

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

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117 **Tropical forests are converted at an alarming rate for agricultural use and pastureland, but also**  
118 **regrow naturally through secondary succession<sup>1</sup>. 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 site<sup>2</sup>. Although the study of succession has a long history<sup>3</sup>, 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<sup>4,5</sup>. 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<sup>6,7</sup>. Late-successional species are expected to have conservative trait values that allow them to  
150 conserve limiting resources and survive under low resource conditions<sup>5,8</sup>. These ideas have been  
151 confirmed in mesic forests, where succession is driven by changes in light availability<sup>9-11</sup>. Yet a recent  
152 study<sup>12</sup> 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 conductivity<sup>13</sup>, carbon gain, and growth<sup>14</sup>, whereas high WD is**  
170 **associated with increased physiological drought tolerance<sup>15</sup>, biomechanical stability<sup>16</sup>, nutrient retention,**  
171 **defense against herbivores, fungi and pathogens<sup>17</sup>, and increased plant survival. For these reasons, WD is**  
172 **an important component of global plant strategies<sup>18</sup>, and the global wood economics spectrum<sup>19</sup>.**  
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<sub>5y</sub>) varied from 0.32 to 1.14 g cm<sup>-3</sup> 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 dependent<sup>20</sup>. **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<sup>15,21</sup> and fire<sup>22</sup>. **Besides, in dry**  
212 **forests resprouting from stumps and roots is an important regeneration mechanism after fire and drought**  
213 **disturbance<sup>23</sup>. Wood density increases survival of resprouts, and hence, the plant, possibly because it**

214 increases resistance to fungi and pathogens and reduces stem decay<sup>24</sup>. 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 conditions<sup>13</sup>. 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 time<sup>9</sup>. In dry forests the situation for early  
228 successional species is characterized by low water availability and high heat load<sup>12,25,26</sup>. As vegetation  
229 regrows the understory becomes cooler and more humid<sup>26</sup>, 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)<sup>27</sup>. 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 P<sup>28</sup>.

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 experimental<sup>29</sup> and theoretical<sup>30</sup> 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 leaves<sup>31</sup>, and may accelerate nutrient cycling through faster decomposition  
255 of soft stem litter<sup>32</sup>. 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 productivity<sup>33</sup>. It may also buffer ecosystem functioning to environmental change and enhance  
260 ecosystem resilience<sup>34</sup>.

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 km<sup>2</sup> by 2030, to enhance biodiversity, site productivity, water quality and flows, and**  
265 **carbon storage<sup>35</sup>.** 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<sup>10,36</sup>. Succession is governed by various processes such as dispersal, facilitation,  
268 competition, and tolerance<sup>37</sup>. In areas with sufficient high surrounding forest cover, it is ecologically best  
269 and economically most cost-efficient to rely on natural regeneration<sup>38</sup>. However, in fragmented or  
270 degraded areas that suffer dispersal limitation, direct seeding or planting can accelerate establishment of  
271 an initial layer<sup>39</sup>. Species selected for initial planting should fulfil many criteria (such as economic and  
272 cultural values, being native, or attracting frugivore dispersers<sup>40</sup>), 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 trees<sup>41</sup>, as their canopy improves microclimate and may protect target plants  
283 against grazing, while hydraulic lift and litter accumulation may increase water and nutrient availability<sup>42</sup>  
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 coupled<sup>43</sup>, whereas others show that they are uncoupled<sup>44</sup>. 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.

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412

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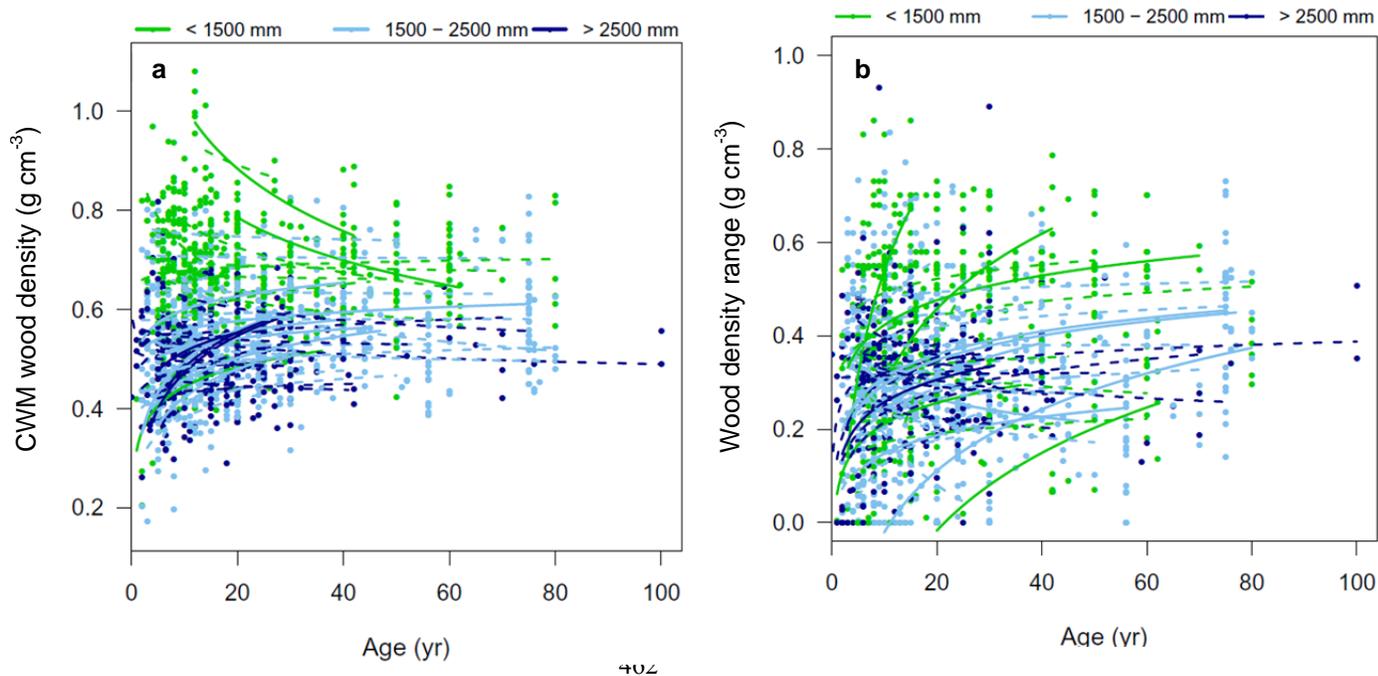
442

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.

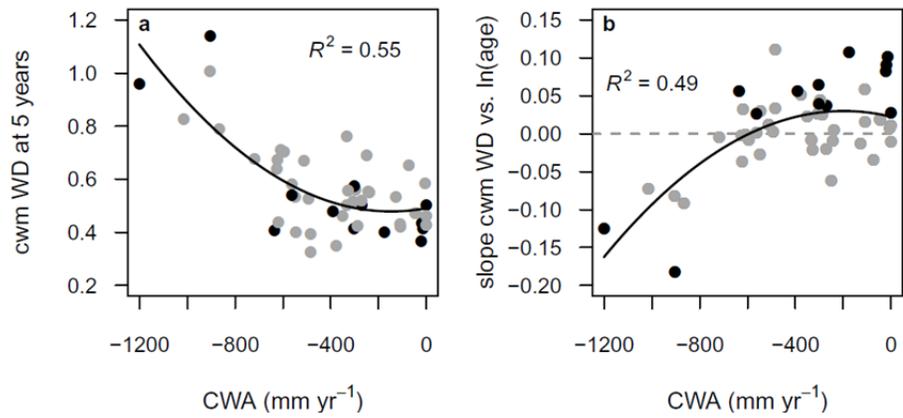
448

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 90<sup>th</sup> percentile minus the trait value of the 10<sup>th</sup> 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  
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474

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

476

477

| Variable | CWA     |       | CWA <sup>2</sup> |       | CEC     |       | R <sup>2</sup> |
|----------|---------|-------|------------------|-------|---------|-------|----------------|
|          | 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 (CWA<sup>2</sup>) 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 (R<sup>2</sup>) 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 sites<sup>27</sup> 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<sup>-1</sup> across sites, topsoil cation exchange capacity (CEC) from  
494 1.7-64.6 cmol(+) kg<sup>-1</sup>, 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  $\geq 5$  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<sup>-3</sup>), 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<sup>43,45</sup>. 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%**<sup>46</sup>.

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 sites<sup>47</sup>. 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 conserved<sup>48</sup>, **although**  
529 **WD can also vary substantially within coexisting genera or families, due to adaptive radiation**<sup>49</sup>. 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 90<sup>th</sup> percentile minus the 10<sup>th</sup> percentile of  
540 WD values in the community, thus ignoring extreme, outlying species.

541  
542 **Environmental conditions.** Annual rainfall (mm yr<sup>-1</sup>) 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 rainfall<sup>50</sup>, we obtained climatic water availability (CWA; in mm yr<sup>-1</sup>, also referred  
545 to as climatic water deficit) from [http://chave.ups-tlse.fr/pantropical\\_allometry.htm](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*<sup>2</sup> = 0.49).

552 Topsoil cation exchange capacity (CEC; in cmol(+) kg<sup>-1</sup>) 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** database<sup>51</sup> 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 ISRIC<sup>51</sup>. SoilGrids did not contain data on soil N and P. Across sites, CEC and CWA were not  
568 significantly correlated (Pearson  $r=-0.08$ ,  $N=50$ ,  $P=0.587$ ).

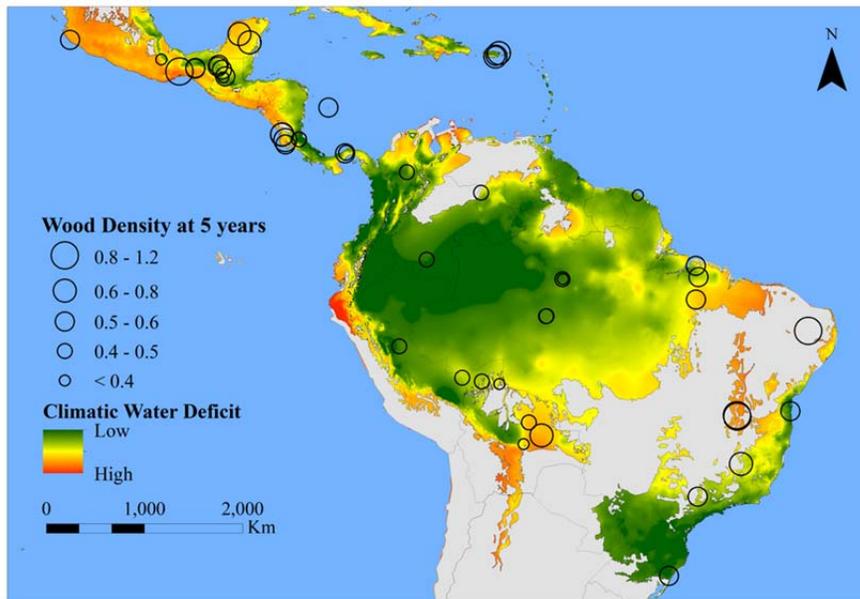
569  
570 **Statistical analyses.** Successional changes in functional composition were assessed for each  
571 chronosequence using secondary forest plots only. We related the functional properties of the plot (CWM  
572 WD, WD range) to time since abandonment using linear regressions. Time since abandonment 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 ( $WD_{\beta}$ ) 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  $WD_{\beta}$  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 package<sup>52</sup>. 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 time<sup>53</sup>, 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

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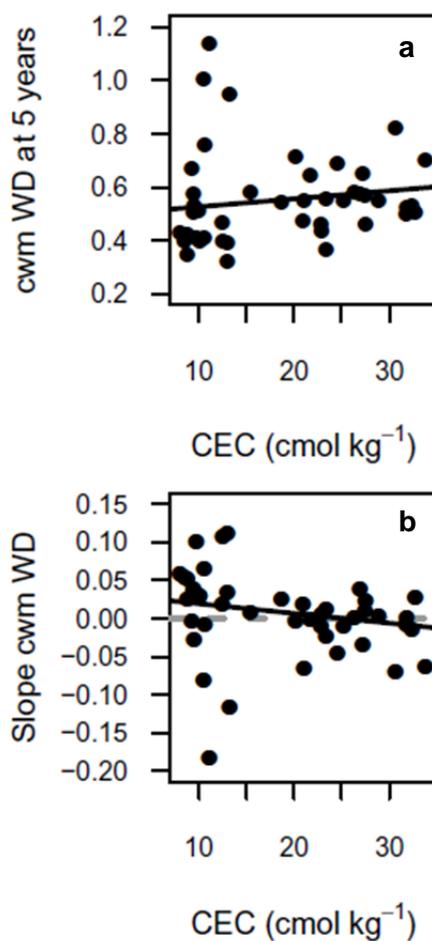
608 **Extended Data Figure 2. Relationships between community-weighted mean wood density (CWM**  
609 **WD) at 5 years (a) and successional changes in wood density (slope) (b) versus cation exchange**  
610 **capacity (CEC) for 50 chronosequence sites.** Continuous lines indicate a significant ( $P \leq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

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614

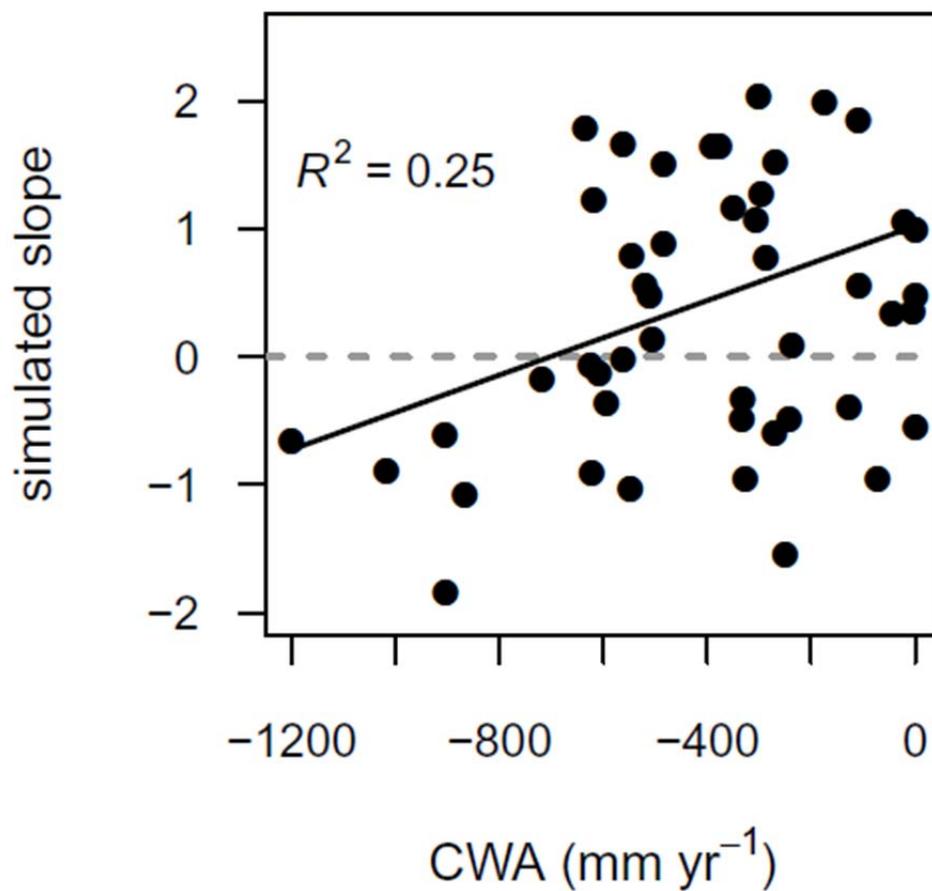
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617 **Extended Data Fig 3.** Successional changes in WD (slope) versus CWA for 50 Neotropical  
618 chronosequence sites. The standardized slope of CWM WD versus  $\ln(\text{time})$  are shown, which correct for  
619 the species accumulation effect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

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

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| Site                                      | Country       | Lat.<br>(°) | Long.<br>(°) | Rainfall<br>(mm/yr) | CWA<br>(mm/yr) | CEC<br>(cmol/kg) | FC<br>(%) | LU<br>(-) | Plots<br>(#) | Age<br>(yr) | WD <sub>5y</sub><br>(g/cm <sup>3</sup> ) | 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                                     |       |

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629 The name of the chronosequence site, country, latitude (Lat.) and longitude (Long.), annual rainfall (in  
630 mm yr<sup>-1</sup>), climatic water availability (in other studies referred to as climatic water deficit (CWA; in mm  
631 yr<sup>-1</sup>), cation exchange capacity (CEC; in cmol(+) kg<sup>-1</sup>), 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<sup>-3</sup>). A reference (Ref.) is given for each site.

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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 <sup>2</sup> |       | CEC     |       | Δ AIC | R <sup>2</sup> |
|-------|----------|------------------------------|---------|-------|------------------|-------|---------|-------|-------|----------------|
|       |          |                              | beta    | P     | beta             | P     | beta    | P     |       |                |
| WD    | 5y       | CWA + CWA <sup>2</sup> + CEC | 0.0001  | 0.381 | 5.24E-07         | 0.002 | 0.0030  | 0.043 | 0.00  | 0.54           |
| WD    | 5y       | CWA + CWA <sup>2</sup>       | 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 <sup>2</sup> + CEC | -0.0001 | 0.229 | -1.80E-07        | 0.002 | -0.0013 | 0.011 | 0.00  | 0.51           |
| WD    | slope    | CWA + CWA <sup>2</sup>       | 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 (CWA<sup>2</sup>) 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 (R<sup>2</sup>) 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 soils<sup>54</sup>.  
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