



MACQUARIE
University

Macquarie University PURE Research Management System

This is a post-peer-review, pre-copyedit version of an article published in *Nature Ecology & Evolution*. The final authenticated version is available online at:

Poorter, L., Rozendaal, D.M.A., Bongers, F. et al. (2019) Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. *Nature Ecology & Evolution*, vol. 3, pp. 928–934.

<https://doi.org/10.1038/s41559-019-0882-6>

Copyright: © Springer 2019.

1 **Wet and dry tropical forests show opposite successional pathways** 2 **in wood density but converge over time**

3
4
5 **Authors:** Lourens Poorter¹, Danaë M.A. Rozendaal^{1,2}, Frans Bongers¹, Jarcilene S. de Almeida-Cortez³, Angélica
6 María Almeyda Zambrano⁴, Francisco S. Álvarez⁵, José Luís Andrade⁶, Luis Felipe Arreola Villa⁷, Patricia
7 Balvanera⁷, Justin M. Becknell⁸, Tony V. Bentos⁹, Radika Bhaskar^{7,10}, Vanessa Boukili¹¹, Pedro H.S. Brancalion¹²,
8 Eben N. Broadbent⁴, Ricardo G. César¹², Jerome Chave¹³, Robin L. Chazdon^{11,14}, Gabriel Dalla Colletta¹⁵, Dylan
9 Craven^{16,17,18,60}, Ben H.J. de Jong¹⁹, Julie S. Denslow²⁰, Daisy H. Dent^{21,22}, Saara J. DeWalt²³, Elisa Díaz García¹²,
10 Juan Manuel Dupuy⁶, Sandra M. Durán^{24,25}, Mário M. Espírito Santo²⁶, María C. Fandiño²⁷, Geraldo Wilson
11 Fernandes²⁸, Bryan Finegan⁵, Vanessa Granda Moser⁵, Jefferson S. Hall¹⁶, José Luis Hernández-Stefanoni⁶, Catarina
12 C. Jakovac^{9,29,30}, André B. Junqueira^{29,30}, Deborah Kennard³¹, Edwin Lebrija-Trejos³², Susan G. Letcher³³, Madelon
13 Lohbeck^{1,34}, Omar R. Lopez^{21,35}, Erika Marín-Spiotta³⁶, Miguel Martínez-Ramos⁷, Sebastião V. Martins³⁷, Paulo
14 E.S. Massoca⁹, Jorge A. Meave³⁸, Rita Mesquita⁹, Francisco Mora⁷, Vanessa de Souza Moreno¹², Sandra C.
15 Müller³⁹, Rodrigo Muñoz³⁸, Robert Muscarella^{40,41}, Silvio Nolasco de Oliveira Neto⁴², Yule R.F. Nunes⁴³, Susana
16 Ochoa-Gaona⁴⁴, Horacio Paz⁷, Marielos Peña-Claros¹, Daniel Piotto⁴⁵, Jorge Ruíz⁴⁷, Lucía Sanaphre-Villanueva⁶,
17 Arturo Sanchez-Azofeifa²⁴, Naomi B. Schwartz⁴⁶, Marc K. Steininger⁴⁸, William Wayt Thomas⁴⁹, Marisol Toledo⁵⁰,
18 Maria Uriarte⁴⁰, Luis P. Utrera⁵, Michiel van Breugel^{16,51,52}, Masha T. van der Sande^{1,17,18}, Hans van der Wal⁵³,
19 Maria D.M. Veloso²⁶, Hans F.M. Vester⁵⁴, Ima C. G. Vieira⁵⁵, Pedro Manuel Villa^{37,56}, G. Bruce Williamson^{28,57}, S.
20 Joseph Wright²¹, Kátia J. Zanini³⁹, Jess K. Zimmerman⁵⁸, Mark Westoby⁵⁹

21 22 **Affiliations:**

23 ¹ Forest Ecology and Forest Management Group, Wageningen University and Research, P.O. Box 47, 6700 AA
24 Wageningen, The Netherlands.

25 ² Laboratory of Geo-Information Science and Remote Sensing, Wageningen University and Research, P.O. Box 47,
26 6700 AA Wageningen, The Netherlands.

27 ³ Departamento de Botânica-CCB, Universidade Federal de Pernambuco, Pernambuco, CEP 50670-901, Brazil.

28 ⁴ School of Forest Resources and Conservation, University of Florida, 303 Reed Lab, Gainesville, FL 32611, USA.

29 ⁵ Forests, Biodiversity and Climate Change Programme, CATIE, Turrialba, Costa Rica.

30 ⁶ Centro de Investigación Científica de Yucatán A.C. Unidad de Recursos Naturales, Calle 43 No 130 x 32 y 34,
31 Colonia Chuburná de Hidalgo, C.P. 97205, Mérida, Yucatán, México.

32 ⁷ Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, CP
33 58089, Morelia, Michoacán, México.

34 ⁸ Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912, USA.

35 ⁹ Instituto Nacional de Pesquisas da Amazônia, Av. André Araujo, 2936, 69083-000, Manaus, Brazil.

36 ¹⁰ College of Design, Engineering, and Commerce, Philadelphia University, Gibbs Hall, 4201 Henry Avenue,
37 Philadelphia, Pennsylvania 19144, USA.

38 ¹¹ Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA.

39 ¹² Department of Forest Sciences, “Luiz de Queiroz” College of Agriculture, University of São Paulo, Av. Pádua
40 Dias, 11, 13418-900, Piracicaba, São Paulo, Brazil.

41 ¹³ Laboratoire Evolution et Diversité Biologique, UMR5174, CNRS/ Université Paul Sabatier Bâtiment 4R1, 118
42 route de Narbonne F-31062 Toulouse cedex 9, France.

43 ¹⁴ Tropical Forests and People Research Centre, University of the Sunshine Coast, 90 Sippy Downs Dr,
44 Sippy Downs QLD 4556, Australia.

45 ¹⁵ Institute of Biology, University of Campinas - UNICAMP, Cidade Universitária Zeferino Vaz - Barão Geraldo,
46 Campinas - SP, Zip code 13083-970, Brazil.

47 ¹⁶ SI ForestGEO, Smithsonian Tropical Research Institute, Roosevelt Ave. 401 Balboa, Ancon, Panama.

48 ¹⁷ German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103
49 Leipzig, Germany.

50 ¹⁸ Department of Community Ecology, Helmholtz Centre for Environmental Research - UFZ, Theodor-Lieser-
51 Straße 4, 06120 Halle (Saale), Germany

52 ¹⁹ Department of Sustainability Science, El Colegio de la Frontera Sur, Av. Rancho Polígono 2-A, Ciudad Industrial,
53 Lerma 24500, Campeche, Mexico.

54 ²⁰ Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA 70118, USA.

55 ²¹ Smithsonian Tropical Research Institute, Roosevelt Ave. 401 Balboa, Ancon, Panamá.

56 ²² Biological and Environmental Sciences, University of Stirling, FK9 4LA, UK.

57 ²³ Department of Biological Sciences, Clemson University, 132 Long Hall, Clemson, SC 29634, USA.

58 ²⁴ Earth and Atmospheric Sciences Department, University of Alberta, Edmonton, AB Canada T6G 2EG.

59 ²⁵ Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, U.S.A.

60 ²⁶ Departamento de Biologia Geral, Universidade Estadual de Montes Claros, Montes Claros, Minas Gerais, CEP
61 39401-089, Brazil.

62 ²⁷ Fondo Patrimonio Natural, Calle 72 No. 12-65 Piso Sexto, Bogotá, Colombia

63 ²⁸ Ecologia Evolutiva & Biodiversidade/DBG, ICB/Universidade Federal de Minas Gerais, Belo Horizonte MG
64 30161-901, Brazil.

65 ²⁹ International Institute for Sustainability, Rio de Janeiro, 22460-320, Brazil.

66 ³⁰ Centre for Conservation and Sustainability Science (CSRio), Department of Geography and the Environment,
67 Pontifical Catholic University of Rio de Janeiro, Rio de Janeiro, 22451-900.

68 ³¹ Department of Physical and Environmental Sciences, Colorado Mesa University, 1100 North Avenue, Grand
69 Junction, CO 81501 USA.

70 ³² Department of Biology and the Environment, Faculty of Natural Sciences, University of Haifa-Oranim, Tivon,
71 36006, Israel.

72 ³³ College of the Atlantic, 105 Eden St., Bar Harbor, ME 04609 USA.

73 ³⁴ World Agroforestry Centre, ICRAF, United Nations Avenue, Gigiri, Nairobi, Kenya.

74 ³⁵ Instituto de Investigaciones Científicas y Servicios de Alta Tecnología, Panamá.

75 ³⁶ Department of Geography, University of Wisconsin-Madison, 550 North Park St, Madison, Wisconsin, 53706
76 USA.

77 ³⁷ Departamento de Engenharia Florestal, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil.

78 ³⁸ Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de
79 México, Mexico City, C.P. 04510, México.

80 ³⁹ Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, 91540-000, Brazil.

81 ⁴⁰ Department of Ecology, Evolution & Environmental Biology, Columbia University, New York, NY, 10027,
82 USA.

83 ⁴¹ Section of Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Aarhus, Denmark.

84 ⁴² Departamento de Engenharia Florestal, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil.

85 ⁴³ Departamento de Biologia Geral, Universidade Estadual de Montes Claros, Montes Claros, Minas Gerais, CEP
86 39401-089, Brazil.

87 ⁴⁴ Department of Sustainability Science, El Colegio de la Frontera Sur, Av. Rancho Polígono 2-A, Ciudad Industrial,
88 Lerma 24500, Campeche, Mexico.

89 ⁴⁵ Centro de Formação em Ciências Agroflorestais, Universidade Federal do Sul da Bahia, Itabuna-BA, 45613-204,
90 Brazil.

91 ⁴⁶ Department of Ecology, Evolution, & Behavior and Plant Biology, University of Minnesota, Saint Paul, MN
92 55108 USA.

93 ⁴⁷ School of Social Sciences, Geography Area, Universidad Pedagógica y Tecnológica de Colombia (UPTC), Tunja,
94 Colombia.

95 ⁴⁸ Department of Geographical Sciences, University of Maryland, College Park, MD 20742, USA.

96 ⁴⁹ Institute of Systematic Botany, The New York Botanical Garden, 2900 Southern Blvd., Bronx, NY 10458-5126,
97 USA.

98 ⁵⁰ FCA-UAGRM, Santa Cruz de la Sierra, Bolivia.

99 ⁵¹ Yale-NUS College, 16 College Avenue West, Singapore 138610, Singapore.

100 ⁵² Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543,
101 Singapore.

102 ⁵³ Departamento de Agricultura, Sociedad y Ambiente, El Colegio de la Frontera Sur - Unidad Villahermosa, 86280
103 Centro, Tabasco, México.

104 ⁵⁴ Bonhoeffer College, Bruggertstraat 60, 7545 AX Enschede, The Netherlands.

105 ⁵⁵ Museu Paraense Emilio Goeldi, C.P. 399, CEP 66040-170, Belém, Pará, Brazil.

106 ⁵⁶ Fundación para la Conservación de la Biodiversidad, 5101, Mérida, estado Mérida, Venezuela.

107 ⁵⁷ Department of Biological Sciences, Louisiana State University, Baton Rouge, LA, 70803-1705, U.S.A.

108 ⁵⁸ Department of Environmental Sciences, University of Puerto Rico, Río Piedras Campus, San Juan, Puerto Rico
109 00936, USA.

110 ⁵⁹ Department of Biological Sciences Macquarie University, Sydney, NSW 2109, Australia.

111 ⁶⁰ Biodiversity, Macroecology & Biogeography, Faculty of Forest Sciences and Forest Ecology, University of
112 Göttingen, Göttingen, Germany

113

114 *Correspondence to: lourens.poorter@wur.nl; Forest Ecology and Forest Management group,
115 Wageningen University and Research, P.O. Box 47, 6700 AA Wageningen, The Netherlands

116

117 **Tropical forests are converted at an alarming rate for agricultural use and pastureland, but also**
118 **regrow naturally through secondary succession¹. For successful forest restoration it is essential to**
119 **understand the mechanisms of secondary succession. These mechanisms may vary across forest**
120 **types but analyses across broad spatial scales are lacking. Here we analyse forest recovery using**
121 **1410 plots from 50 chronosequence sites across the Neotropics. We analyse changes in community**
122 **composition using species-specific stemwood density (WD), which is a key trait for plant growth,**
123 **survival, and forest carbon storage. In wet forest, succession proceeds from low towards high**
124 **community WD (acquisitive towards conservative trait values), in line with standard successional**
125 **theory. In dry forest, however, succession proceeds from high towards low WD (conservative**
126 **towards acquisitive) probably because high WD reflects drought tolerance in harsh early-**
127 **successional environments. Dry season intensity drives WD recovery by influencing the start and**
128 **trajectory of succession, resulting in convergence of community trait mean over time as vegetation**
129 **cover builds up. These ecological insights can be used to improve species selection for reforestation.**
130 **Reforestation species should, amongst others, ideally have a similar WD as the early-successional**
131 **communities that dominate under the prevailing macroclimatic conditions to establish a first**
132 **protective canopy layer.**

133

134 During succession the structure and complexity of vegetation increase, modifying environmental
135 conditions and leading to shifts in species performance and composition. Successional pathways depend

136 on the traits of the individual species, which determine their ability to establish, grow, survive and
137 reproduce at a site². Although the study of succession has a long history³, we currently lack tests of
138 successional hypotheses across broad biogeographic scales because biogeographically distinct areas have
139 different taxonomic species composition. **It is difficult to generalize successional patterns based on**
140 **different species lists, whereas such a direct and quantitative comparison across regions can be made**
141 **using species traits.** Species traits also provide important insights into mechanisms of succession and
142 community assembly, and ecosystem recovery in carbon, water and nutrient cycling.

143
144 Open space and light, water and nutrient availability all tend to decline over time during forest succession.
145 Successional change is therefore thought to be partly governed by trade-offs between resource acquisition
146 and conservation^{4,5}. Life history and resource use theory predict a spectrum of plant strategies between
147 early and late successional species. Early-successional species are expected to have acquisitive trait
148 values that allow them to acquire resources, grow fast and complete their life cycle under high resource
149 conditions^{6,7}. Late-successional species are expected to have conservative trait values that allow them to
150 conserve limiting resources and survive under low resource conditions^{5,8}. These ideas have been
151 confirmed in mesic forests, where succession is driven by changes in light availability⁹⁻¹¹. Yet a recent
152 study¹² showed that succession may be fundamentally different in environments that differ in water
153 availability. In wet forests, **where there is no seasonal water stress**, early-successional species indeed had
154 acquisitive trait values to take advantage of ample light and water resources, but in the low-resource
155 environment of a dry forest, early-successional species had conservative trait values such as dense wood
156 and tough leaves to tolerate drought and heat and enhance tissue longevity. These preliminary results
157 **from two sites** would imply that **traditional successional theory holds for wet but not for dry forests and**
158 **that we should reconsider one of the successional paradigms.** The question is, **however**, to what extent
159 **these results** can be generalized. Here we report the first study measuring recovery **in wood density** in a
160 systematic way at a **continental** scale, and assess how **recovery** is driven by variation in rainfall and soil
161 fertility across sites.

162
163 We analysed **wood density** recovery at an unprecedented **spatial** scale, using original data from 50 sites,
164 1410 plots and >16,000 trees, covering most of the latitudinal, climatic, and soil fertility gradients in
165 lowland Neotropical forests. To provide a long-term perspective on succession, we used chronosequences
166 (“sites”) where plots that differ in time since agricultural abandonment (0-100 years) were compared. We
167 focused on stemwood density (WD) because it **is a key trait** shapes plant responses to the environment
168 **and impacts carbon cycling. WD is a key trait as it is at the nexus of many plant functions; low WD**
169 **facilitates water storage, hydraulic conductivity¹³, carbon gain, and growth¹⁴, whereas high WD is**
170 **associated with increased physiological drought tolerance¹⁵, biomechanical stability¹⁶, nutrient retention,**
171 **defense against herbivores, fungi and pathogens¹⁷, and increased plant survival. For these reasons, WD is**
172 **an important component of global plant strategies¹⁸, and the global wood economics spectrum¹⁹.**
173 **Moreover, WD has been measured across many sites, making cross-site comparisons possible.** For each
174 plot, the average and variation in community WD was calculated based on the proportional basal area and
175 WD values of the species. For each site, recovery was analysed by regressing community WD values
176 against time since land abandonment. The start (interpolated value at 5 years) and direction (slope of the
177 fitted time-course) of succession were then related to climatic water availability (CWA) and to cation
178 exchange capacity (CEC) as an indicator of soil fertility.

179

180 **Results**

181 Community-level mean WD varied widely across all plots early in succession and more narrowly later in
182 succession (Figure 1a). The funnel shape arises because sites differed both in their initial trait values (the
183 intercept) and in their direction of successional change over time (the slope). Initial values and slopes
184 were both driven by climatic water availability and **to a lesser extent** by soil fertility (Table 1).
185 Community wood density at 5 years (WD_{5y}) varied from 0.32 to 1.14 g cm⁻³ across sites (Table 1)
186 covering nearly the whole natural range in wood density, with drier sites having significantly higher
187 initial WD than wetter sites (Table 1, Figure 2a). The direction and slope of successional change in WD

188 varied across sites, in relation to CWA. Drier sites showed a decrease in WD over time and wetter sites
189 an increase (Figure 2b), so that overall, WD values converged over time for wet and dry forests towards
190 more similar values (Figure 1a). **The same results were found after a randomization test (Extended Data**
191 **Figure 3), indicating that our results still hold, independent of species richness (see Methods).**

192

193 **Discussion**

194 Successional theory predicts that fast-growing acquisitive species will be replaced by persistent,
195 conservative species but here we found a variety of patterns. Across all plots, **community WD** values
196 greatly differ in early succession and converge later in succession (i.e., a funnel-shaped relationship).
197 Some sites showed a significant increase in WD over time, other sites a significant decrease or no net
198 change (Figure 1a). Such contrasting results **can** contribute to the idea that succession is highly
199 unpredictable, stochastic, and context dependent²⁰. **However**, we show at the continental scale that this
200 seemingly idiosyncratic behavior is partly caused by opposite patterns in the *start* (i.e., initial state) and
201 *direction* (i.e, trajectory) of succession, largely due to climate. Species with high wood density increase in
202 abundance with time after land abandonment in wet forests, while the reverse occurs in drier forests.
203 These opposing patterns have potentially large implications for recovery of forest functioning during
204 natural regeneration and restoration.

205

206

207 The strong differences in starting values amongst sites may be caused by strong functional constraints
208 imposed by climatic filtering (Figure 2a). Early in succession sparse vegetation cover results in sun-
209 exposed, hot and (atmospherically) dry conditions during the growing season, especially in drier climates.
210 Early-successional species in dry forests are therefore characterized by dense wood, which in this setting
211 is associated with enhanced cavitation resistance and tolerance to drought^{15,21} and fire²². **Besides, in dry**
212 **forests resprouting from stumps and roots is an important regeneration mechanism after fire and drought**
213 **disturbance²³. Wood density increases survival of resprouts, and hence, the plant, possibly because it**

214 increases resistance to fungi and pathogens and reduces stem decay²⁴. In wetter climates, high rainfall and
215 cloud cover lead to more benign microclimatic conditions. Early-successional species in wet forests are
216 therefore characterized by soft wood which enhances water transport, and therefore carbon gain and
217 growth under wet and high-light conditions¹³. Variation in plot WD is large at the start of succession
218 (Figure 1a), not only because of climatic filtering across sites, but also because of large trait variation
219 within sites caused by dispersal limitation (colonising species are not a random selection of the regional
220 species pool), priority effects (the first incoming species have a head start in the developing community)
221 and the resulting high species dominance of such first-comers or better adapted species.

222
223 Neotropical communities also differed strikingly in the *direction* of trait changes during succession. WD
224 increased over time for wetter forests and decreased over time for drier forests (Figure 2b), in other words
225 it tended to converge later during succession (Fig 1a). In wet forests, light availability in the lower forest
226 strata decreases as the forest regrows, dense-wooded late-successional species that persist better in the
227 shade become dominant, and community WD increases over time⁹. In dry forests the situation for early
228 successional species is characterized by low water availability and high heat load^{12,25,26}. As vegetation
229 regrows the understory becomes cooler and more humid²⁶, allowing establishment of late-successional
230 species with softer wood that better compete for light under more benign conditions, resulting in a
231 decrease in community WD over time (Figure 1a).

232
233 Across sites, the start and direction of succession were driven by climatic water availability (CWA) and to
234 a lesser extent by cation exchange capacity (Table 1, for a discussion on CEC see Supplementary
235 Information 1). At these broad biogeographic scales climate seems to be a stronger filter than soils (Table
236 1)²⁷. Alternatively, CEC may have had limited predictive power because at many sites soil fertility was
237 inferred from a global database rather than measured locally, or because tropical forest communities are
238 driven not by CEC and base cations, but rather by N and especially P²⁸.

239

240 For most sites within-plot variation in WD increased over time (Figure 1b) **which** may be caused by 1)
241 weaker environmental filtering, 2) larger diversity over time because of competitive interactions resulting
242 in limiting similarity, 3) finer partitioning or a wider range of niches in a structurally more complex
243 vegetation, 4) species accumulation over time with some species having **extreme** trait values, and 5) **some**
244 **pioneer trees with extreme trait values are still present in the older-successional plots, thus extending the**
245 **WD range. This is partly in line with recent experimental²⁹ and theoretical³⁰ studies on community**
246 **assembly. Under strong environmental filtering community assembly is often more niche-based, but when**
247 **filtering is relaxed, community assembly can be more neutral or dispersal-based.** WD variation increased
248 more strongly over time for drier forests (Figure 1b), perhaps because drier forests start with fewer
249 species, or because of a rapid accumulation of different drought-coping strategies during succession.

250
251 Successional shifts in trait values may also have large impacts on ecosystem functioning. In dry forests,
252 succession proceeds from conservative to acquisitive trait values (decreasing **community** WD with time),
253 which may accelerate water and carbon cycling through faster water transport by lower WD stems and
254 larger carbon assimilation by leaves³¹, and may accelerate nutrient cycling through faster decomposition
255 of soft stem litter³². In wet forests, succession proceeds from acquisitive to conservative trait values
256 (increasing **community** WD with time), which may slow down biogeochemical cycling, and partly offset
257 the positive effects of increased above ground biomass. Increased trait variation during succession in
258 many forests (Figure 1b) may lead to **greater** niche complementarity, more efficient resource use and
259 higher productivity³³. It may also buffer ecosystem functioning to environmental change and enhance
260 ecosystem resilience³⁴.

261
262 Insight into mechanisms of succession can facilitate the design of effective forest restoration strategies
263 adapted to local site conditions. **Efficient reforestation is urgent given global commitments to restore an**
264 **area of 3.5 million km² by 2030, to enhance biodiversity, site productivity, water quality and flows, and**
265 **carbon storage³⁵.** Rapid establishment of an initial vegetation layer is of paramount importance because it

266 ameliorates local microclimate and soil, suppresses weeds, and facilitates establishment of late-
267 successional species^{10,36}. Succession is governed by various processes such as dispersal, facilitation,
268 competition, and tolerance³⁷. In areas with sufficient high surrounding forest cover, it is ecologically best
269 and economically most cost-efficient to rely on natural regeneration³⁸. However, in fragmented or
270 degraded areas that suffer dispersal limitation, direct seeding or planting can accelerate establishment of
271 an initial layer³⁹. Species selected for initial planting should fulfil many criteria (such as economic and
272 cultural values, being native, or attracting frugivore dispersers⁴⁰), depending on the goals of restoration.
273 Nevertheless, species should at least be well adapted to local site conditions to be successful. WD can be
274 used as an additional ecological criterion and an easy proxy for species selection. In dry regions, dense-
275 wooded, drought-tolerant conservative species should be selected that can tolerate the harsh initial
276 conditions, whereas in wet regions soft-wooded, fast-growing acquisitive species should be selected that
277 can rapidly restore vegetation cover and facilitate succession together with dense-wooded shade tolerant
278 species that may replace them on the long-term. Early-successional forests in Latin America show a
279 tremendous variation in CWM WD, and the relationship between CWM WD at 5 years and CWA (Figure
280 2a) can be used to optimize species selection for restoration. Additionally, in climatically harsh
281 environments land managers may use nurse shrubs or perennial grasses to facilitate and increase the
282 survival of planted target trees⁴¹, as their canopy improves microclimate and may protect target plants
283 against grazing, while hydraulic lift and litter accumulation may increase water and nutrient availability⁴²
284
285 In sum, 1) succession proceeds from acquisitive towards conservative WD values in wet forest but from
286 conservative towards acquisitive WD values in dry forest, 2) during succession, there is a shift from
287 strong abiotic filtering in open early-successional environments towards weaker abiotic filtering in
288 benign, closed late-successional environments, and 3) combined these processes lead to trait convergence
289 across sites over time. Future research should demonstrate whether our findings for wood density of long-
290 lived stems also apply to traits of shorter-lived leaves, as some studies show that stem and leaf traits are
291 strongly coupled⁴³, whereas others show that they are uncoupled⁴⁴. This climate-dependence of

292 successional processes should be taken into account in restoration efforts to meet global commitments for
293 forest restoration and climate change mitigation.

294

295

296 **References**

297

- 298 1 Chazdon, R. L. *et al.* Carbon sequestration potential of second-growth forest regeneration in the Latin
299 American tropics. *Sci. Adv.* **2**, 10, doi:10.1126/sciadv.1501639 (2016).
- 300 2 Shipley, B., Vile, D. & Garnier, É. From plant traits to plant communities: a statistical mechanistic
301 approach to biodiversity. *science* **314**, 812-814 (2006).
- 302 3 Clements, F. E. *Plant succession: an analysis of the development of vegetation.* (Carnegie Institution of
303 Washington, 1916).
- 304 4 Bazzaz, F. A. Physiological ecology of plant succession. *Annual Review of Ecology and Systematics* **10**,
305 351-371, doi:10.1146/annurev.es.10.110179.002031 (1979).
- 306 5 Wright, I. J. *et al.* The worldwide leaf economics spectrum. *Nature* **428**, 821-827 (2004).
- 307 6 Pianka, E. On r and K selection (Citation Classic). *American Naturalist* **104**, 592-597. (1970).
- 308 7 Tilman, D. *Plant strategies and the dynamics and structure of plant communities.* (Princeton University
309 Press, 1988).
- 310 8 Kitajima, K. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling
311 shade tolerance of 13 tropical trees. *Oecologia* **98**, 419-428 (1994).
- 312 9 Finegan, B. Pattern and process in neotropical secondary rain forests: The first 100 years of succession.
313 *Trends in Ecology & Evolution* **11**, 119-124, doi:10.1016/0169-5347(96)81090-1 (1996).
- 314 10 Chazdon, R. L. *Second growth: The promise of tropical forest regeneration in an age of deforestation.*
315 (University of Chicago Press, 2014).
- 316 11 Peterson, C. & Carson, W. Processes constraining woody species succession on abandoned pastures in the
317 tropics: on the relevance of temperate models of succession. *Tropical forest community ecology.* Oxford:
318 Wiley-Blackwell, 367-383 (2008).
- 319 12 Lohbeck, M. *et al.* Successional changes in functional composition contrast for dry and wet tropical forest.
320 *Ecology* **94**, 1211-1216 (2013).
- 321 13 Santiago, L. *et al.* Leaf photosynthetic traits scale with hydraulic conductivity and wood density in
322 Panamanian forest canopy trees. *Oecologia* **140**, 543-550 (2004).
- 323 14 Poorter, L. *et al.* The importance of wood traits and hydraulic conductance for the performance and life
324 history strategies of 42 rainforest tree species. *New Phytologist* **185**, 481-492, doi:10.1111/j.1469-
325 8137.2009.03092.x (2010).
- 326 15 Pineda-García, F., Paz, H. & Meinzer, F. C. Drought resistance in early and late secondary successional
327 species from a tropical dry forest: the interplay between xylem resistance to embolism, sapwood water
328 storage and leaf shedding. *Plant Cell and Environment* **36**, 405-418, doi:10.1111/j.1365-
329 3040.2012.02582.x (2013).
- 330 16 van Gelder, H. A., Poorter, L. & Sterck, F. J. Wood mechanics, allometry, and life-history variation in a
331 tropical rain forest tree community. *New Phytologist* **171**, 367-378, doi:10.1111/j.1469-
332 8137.2006.01757.x (2006).
- 333 17 Loehle, C. Tree life history strategies: the role of defenses. *Canadian Journal of Forest Research* **18**, 209-
334 222 (1988).
- 335 18 Díaz, S. *et al.* The global spectrum of plant form and function. *Nature* **529**, 167-171 (2016).
- 336 19 Chave, J. *et al.* Towards a worldwide wood economics spectrum. *Ecology Letters* **12**, 351-366,
337 doi:10.1111/j.1461-0248.2009.01285.x (2009).
- 338 20 Norden, N. *et al.* Successional dynamics in Neotropical forests are as uncertain as they are predictable.
339 *Proc Natl Acad Sci U S A* **112**, 8013-8018, doi:10.1073/pnas.1500403112 (2015).
- 340 21 Markesteijn, L., Poorter, L., Paz, H., Sack, L. & Bongers, F. Ecological differentiation in xylem cavitation
341 resistance is associated with stem and leaf structural traits. *Plant Cell and Environment* **34**, 137-148,
342 doi:10.1111/j.1365-3040.2010.02231.x (2011).
- 343 22 Brando, P. M. *et al.* Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size,
344 wood density and fire behavior. *Global Change Biology* **18**, 630-641, doi:doi:10.1111/j.1365-
345 2486.2011.02533.x (2012).

346 23 Vieira, D. L. & Scariot, A. Principles of natural regeneration of tropical dry forests for restoration.
347 *Restoration Ecology* **14**, 11-20 (2006).

348 24 Poorter, L. *et al.* Resprouting as a persistence strategy of tropical forest trees: relations with carbohydrate
349 storage and shade tolerance. *Ecology* **91**, 2613-2627, doi:10.1890/09-0862.1 (2010).

350 25 Lebrija-Trejos, E., Meave, J. A., Poorter, L., Pérez-García, E. A. & Bongers, F. Pathways, mechanisms and
351 predictability of vegetation change during tropical dry forest succession. *Perspectives in Plant Ecology*
352 *Evolution and Systematics* **12**, 267-275, doi:10.1016/j.ppees.2010.09.002 (2010).

353 26 Lebrija-Trejos, E., Pérez-García, E. A., Meave, J. A., Poorter, L. & Bongers, F. Environmental changes
354 during secondary succession in a tropical dry forest in Mexico. *Journal of Tropical Ecology* **27**, 477-489,
355 doi:10.1017/s0266467411000253 (2011).

356 27 Poorter, L. *et al.* Biomass resilience of Neotropical secondary forests. *Nature* **530**, 211-214 (2016).

357 28 Fyllas, N. M. *et al.* Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and
358 climate. *Biogeosciences* **6**, 2677-2708 (2009).

359 29 Chase, J. M. Drought mediates the importance of stochastic community assembly. *Proceedings of the*
360 *National Academy of Sciences* **104**, 17430-17434 (2007).

361 30 Fukami, T. Historical contingency in community assembly: integrating niches, species pools, and priority
362 effects. *Annual Review of Ecology, Evolution, and Systematics* **46**, 1-23 (2015).

363 31 Finegan, B. *et al.* Does functional trait diversity predict above-ground biomass and productivity of tropical
364 forests? Testing three alternative hypotheses. *Journal of Ecology* **103**, 191-201 (2015).

365 32 Cornwell, W. K. *et al.* Plant species traits are the predominant control on litter decomposition rates within
366 biomes worldwide. *Ecology letters* **11**, 1065-1071 (2008).

367 33 Sande, M. T. *et al.* Biodiversity in species, traits, and structure determines carbon stocks and uptake in
368 tropical forests. *Biotropica* **49**, 593-603, doi:10.1111/btp.12453 (2017).

369 34 Sakschewski, B. *et al.* Amazon forest resilience emerges from plant trait diversity. *Nat. Clim. Chang.*, DOI:
370 10.1038/NCLIMATE3109 (2016).

371 35 Holl, K. D. Restoring tropical forests from the bottom up. *Science* **355**, 455-456,
372 doi:10.1126/science.aam5432 (2017).

373 36 van Breugel, M., Bongers, F. & Martínez-Ramos, M. Species dynamics during early secondary forest
374 succession: Recruitment, mortality and species turnover. *Biotropica* **39**, 610-619, doi:10.1111/j.1744-
375 7429.2007.00316.x (2007).

376 37 Connell, J. H. & Slatyer, R. O. Mechanisms of succession in natural communities and their role in
377 community stability and organization. *The American Naturalist* **111**, 1119-1144 (1977).

378 38 Crouzeilles, R. *et al.* Ecological restoration success is higher for natural regeneration than for active
379 restoration in tropical forests. *Sci. Adv.* **3**, e1701345 (2017).

380 39 Chazdon, R. L. Beyond deforestation: Restoring forests and ecosystem services on degraded lands.
381 *Science* **320**, 1458-1460, doi:10.1126/science.1155365 (2008).

382 40 Quesada, M. *et al.* Succession and management of tropical dry forests in the Americas: Review and new
383 perspectives. *Forest Ecology and Management* **258**, 1014-1024 (2009).

384 41 Gómez-Aparicio, L. *et al.* Applying plant facilitation to forest restoration: a meta-analysis of the use of
385 shrubs as nurse plants. *Ecological Applications* **14**, 1128-1138 (2004).

386 42 Padilla, F. M. & Pugnaire, F. I. The role of nurse plants in the restoration of degraded environments.
387 *Frontiers in Ecology and the Environment* **4**, 196-202 (2006).

388 43 Reich, P. B. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology*
389 **102**, 275-301 (2014).

390 44 Baraloto, C. *et al.* Decoupled leaf and stem economics in rain forest trees. *Ecology letters* **13**, 1338-1347
391 (2010).

392 45 Lambers, H. & Poorter, H. Inherent variation in growth rate between higher plants: a search for
393 physiological causes and ecological consequences. *Advances in ecological research* **23**, 187-261 (1992).

394 46 Pérez-Harguindeguy, N. *et al.* New handbook for standardised measurement of plant functional traits
395 worldwide. *Australian Journal of botany* **61**, 167-234 (2013).

396 47 Zanne, A. E. *et al.* Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository.
397 doi:10.5061/dryad.234. (2009).

398 48 Coelho de Souza, F. *et al.* Evolutionary heritage influences Amazon tree ecology. *Proceedings of the Royal*
399 *Society B: Biological Sciences* **283**, doi:10.1098/rspb.2016.1587 (2016).

400 49 Thomas, S. C. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain
401 forest trees. *American Journal of Botany* **83**, 556-566 (1996).

402 50 ter Steege, H. *et al.* Continental-scale patterns of canopy tree composition and function across Amazonia.
403 *Nature* **443**, 444-447, doi:10.1038/nature05134 (2006).

404 51 Hengl, T. *et al.* SoilGrids250m: global gridded soil information based on Machine Learning. *PLOS ONE*
405 (2017).

406 52 Laliberté, E., Legendre, P. & Shipley, B. FD: measuring functional diversity from multiple traits, and other
407 tools for functional ecology. *R package version 1.0-12* (2014).

408 53 Rozendaal, D. M. A., Bongers, F., Aide, T. M., others & Poorter, L. Biodiversity recovery of Neotropical
409 secondary forests. *Sci. Adv.* (in press).

410 54 Mitchard, E. T. A. *et al.* Markedly divergent estimates of Amazon forest carbon density from ground plots
411 and satellites. *Global Ecology and Biogeography* **23**, 935-946, doi:10.1111/geb.12168 (2014).

412

413 **Acknowledgments:** This paper is a product of the 2ndFOR collaborative research network on
414 secondary forests. We thank the owners of the secondary forest sites and the local communities
415 for access to their forests, all the people who have established and measured the plots, the
416 institutions and funding agencies that supported them **and three anonymous reviewers for their**
417 **helpful comments.** We thank the following agencies for financial support: Netherlands
418 Foundation for Scientific research (NWO-ALW.OP241), Wageningen University and Research
419 (INREF FOREFRONT and Terra Preta programs), Macquarie University Visiting Researcher
420 grant to LP, Biological Dynamics of Forest Fragments Project (BDFFP), CIFOR,
421 COLCIENCIAS grant 1243-13-16640, CONACYT Ph.D. grant 169510, Conselho Nacional de
422 Desenvolvimento Científico e Tecnológico (CNPq, grant #481576/2009-6, #304817/2015-5,
423 #309874/2015-7), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES,
424 grant #88881.064976/2014-01), DAAD (German Academic Exchange Service), Fapemig,
425 Garden Club of America Award in Tropical Botany, Global Environment Facility (GEF-grant
426 VEN/SGP/2010-2015), ICETEX, Instituto Nacional de Investigaciones Agrícolas (INIA-
427 Amazonas), Instituto Nacional de Ciência e Tecnologia dos Serviços Ambientais da Amazônia
428 (INCT/Servamb), International Climate Initiative (IKI) of the German Federal Ministry for the
429 Environment; Nature Conservation, Building and Nuclear Safety (BMUB), Lewis and Clark
430 Fund for Exploration and Field Research, NASA ROSES Grant NNH08ZDA001N-TE, ,
431 Norwegian Agency for Development Cooperation (Norad), NUFFIC, NUS College (grant R-
432 607-265-054-121), FOMIX-Yucatan (YUC-2008-C06-108863), OTS and the Christiane and
433 Christopher Tyson Fellowship, PAPIIT-UNAM (218416, 211114). Ronald Bamford
434 Endowment, São Paulo Research Foundation (FAPESP, grants #2011/06782-5 and 2014/14503-

435 7), SENACYT grant COL10-052, SEP-CONACYT (CB-2009-128136, CB 2015- 255544),
436 Stichting Het Kronendak, Tropenbos International, United Nations Development Program
437 (Venezuela). US National Science Foundation (DEB-0639114, DEB-1147434, DEB-0424767,
438 DEB-0639393, DEB-1147429, DEB- 1110722, NSF-0946618, NSF-9208031). This is
439 publication #____ in the Technical Series of the Biological Dynamics of Forest Fragments
440 Project BDFFP-INPA-SI and publication #____ from 2ndFOR. The data reported in this paper
441 are archived at _____.

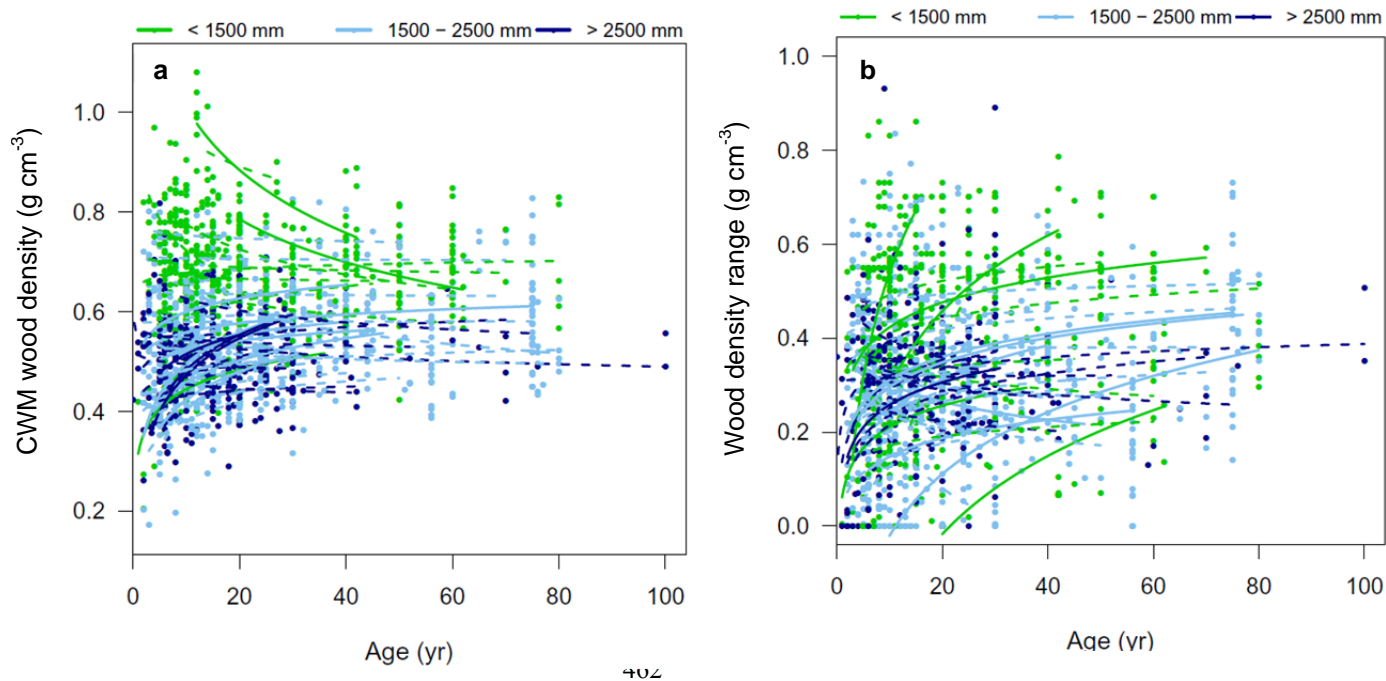
442

443 **Author contributions** L.P. and M.W. conceived the idea, L.P. and D.R. coordinated the data
444 compilations, D.R. carried out the data analysis, L.P., D.R., F.B., and M.W. contributed to
445 analytical tools used in the analysis, E.N.B. and A.M.A.Z made the map, L.P. wrote the paper,
446 and all co-authors collected field data, discussed the results, gave suggestions for further
447 analyses and commented on the manuscript.

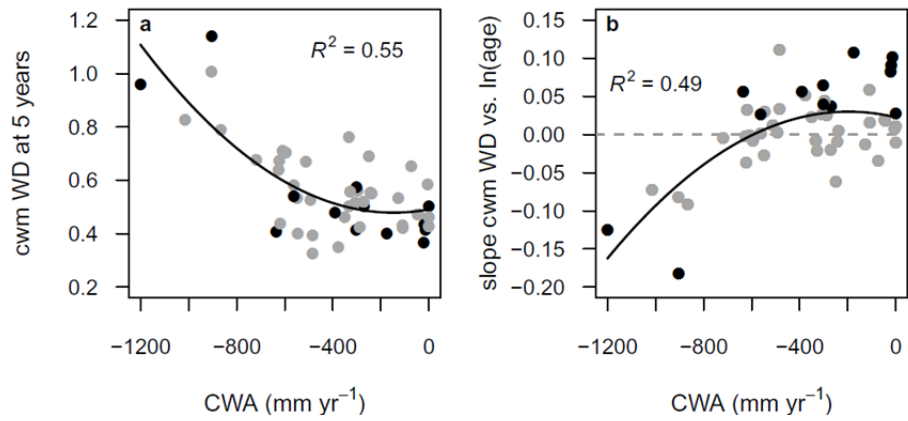
448

449 **Data information** CWM WD data of 50 sites are available from _____. The authors declare no
450 competing financial interests. Readers are welcome to comment on the online version of the
451 paper. Correspondence and requests for materials should be addressed to L.P.
452 (lourens.poorter@wur.nl).

453 **Figure 1. Recovery of functional trait values and trait variation with time since abandonment in**
 454 **Neotropical secondary forest sites. a,** Community-weighted mean wood density; **b,** wood density range
 455 within each community (i.e., plot). Each line represents a different chronosequence (N=50). Significant
 456 changes over time are indicated by continuous lines, non-significant changes by broken lines. Lines and
 457 dots (individual plots, N=1410) are colour coded according to the forest type as dry forest (700-1500
 458 mm/y, green), moist forest (1500-2500 mm/y, light blue) and wet forest (>2500 mm/y, dark blue). The
 459 range is calculated per plot as trait value of the 90th percentile minus the trait value of the 10th percentile
 460 of trait values in a plot.
 461



463 **Figure 2 a, Community-weighted mean wood density at 5 years (WD_{5y}) versus climatic water**
464 **availability (CWA); b, successional changes in WD (slope) versus CWA for 50 Neotropical sites.**
465 Black symbols indicate sites with significant slopes. CWA indicates the water deficit during the dry
466 season, with zero meaning no water deficit.
467



468
469
470
471
472
473
474

475 **Table 1 Environmental predictors of community wood density across Neotropical forest sites.**

476

477

Variable	CWA		CWA ²		CEC		R ²
	beta	P	beta	P	beta	P	
WD5y	0.0001	0.381	5.24E-07	0.002	0.0030	0.043	0.54
slope	-0.0001	0.229	-1.80E-07	0.002	-0.0013	0.011	0.51

478

479

480 Community weighted mean wood density at 5 years (WD5y) and its change over time (slope) were
 481 evaluated. Predictors are climatic water availability (CWA), its squared value (CWA²) and Cation
 482 Exchange Capacity (CEC). All possible combinations of predictors were compared, and the best-
 483 supported model with lowest Akaike’s Information Criterion (AICc) adjusted for small sample sizes was
 484 selected (Extended Data Table S2). The parameter estimate (beta), P-value (P) and explained variation
 485 (R²) are shown. See Extended Data Figure 2 for bivariate relationships.

486 **METHODS**

487

488 **Study sites.** We compiled chronosequence data for 50 Neotropical lowland forest sites²⁷ covering the
489 entire latitudinal gradient in the Neotropics (Fig. 2C, Extended Data Table 1). We focused on the
490 Neotropics, i.e., tropical South America and Mesoamerica, because (1) shifting cultivation is an important
491 land use type there, (2) the region has a relatively shared biogeographic history, thus reducing
492 confounding historical effects, and (3) many chronosequence studies have been established in the area.
493 Annual rainfall varied from 750-4000 mm y⁻¹ across sites, topsoil cation exchange capacity (CEC) from
494 1.7-64.6 cmol(+) kg⁻¹, and percent forest cover in the landscape matrix ranged from 9-100% (Extended
495 Data Table 1).

496

497 **Plots.** On average 28 plots (range 5-251) were established per chronosequence, with the age of the
498 youngest plot ranging from 0 to 20 years in time since abandonment. The age range covered by
499 chronosequence plots varied from 9 to 80 years across sites (Extended Data Table 1) and plot sizes ranged
500 from 0.01 to 1 ha, with an average of 0.1 ha across all plots. Per site, plots were of the same size. For
501 trees, palms and shrubs all stems ≥ 5 cm stem diameter at breast height (dbh) were measured for dbh and
502 identified to species, except for six sites where minimum dbh was 10 cm. Across chronosequences, on
503 average 94.5 % of stems were identified to species (range 71-100 %), and 99.5 % (range 94-100 %) to
504 family, genus, species or morphospecies.

505

506 **Wood density.** We focused on stemwood density as a key response trait (indicating how communities are
507 assembled during succession) and a key effect trait (determining how ecosystems function in terms of
508 carbon, water and nutrient stocks and cycling). Wood density (WD, in g cm⁻³), which is also known as
509 wood specific gravity, is the wood dry mass divided by the wood green volume. It reflects a trade-off
510 between fast volumetric growth of soft-wooded species and high survival because of resistance against
511 biophysical hazards and drought in dense-wooded species. Soft wood is associated with high resource

512 acquisition and fast growth and returns on investment, whereas dense wood is associated with resource
513 conservation and persistence^{43,45}. WD also has an important effect on carbon, water, and nutrient stocks
514 and cycling. High WD is associated with narrow vessels and hence lower water transport capacity, but
515 also with longer-lived tissues that are difficult to decompose, hence WD increases carbon and nutrient
516 stocks in the stand.

517
518 **Community functional composition.** For each plot we calculated community functional composition
519 based on species-specific WD values. Traits can be plastic and respond to environmental gradients. To
520 take trait acclimation and adaptation to local site conditions into account, WD data were, as far as
521 possible, locally collected at the site. Because WD data were collected at the site level and not at the plot
522 level, plasticity in response to successional stage could not be accounted for, **although within species**
523 **variation in wood density tends to be small, with an average coefficient of variation of 5-9%**⁴⁶.

524 Successional changes in community WD as reported here are therefore only due to species turnover and
525 not due to plasticity.

526 Species-specific WD data were collected for 22 sites and taken from a wood density database for
527 the remaining sites⁴⁷. When local species data were not available, we used the average local site data at
528 genus or family level, as WD values of tropical trees are strongly phylogenetically conserved⁴⁸, **although**
529 **WD can also vary substantially within coexisting genera or families, due to adaptive radiation**⁴⁹. For on
530 **average 23.7% of the trees we use average site-specific genus level data and for 8.7% of the trees we use**
531 **average site-specific family level data, and for 3.6% of the trees we used mean plot-specific WD data.**
532 **The imputed data have only little effect on the calculated community-weighted wood density; plot CWM**
533 **WD with and without imputed data are strongly correlated (Pearsons $r=0.88, P<0.0001$).** The remaining
534 species without trait values were excluded from the analysis.

535 For each plot we calculated community-weighted mean (CWM) WD values, based on the
536 proportional basal area of the species in the plots and their species-level WD values. We weighted by
537 basal area, since basal area scales closely with total leaf area and with water transport capacity of trees,

538 and therefore with the effects that trees have on ecosystem functioning. To describe trait variation in each
539 community we calculated for each plot the WD range as the 90th percentile minus the 10th percentile of
540 WD values in the community, thus ignoring extreme, outlying species.

541
542 **Environmental conditions.** Annual rainfall (mm yr⁻¹) was obtained for each site from the nearest
543 weather station. As seasonality in water availability is a stronger determinant of forest composition and
544 functioning than annual rainfall⁵⁰, we obtained climatic water availability (CWA; in mm yr⁻¹, also referred
545 to as climatic water deficit) from http://chave.ups-tlse.fr/pantropical_allometry.htm. CWA indicates the
546 **cumulative** amount of water lost **to the atmosphere** during the months when evapotranspiration exceeds
547 rainfall, i.e., **the sum of (evapotranspiration minus rainfall) over the course of the dry season**. It reflects
548 **therefore** the dry season intensity. CWA is by definition negative, and sites with a CWA of 0 do not
549 experience seasonal drought stress. For one site where CWA was not available (Providencia Island), we
550 estimated CWA from a linear regression between CWA and rainfall based on the other chronosequence
551 sites (CWA = -924 + 0.271 × rainfall; $n = 49$, $P < 0.0001$, $R^2 = 0.49$).

552 Topsoil cation exchange capacity (CEC; in cmol(+) kg⁻¹) over the first 30 cm of the soil was used
553 as an indicator of soil nutrient availability as it scales well with the total concentrations of base cations,
554 and it was available for part of the sites, and could be obtained from the global **SoilGrids** database⁵¹ for
555 the rest of the sites. It should be said that CEC not only includes the base cations Ca, Mg and K, but also
556 Na and Al, which can impair plant growth. In general, however, CEC scales positively with the total
557 concentration of base cations, and is therefore a reasonable indicator of soil fertility. Soil clay content was
558 also available in the global database, and had similar effects on community traits as CEC. We preferred to
559 use CEC instead, as it is a more direct measure of nutrient resource availability, than clay, which can also
560 affect soil aeration, stability, and water retention capacity. We acknowledge that soil N or P might be
561 stronger drivers of forest recovery as N might especially be limiting in early stages of succession and P is
562 thought to limit plant growth in highly weathered and leached tropical soils. We preferably included local
563 CEC data from old-growth forest plots (instead of secondary forest plots), because it **allows to rank the**

564 sites based on their potential soil fertility, and in that respect it is consistent with the SoilGrids database
565 which for these tropical areas also mostly includes soil characteristics associated with mature forest. For
566 34 sites for which no local CEC data were available, CEC was obtained from the SoilGrids database from
567 ISRIC⁵¹. SoilGrids did not contain data on soil N and P. Across sites, CEC and CWA were not
568 significantly correlated (Pearson $r=-0.08$, $N=50$, $P=0.587$).

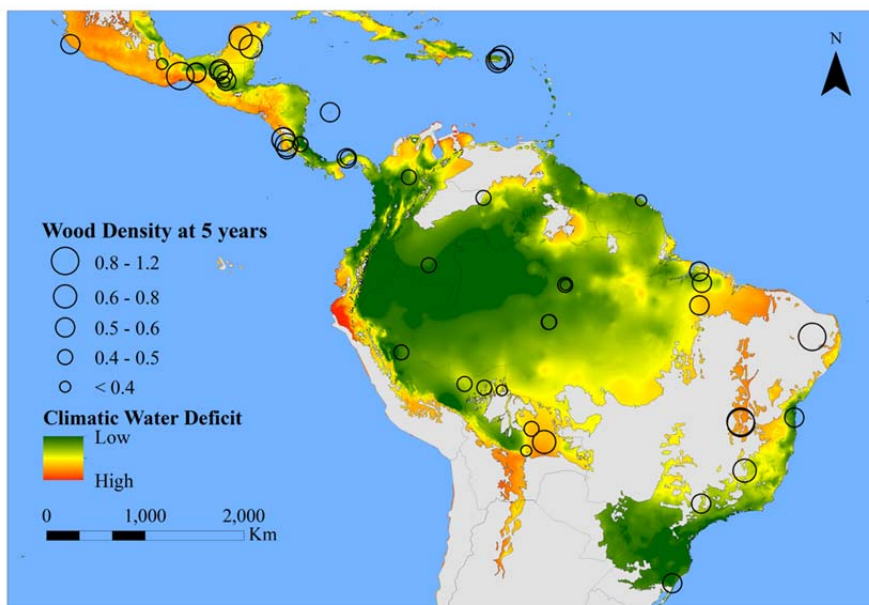
569
570 **Statistical analyses.** Successional changes in functional composition were assessed for each
571 chronosequence using secondary forest plots only. We related the functional properties of the plot (CWM
572 WD, WD range) to time since abandonment using linear regressions. Time since abandonment was ln-
573 transformed prior to analysis because forest structure, environmental conditions, and species composition
574 typically change non-linearly over time with rapid initial changes and slow changes afterwards. The
575 regression slope (WD_{β}) indicates direction and pace of functional change during succession. We used the
576 site-specific regression equations to predict CWM WD at 5 years (WD_{5y}), reflecting the early-
577 successional community that is filtered out by the macroenvironment. WD_{5y} and WD_{β} were then related
578 to CWA (as an indicator of water availability), CWA squared (to account for non-linear relationships) and
579 CEC (as an indicator of soil fertility), using subsets multiple regression analysis. Different models of
580 predictor combinations were compared using Akaike's Information Criterion adjusted for small sample
581 sizes (AICc), and the best-supported model with lowest AICc given the number of predictors was
582 selected. All analyses were performed in R 3.3.2. CWM WD was calculated using the FD package⁵². In
583 our results we observed a convergence of WD values from different forests over time. Converge over
584 time may also arise from a sampling effect; as at our sites species richness increases logarithmically over
585 time⁵³, a larger number of species may lead to a convergence in the trait distributions between forests over
586 time and, hence, a more central CWM WD value, as WD is averaged across many species. To test to what
587 extent species accumulation over time drives the observed relationships we performed a randomization
588 test in which we randomized species identity within sites. For each plot we maintained the community

589 structure (i.e., the number of species and their abundances) but randomized the species names and, hence,
590 WD values within a site, based on species pool occurring in the plots within in a site. We did 999
591 iterations per site, and in each iteration calculated the CWM WD for all plots of that site. After each
592 iteration we calculated for the site the slope of CWM WD versus $\ln(\text{age})$, and calculated the average slope
593 over 999 iterations. This randomized slope represents the change in CWM WD over time if changes were
594 only driven by species accumulation, and a strong deviation between the random and observed slopes
595 indicates that the pattern is largely independent of species accumulation. In fact, the randomized slopes
596 were close to- and not significantly different from zero. To quantify the deviation from random, we then
597 calculated the standardized slope per site as: $(\text{observed slope} - \text{average of random slopes}) / \text{standard}$
598 $\text{deviation of random slopes}$. We then plotted the standardized slopes against CWA.

599

600

601 **Extended Data Figure 1.** Map of the 50 study sites are indicated by black circles (the symbol on the
602 ocean belongs to an island) and the size of the symbols scales with the CWM WD at 5 years. The colored
603 areas indicate the lowland tropical forest biome (altitude < 1000 m). The colors indicate the climatic
604 water availability (also known as climatic water deficit); orange colors indicate low water availability,
605 green colors indicate high water availability).



606

607

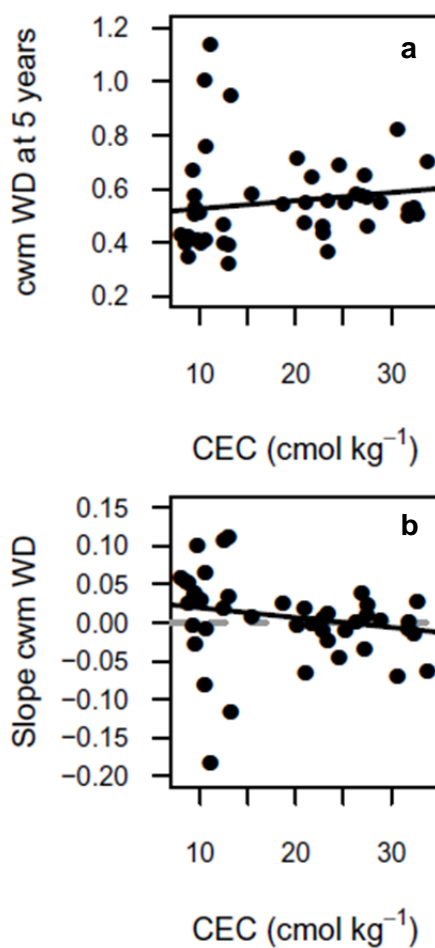
608 **Extended Data Figure 2. Relationships between community-weighted mean wood density (CWM**
609 **WD) at 5 years (a) and successional changes in wood density (slope) (b) versus cation exchange**
610 **capacity (CEC) for 50 chronosequence sites.** Continuous lines indicate a significant ($P \leq 0.05$)
611 relationship according to the multiple regression models (Extended Data Table 2). Grey dotted lines
612 indicate a successional slope of zero.

613

614

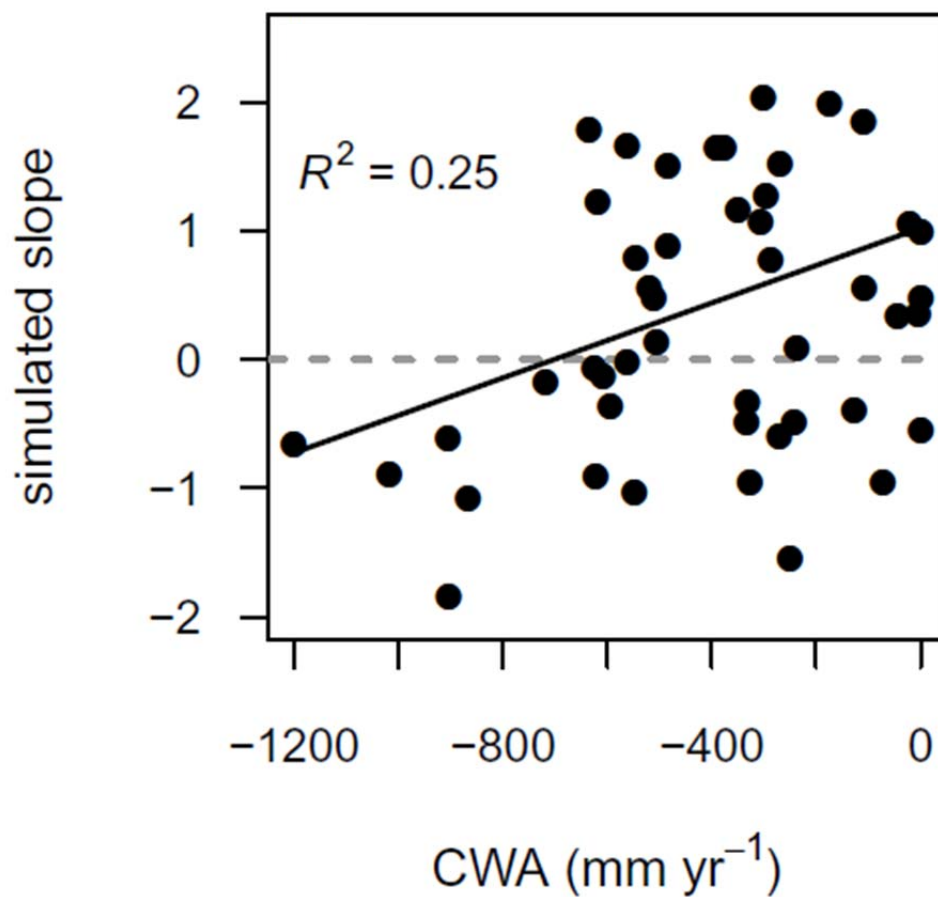
615

616



617 **Extended Data Fig 3.** Successional changes in WD (slope) versus CWA for 50 Neotropical
618 chronosequence sites. The standardized slope of CWM WD versus $\ln(\text{time})$ are shown, which correct for
619 the species accumulation effect (see methods).

620



621

622

623

624

625 **Extended Data Table 1** Characteristics of the included Neotropical secondary forest sites

626

Site	Country	Lat. (°)	Long. (°)	Rainfall (mm/yr)	CWA (mm/yr)	CEC (cmol/kg)	FC (%)	LU (-)	Plots (#)	Age (yr)	WD _{5y} (g/cm ³)	Ref.
Bolpebra	Bolivia	-11.42	-69.13	1800	-303	10.5	97.5	SA	15	(4-47)	0.41	
El Tigre	Bolivia	-11.98	-65.72	1780	-378	8.8	90.3	SA	6	(3-25)	0.35	1
El Turi	Bolivia	-11.75	-67.33	1833	-288	8.8	99.7	SA	6	(2-40)	0.42	1
Salvatierra	Bolivia	-15.50	-63.03	1200	-635	8.5	98.8	SA	28	(1-36)	0.40	2
San Lorenzo	Bolivia	-16.70	-61.87	1129	-719	9.3	94.5	SA	10	(5-50)	0.67	3
Surutu 1	Bolivia	-17.50	-63.50	1600	-484	13.0	72.3	SA	8	(4-20)	0.39	
Surutu 2	Bolivia	-17.50	-63.50	1600	-484	13.0	72.3	SA	5	(6-25)	0.32	
Bahia	Brazil	-14.48	-39.09	2000	-6	15.4	94.5	SA	27	(10-40)	0.58	4
Cajueiro	Brazil	-14.98	-43.95	840	-906	10.5	73.9	PA	6	(14-27)	1.01	
Serra do Cipo	Brazil	-19.30	-43.61	1519	-334	10.6	27.8	PA	9	(4-50)	0.76	
Eastern Pará 1	Brazil	-4.26	-47.73	1898	-549	9.5	63.1	SA&PA	15	(5-25)	0.53	5
Eastern Pará 2	Brazil	-2.19	-47.50	2460	-270	9.4	64.6	SA&PA	25	(5-40)	0.50	5
Eastern Pará 3	Brazil	-1.17	-47.75	2785	-306	10.0	73.6	PA	12	(2-70)	0.51	5
Manaus (Cecropia pathway)	Brazil	-2.38	-59.91	2400	-22	2.0	98.4	SA	13	(5-31)	0.37	6
Manaus (Vismia pathway)	Brazil	-2.39	-59.94	2400	-20	2.0	99	PA	15	(2-25)	0.43	6
Maquiné	Brazil	-29.57	-50.20	1720	0	32.7	94.6	SA	20	(6-45)	0.50	7
Mata Seca	Brazil	-14.85	-43.99	825	-904	11.1	86.6	PA	12	(12-42)	1.14	8
Patos	Brazil	-7.12	-37.47	750	-1201	13.2	34.2	SA&PA	15	(20-62)	0.95	10
Middle Madeira River (anthropogenic soil)	Brazil	-5.78	-61.46	2507	-109	3.8	86.9	SA	26	(5-30)	0.42	9
Middle Madeira River (oxisol)	Brazil	-5.76	-61.41	2507	-110	8.0	86	SA	26	(6.5-30)	0.43	9
Sao Paulo	Brazil	-22.32	-47.57	1367	-297	9.4	22.8	PA	18	(11-45)	0.57	
Aracuara	Colombia	-0.60	-72.37	3059	-14	9.7	92.1	SA	4	(7-30)	0.41	11
Providencia Island	Colombia	13.35	-81.37	1584	-494	31.8	9.4	SA&PA	100	(6-56)	0.53	12
Nicoya Peninsula	Costa Rica	9.97	-85.30	2130	-619	27.4	69.9	SA&PA	53	(5-35)	0.57	
Santa Rosa (oak forest)	Costa Rica	10.89	-85.60	1765	-609	20.1	75.7	PA	22	(5-70)	0.71	14
Palo Verde	Costa Rica	10.36	-85.31	1444	-623	24.5	42.8	PA	19	(7-60)	0.69	14
Santa Rosa 1	Costa Rica	10.85	-85.61	1765	-626	21.7	74.1	PA	40	(6-70)	0.64	14
Sarapiquí 1	Costa Rica	10.43	-84.07	4000	0	22.8	89.1	PA	6	(10-41)	0.46	16
Sarapiquí 2	Costa Rica	10.42	-84.05	4000	0	22.9	88.3	PA	23	(10-42)	0.43	17
ArboceI	French Guiana	5.30	-53.05	3040	-176	12.5	99.9	SA	5	(3.5-28.5)	0.40	18
Chajul	Mexico	16.09	-90.99	3000	-272	23.3	88.6	SA	17	(0-27)	0.37	19
Chamela	Mexico	19.54	-105.00	788	-867	21.0	65.7	PA	8	(3-15)	0.55	20
Chinantla	Mexico	17.75	-96.65	1593	-546	10.1	99.5	SA	26	(5-50)	0.40	
El Ocote 1	Mexico	16.92	-93.54	1500	-563	26.3	91.7	SA	29	(2-75)	0.58	21
El Ocote 2	Mexico	16.97	-93.55	2000	-563	18.6	89.4	SA	63	(3-75)	0.54	21
Comunidad Lacandona	Mexico	16.81	-91.10	2500	-333	31.7	95.6	SA&PA	42	(1-30)	0.50	
Marqués de Comillas	Mexico	16.20	-90.80	2250	-302	26.9	87.2	SA&PA	74	(2-40)	0.57	
Nizanda	Mexico	16.65	-95.01	878	-1016	30.6	60.1	SA	12	(7-60)	0.82	23
JM Morelos	Mexico	19.31	-88.58	1250	-512	64.6	92.3	SA&PA	60	(2-80)	0.66	
Tenosique	Mexico	17.27	-91.41	2750	-238	28.8	93.4	SA	24	(6-15)	0.55	
Kaxil Kiuic	Mexico	20.08	-89.51	1100	-595	39.9	97.8	SA	274	(3-70)	0.70	22
Zona Norte of Selva Lacandona	Mexico	17.09	-91.47	2750	-243	25.2	85.7	SA&PA	39	(2-52)	0.55	
Agua Salud	Panama	9.21	-79.75	2700	-350	27.5	91.1	SA&PA	45	(2-31)	0.46	24,25
Barro Colorado Nature Monument	Panama	9.14	-79.85	2600	-328	23.3	54.1	SA&PA	8	(20-100)	0.56	26
Playa Venado	Panama	7.43	-74.18	1550	-47	20.9	25.1	PA	13	(6-80)	0.47	
Pucallpa	Peru	-8.53	-74.88	1570	-45	12.4	71.8	SA&PA	14	(5-30)	0.47	
Cayey	Puerto Rico	18.02	-66.08	2000	-251	33.8	71.4	PA	15	(10-80)	0.70	27
El Carite	Puerto Rico	18.08	-66.07	1822	-128	32.3	91.1	PA	28	(4-77)	0.53	28
Luquillo	Puerto Rico	18.34	-65.76	2660	-73	27.2	75.6	PA	12	(9-76)	0.65	28
Gavilán	Venezuela	5.55	-67.40	2673	-391	1.7	99.3	SA	12	(5-20)	0.48	

627

628

629 The name of the chronosequence site, country, latitude (Lat.) and longitude (Long.), annual rainfall (in

630 mm yr⁻¹), climatic water availability (in other studies referred to as climatic water deficit (CWA; in mm

631 yr⁻¹), cation exchange capacity (CEC; in cmol(+) kg⁻¹), forest cover in the landscape matrix (FC; in %),

632 previous land use (LU; SC = shifting cultivation, SC & PA = some plots shifting cultivation, some plots

633 pasture, PA = pasture), the number of secondary forest (SF) plots, the minimum age and maximum age of
634 secondary forests (in yr) included in the chronosequence, and community trait values at 5 years. Trait
635 values are given for wood density (WD; in g cm⁻³). A reference (Ref.) is given for each site.

636

637

638 1 Peña-Claros, M. Changes in forest structure and species composition during secondary forest
639 succession in the Bolivian Amazon. *Biotropica* 35, 450-461, doi:10.1111/j.1744-7429.2003.tb00602.x
640 (2003).

641 2 Toledo, M. & Salick, J. Secondary succession and indigenous management in semideciduous
642 forest fallows of the Amazon basin. *Biotropica* 38, 161-170, doi:10.1111/j.1744-7429.2006.00120.x
643 (2006).

644 3 Kennard, D. K. Secondary forest succession in a tropical dry forest: patterns of development
645 across a 50-year chronosequence in lowland Bolivia. *J. Trop. Ecol.* 18, 53-66 (2002).

646 4 Piotto, D. Spatial dynamics of forest recovery after swidden cultivation in the Atlantic forest of
647 Southern Bahia, Brazil. (PhD Thesis, Yale University, New Haven, USA, 2011).

648 5 Vieira, I. C. G. et al. Classifying successional forests using Landsat spectral properties and
649 ecological characteristics in eastern Amazonia. *Remote Sens. Environ.* 87, 470-481,
650 doi:10.1016/j.rse.2002.09.002 (2003).

651 6 Williamson, G. B., Bentos, T. V., Longworth, J. B. & Mesquita, R. C. G. Convergence and
652 divergence in alternative successional pathways in Central Amazonia. *Plant Ecology & Diversity* 7, 341-
653 348, doi:10.1080/17550874.2012.735714 (2014).

654 7 Zanini, K. J., Bergamin, R. S., Machado, R. E., Pillar, V. D. & Muller, S. C. Atlantic rain forest
655 recovery: successional drivers of floristic and structural patterns of secondary forest in Southern Brazil. *J.*
656 *Veg. Sci.* 25, 1056-1068, doi:10.1111/jvs.12162 (2014).

657 8 Madeira, B. et al. Changes in tree and liana communities along a successional gradient in a
658 tropical dry forest in south-eastern Brazil. *Plant Ecol.* 201, 291-304, doi:10.1007/s11258-009-9580-9
659 (2009).

660 9 Junqueira, A. B., Shepard, G. H. & Clement, C. R. Secondary forests on anthropogenic soils in
661 Brazilian Amazonia conserve agrobiodiversity. *Biodivers. Conserv.* 19, 1933-1961, doi:10.1007/s10531-
662 010-9813-1 (2010).

663 10 Cabral, G. A. L., de Sá Barreto-Sampaio, E. V. & de Almeida-Cortez, J. S. Estrutura espacial e
664 biomassa da parte aérea em diferentes estádios sucessionais de caatinga, em Santa Terezinha, Paraíba.
665 *Rev. Bras. Geogr. Fis.* 6, 566-574 (2013).

666 11 Vester, H. F. M. & Cleef, A. M. Tree architecture and secondary tropical rain forest development
667 - A case study in Araracuara, Colombian Amazonia. *Flora* 193, 75-97 (1998).

668 12 Ruiz, J., Fandino, M. C. & Chazdon, R. L. Vegetation structure, composition, and species
669 richness across a 56-year chronosequence of dry tropical forest on Providencia island, Colombia.
670 *Biotropica* 37, 520-530, doi:10.1111/j.1744-7429.2005.00070.x (2005).

671 13 Morales-Salazar, M. et al. Diversidad y estructura horizontal en los bosques tropicales del
672 Corredor Biológico de Osa, Costa Rica. *Rev. For. Mesoamericana Kurú* 9, 19-28 (2012).

673 14 Powers, J. S., Becknell, J. M., Irving, J. & Perez-Aviles, D. Diversity and structure of
674 regenerating tropical dry forests in Costa Rica: Geographic patterns and environmental drivers. *For. Ecol.*
675 *Manage.* 258, 959-970, doi:10.1016/j.foreco.2008.10.036 (2009).

676 15 Hilje, B., Calvo-Alvarado, J., Jiménez-Rodríguez, C. & Sánchez-Azofeifa, A. Tree species
677 composition, breeding systems, and pollination and dispersal syndromes in three forest successional
678 stages in a tropical dry forest in Mesoamerica. *Trop. Conserv. Sci.* 8, 76-94 (2015).

679 16 Chazdon, R. L., Brenes, A. R. & Alvarado, B. V. Effects of climate and stand age on annual tree
680 dynamics in tropical second-growth rain forests. *Ecology* 86, 1808-1815, doi:10.1890/04-0572 (2005).

681 17 Letcher, S. G. & Chazdon, R. L. Rapid recovery of biomass, species richness, and species
682 composition in a forest chronosequence in northeastern Costa Rica. *Biotropica* 41, 608-617,
683 doi:10.1111/j.1744-7429.2009.00517.x (2009).

684 18 Maury-Lechon, G. Régénération forestière en Guyane Française: recrû sur 25 ha de coupe
685 papetière de forêt dense humide (ARBOCEL). *Revue Bois et Forêts des Tropiques* 197, 3-21 (1982).

686 19 van Breugel, M., Martínez-Ramos, M. & Bongers, F. Community dynamics during early
687 secondary succession in Mexican tropical rain forests. *J. Trop. Ecol.* 22, 663-674,
688 doi:10.1017/s0266467406003452 (2006).

689 20 Mora, F. et al. Testing chronosequences through dynamic approaches: time and site effects on
690 tropical dry forest succession. *Biotropica*, 38-48 (2015).

691 21 Orihuela-Belmonte, D. E. et al. Carbon stocks and accumulation rates in tropical secondary
692 forests at the scale of community, landscape and forest type. *Agric., Ecosyst. Environ.* 171, 72-84,
693 doi:10.1016/j.agee.2013.03.012 (2013).

694 22 Dupuy, J. M. et al. Patterns and correlates of tropical dry forest structure and composition in a
695 highly replicated chronosequence in Yucatan, Mexico. *Biotropica* 44, 151-162, doi:10.1111/j.1744-
696 7429.2011.00783.x (2012).

697 23 Lebrija-Trejos, E., Bongers, F., Pérez-García, E. A. & Meave, J. A. Successional change and
698 resilience of a very dry tropical deciduous forest following shifting agriculture. *Biotropica* 40, 422-431,
699 doi:10.1111/j.1744-7429.2008.00398.x (2008).

700 24 van Breugel, M. et al. Succession of ephemeral secondary forests and their limited role for the
701 conservation of floristic diversity in a human-modified tropical landscape. *PLoS One* 8,
702 doi:10.1371/journal.pone.0082433 (2013).

703 25 Hubbell, S. P., Condit, R. & Foster, R. B. Barro Colorado Forest Census Plot Data. URL
704 <http://ctfs.si.edu/webatlas/datasets/bci> (2005).

705 26 Dent, D. H., DeWalt, S. J. & Denslow, J. S. Secondary forests of central Panama increase in
706 similarity to old-growth forest over time in shade tolerance but not species composition. *J. Veg. Sci.* 24,
707 530-542, doi:10.1111/j.1654-1103.2012.01482.x (2013).

708 27 Marín-Spiotta, E., Ostertag, R. & Silver, W. L. Long-term patterns in tropical reforestation: plant
709 community composition and aboveground biomass accumulation. *Ecol. Appl.* 17, 828-839,
710 doi:10.1890/06-1268 (2007).

711 28 Aide, T. M., Zimmerman, J. K., Pascarella, J. B., Rivera, L. & Marcano-Vega, H. Forest
712 regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology.
713 *Restor. Ecol.* 8, 328-338, doi:10.1046/j.1526-100x.2000.80048.x (2000).

714

715

716

717

718

719

720

721

722

723

724

725

726

727

728 **Extended Data Table 2** Effects of environmental predictors on community functional properties (values
 729 in early-successional forests (5y) and the rate of change during succession (slope)) across Neotropical
 730 forest sites (N=50).

731

Trait	Variable	Model	CWA		CWA ²		CEC		Δ AIC	R ²
			beta	P	beta	P	beta	P		
WD	5y	CWA + CWA ² + CEC	0.0001	0.381	5.24E-07	0.002	0.0030	0.043	0.00	0.54
WD	5y	CWA + CWA ²	0.0001	0.580	4.80E-07	0.006			2.02	0.49
WD	5y	CWA + CEC	-0.0004	0.000			0.0024	0.137	7.90	0.43
WD	5y	CWA	-0.0004	0.000					7.91	0.40
WD	5y	CEC					0.0031	0.131	31.13	0.05
WD	slope	CWA + CWA ² + CEC	-0.0001	0.229	-1.80E-07	0.002	-0.0013	0.011	0.00	0.51
WD	slope	CWA + CWA ²	0.0000	0.438	-1.61E-07	0.007			4.56	0.43
WD	slope	CWA + CEC	0.0001	0.000			-0.0011	0.050	8.35	0.39
WD	slope	CWA	0.0001	0.000					10.10	0.34
732	WD	slope					-0.0013	0.054	26.65	0.08

733

734 Community functional properties at 5 years (5y) and their change over time (slope) were evaluated.

735 Predictors are climatic water availability (CWA), climatic water availability squared (CWA²) and Cation

736 Exchange Capacity (CEC). Community functional properties refer to community mean wood density

737 (WD). All possible combinations of predictors were compared, and the best-supported model with lowest

738 Akaike's Information Criterion adjusted for small sample sizes (AICc) given the number of variables

739 included, was selected (models highlighted in grey). The parameter estimate (beta), P-value (P) and

740 explained variation (R²) are shown.

741

742 **Supplementary Information 1** Relationships between WD and soil fertility

743

744 Across sites, WD at 5 years decreased most strongly with CWA (as discussed in the main text) and it
745 increased weakly with CEC (i.e., the model with CEC was only marginally better than a model without
746 CEC, Extended Data Table 2). High WD of early-successional communities on fertile soils is surprising,
747 as studies in Amazonian old-growth forest have found that community WD is highest on infertile soils⁵⁴.
748 High WD may protect trees against insects and pathogens, increase nutrient residence time in the plant,
749 and enhance tree longevity in low resource environments. Perhaps our results are different compared to
750 the Amazonian study, because (1) we studied a larger rainfall- and soil fertility gradient, and (2) early-
751 successional communities show different responses to soil fertility than old-growth communities.

752 Community WD increased with time for infertile sites, which is in line with successional hypotheses, but
753 hardly changed over time for fertile sites (Extended Data Figure 2, although again, a model with CEC was
754 only marginally better than a model without CEC, Extended Data Table 2). In some fertile, hurricane
755 prone areas such as Puerto Rico, WD of the “old-growth” forests may be low, as these forests have been
756 frequently disturbed by hurricanes, and are characterized by many light demanding species. However, this
757 is not a likely explanation for other sites. **Alternatively, fertile soils increase the success of soft-wooded**
758 **fast growing, light demanding gap specialists, that can be very abundant in the canopy.**

759