AFROTROPICS -
14 Korup (Korup National Park, Cameroon), Bwindi (Bwindi Impenetrable National Park,
15 Uganda), Udzungwa (Udzungwa Mountains National Park, Tanzania); MADAGASCAR -
16 Ranomafana (Ranomafana National Park, Madagascar).

17 We selected seven sites containing information of tree composition and abundance in
18 tropical rainforests. For each site, we used the inventory data that ranged between Aug 2010
19 and May 2011. The TEAM Network sampling design for trees consists of tropical rainforest
20 sites with five to seven 1-ha plots (100 x 100 m), each subdivided in 25 subplots of 400 m²
21 (20 x 20 m), where trees with diameter at breast height ≥ 10 cm were recorded. Plots were
22 placed in closed-canopy moist forest habitats. Each of the selected sites was composed by six

23 plots of 1 ha, except for Korup and Volcán Barva, which were composed by five and nine
24 plots, respectively. The data from all these plots were gathered using a defined, shared and
25 therefore comparable method, which follows quality controls, such as including late
26 successional forests with little anthropogenic impact. Further information can be found in
27 TEAM Network (2010) and at <http://www.teamnetwork.org>.

28

29 **(b) Alwyn Gentry's sites (codes in parentheses):** AFROTROPICS – Banyong (Afr1),
30 Belinga (Afr6), Makokou 1 (Afr7), Makokou 2 (Afr8), Mount Cameroun (Afr3), Ndakan
31 (Afr4), Pande Forest Reserve (Afr17), Pugu Forest Reserve (Afr18); MADAGASCAR –
32 Nosy Mangabe (Afr13), Perinet Forestry Station (Afr14); NEOTROPICS - Allpahuayo
33 (SAm89), Alter de Chao (SAm20), Alto de Cuevas (SAm33), Alto de Mirador (SAm35), Alto
34 Madidi (SAm10), Alto Madidi – Ridge Top (SAm11), Anchicayá (SAm36), Antado
35 (SAm37), Araracuara (SAm39), Araracuara - High Campina (SAm38), Bajo Calima
36 (SAm40), Belém-Mocambo (SAm29), Berbice River (SAm87), Bosque de la Cueva
37 (SAm41), Bosque Nacional von Humboldt (SAm90), Cabeza de Mono (SAm91), Candamo
38 (SAm108), Carajas (SAm23), Carara National Park (CAM6), Centinela (SAm70), Cerro de la
39 Neblina 1 (SAm124), Cerro de la Neblina 2 (SAm125), Cerro El Picacho (CAM24), Cerro
40 Olumo (CAM23), Cochacashu (SAm96), Constancia (SAm97),Cuangos (SAm71),Curundu
41 (CAM25), Cuzco Amazónico (SAm99), Dureno (SAm72), Fila de Bilsa (SAm68), Huamaní
42 (SAm75), Indiana (SAm101), Jatun Sacha (SAm76), Jenaro Herrera (SAm102), La Planada
43 (SAm54), Madden Forest (CAM26), Maquipucuna (SAm78), Miazí (SAm79), Mishana -
44 Tahuampa (SAm104), Mishana Old Floodplain (SAm105), Mishana White Sand (SAm106),
45 Murri (SAm59), Osa-Sirena (CAM8), Pampas del Heath (SAm109), Pipeline Road (CAM27),
46 Quebrada Sucusari (SAm112), Rancho Quemado (CAM7), Río Manso (SAm61), Río

47 Nangaritza (SAm82), Río Palenque 1 (SAm83), Río Palenque 2 (SAm84), Río Távora
48 (SAm110), San Sebastián (SAm85), Saul (SAm86), Shiringamazú (SAm111), Tambopata
49 Alluvial (SAm114), Tambopata Lateritic (SAm116), Tambopata Swamp Trail (SAm115),
50 Tambopata Upland Sandy (SAm113), Tutunendo (SAm65), Yanamono 1 (SAm120),
51 Yanamono 2 (SAm121), Yanamono Tahuampo (SAm119).

52

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126 583.

127

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128 **Table A1.** Criteria of inclusion used in the different data sources.

| Data source | DBH |
|----------------------------|--------|
| Alarcon & Peixoto 2007 | ≥10 cm |
| Amaral et al. 2009 | ≥10 cm |
| Bongers et al. 1988 | ≥10 cm |
| Chapman et al 1997 | ≥10 cm |
| Espírito-Santo et al. 2005 | ≥10 cm |
| Fashing & Gathua 2004 | ≥15 cm |
| Gentry_Allpahua | ≥5 cm |
| Gentry_Alterdoc | ≥5 cm |
| Gentry_Altocuevas | ≥5 cm |
| Gentry_Altodemi | ≥5 cm |
| Gentry_Anchicay | ≥5 cm |
| Gentry_Antado | ≥5 cm |
| Gentry_Araracua | ≥5 cm |
| Gentry_Arcating | ≥5 cm |
| Gentry_Banyong | ≥5 cm |
| Gentry_Belem | ≥5 cm |
| Gentry_Belinga | ≥5 cm |
| Gentry_Berbicer | ≥5 cm |
| Gentry_Bilsa | ≥5 cm |
| Gentry_Bosqueva | ≥5 cm |
| Gentry_Cabezade | ≥5 cm |
| Gentry_Calima | ≥5 cm |
| Gentry_Candamo | ≥5 cm |
| Gentry_Carajas | ≥5 cm |
| Gentry_Carara | ≥5 cm |
| Gentry_Centinel | ≥5 cm |
| Gentry_Ceroneb1 | ≥5 cm |
| Gentry_Ceroneb2 | ≥5 cm |
| Gentry_Cerroelp | ≥5 cm |
| Gentry_Cerroolu | ≥5 cm |
| Gentry_Cochacas | ≥5 cm |
| Gentry_Constanc | ≥5 cm |
| Gentry_Cuangos | ≥5 cm |
| Gentry_Curundu | ≥5 cm |
| Gentry_Cuzcoama | ≥5 cm |
| Gentry_Dureno | ≥5 cm |
| Gentry_Huamani | ≥5 cm |
| Gentry_Humboldt | ≥5 cm |
| Gentry_Indiana | ≥5 cm |
| Gentry_Jatunsac | ≥5 cm |
| Gentry_Jenarohe | ≥5 cm |
| Gentry_Laplanad | ≥5 cm |

| | |
|---------------------|--------|
| Gentry_Madden | ≥5 cm |
| Gentry_Madidi | ≥5 cm |
| Gentry_Madidiri | ≥5 cm |
| Gentry_Makokou1 | ≥5 cm |
| Gentry_Makokou2 | ≥5 cm |
| Gentry_Maquipuc | ≥5 cm |
| Gentry_Miazi | ≥5 cm |
| Gentry_Mishnfl | ≥5 cm |
| Gentry_Mishws | ≥5 cm |
| Gentry_Mtcam | ≥5 cm |
| Gentry_Murri | ≥5 cm |
| Gentry_Nangarit | ≥5 cm |
| Gentry_Ndakani | ≥5 cm |
| Gentry_Nosymang | ≥5 cm |
| Gentry_Osasiren | ≥5 cm |
| Gentry_Pande | ≥5 cm |
| Gentry_Perinet | ≥5 cm |
| Gentry_Pipeline | ≥5 cm |
| Gentry_Pugu | ≥5 cm |
| Gentry_Ranchoqu | ≥5 cm |
| Gentry_Rioheath | ≥5 cm |
| Gentry_Riomanso | ≥5 cm |
| Gentry_Riopal1 | ≥5 cm |
| Gentry_Riopal2 | ≥5 cm |
| Gentry_Riotavar | ≥5 cm |
| Gentry_Sansebas | ≥5 cm |
| Gentry_Saul | ≥5 cm |
| Gentry_Shiringa | ≥5 cm |
| Gentry_Sucusari | ≥5 cm |
| Gentry_Tahuampa | ≥5 cm |
| Gentry_Tamblat2 | ≥5 cm |
| Gentry_Tambo | ≥5 cm |
| Gentry_Tamboall | ≥5 cm |
| Gentry_Tambupl | ≥5 cm |
| Gentry_Tutunend | ≥5 cm |
| Gentry_Yanam1 | ≥5 cm |
| Gentry_Yanam2 | ≥5 cm |
| Gentry_Yanamtah | ≥5 cm |
| Salomão et al. 2007 | ≥5cm |
| Sheil et al. 2000 | ≥10cm |
| Silva et al. 2008 | ≥20cm |
| Stropp et al. 2011 | ≥10cm |
| TEAM_Bwindi | ≥10 cm |
| TEAM_Caxiuanã | ≥10 cm |
| TEAM_Korup | ≥10 cm |

| | |
|--------------------------|--------|
| TEAM_Manaus | ≥10 cm |
| TEAM_Ranomafana | ≥10 cm |
| TEAM_Udzungwa | ≥10 cm |
| TEAM_Volcán Barva | ≥10 cm |
| ter Steege et al. 2007 | ≥10cm |
| van Gemergen et al. 2003 | ≥10cm |
| Webb & Peralta 1998 | ≥10cm |

129

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130 **Appendix 2.** Analyses of the influence of data source on phylogenetic structure patterns.

131

132 Considering that our data came from different sources with different sampling sizes
133 and inclusion criteria (minimum stem diameter), we tested for the influence of data source on
134 net relatedness index (NRI), our measure of phylogenetic structure. Among the data sources
135 used, the sites sampled by Alwyn Gentry had the smallest sampling size, with each site
136 having one transect with 0.1 ha. TEAM Network's sites in turn had 5 to 9 ha sampled, while
137 the surveys from the literature had variable sampling effort (but mostly 1 ha). See Table A1 in
138 Supplementary material Appendix 1. Thus, one could wonder about the effect of small
139 sampling effort in Gentry's sites over NRI.

140 In order to test for this possible sampling effect, we compared NRI values between
141 data sources. For this, we used a two-way ANOVA, in which the factors were Source (Gentry
142 vs. TEAM vs. Literature) and Andes (sites in the Andes vs. sites in other regions). Since the
143 design was unbalanced, we used an ANOVA with randomization tests (Pillar and Orłóci
144 1996) to test for significance of the contrasts between groups of each factor. Analyses were
145 performed using the software MULTIV v. 3.1 by V. Pillar (available at
146 <http://ecoqua.ecologia.ufrgs.br/software.html>).

147 Gentry's sites had lower NRI values than TEAM's sites and surveys from the
148 literature (Table A2; Fig. A1). Moreover, Andes sites had lower NRI values than other sites
149 (Table A2; Fig. A2).

150 Given that all data on Andean sites came from Gentry's database, we were not able to
151 decouple the effect of data source from biogeographic causation using only the data from
152 Andean sites. Thus, we compared NRI values between Gentry's non-Andean sites and non-
153 Andean sites from other data sources. If Gentry's sites are not biased toward low NRI values,
154 then there should be no difference in NRI between Gentry's non-Andean sites and all other
155 non-Andean sites.

156 Indeed, there were no significant differences in NRI between non-Andean sites from
157 different data sources (Table A3; Fig. A3). Hence, Gentry's sites in general presented lower
158 NRI values than other data sources probably because of Andes, which typically had low NRI
159 values (see Results in the main text). Therefore, we conclude that Gentry's sites are unbiased

160 and can be used together with TEAM Network's sites and the surveys from the literature in
161 the analyses.

162

163 **References**

164 Pillar, V. D. and Orlóci, L. 1996. On randomization testing in vegetation science: multifactor
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166

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167 **Table A2.** Results of the two-way ANOVA with randomization tests, comparing NRI values between
 168 Andean and non-Andean sites and between sites from different data sources.

| Source of variation | Sum of squares (Q) | $P(Qb_{null} \geq Qb)$ |
|------------------------------|------------------------|------------------------|
| Factor Andes | | |
| Andean sites vs. other sites | 40.721 | 0.002 |
| Factor Source | | |
| Between groups | 30.391 | 0.034 |
| Contrasts: | | |
| Gentry vs. Literature | 17.188 | 0.048 |
| Gentry vs. TEAM | 16.656 | 0.036 |
| Literature vs. TEAM | 0.61308 | 0.672 |
| Andes vs. Source * | -18.8 | 0.973 |
| Between groups | 52.312 | 0.001 |
| Within groups | 158.17 | |
| Total | 210.48 | |

169 *Note that the interaction between Andes and Source does not contain all the
 170 combinations of levels, because all Andean sites came from Gentry's database.

171

172

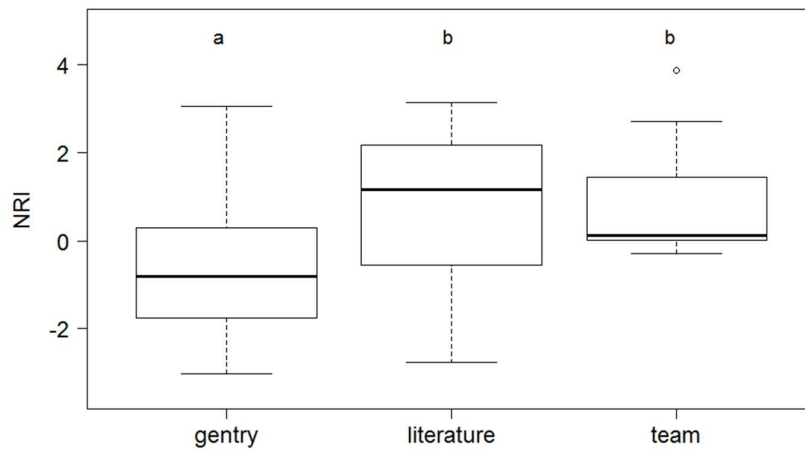
173 **Table A3.** Results of the one-way ANOVA with randomization tests, comparing NRI values between
 174 non-Andean sites from different data sources.

| Source of variation | Sum of squares (Q) | $P(Qb_{mult} \geq Qb)$ |
|-----------------------|------------------------|------------------------|
| Factor Source | | |
| Between groups | 11.591 | 0.084 |
| Contrasts | | |
| Gentry vs. Literature | 5.9116 | 0.096 |
| Gentry vs. TEAM | 7.7806 | 0.061 |
| Literature vs. TEAM | 0.61308 | 0.669 |
| Within groups | 129.01 | |
| Total | 140.6 | |

175

176

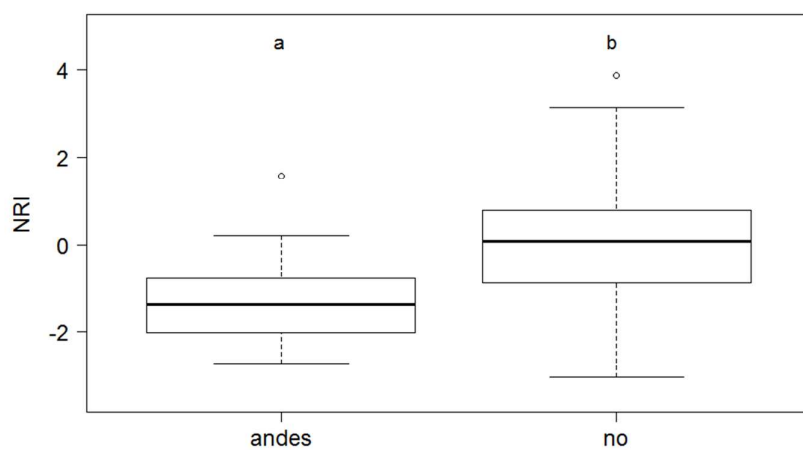
177



178

179 **Figure A1.** Comparison of NRI values between different sources of data: Gentry's transects, surveys
180 from the literature, and TEAM Network's plots. Different letter above boxes mean significant
181 differences between data sources ($P < 0.05$).

182

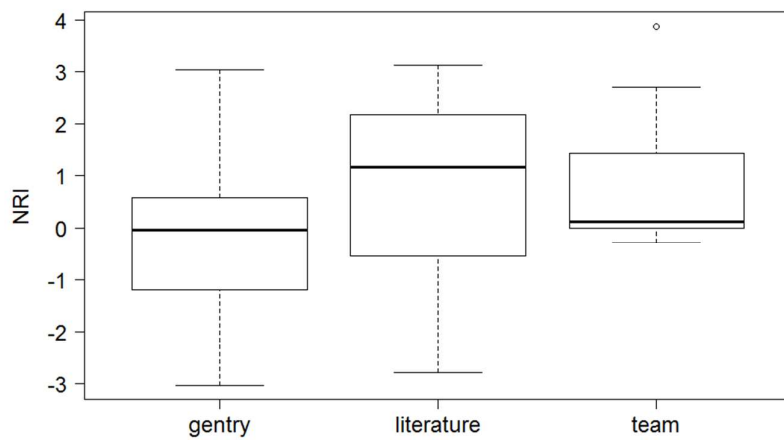


183

184 **Figure A2.** Comparison of NRI values between groups of sites in Andes and in other regions.185 Different letter above boxes mean significant differences between data sources ($P < 0.05$).

186

187



188

189 **Figure A3.** Comparison of NRI values between non-Andean sites from different data sources. NRI did
190 not differ between groups.

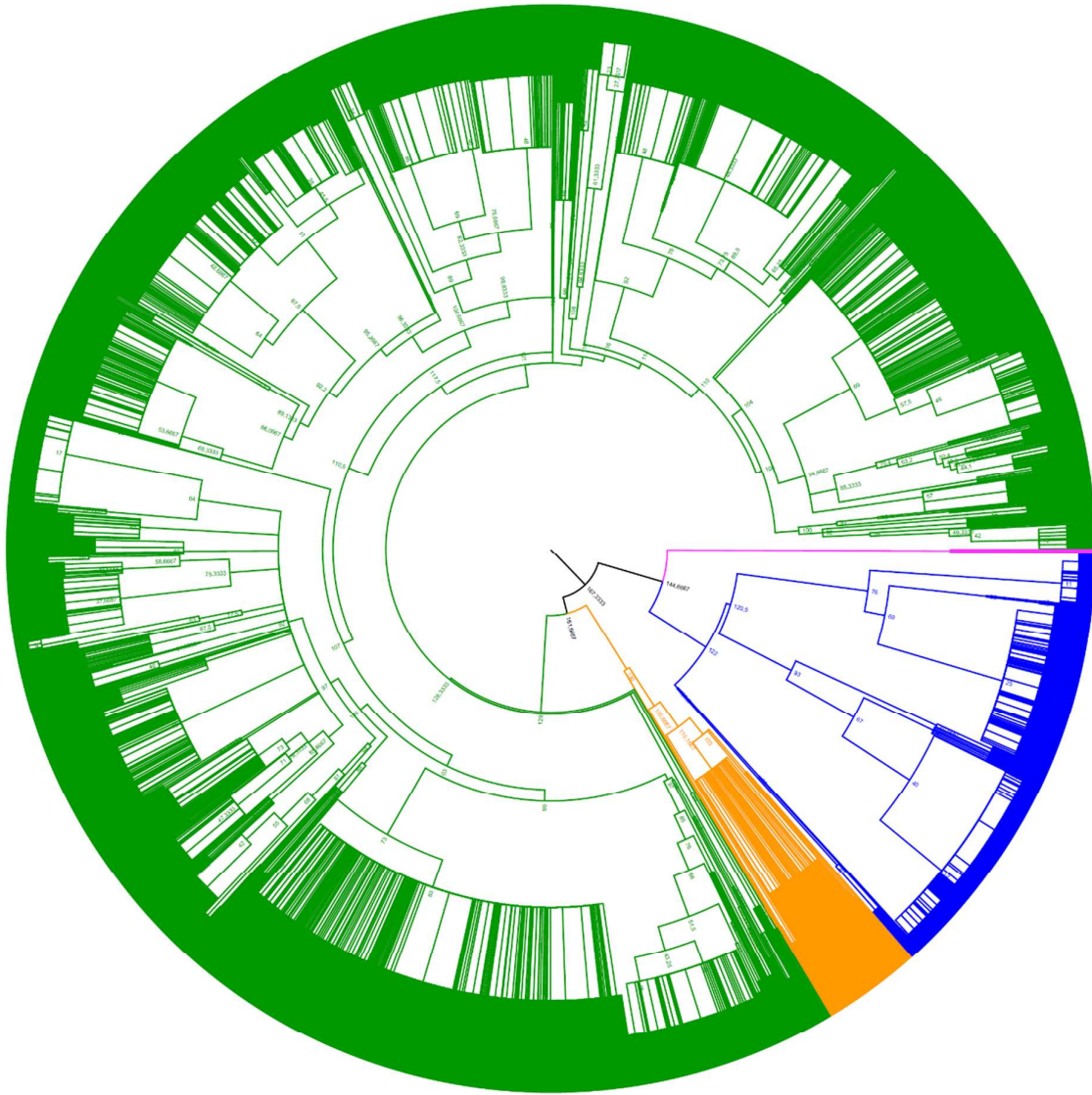
191

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193 **Appendix 3.** Figure of the phylogenetic tree.

194

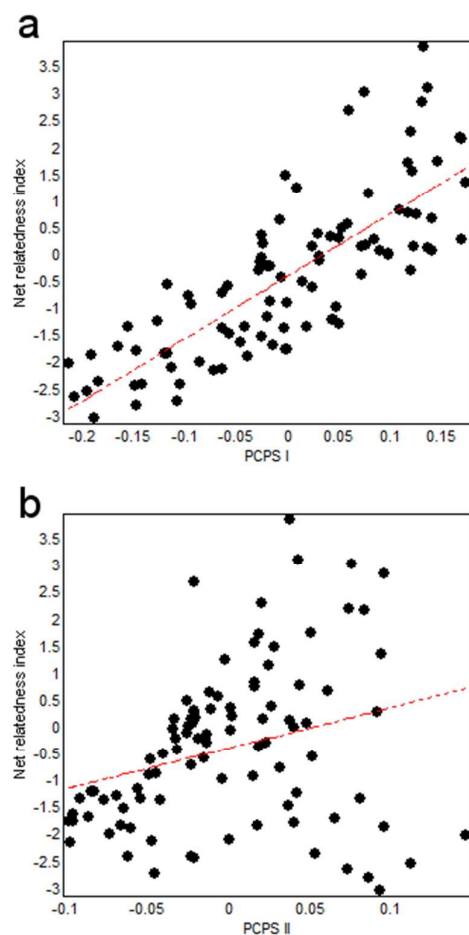


195

196 **Figure A4.** Phylogenetic tree for 6,056 rainforest tree species occurring in 115 Neotropical,
197 Afrotropical and Malagasy communities (including the 94 with species abundance data and 21 with
198 only species occurrence data). Pink, Chloranthales; Blue, magnoliids; orange, monocots; Green,
199 eudicots.

200 **Appendix 4.** Correlation between PCPS (principal coordinates of phylogenetic structure) and
201 NRI (net relatedness index).

202



203

204 **Figure A5.** Scatter plot between phylogenetic composition and local phylogenetic structure of tropical
205 rainforest tree communities ($n=94$), measured using PCPS and NRI, respectively. Pearson's
206 correlation was significant for the comparisons of NRI with both main phylogenetic composition
207 vectors: (a) PCPS I vs. NRI, $r = 0.791$, $F_{30,2} = 50.35$, $P < .001$; (b) PCPS II vs. NRI, $r = 0.28$, $F_{52,1} =$
208 4.42 , $P = 0.04$. Correlation statistics and significance were obtained after accounting for the influence
209 of spatial autocorrelation on the number of degrees of freedom by using Dutilleul's correction
210 (Dutilleul 1993).

211

212 **References**

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