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Evolutionary heritage influences Amazon tree ecology

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Complete List of Authors:	<p>Coelho de Souza, Fernanda; University of Leeds School of Geography Dexter, Kyle; University of Edinburgh School of GeoSciences; Royal Botanic Garden Edinburgh Phillips, Oliver; University of Leeds School of Geography Brienen, Roel; University of Leeds School of Geography Chave, Jérôme; Université Paul Sabatier, Laboratoire Evolution et Diversité Biologique Galbraith, David; University of Leeds School of Geography Lopez-Gonzalez, Gabriela; University of Leeds School of Geography Monteagudo Mendoza, Abel; Jardín Botánico de Missouri, Pennington, Toby; Royal Botanic Garden Edinburgh, Poorter, Lourens; Wageningen University, Forest Ecology and Forest Management Group Alexiades, Miguel; University of Kent, School of Anthropology and Conservation Álvarez-Dávila, Esteban; Fundación Con Vida Segalin de Andrade, Ana; Instituto Nacional de Pesquisas da Amazônia, Aragao, Luiz; University of Exeter; Instituto Nacional de Pesquisas Espaciais Araujo-Murakami, Alejandro; Museo de Historia Natural Noel Kempff Mercado, Arets, Eric; Alterra, Wageningen University and Research Centre, Aymard, Gerardo; UNELLEZ-Guanare, Programa del Agro y el Mar, Herbario Universitario (PORT), Baraloto, Christopher; Florida International University, Department of Biological Sciences Barroso, Jorcely; Universidade Federal do Acre Bonal, Damien; Institut National de la Recherche Agronomique, UMR EEF INRA-Université de Lorraine, Boot, Rene; Tropenbos International Camargo, José; Instituto Nacional de Pesquisas da Amazônia, Biological Dynamics of Forest Fragment Project Comiskey, James; National Park Service; Smithsonian Institution Cornejo Valverde, Fernando; Proyecto Castaña Camargo, Plinio; Universidade de Sao Paulo Centro de Energia Nuclear na Agricultura Di Fiore, Anthony; University of Texas, Department of Anthropology Elias, Fernando; Universidade Federal do Mato Grosso Erwin, Terry; Smithsonian Institution, Department of Entomology Feldpausch, Ted; University of Exeter,</p>

	<p>Ferreira, Leandro; Museu Paraense Emilio Goeldi Fyllas, Nikolaos; University of Leeds, School of Geography Gloor, Manuel; University of Leeds, School of Geography Herault, Bruno; Cirad, UMR EcoFoG (AgroParisTech, CNRS, Inra, U Antilles, U Guyane) Herrera, Rafael; Centro de Ecología IVIC; Universitat Wien Institut fur Geographie und Regionalforschung Higuchi, Niro; Instituto Nacional de Pesquisas da Amazonia Honorio Coronado, Euridice; University of Leeds, School of Geography; Instituto de Investigaciones de la Amazonia Peruana, Killeen, Timothy; GTECA-Amazonica Laurance, William; James Cook University, Centre for Tropical Environmental and Sustainability Science (TESS) and College of Science and Engineering Laurance, Susan; James Cook University, Centre for Tropical Environmental and Sustainability Science (TESS) and College of Science and Engineering Lloyd, Jon; Imperial College London, Department of Life Sciences Lovejoy, Thomas; George Mason University, Environmental Science and Policy Department and the Department of Public and International Affairs Malhi, Yadvinder; University of Oxford, Environmental Change Institute; Maracahipes, Leandro; Universidade Federal de Goias, Ecologia e Evolução Marimon, Beatriz; Universidade do Estado de Mato Grosso, Marimon-Junior, Ben Hur; Universidade do Estado de Mato Grosso, Mendoza, Casimiro; Universidad Mayor de San Simon, Escuela de Ciencias Forestales Morandi, Paulo; Universidade do Estado de Mato Grosso Neill, David; Universidad Estatal Amazónica, Núñez Vargas, Percy; Universidad Nacional de San Antonio Abad Oliveira, Edmar; Universidade Federal do Mato Grosso Oliveira, Eddie; Universidade Federal do Mato Grosso Palacios Cuenca, Walter; Universidad Técnica del Norte & Herbario Nacional del Ecuador, FICAYA Peñuela-Mora, Maria; Universidad Regional Amazónica IKIAM Pipoly III, John; Broward County Parks & Recreation Pitman, Nigel; Duke University, Prieto, Adriana; Universidad Nacional de Colombia, Quesada, Carlos; Instituto Nacional de Pesquisas da Amazônia Ramirez Angulo, Hirma; Instituto de Investigaciones para el Desarrollo Forestal, Universidad de Los Ande, Rudas, Agustin; Universidad Nacional de Colombia Ruokolainen, Kalle; University of Turku, Department of Biology Salomão, Rafael; Museu Paraense Emilio Goeldi, Coordenadoria de Botânica Silveira, Marcos; Universidade Federal do Acre Stropp, Juliana; Joint Research Centre, Institute for Environment and Sustainability, European Commission, Directorate General ter Steege, Hans; Naturalis Nationaal Natuurhistorisch Museum Thomas-Caesar, Raquel; Iwokrama Intertiol Centre for Rainforest Conservation and Development van der Hout, Peter; Van der Hout Forestry Consulting, Jan Trooststraat van der Heijden , Geertje; University of Nottingham, School of Geography van der Meer, Peter; Van Hall Larenstein University of Applied Sciences Vasquez, Rodolfo; Jardín Botánico de Missouri, Peru Vieira, Simone; UNICAMP, NEPAM Vilanova Torre, Emilio; Instituto de Investigaciones para el Desarrollo Forestal, Universidad de Los Andes, Vos, Vincent; Centro de Investigación y Promoción del Campesinado - regional Norte Amazónico Wang, Ophelia; Northern Arizona University Young, Ken; University of Texas at Austin, Geography and the Environment</p>
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	Zagt, Roderick; Tropenbos International Baker, Tim; University of Leeds, Geography
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Evolutionary heritage influences Amazon tree

ecology

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3 Fernanda Coelho de Souza¹, Kyle G. Dexter^{2,3}, Oliver L. Phillips¹, Roel J.W. Brienen¹, Jerome
4 Chave⁴, David R. Galbraith¹, Gabriela Lopez-Gonzalez¹, Abel Monteagudo-Mendoza⁵, R.
5 Toby Pennington³, Lourens Poorter⁶, Miguel Alexiades⁷, Esteban Álvarez-Dávila⁸, Ana
6 Andrade⁹, Luis E.O.C. Aragão^{10,11}, Alejandro Araujo-Murakami¹², Eric J.M.M. Arets¹³,
7 Gerardo A. Aymard C.¹⁴, Christopher Baraloto¹⁵, Jorcely Barroso¹⁶, Damien Bonal¹⁷, Rene
8 G.A. Boot¹⁸, José L.C. Camargo⁹, James A. Comiskey^{19,20}, Fernando Cornejo Valverde²¹, Plínio
9 B. de Camargo²², Anthony Di Fiore²³, Fernando Elias²⁴, Terry L. Erwin²⁵, Ted R. Feldpausch¹⁰,
10 Leandro Ferreira²⁶, Nykolos M.F. Fyllas¹, Emanuel Gloor¹, Bruno Herault²⁷, Rafael
11 Herrera^{28,29}, Niro Higuchi³⁰, Eurídice N. Honorio Coronado³¹, Timothy J. Killeen³², William F.
12 Laurance³³, Susan Laurance³³, Jon Lloyd³⁴, Thomas E. Lovejoy³⁵, Yadvinder Malhi³⁶, Leandro
13 Maracahipes³⁷, Beatriz S. Marimon²⁴, Ben H. Marimon-Junior²⁴, Casimiro Mendoza³⁸, Paulo
14 Morandi²⁴, David A. Neill³⁹, Percy Núñez Vargas⁴⁰, Edmar A. Oliveira²⁴, Eddie L. Oliveira²⁴,
15 Walter A. Palacios⁴¹, Maria C. Peñuela-Mora⁴², John J. Pipoly III⁴³, Nigel C.A. Pitman⁴⁴,
16 Adriana Prieto⁴⁵, Carlos A. Quesada³⁰, Hirma Ramirez-Angulo⁴⁶, Agustin Rudas⁴⁵, Kalle
17 Ruokolainen⁴⁷, Rafael P. Salomão²⁶, Marcos Silveira⁴⁸, Juliana Stropp⁴⁹, Hans ter Steege⁵⁰,
18 Raquel Thomas-Caesar⁵¹, Peter van der Hout⁵², Geertje M.F. van der Heijden⁵³, Peter J. van
19 der Meer⁵⁴, Rodolfo V. Vasquez⁵, Simone A. Vieira⁵⁵, Emilio Vilanova⁵⁶, Vincent A. Vos^{57,58},
20 Ophelia Wang⁵⁹, Kenneth R. Young⁶⁰, Roderick J. Zagt¹⁸, Timothy R. Baker¹

21 ¹School of Geography, University of Leeds, Leeds, LS2 9JT, UK

22 ²School of Geosciences, University of Edinburgh, 201 Crew Building, King's Buildings,
23 Edinburgh EH9 3FF, UK

24 ³Royal Botanic Garden Edinburgh, 20a Inverleith Row, Edinburgh EH3 5LR, UK

25 ⁴Université Paul Sabatier CNRS, UMR 5174 Evolution et Diversité Biologique, bâtiment
26 4R1, 31062 Toulouse, France

27 ⁵Jardín Botánico de Missouri, Prolongacion Bolognesi Mz.e, Lote 6, Oxapampa, Pasco,
28 Peru

29 ⁶Forest Ecology and Forest Management Group, Wageningen University, P.O. Box 47,
30 6700 AA Wageningen, The Netherlands

31 ⁷School of Anthropology and Conservation, University of Kent, Marlowe Building,
32 Canterbury, Kent CT2 7NR, UK

33 ⁸Fundación Con Vida, Medellin Cra 48: 20-114, Colombia

34 ⁹Biological Dynamics of Forest Fragment Project (INPA &STRI), C.P. 478, Manaus AM
35 69.011-970, Brazil

36 ¹⁰Geography, College of Life and Environmental Sciences, University of Exeter, Rennes,
37 Drive, Exeter, EX4 4RJ, UK

38 ¹¹National Institute for Space Research (INPE), São José dos Campos, São Paulo, Brazil

39 ¹²Museo de Historia Natural Noel Kempff Mercado, Universidad Autonoma Gabriel
40 Rene Moreno, Casilla 2489, Av. Irala 565, Santa Cruz, Bolivia

- 41 ¹³Alterra, Wageningen University and Research Centre, PO box 47, 6700 AA
42 Wageningen, The Netherlands
- 43 ¹⁴UNELLEZ-Guanare, Programa del Agro y del Mar, Herbario Universitario (PORT),
44 Mesa de Cavacas, Estado Portuguesa 3350, Venezuela
- 45 ¹⁵International Center for Tropical Botany, Department of Biological Sciences, Florida
46 International University, Miami, FL 33199, USA
- 47 ¹⁶Universidade Federal do Acre, Campus de Cruzeiro do Sul, Rio Branco, Brazil
- 48 ¹⁷INRA, UMR 1137 "Ecologie et Ecophysiologie Forestiere" 54280 Champenoux,
49 France
- 50 ¹⁸Tropenbos International, P.O. Box 232, 6700 AE Wageningen, The Netherlands
- 51 ¹⁹National Park Service, 120 Chatham Lane, Fredericksburg, VA 22405
- 52 ²⁰Smithsonian Institution, 1100 Jefferson Dr, SW, Washington DC 20560
- 53 ²¹Proyecto Castaña. Madre de Dios, Peru
- 54 ²²Centro de Energia Nuclear na Agricultura, Universidade de São Paulo, São Paulo, SP,
55 Brazil
- 56 ²³Department of Anthropology, University of Texas at Austin, SAC Room 5.150, 2201
57 Speedway Stop C3200, Austin, TX 78712, USA
- 58 ²⁴Universidade do Estado de Mato Grosso, Campus de Nova Xavantina, Caixa Postal
59 08, 78.690-000, Nova Xavantina, MT, Brazil

60 ²⁵Department of Entomology, Smithsonian Institution, PO Box 37012, MRC
61 187, Washington DC 20013-7012, USA

62 ²⁶Museu Paraense Emilio Goeldi, C.P. 399, 66.040-170, Belém, PA, Brazil

63 ²⁷Cirad, UMR EcoFoG (AgroParisTech, CNRS, Inra, U Antilles, U Guyane), Campus
64 Agronomique, 97310 Kourou, French Guiana

65 ²⁸Centro de Ecología IVIC, Caracas, Venezuela

66 ²⁹Institut für Geographie und Regionalforschung, University of Vienna, Austria

67 ³⁰INPA, Av. André Araújo, 2.936 - Petrópolis – 69.067-375 - Manaus -AM, Brasil

68 ³¹Instituto de Investigaciones de la Amazonia Peruana, Apartado 784, Iquitos, Peru

69 ³²GTECA - Amazonica, Santa Cruz, Bolivia

70 ³³Centre for Tropical Environmental and Sustainability Science (TESS) and College of
71 Science and Engineering, James Cook University, Cairns, Queensland 4878, Australia

72 ³⁴Department of Life Sciences, Imperial College London, Silwood Park Campus,
73 Buckhurst, Road, Ascot, Berkshire SL5 7PY, UK

74 ³⁵Environmental Science and Policy Department and the Department of Public and
75 International Affairs at George Mason University (GMU), Washington, DC, USA

76 ³⁶Environmental Change Institute, School of Geography and the Environment,
77 University of Oxford, UK

78 ³⁷Programa de Pós-graduação em Ecologia e Evolução, Universidade Federal de Goias,
79 Goiânia, Goias, Brazil

80 ³⁸Universidad Mayor de San Simón, Escuela de Ciencias Forestales, Unidad Académica
81 del Trópico, Sacta, Bolivia

82 ³⁹Universidad Estatal Amazónica, Facultad de Ingeniería Ambiental, Paso lateral km 2
83 1/2 via po, Puyo, Pastaza, Ecuador

84 ⁴⁰Universidad Nacional San Antonio Abad del Cusco, Av. de la Cultura N° 733. Cusco,
85 Peru

86 ⁴¹Universidad Técnica del Norte & Herbario Nacional del Ecuador, Casilla 17-21-1787,
87 Av. Río Coca E6-115, Quito, Ecuador

88 ⁴²Universidad Regional Amazónica IKIAM, Tena, Ecuador

89 ⁴³Broward Broward County Parks & Recreation, 950 NW 38th St, Oakland Park, FL
90 33309

91 ⁴⁴Center for Tropical Conservation, Duke University, Box 90381, Durham, NC 27708,
92 USA

93 ⁴⁵Doctorado Instituto de Ciencias Naturales, Universidad ciol de Colombia, Colombia

94 ⁴⁶Instituto de Investigaciones para el Desarrollo Forestal (INDEFOR), Universidad de
95 Los Andes, Facultad de Ciencias Forestales y Ambientales, Conjunto Forestal, C.P.
96 5101, Mérida, Venezuela

- 97 ⁴⁷Department of Biology, University of Turku, Turku FI-20014, Finland
- 98 ⁴⁸Museu Universitário, Universidade Federal do Acre, Rio Branco AC, 69910-900, Brazil
- 99 ⁴⁹European Commission, Directorate General - Joint Research Centre, Institute for
100 Environment and Sustainability, Ispra, Italy
- 101 ⁵⁰Naturalis Biodiversity Center, Vondellaan 55, Postbus 9517, 2300 RA Leiden, The
102 Netherlands
- 103 ⁵¹Iwokrama Intertiol Centre for Rainforest Conservation and Development, 77 High
104 Street Kingston, Georgetown, Guyana
- 105 ⁵²Van der Hout Forestry Consulting, Jan Trooststraat 6, 3078 HP Rotterdam, The
106 Netherlands
- 107 ⁵³School of Geography, University of Nottingham, University Park, NG7 2RD,
108 Nottingham, UK
- 109 ⁵⁴Van Hall Larenstein University of Applied Sciences, Velp, PO Box 9001, 6880 GB, The
110 Netherlands
- 111 ⁵⁵Universidade Estadual de Campinas, Núcleo de Estudos e Pesquisas Ambientais -
112 NEPAM
- 113 ⁵⁶Universidad de Los Andes, Facultad de Ciencias Forestales y Ambientales, Mérida,
114 Venezuela

115 ⁵⁷Centro de Investigación y Promoción del Campesinado - regional Norte Amazónico,
116 C/ Nicanor Gonzalo Salvatierra N° 362, Casilla 16, Riberalta, Bolivia

117 ⁵⁸Universidad Autónoma del Beni, Campus Universitario, Riberalta, Bolivia

118 ⁵⁹Northern Arizona University, Flagstaff, AZ 86011, USA

119 ⁶⁰Department of Geography and the Environment, University of Texas at Austin,
120 Austin, TX 78712 USA

121 Author for correspondence: Fernanda Coelho de Souza, email: fecoelhos@gmail.com

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124 phylogenetic signal

125 **Summary**

126 Lineages tend to retain ecological characteristics of their ancestors through time. However,
127 for some traits, selection during evolutionary history may have also played a role in
128 determining trait values. To address the relative importance of these processes requires
129 large-scale quantification of traits and evolutionary relationships amongst species. The
130 Amazonian tree flora comprises a high diversity of angiosperm lineages and species with
131 widely differing life history characteristics, providing an excellent system to investigate the
132 combined influences of evolutionary heritage and selection in determining trait variation.
133 We used trait data related to the major axes of life history variation among tropical trees
134 (e.g. growth and mortality rates) from 577 inventory plots in closed-canopy forest, mapped

135 onto a phylogenetic hypothesis spanning >300 genera including all major angiosperm clades
136 to test for evolutionary constraints on traits. We found significant phylogenetic signal for all
137 traits, consistent with evolutionarily related genera having more similar characteristics than
138 expected by chance. Although there is also evidence for repeated evolution of similar,
139 pioneer and shade tolerant life history strategies within independent lineages, the existence
140 of significant phylogenetic signal allows clearer predictions of the links between
141 evolutionary diversity, ecosystem function and the response of tropical forests to global
142 change.

143 **1. Introduction**

144 Evolutionary heritage may act as a major constraint on the ecological roles that species in a
145 lineage can occupy. Even under a random model of trait evolution where functional traits
146 drift in state over time (e.g. a Brownian motion model), we would expect closely related
147 species to have similar functional trait values and similar ecologies due to their shared
148 common ancestry [1, 2]. However, both divergent selection and convergent evolution lead
149 to weaker relationships between species relatedness and their ecological similarity [1, 3, 4].
150 Hence, although it is often assumed that close relatives are more similar because they retain
151 the ecological characteristics of their ancestors, in many clades the ancestral character state
152 may not be conserved. Thus, rather than being simply assumed, the tendency of closely
153 related species to have similar ecological characteristics needs to be tested.

154 The strength of the link between trait variation and phylogenetic relatedness has a wide
155 range of implications for understanding ecological and evolutionary processes and can be
156 measured by the magnitude of phylogenetic signal (PS) [1, 2]. For example, if a selected trait

157 has significant PS, the relatedness of species can help us to understand the underlying
158 mechanisms that drive community structure [5-7]. The presence of significant PS also
159 suggests that the sum of phylogenetic distances among species that occur within a
160 community (i.e. phylogenetic diversity) is a useful proxy for functional diversity and that, in
161 turn, phylogenies of tree taxa may contribute to understanding ecosystem function [8, 9]. In
162 addition, if trait values are more similar than expected by chance among closely related
163 lineages, we can predict the trait values for species where trait data are not available.

164 To understand the relative importance of evolutionary heritage versus selection in
165 determining trait variation requires large-scale quantification of traits and evolutionary
166 relationships amongst species. The Amazonian tree flora comprises a high diversity of
167 angiosperm lineages and species with widely differing life history characteristics, providing
168 an excellent system to investigate these processes. Previous studies of the degree of
169 phylogenetic signal among traits of tropical trees, such as seed mass, leaf structure and
170 chemistry, trunk characteristics and range size, have shown variable results [6, 7, 10-13].
171 For example, some studies show significant PS [6, 7, 13], while for the same traits other
172 studies have failed to detect any PS, with closely related species exhibiting rather different
173 trait values [10, 11]. A key limitation of many of these studies is the limited spatial and
174 phylogenetic scale of study, as well as the resolution of the phylogeny that they have used
175 [14]. Here, we explore patterns of PS at large spatial and phylogenetic scales using a
176 sequence-based phylogeny to test whether there are significant levels of PS for four key
177 traits related to the major axes of life history variation among tropical trees: tree growth
178 and mortality rates, wood density and potential tree size. These traits are related to
179 resource acquisition and allocation, defence, and dispersal ability [15, 16] and represent

180 important axes of functional variation which drive variation in plant performance and
181 function in many ecosystems [17]. Moreover, those traits are strongly related to differences
182 in carbon fluxes and storage among species [18]. As a result, understanding PS in these traits
183 may help to understand and model ecosystem processes in such highly diverse tropical
184 forests such as Amazonia, which may harbour more than 16,000 tree species [19].

185 Studying PS at large spatial scales is important because the scale of study affects the
186 strength of PS. At small scales, patterns of PS can be obscured because co-occurring species
187 represent just a small fraction of the species richness of clades [20, 21]. Small spatial scales
188 encompass limited environmental variation, so the species pool is limited to representatives
189 of different lineages that may have similar ecological traits and environmental
190 requirements: this pattern results in a lower range in traits and low PS. The strength of this
191 effect depends on how environmental variability changes with spatial scale, on the degree
192 of habitat specialization by species and the proportion of clades that are sampled in small-
193 scale studies [6, 7]. However, in general, larger spatial scales incorporate greater
194 environmental heterogeneity and encompass a larger number of lineages with a wider
195 range of trait values. Inferring patterns of PS that are more representative of evolutionary
196 trends therefore typically requires measurement across large spatial scales, including a wide
197 range of environmental conditions and taxa from a broad array of clades [22].

198 The patterns of PS also depend on traits under investigation and their specific evolutionary
199 history. Some traits may exhibit phylogenetic conservatism where traits in specific lineages
200 are constrained to certain trait values. For example, complex traits, such as growth and
201 mortality, may depend in complex ways on multiple, interacting gene loci [23, 24] which

202 impose strong constraints on trait variation. Alternatively, traits may show no PS because
203 they are under strong selective pressure and/or because they show phenotypic plasticity in
204 response to environmental conditions [20, 25].

205 Here, we use a large dataset of several hundred permanent forest plots that occur across a
206 wide range of the environmental conditions from all nine Amazonian countries [26], to
207 quantify key demographic traits of more than 300 lineages of tropical trees, and explore the
208 PS of these traits using recently published molecular genus- [13] and species-level
209 phylogenies [27, Dexter & Pennington, unpubl.]. By exploring how traits are correlated and
210 the strength of PS, our goal is to address the fundamental question of whether repeated
211 convergent and divergent evolution of life history strategies has erased phylogenetic signal
212 for life history-related traits in tropical trees, or whether phylogenetic information can be
213 used to understand ecosystem function in the world's most diverse and ecologically
214 important forest.

215 **2. Methods**

216 **Plot data**

217 This study used inventory data from all trees and palms ≥ 10 cm diameter (DBH) in 577
218 forest plots from the RAINFOR forest plot network (figure 1; electronic supplementary
219 material S1) across lowland closed-canopy South American tropical forests. This network is
220 centred on Amazonia and includes plots in forests on the Guiana Shield, in the Choco and
221 northern South America; however, hereafter for simplicity we refer to this sampling region
222 as 'Amazonia'. Plots are located in old growth, unlogged forests and range in size from 0.04
223 to 25 ha (most being 1 ha). They span a precipitation gradient from 1300 to 7436 mm yr⁻¹

224 [28], a broad range of soil types [29], and are found below 500 m in elevation. Data were
225 extracted from the ForestPlots.net database which curates tree-by-tree records from
226 RAINFOR and other plot networks [26, 30].

227 For productivity and mortality analyses, we used a subset of 257 repeated census plots with
228 a minimum monitoring period of 2 years from 1962 to 2014. Mean census interval length is
229 4.4 years and plot mean total monitoring period is 9.9 years. During each census, all
230 surviving trees and palms were measured, dead trees were documented and new trees with
231 ≥ 10 cm dbh were recorded. More detailed measurement methods and plot characteristics
232 have been previously published [e.g. 31, 32]. All recorded species and genus names were
233 checked and standardized using the Taxonomic Name Resolution Service [33]. We excluded
234 all trees and palms not identified to genus-level (7.9% of stems).

235 **Trait data**

236 Trait mean values of potential tree size, mean and maximum growth rates, mortality rates
237 and wood density were calculated at both the genus and species-level. Our main analyses
238 were performed at the genus-level and covered all genera present in a recently published
239 genus-level phylogeny for Amazonian trees [13]. Species-level trait data for those clades
240 where we had species-level phylogenies with sufficient sampling of species in our dataset
241 (>20 species): Burseraceae [27] and *Inga* (Dexter & Pennington, unpubl.), were used to
242 investigate whether patterns of PS at the genus-level were consistent with species level
243 patterns. Species-level trait data was also used to account for intrageneric variation in the
244 genus-level analyses of PS: the species-level data was used to calculate the standard error of
245 each trait within each genus and these values were incorporated into the calculations of PS

246 (described below) [34]. In the methods below, all the details are given for trait values
247 calculated at the genus-level; similar calculations and methods were used at the species-
248 level.

249 Potential tree size, mean and maximum growth rates were all calculated in terms of tree
250 diameter, basal area and biomass for each genus with at least 20 individuals across multiple
251 censuses.

252 Potential tree size was estimated as the 95th percentile of the size distribution of all trees
253 within each genus. For trees with multiple measurements, we selected the maximum size
254 across different censuses to define these distributions. Tree aboveground biomass (AGB)
255 per stem was calculated using the pan-tropical, three parameter allometric equation
256 (diameter, wood density and E) of Chave, Rejou-Mechain [35], which assumes that tree
257 diameter-height relationships depend linearly on bioclimatic variables (E), where E is a
258 measurement of environmental stress based on measures of temperature seasonality and
259 precipitation seasonality derived from the WorldClim dataset [28] and a measure of Climatic
260 Water Deficit extracted from a global gridded dataset [35]. Palm biomass was estimated
261 using a palm-specific allometric equation based on diameter [36].

262 For each genus, we computed both mean growth rate and the 95th percentile of growth
263 rates, to represent maximum growth rates within each genus, across all stems. To calculate
264 these parameters, mean stem-level growth rate was first estimated as the mean growth per
265 year across multiple censuses and maximum stem-level growth as the maximum growth
266 rate per year calculated across multiple censuses. Trees with mean negative growth rates
267 (0.9% of stems) were excluded in order to normalize the data [similar to 37]. We also

268 excluded palms, which do not have secondary growth, nine trees exhibiting diameter
269 growth greater than 80 mm yr^{-1} which likely represents recording errors and stems where
270 diameter measurements were not made using a tape measure (0.12 % of all stems). If a
271 change in the point of measurement (POM) was made during the measurement record of
272 any given tree, we calculated growth rates using the arithmetic mean of the diameter
273 measured at the original POM and the diameter at the new POM [38].

274 Mortality rates were estimated for all genera with a minimum of 100 individuals in the plot
275 data, based on the number of individuals found alive in the initial and final censuses of each
276 plot. To estimate average mortality rates within each genus, the survival probability of
277 individual trees within each clade was modelled as an exponentially declining function of
278 the monitoring period whilst accounting for variation in tree size [39, 40].

279 To account for the wide range of environmental conditions across plots [29], we used mixed
280 models to calculate genus-level values of potential tree size, mean and maximum growth
281 rates and mortality rates whilst accounting for systematic variation in these parameters
282 among plots [40] (see electronic supplementary material, S2).

283 Wood density data were extracted from the Global Wood Density database [41, 42] and
284 average values calculated for each genus in the phylogeny [43].

285 **Trait correlations**

286 To identify relationships amongst genus-level traits we conducted a Phylogenetic Principal
287 Component Analysis PPCA [44] including genera where we have a complete set of trait data.
288 PPCA incorporates the expected correlation among traits due to their shared evolutionary

289 history into the principal component analyses [45]. We standardized trait values to a mean
290 of zero and unit variance to ensure that each trait contributed equally to the PPCA.

291 **Phylogenetic Signal**

292 In order to estimate phylogenetic signal (PS) for traits, we used Blomberg's K [1]. This metric
293 quantifies the amount of variance in an observed trait in relation to the expected trait
294 variance under a Brownian motion model of evolution [1, 4]. Under this model of evolution,
295 trait values drift randomly over time, with small changes being more likely than large
296 changes within a given unit of time (trait values at t_1 are chosen from a normal distribution
297 centred on the trait value at t_0). This model generates trait data where the covariance
298 among trait values for taxa is proportional to the duration of their shared evolutionary
299 history [4]. Values of K equal to 0 indicate that there is no phylogenetic signal, whilst K equal
300 to 1 indicates high phylogenetic signal and is the expected value under a Brownian motion
301 model of evolution. Intermediate values ($0 < K < 1$) indicate intermediate levels of
302 phylogenetic signal. To assess significance in K , we recalculated K on the tree with
303 randomized tips a thousand times, and compared the simulated values with the observed
304 value of K . If the observed value fell outside the range given by 2.5-97.5 percentiles of the
305 simulated values, this value was considered significant.

306 We accounted for intra-generic trait variation in the calculation of K by measuring the
307 standard error for each genus, treating individual genera as species and intrageneric
308 variation as intraspecific variation *sensu* [34]. For genera where the standard error could not
309 be computed, we assigned the mean value of the standard error for all genera with
310 estimates for multiple species [34]. Including this within-genus variation allows us to

311 account for uncertainty in trait estimation (e.g. population variation and measurement
312 error), improve parameter estimation and reduce bias in the calculation of PS [1, 34].

313 We also calculated PS using Pagel's λ [46] in order to explore whether our results were
314 dependent on the particular method used to calculate phylogenetic signal (see electronic
315 supplementary material, S3).

316 **Sensitivity analysis**

317 To investigate whether our results were affected by the spatial scale of our study, we
318 repeated our analyses using 26 plots within 55 km of each other near Manaus. Similarly, to
319 verify whether our results were affected by our use of genus-level data, we conducted the
320 same analyses at the species level for the genus *Inga* and the Protieae (Burseraceae).
321 Likewise, to investigate whether the number of lineages included in the analyses affected
322 the extent of PS, we repeated the calculations of PS with just the genera with a complete set
323 of trait values (214).

324 Statistical analyses were performed in the R 3.1.1 program [47], using ape [48], phytools
325 [44] and data.table [49] packages.

326 **3. Results**

327 **Trait data**

328 All traits measured varied substantially among genera (table 1, figure 2): wood density
329 varied eight-fold, potential size in tree diameter 12-fold, potential size in biomass 814-fold,
330 maximum growth rates in tree diameter 23-fold, mean diameter growth rates 35-fold, and

331 mortality rates 275-fold. Overall, the trait values after correcting for environmental variation
332 and those estimated directly from the database without accounting for variation among
333 plots were highly correlated with each other ($p < 0.001$ in all cases and τ ranging from 0.59-
334 0.79).

335 **Trait relationships**

336 Trait associations among lineages were analysed with a phylogenetic principal component
337 analysis (PPCA): eighty-three percent of the variation in the four dimensional space was
338 accounted for by the first two axes (figure 3). The first axis (PPCA1) explained 52.8% of the
339 variation and shows strong positive loadings for mortality and maximum growth rates,
340 whilst wood density was negatively associated with this axis (electronic supplementary
341 material S4). PPCA1 thus represents a continuum from pioneer and light demanding
342 lineages with low wood density and fast demographic traits (e.g. high mortality and growth
343 rates) to non-pioneer lineages with high wood density and slow demographic rates. The
344 second axis (PPCA2) explained 30.5% of the variation and was associated more closely with
345 potential tree size, and reflects the variation from individuals of understory genera, to
346 individuals of canopy and emergent lineages (figure 3).

347 **Phylogenetic signal**

348 All traits and the first two PPCA axes exhibited significant PS, with closely related genera
349 being more similar than expected by chance, using either Bloomberg's K (table 1) or Pagel's
350 λ (electronic supplementary material S3). Because estimates of Pagel's λ and Blomberg's K
351 are strongly correlated and most studies of phylogenetic signal in tropical trees have

352 focused on the K metric rather than λ , we focus our results and discussion on the
353 calculations using Blomberg's K -value.

354 Traits showed significant and similar values for K , varying from 0.25 to 0.39 and from 0.18 to
355 0.27, with and without accounting for intrageneric variation respectively. These K -values
356 indicate that evolutionarily related genera tend to be more similar to each other, but less
357 than expected under a BM model of evolution (table 1). Finally, removing the environmental
358 contribution to trait variation did not substantially alter the magnitude of PS (table 1).

359 **Sensitivity analyses**

360 Although selecting just the Manaus data significantly reduced the number of genera,
361 species, and individual trees included in the analyses, PS at smaller spatial scales showed
362 similar patterns to PS calculated using the whole dataset (electronic supplementary material
363 S5). Similarly, reducing the number of lineages to genera we had all trait values showed
364 congruent patterns of PS (electronic supplementary material S5). In addition, all traits
365 showed similar or slightly higher Blomberg's K values for just *Inga* or *Protieae* than for all
366 taxa together (electronic supplementary material S5).

367 **4. Discussion**

368 This is the first study, to our knowledge, to investigate the extent of phylogenetic signal (PS)
369 for traits that quantify the main axes of life history variation in survival and growth of trees
370 at such a large phylogenetic and spatial scale. Our results demonstrate that for Amazonian
371 forests, closely related genera have similar life history strategies, with all traits showing
372 similar levels of PS (table 1, figure 2 and electronic supplementary material S6). The similar

373 level of PS found across all the different, correlated traits suggests that the main axes of life-
374 history variation among lineages of Amazonian trees may represent the result of repeated
375 evolution of a suite of coordinated functional characteristics.

376 **Relationships amongst Traits**

377 Strong correlations amongst traits were represented by two major axes of variation, which
378 are likely to be associated with adaptations to horizontal and vertical light gradients.
379 Ecological differences among species adapted to gaps versus the shaded understory or to
380 the understory versus the canopy are well-established as the principal axes of functional
381 variation among tropical forest tree species [50, 51]. The first axis runs from pioneer and
382 light demanding genera with low wood density and fast demographic traits (e.g. high
383 mortality and high growth rates) to shade tolerant genera with heavy wood and slow
384 demographic traits. The second axis represents variation in tree size and contrasts
385 understorey genera, from lineages of canopy trees. For example, these axes distinguish
386 *Cecropia* and *Croton*, classic pioneers with low wood density and fast demographic traits,
387 from *Hirtella* - a typically dense-wooded and slow-growing understory genus of trees.
388 Lineages of emergent trees which all achieve very large potential tree sizes (e.g. *Bertholletia*,
389 *Ceiba*, *Hura*, *Dipteryx*) , are also distinguished in this analysis by their different wood
390 densities and growth rates (figure 3).

391 **Phylogenetic Signal**

392 Our results demonstrate significant levels of PS among demographic and structural traits of
393 tropical trees, with Blomberg's K ranging from 0.25 to 0.32. This pattern suggests that
394 evolutionary relationships provide useful information about the ecological similarity of

395 these lineages. However, while our analyses of PS shows that evolutionarily related lineages
396 have more similar traits than expected by chance, their values are lower than expected
397 under a pure BM model of evolution (table 1 and figure 2) under which K -values would be
398 close to 1. PS can be lower than expected under BM if there is convergent evolution across
399 distantly related lineages and/or divergent selection among closely related groups [3, 4].
400 This result therefore suggests that there has been repeated convergent evolution and/or
401 divergent selection, along the two main axes of variation identified by the PPCA analysis
402 (figure 3). This finding suggests that adaptations to light gaps, or understorey and canopy
403 light environments, have repeatedly evolved within multiple lineages of tropical trees as
404 shown by the different pioneer and shade tolerant genera within a series of unrelated
405 families (e.g. *Cecropia* versus *Brosimum* (Urticaceae/Moraceae), *Vismia* versus *Calophyllum*
406 (Clusiaceae), and *Inga* versus *Dipteryx/Parkia* (Fabaceae); figure 2).

407 **Sensitivity analyses**

408 The PS found here for trees across lowland closed-canopy South American forests is
409 generally stronger than previously reported in the literature for tropical forests in smaller-
410 scale analyses (electronic supplementary material S7). In previous studies, some traits
411 showed low but significant PS [6, 7, 13], while others have even found that traits are
412 randomly dispersed over the phylogeny [10, 11]. However, although K -values are
413 standardized to allow comparison between traits and phylogenetic trees [1, 4], direct
414 comparisons of PS are affected by differences in the spatial and taxonomic scale of the
415 studies, the number of lineages and the use of different kinds of phylogenies.

416 A first issue for comparing the extent of PS among studies is variation in spatial scales.
417 However, here we show that the higher PS in the present study is unlikely to be an artefact
418 of our larger spatial scale: restricting our analyses to 26 plots around Manaus shows
419 consistent patterns, with similar levels of PS for all traits compared to analyses for the whole
420 Amazon (electronic supplementary material S5).

421 Secondly, different numbers of lineages in different studies may play a role in determining
422 variation in the extent of PS. Although Blomberg's K is efficient at detecting the strength of
423 similarity among closely related lineages for sample sizes greater than 20 [1], the ability to
424 detect different levels of PS may increase with larger sample sizes [52]. In order to address
425 this issue, we conducted a set of analyses restricted to genera for which we had all trait
426 values (214 genera). Since estimates of K are highly consistent when we include fewer
427 genera (electronic supplementary material S5), it appears that the number of lineages is
428 unlikely to have caused the observed trends of high levels of PS for our traits.

429 Thirdly, most of previous studies [6, 7, 10-12] were conducted at the species-level, and
430 taxonomic scale can also affect the degree of PS. Phylogenetic signal in any trait may vary at
431 different taxonomic scales; a single trait can have high similarity at one level (e.g. genus
432 level) but this pattern can break down at higher or lower taxonomic levels [52]. Here, the
433 phylogenetic signal of these traits at the species level within the *Protieae* and *Inga* were
434 similar or slightly greater than for the genus-level results (electronic supplementary material
435 S5), suggesting that our results are consistent at finer taxonomic levels. However, since our
436 analyses at low taxonomic levels were limited to two lineages it remains to be fully tested
437 whether the result indeed holds within all clades of Neotropical trees.

438 Finally, the use of different kinds of phylogenies is likely to affect the extent of similarity
439 among related species that is reported in different studies (electronic supplementary
440 material S7). Much previous work was carried out using community-level phylogenies,
441 restricted to locally co-occurring species [6, 12] and in many cases using unresolved
442 phylogenies with relationships represented as polytomies [11]. Such community level
443 phylogenies may lack sister lineages for many clades that may be critical to effectively
444 measure PS. In addition, the use of trees with many polytomies, e.g. those which add genera
445 and species as polytomies onto backbone family-level trees [53], leads to uncertainty in
446 phylogenetic signal estimates [14]. More importantly, phylogenetic sampling may play a
447 major role in determining the extent of PS. Although the genus level phylogeny used here is
448 far from complete, our analyses do encompass a far wider range of lineages than previous
449 studies, including the major angiosperm lineages present in the Amazon basin.

450 Our results demonstrate that there is significant PS for key demographic and structural traits
451 in tropical forests. This finding opens the way for clearer predictions of how evolutionary
452 diversity relates to ecosystem structure and function, and how different drivers will, in turn,
453 affect the evolutionary diversity of Amazonian forests. For example, this study suggests that
454 community-level measures of evolutionary relatedness among species are likely to be good
455 predictors of the structure and functioning of these ecosystems [8, 9]. These results also
456 indicate that changes in environmental conditions or disturbance regimes that favour
457 particular life history strategies will ultimately erode evolutionary diversity [54, 55],
458 although the presence of some convergent evolution across lineages may prevent significant
459 loss of phylogenetic diversity over some scales of anthropogenic disturbance [56]. Our
460 results may therefore help to resolve why different studies of the effect of disturbance on

461 phylogenetic diversity have obtained contrasting results [54-56]: in particular, this study
462 suggests that investigating the PS of traits that influence species ability to persist after
463 disturbance within the species pool of interest will be critical to understand how
464 disturbance will alter phylogenetic diversity. Finally, our results also suggest that any long-
465 term changes in the evolutionary diversity of intact Amazonian forests may help to uncover
466 functional shifts in these diverse ecosystems. Overall, the phylogenetic structure of life
467 history strategies within Amazon tree communities described in this study helps to provide a
468 predictive framework to understand how such complex systems will respond to global
469 change and anthropogenic disturbance.

470 **Author contributions**

471 F.C.S and T.R.B. conceived the study, F.C.S, T.R.B. and K.G.D. designed the study; F.C.S.
472 analyzed data and wrote the paper; all co-authors collected field data or data management
473 and analyses tools. O.L.P., Y.M. and J.L conceived the RAINFOR forest census plot network.
474 K.G.D, J.C. and R.T.P contributed phylogenetic data used in this study. All co-authors
475 commented and/or approved the manuscript.

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496 will be made freely available and can be accessed at
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674

675 **Table and figure captions**

676 Table 1. Summary of trait data, including number of genera per trait, number of species, and
677 number of individuals used for selection criterion, minimum, maximum and mean trait
678 values per genera. In addition, phylogenetic signal for absolute trait values, accounting for
679 intrageneric variation, environmental variation, and both environmental and intrageneric
680 variation. Phylogenetic signal measured using Blomberg's K. *** $p < 0.001$; ** $p < 0.05$; * $p < 0.1$.

681 Figure 1. Map of location of 577 selected plots in lowland tropical South America over a
682 backcloth of the precipitation gradient (Annual precipitation, from the WorldClim dataset).
683 The map shows plots, with annual precipitation greater than 1300 mm year⁻¹ and altitude
684 less than 500 m. Black circles – single census, plots used exclusively for wood density and

685 potential tree size; grey circles – multi censuses, plots used for wood density, potential tree
686 size, growth and mortality rates.

687 Figure 2. Phylogeny (based on *rbcl* and *matK* plastid gene) of 497 Amazonian tree and palm
688 genera. Number of genera varied in the different phylogenies according to the selection
689 criterion for each trait (see Material and Methods). Branches are coloured according to (a)
690 wood density ($wd \text{ g.cm}^3$), (b) potential tree size in diameter (Max D cm), (c) maximum tree
691 growth in diameter (Max gr cm) and (d) mortality rates (%). Continuous traits were coloured
692 using a continuous colour gradient, with colour codes indicate the wide range of trait values,
693 from blue to red, indicating higher and lower trait values respectively. Phylogenies for each
694 trait with all tips labelled are available in the supplementary material (S6).

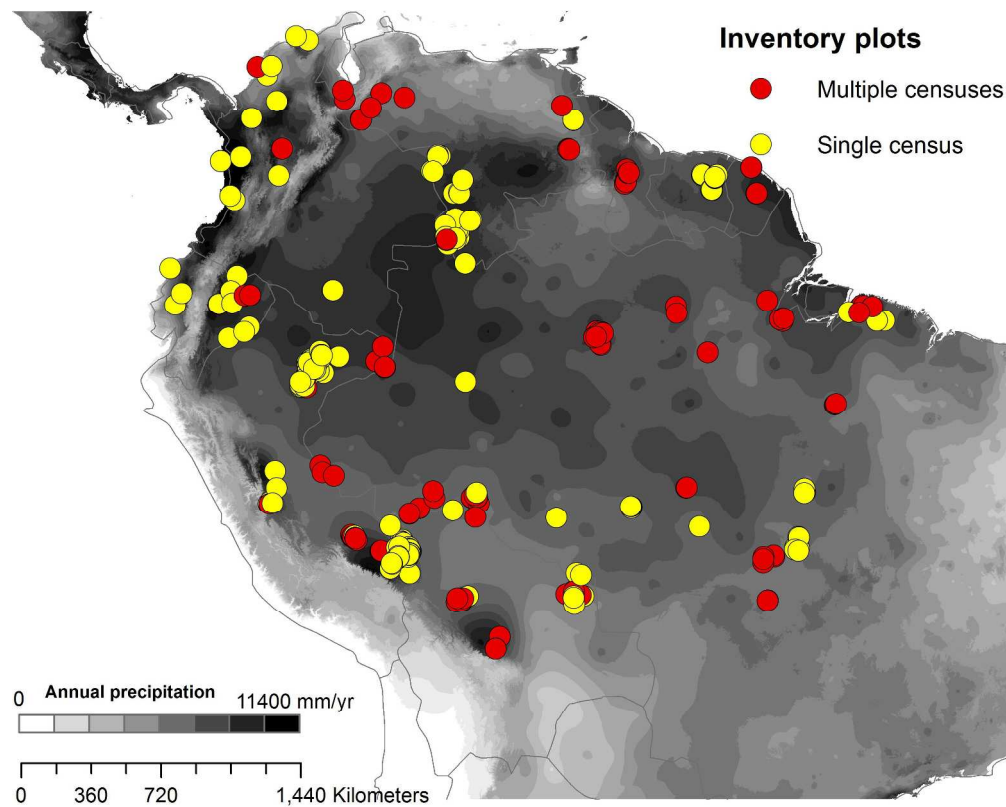
695 Figure 3. Phylogenetic Principal Component Analyses (PPCA) for the first two principal
696 components with PC loadings for the four traits studied here: Wood density (*wd*), potential
697 tree size in terms of diameter (Max.D), potential growth rates in terms of diameter
698 (Maxgr.D) and annual mortality rates (Mortality).

699 Table 1

	Traits	Units	N° ind	N° Genera	N° Species	Range	Mean	Phylogenetic Signal (<i>K</i>)			
								Intragenetic variation			
								no	yes	no	yes
								Environmental variation			
							no	no	yes	yes	
Wood density	wd	g.cm ³	-	497	1324	0.15-1.21	0.61	0.26***	0.30***	-	-
	Maximum diameter	cm	244362	383	1412	14.5-171.1	459.4	0.23***	0.31***	0.20***	0.29***
	Maximum diameter * wd	-	244362	383	1412	4.94-154.69	28.08	0.27***	0.34***	0.25***	0.32***
Potential size	Maximum basal area	m ²	244362	383	1412	0.02-2.3	0.21	0.23***	0.31***	0.21**	0.26***
	Maximum basal area * wd	-	244362	383	1412	0.01-0.13	0.13	0.26***	0.32***	0.23***	0.29***
	Maximum biomass	kg	244362	383	1412	54.63-44443.1	2760.6	0.25***	0.28***	0.22***	0.28***
	Maximum growth in diameter	cm	134303	329	1024	0.19-4.38	0.93	0.19***	0.25***	0.18***	0.25***
	Maximum growth in basal area	m ²	134303	329	1024	0.003-0.03	0.005	0.22***	0.32***	0.21***	0.29***
Growth rates	Maximum growth in biomass	kg	134303	329	1024	0.21-95.23	6.17	0.25***	0.39***	0.23***	0.33***
	Mean growth in diameter	cm	133656	327	1000	0.05-1.74	0.26	0.18***	0.25***	0.19***	0.29***
	Mean growth in basal area	m ²	133656	327	1000	0-0.01	0	0.20***	0.27***	0.19***	0.29***
	Mean growth in biomass	kg	133656	327	1000	0.15-21.76	1.67	0.23***	0.30***	0.19***	0.25***
Mortality	Mean stem mortality	%	156495	221	306	0.04-10.98	1.08	0.17**	0.25**	-	-
PPCA1	-	-	-	214	-	-	-	0.18**	-	-	-
PPCA2	-	-	-	214	-	-	-	0.21***	-	-	-

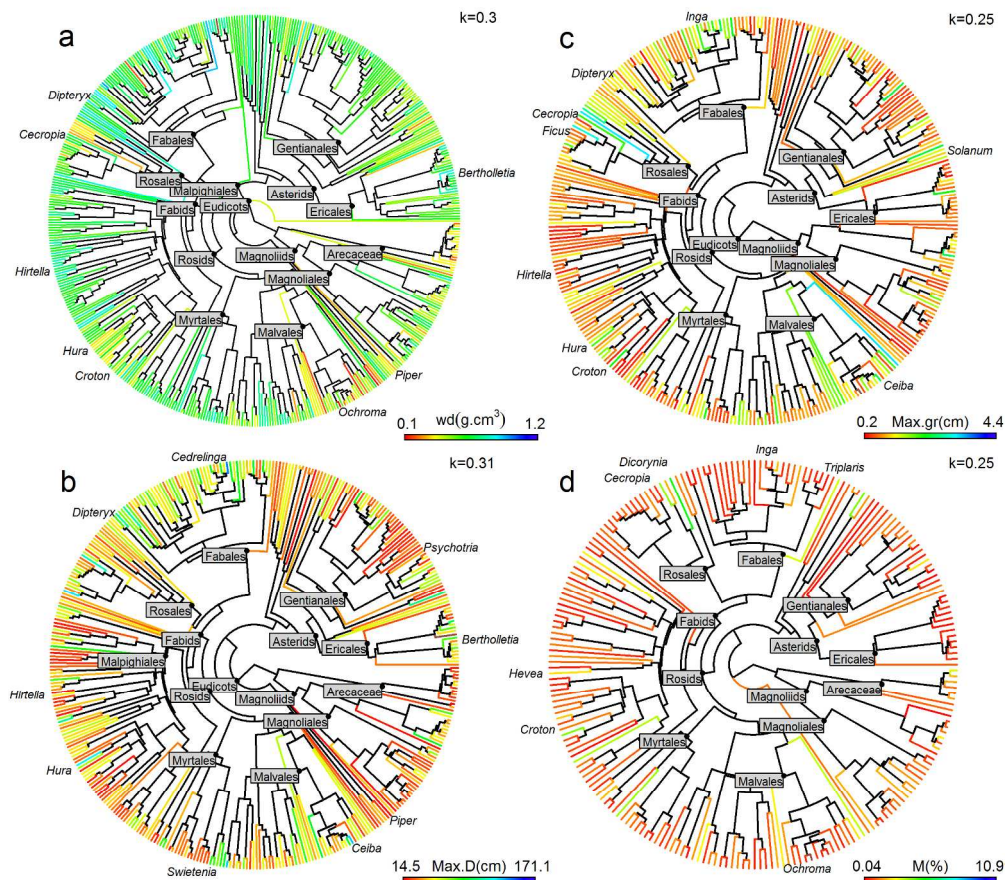
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Map of location of 577 selected plots in lowland tropical South America over a backcloth of the precipitation gradient (Annual precipitation, from the WorldClim dataset). The map shows plots, with annual precipitation greater than 1300 mm year⁻¹ and altitude less than 500 m. Black circles – single census, plots used exclusively for wood density and potential tree size; grey circles – multi censuses, plots used for wood density, potential tree size, growth and mortality rates.

Map of location of 577 plots
4127x3302mm (20 x 20 DPI)

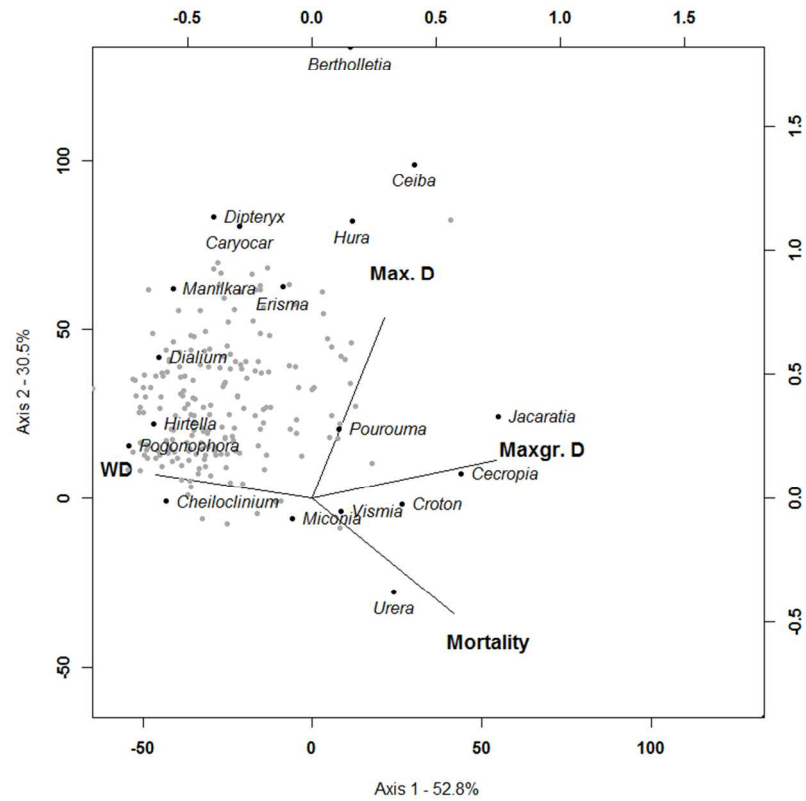


. Phylogeny (based on *rbcl* and *matK* plastid gene) of 497 Amazonian tree and palm genera. Number of genera varied in the different phylogenies according to the selection criterion for each trait (see Material and Methods). Branches are coloured according to (a) wood density (*wd* g.cm³), (b) potential tree size in diameter (Max D cm), (c) maximum tree growth in diameter (Max gr cm) and (d) mortality rates (%).

Continuous traits were coloured using a continuous colour gradient, with colour codes indicate the wide range of trait values, from blue to red, indicating higher and lower trait values respectively. Phylogenies for each trait with all tips labelled are available in the supplementary material (S6).

Phylogeny

235x209mm (300 x 300 DPI)



Phylogenetic Principal Component Analyses (PPCA) for the first two principal components with PC loadings for the four traits studied here: Wood density (wd), potential tree size in terms of diameter (Max.D), potential growth rates in terms of diameter (Maxgr.D) and annual mortality rates (Mortality)

PPCA

341x284mm (72 x 72 DPI)