1   # Wet and dry tropical forests show opposite successional pathways

2   # in wood density but converge over time

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116

117   **Tropical forests are converted at an alarming rate for agricultural use and pastureland, but also**

118   **regrow naturally through secondary succession[1]. 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

5

136 on the traits of the individual species, which determine their ability to establish, grow, survive and

137 reproduce at a site[2]. Although the study of succession has a long history[3], 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 availability[9-11]. Yet a recent

152 study[12] 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

We analysed wood density recovery at an unprecedented spatial scale, using original data from 50 sites,

1410 plots and >16,000 trees, covering most of the latitudinal, climatic, and soil fertility gradients in

lowland Neotropical forests. To provide a long-term perspective on succession, we used chronosequences

("sites") where plots that differ in time since agricultural abandonment (0-100 years) were compared. We

focused on stemwood density (WD) because it is a key trait shapes plant responses to the environment

and impacts carbon cycling. WD is a key trait as it is at the nexus of many plant functions; low WD

facilitates water storage, hydraulic conductivity[13], carbon gain, and growth[14], whereas high WD is

associated with increased physiological drought tolerance[15], biomechanical stability[16], nutrient retention,

defense against herbivores, fungi and pathogens[17], and increased plant survival. For these reasons, WD is

an important component of global plant strategies[18], and the global wood economics spectrum[19].

Moreover, WD has been measured across many sites, making cross-site comparisons possible. For each

plot, the average and variation in community WD was calculated based on the proportional basal area and

WD values of the species. For each site, recovery was analysed by regressing community WD values

against time since land abandonment. The start (interpolated value at 5 years) and direction (slope of the

fitted time-course) of succession were then related to climatic water availability (CWA) and to cation

exchange capacity (CEC) as an indicator of soil fertility.

179

Results

Community-level mean WD varied widely across all plots early in succession and more narrowly later in

succession (Figure 1a). The funnel shape arises because sites differed both in their initial trait values (the

intercept) and in their direction of successional change over time (the slope). Initial values and slopes

were both driven by climatic water availability and to a lesser extent by soil fertility (Table 1).

Community wood density at 5 years (WD_{5y}) varied from 0.32 to 1.14 g cm^{-3} across sites (Table 1)

covering nearly the whole natural range in wood density, with drier sites having significantly higher

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[20]. 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   Eearly-succesional 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 fire[22]. Besides, in dry

212   forests resprouting from stumps and roots is an important regeneration mechanism after fire and drought

213   disturbance[23]. Wood density increases survival of resprouts, and hence, the plant, possibly because it

214 increases resistance to fungi and pathogens and reduces stem decay[24]. In wetter climates, high rainfall and

215 cloud cover lead to more benign microclimatic conditions. Early-succesional 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[13]. 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[9]. 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 humid[26], 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 P[28].

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[29] and theoretical[30] 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[31], and may accelerate nutrient cycling through faster decomposition

255   of soft stem litter[32]. 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[33]. It may also buffer ecosystem functioning to environmental change and enhance

260   ecosystem resilience[34].

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^2 by 2030, to enhance biodiversity, site productivity, water quality and flows, and

265   carbon storage[35]. 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 tolerance[37]. In areas with sufficient high surrounding forest cover, it is ecologically best

269   and economically most cost-efficient to rely on natural regeneration[38]. However, in fragmented or

270   degraded areas that suffer dispersal limitation, direct seeding or planting can accelerate establishment of

271   an initial layer[39]. Species selected for initial planting should fulfil many criteria (such as economic and

272   cultural values, being native, or attracting frugivore dispersers[40]), 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[41], 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[42]

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[43], whereas others show that they are uncoupled[44]. This climate-dependence of

11

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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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).

Figure 1. Recovery of functional trait values and trait variation with time since abandonment in

Neotropical secondary forest sites. a, Community-weighted mean wood density; **b,** wood density range

within each community (i.e., plot). Each line represents a different chronosequence (N=50). Significant

changes over time are indicated by continuous lines, non-significant changes by broken lines. Lines and

dots (individual plots, N=1410) are colour coded according to the forest type as dry forest (700-1500

mm/y, green), moist forest (1500-2500 mm/y, light blue) and wet forest (>2500 mm/y, dark blue). The

range is calculated per plot as trait value of the 90th percentile minus the trait value of the 10th percentile

of trait values in a plot.

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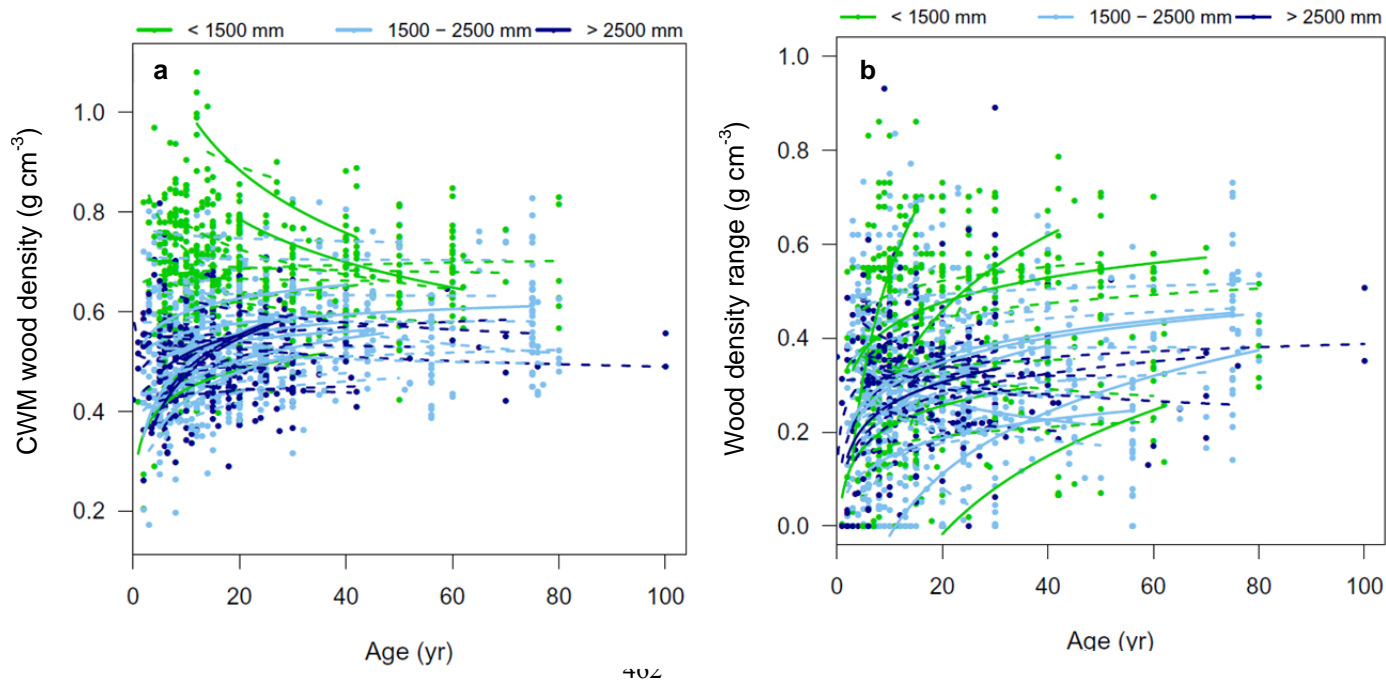
Figure 2 a, Community-weighted mean wood density at 5 years (WD$_{5y}$) versus climatic water

availability (CWA); b, successional changes in WD (slope) versus CWA for 50 Neotropical sites.
Black symbols indicate sites with significant slopes. CWA indicates the water deficit during the dry

season, with zero meaning no water deficit.

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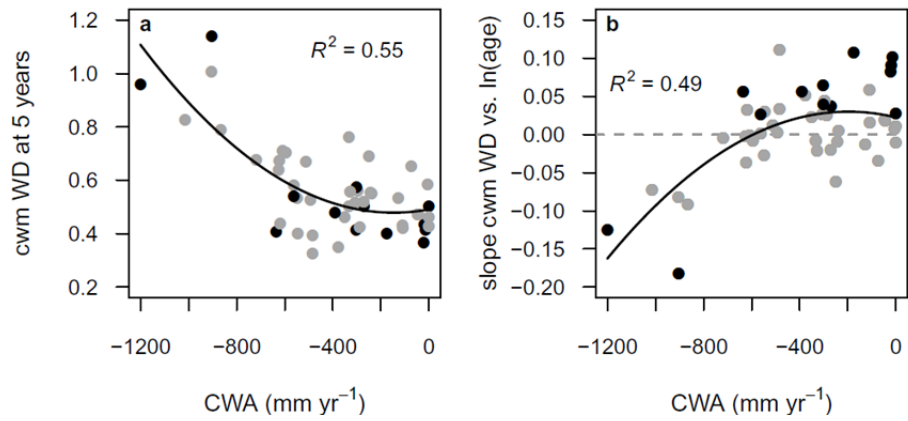
475 **Table 1 Environmental predictors of community wood density across Neotropical forest sites.**

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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 (CWA^2) 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^2) are shown. See Extended Data Figure 2 for bivariate relationships.

METHODS

Study sites. We compiled chronosequence data for 50 Neotropical lowland forest sites[27] covering the entire latitudinal gradient in the Neotropics (Fig. 2C, Extended Data Table 1). We focused on the Neotropics, i.e., tropical South America and Mesoamerica, because (1) shifting cultivation is an important land use type there, (2) the region has a relatively shared biogeographic history, thus reducing confounding historical effects, and (3) many chronosequence studies have been established in the area. Annual rainfall varied from 750-4000 mm y^{-1} across sites, topsoil cation exchange capacity (CEC) from 1.7-64.6 cmol(+) kg^{-1}, and percent forest cover in the landscape matrix ranged from 9-100% (Extended Data Table 1).

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

Wood density. We focused on stemwood density as a key response trait (indicating how communities are assembled during succession) and a key effect trait (determining how ecosystems function in terms of carbon, water and nutrient stocks and cycling). Wood density (WD, in g cm^{-3}), which is also known as wood specific gravity, is the wood dry mass divided by the wood green volume. It reflects a trade-off between fast volumetric growth of soft-wooded species and high survival because of resistance against 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 sites[47]. 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[48], 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 rainfall[50], 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 database[51] 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

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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[51]. 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 package[52]. 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[53], 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

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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(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: (observed slope– average of random slopes) / standard

598   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).
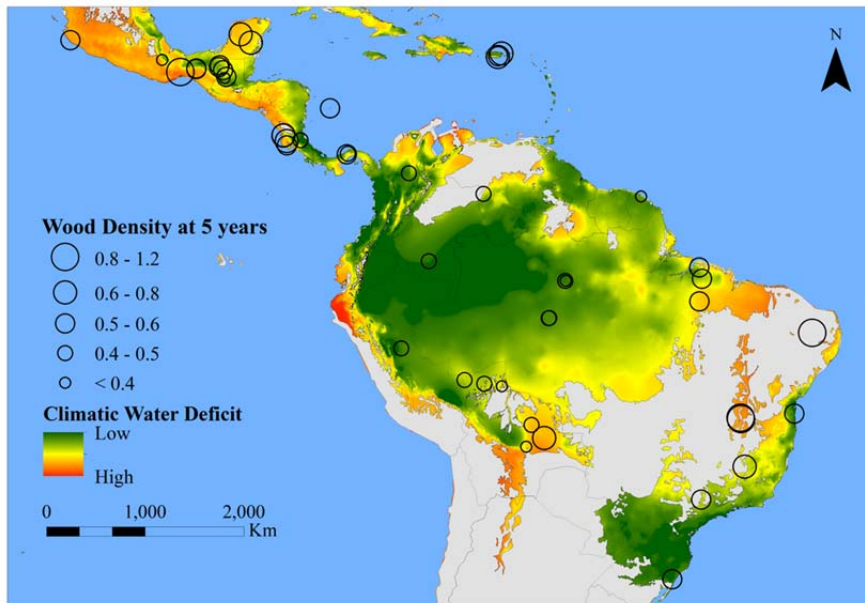
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608   **Extended Data Figure 2. Relationships between community-weighted mean wood density (CWM**

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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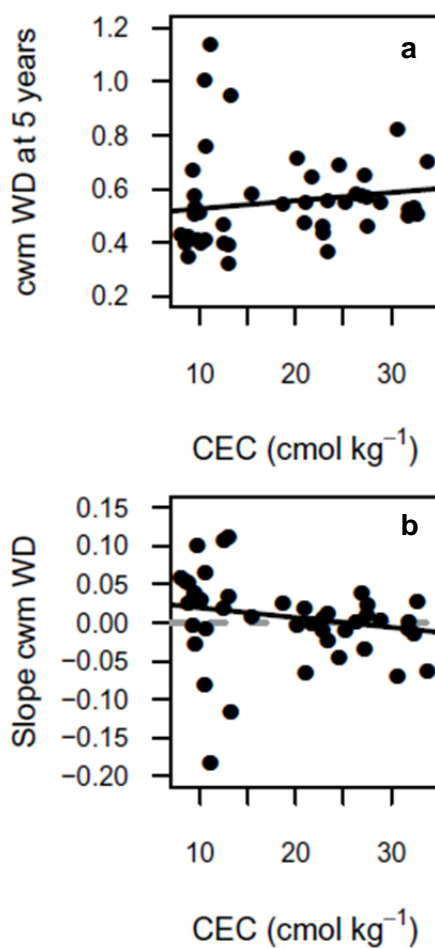
617   **Extended Data Fig 3**. Successional changes in WD (slope) versus CWA for 50 Neotropical

618   chronosequence sites. The standardized slope of CWM WD versus ln(time) are shown, which correct for

619   the species accumulation effect (see methods).

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

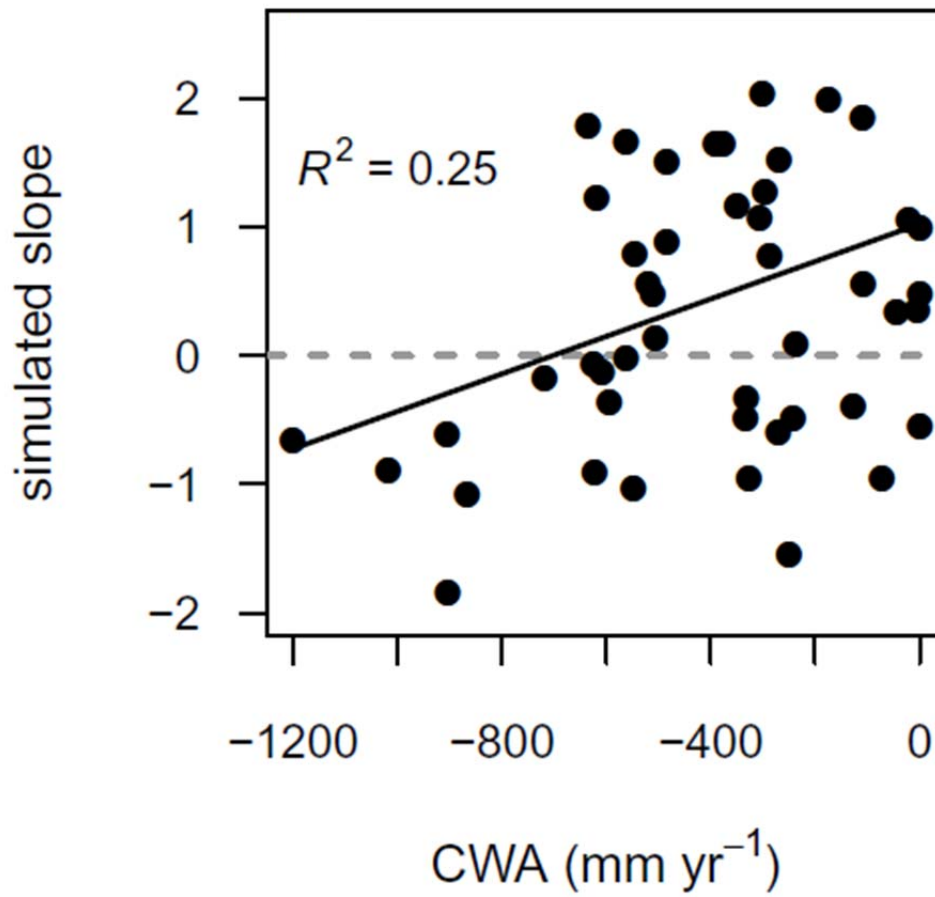| Site	Country	Lat. (°)	Long. (°)	Rainfall (mm/yr)	CWA (mm/yr)	CEC (cmol/kg)	FC (%)	LU (-)	Plots (#)	Age (yr)	WD$_{5y}$ (g/cm^3)	Ref.
Bolpebra	Bolivia	-11.42	-69.13	1800	-303	10.5	97.5	SA	15	(4-47)	0.41	
El Tigre	Bolivia	-11.98	-65.72	1780	-378	8.8	90.3	SA	6	(3-25)	0.35	1
El Turi	Bolivia	-11.75	-67.33	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	PA	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	
Araracuara	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
Arbocel	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	

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

mm yr^{-1}), climatic water availability (in other studies reffered to as climatic water deficit (CWA; in mm

yr^{-1}), cation exchange capacity (CEC; in cmol(+) kg^{-1}), forest cover in the landscape matrix (FC; in %),

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.

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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 beta	P	CWA^2 beta	P	CEC beta	P	Δ AIC	R^2
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
WD	slope	CEC					-0.0013	0.054	26.65	0.08

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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^2) 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^2) are shown.

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

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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[54].

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.

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