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

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

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

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

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 conductivity¹³, carbon gain, and growth¹⁴, whereas high WD is associated with increased physiological drought tolerance¹⁵, biomechanical stability¹⁶, nutrient retention, defense against herbivores, fungi and pathogens¹⁷, and increased plant survival. For these reasons, WD is an important component of global plant strategies¹⁸, and the global wood economics spectrum¹⁹. 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.

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

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

Discussion

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

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

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

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

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

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

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

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

ameliorates local microclimate and soil, suppresses weeds, and facilitates establishment of late-successional species^{10,36}. Succession is governed by various processes such as dispersal, facilitation, competition, and tolerance³⁷. In areas with sufficient high surrounding forest cover, it is ecologically best and economically most cost-efficient to rely on natural regeneration³⁸. However, in fragmented or degraded areas that suffer dispersal limitation, direct seeding or planting can accelerate establishment of an initial layer³⁹. Species selected for initial planting should fulfil many criteria (such as economic and cultural values, being native, or attracting frugivore dispersers⁴⁰), depending on the goals of restoration. Nevertheless, species should at least be well adapted to local site conditions to be successful. WD can be used as an additional ecological criterion and an easy proxy for species selection. In dry regions, dense-wooded, drought-tolerant conservative species should be selected that can tolerate the harsh initial conditions, whereas in wet regions soft-wooded, fast-growing acquisitive species should be selected that can rapidly restore vegetation cover and facilitate succession together with dense-wooded shade tolerant species that may replace them on the long-term. Early-successional forests in Latin America show a tremendous variation in CWM WD, and the relationship between CWM WD at 5 years and CWA (Figure 2a) can be used to optimize species selection for restoration. Additionally, in climatically harsh environments land managers may use nurse shrubs or perennial grasses to facilitate and increase the survival of planted target trees⁴¹, as their canopy improves microclimate and may protect target plants against grazing, while hydraulic lift and litter accumulation may increase water and nutrient availability⁴².

In sum, 1) succession proceeds from acquisitive towards conservative WD values in wet forest but from conservative towards acquisitive WD values in dry forest, 2) during succession, there is a shift from strong abiotic filtering in open early-successional environments towards weaker abiotic filtering in benign, closed late-successional environments, and 3) combined these processes lead to trait convergence across sites over time. Future research should demonstrate whether our findings for wood density of long-lived stems also apply to traits of shorter-lived leaves, as some studies show that stem and leaf traits are strongly coupled⁴³, whereas others show that they are uncoupled⁴⁴. This climate-dependence of

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

References

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

- 23 Vieira, D. L. & Scariot, A. Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology* **14**, 11-20 (2006).
- 24 Poorter, L. *et al.* Resprouting as a persistence strategy of tropical forest trees: relations with carbohydrate storage and shade tolerance. *Ecology* **91**, 2613-2627, doi:10.1890/09-0862.1 (2010).
- 25 Lebrija-Trejos, E., Meave, J. A., Poorter, L., Pérez-García, E. A. & Bongers, F. Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession. *Perspectives in Plant Ecology Evolution and Systematics* **12**, 267-275, doi:10.1016/j.ppees.2010.09.002 (2010).
- 26 Lebrija-Trejos, E., Pérez-García, E. A., Meave, J. A., Poorter, L. & Bongers, F. Environmental changes during secondary succession in a tropical dry forest in Mexico. *Journal of Tropical Ecology* **27**, 477-489, doi:10.1017/s0266467411000253 (2011).
- 27 Poorter, L. *et al.* Biomass resilience of Neotropical secondary forests. *Nature* **530**, 211-214 (2016).
- 28 Fyllas, N. M. *et al.* Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. *Biogeosciences* **6**, 2677-2708 (2009).
- 29 Chase, J. M. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences* **104**, 17430-17434 (2007).
- 30 Fukami, T. Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics* **46**, 1-23 (2015).
- 31 Finegan, B. *et al.* Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *Journal of Ecology* **103**, 191-201 (2015).
- 32 Cornwell, W. K. *et al.* Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology letters* **11**, 1065-1071 (2008).
- 33 Sande, M. T. *et al.* Biodiversity in species, traits, and structure determines carbon stocks and uptake in tropical forests. *Biotropica* **49**, 593-603, doi:10.1111/btp.12453 (2017).
- 34 Sakschewski, B. *et al.* Amazon forest resilience emerges from plant trait diversity. *Nat. Clim. Chang.*, DOI: 10.1038/NCLIMATE3109 (2016).
- 35 Holl, K. D. Restoring tropical forests from the bottom up. *Science* **355**, 455-456, doi:10.1126/science.aam5432 (2017).
- 36 van Breugel, M., Bongers, F. & Martínez-Ramos, M. Species dynamics during early secondary forest succession: Recruitment, mortality and species turnover. *Biotropica* **39**, 610-619, doi:10.1111/j.1744-7429.2007.00316.x (2007).
- 37 Connell, J. H. & Slatyer, R. O. Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist* **111**, 1119-1144 (1977).
- 38 Crouzeilles, R. *et al.* Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Sci. Adv.* **3**, e1701345 (2017).
- 39 Chazdon, R. L. Beyond deforestation: Restoring forests and ecosystem services on degraded lands. *Science* **320**, 1458-1460, doi:10.1126/science.1155365 (2008).
- 40 Quesada, M. *et al.* Succession and management of tropical dry forests in the Americas: Review and new perspectives. *Forest Ecology and Management* **258**, 1014-1024 (2009).
- 41 Gómez-Aparicio, L. *et al.* Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* **14**, 1128-1138 (2004).
- 42 Padilla, F. M. & Pugnaire, F. I. The role of nurse plants in the restoration of degraded environments. *Frontiers in Ecology and the Environment* **4**, 196-202 (2006).
- 43 Reich, P. B. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**, 275-301 (2014).
- 44 Baraloto, C. *et al.* Decoupled leaf and stem economics in rain forest trees. *Ecology letters* **13**, 1338-1347 (2010).
- 45 Lambers, H. & Poorter, H. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in ecological research* **23**, 187-261 (1992).
- 46 Pérez-Harguindeguy, N. *et al.* New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of botany* **61**, 167-234 (2013).
- 47 Zanne, A. E. *et al.* Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository. doi:10.5061/dryad.234. (2009).
- 48 Coelho de Souza, F. *et al.* Evolutionary heritage influences Amazon tree ecology. *Proceedings of the Royal Society B: Biological Sciences* **283**, doi:10.1098/rspb.2016.1587 (2016).
- 49 Thomas, S. C. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. *American journal of Botany* **83**, 556-566 (1996).
- 50 ter Steege, H. *et al.* Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* **443**, 444-447, doi:10.1038/nature05134 (2006).
- 51 Hengl, T. *et al.* SoilGrids250m: global gridded soil information based on Machine Learning. *PLOS ONE* (2017).
- 52 Laliberté, E., Legendre, P. & Shipley, B. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. *R package version 1.0-12* (2014).
- 53 Rozendaal, D. M. A., Bongers, F., Aide, T. M., others & Poorter, L. Biodiversity recovery of Neotropical secondary forests. *Sci. Adv.* (in press).
- 54 Mitchard, E. T. A. *et al.* Markedly divergent estimates of Amazon forest carbon density from ground plots and satellites. *Global Ecology and Biogeography* **23**, 935-946, doi:10.1111/geb.12168 (2014).

412

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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.

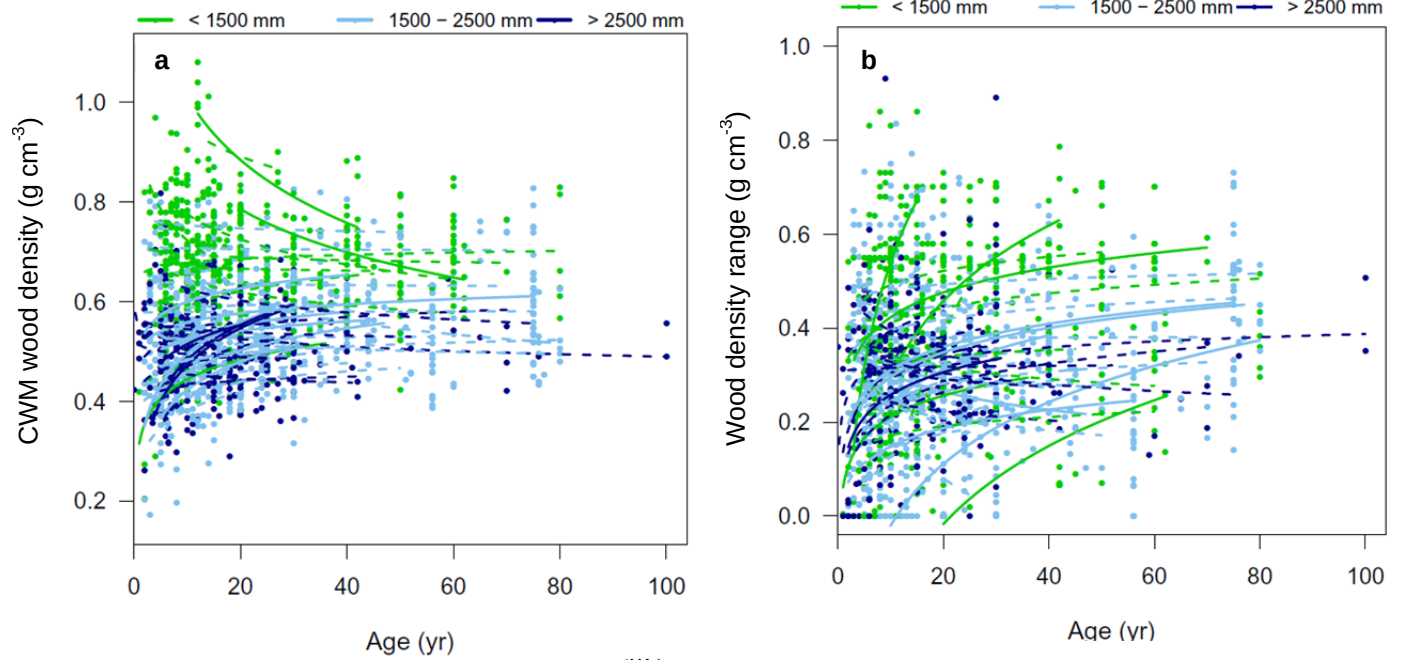


Figure 2 a, Community-weighted mean wood density at 5 years (WD_{5y}) versus climatic water availability (CWA); b, successional changes in WD (slope) versus CWA for 50 Neotropical sites.

Black symbols indicate sites with significant slopes. CWA indicates the water deficit during the dry season, with zero meaning no water deficit.

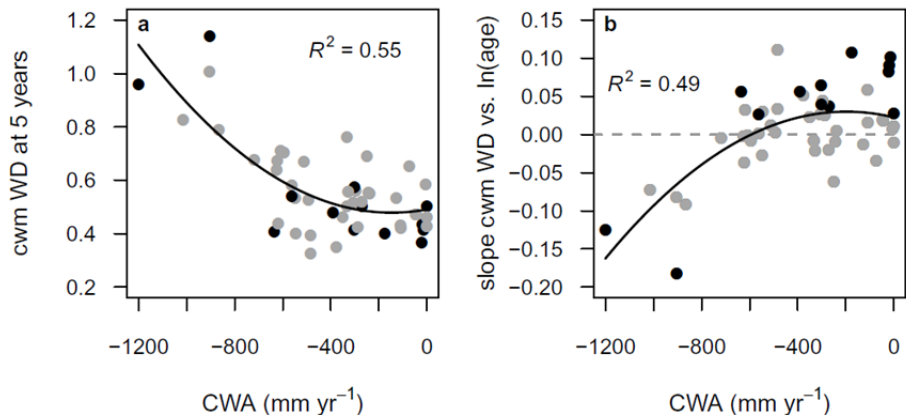


Table 1 Environmental predictors of community wood density across Neotropical forest sites.

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

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

METHODS

Study sites. We compiled chronosequence data for 50 Neotropical lowland forest sites²⁷ 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

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

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

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

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

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

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

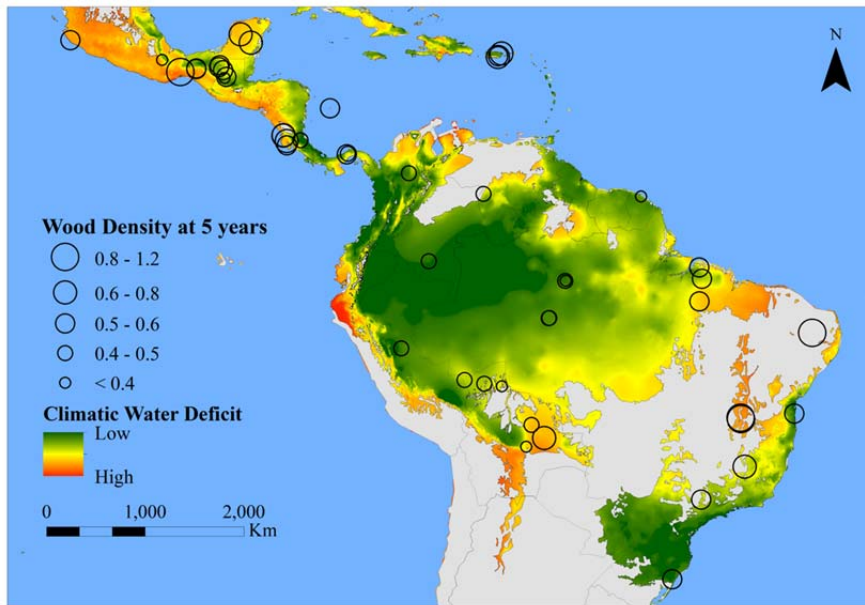
Topsoil cation exchange capacity (CEC; in cmol(+) kg⁻¹) over the first 30 cm of the soil was used as an indicator of soil nutrient availability as it scales well with the total concentrations of base cations, and it was available for part of the sites, and could be obtained from the global SoilGrids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

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

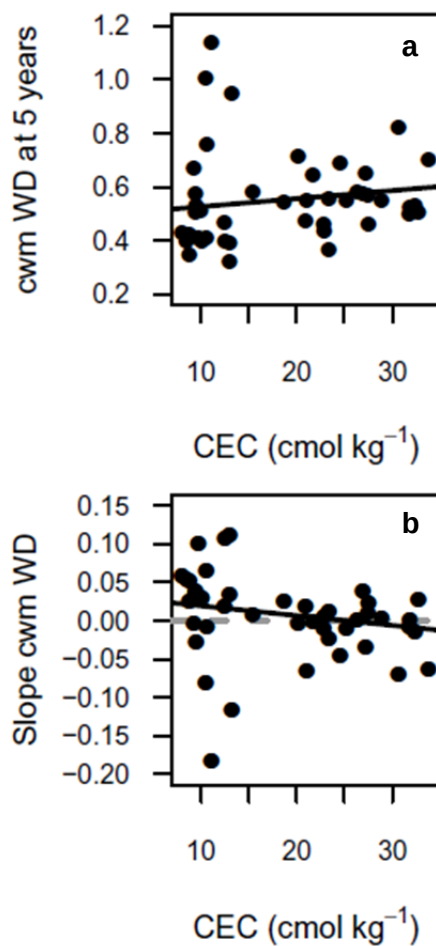
Statistical analyses. Successional changes in functional composition were assessed for each chronosequence using secondary forest plots only. We related the functional properties of the plot (CWM WD, WD range) to time since abandonment using linear regressions. Time since abandonment was ln-transformed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

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

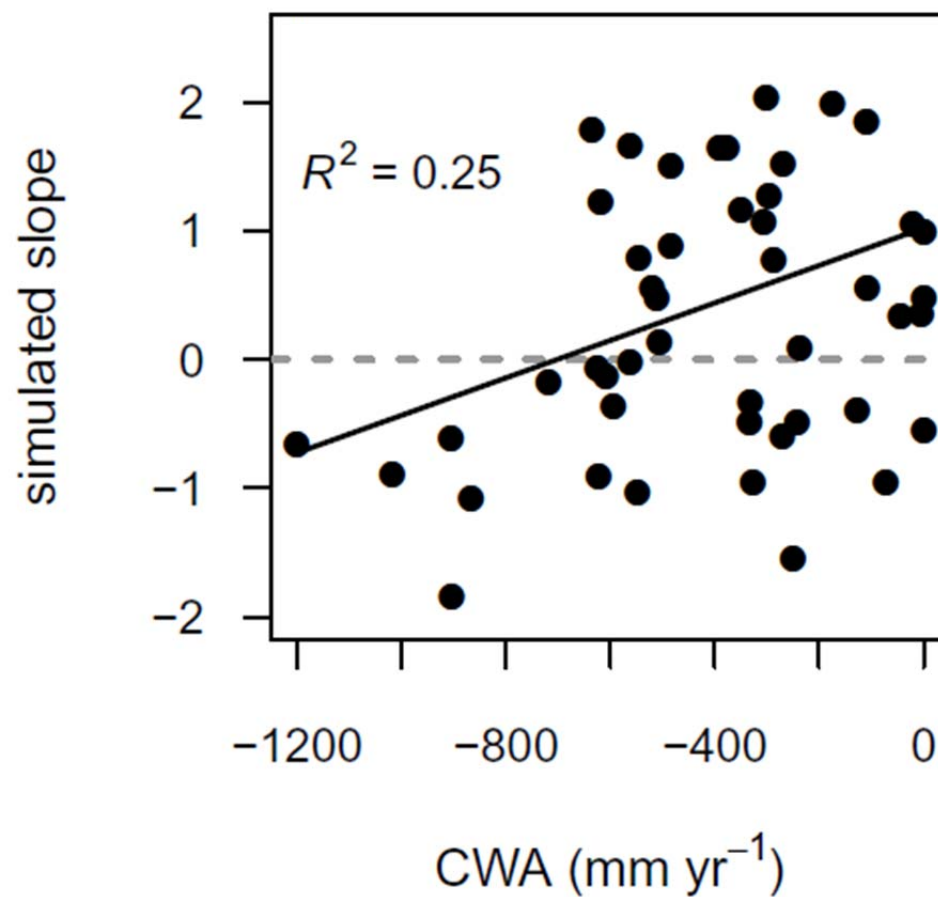
Extended Data Figure 1. Map of the 50 study sites are indicated by black circles (the symbol on the ocean belongs to an island) and the size of the symbols scales with the CWM WD at 5 years. The colored areas indicate the lowland tropical forest biome (altitude < 1000 m). The colors indicate the climatic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



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



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



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 _{sy} (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 (<i>Cecropia</i> pathway)	Brazil	-2.38	-59.91	2400	-22	2.0	98.4	SA	13	(5-31)	0.37	6
Manaus (<i>Vismia</i> 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	
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 referred 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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

- 26 Dent, D. H., DeWalt, S. J. & Denslow, J. S. Secondary forests of central Panama increase in
similarity to old-growth forest over time in shade tolerance but not species composition. *J. Veg. Sci.* 24,
530-542, doi:10.1111/j.1654-1103.2012.01482.x (2013).
- 27 Marín-Spiotta, E., Ostertag, R. & Silver, W. L. Long-term patterns in tropical reforestation: plant
community composition and aboveground biomass accumulation. *Ecol. Appl.* 17, 828-839,
doi:10.1890/06-1268 (2007).
- 28 Aide, T. M., Zimmerman, J. K., Pascarella, J. B., Rivera, L. & Marciano-Vega, H. Forest
regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology.
Restor. Ecol. 8, 328-338, doi:10.1046/j.1526-100x.2000.80048.x (2000).

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

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

Community functional properties at 5 years (5y) and their change over time (slope) were evaluated. Predictors are climatic water availability (CWA), climatic water availability squared (CWA²) and Cation Exchange Capacity (CEC). Community functional properties refer to community mean wood density (WD). All possible combinations of predictors were compared, and the best-supported model with lowest Akaike's Information Criterion adjusted for small sample sizes (AICc) given the number of variables included, was selected (models highlighted in grey). The parameter estimate (beta), P-value (P) and explained variation (R²) are shown.

Supplementary Information 1 Relationships between WD and soil fertility

Across sites, WD at 5 years decreased most strongly with CWA (as discussed in the main text) and it increased weakly with CEC (i.e., the model with CEC was only marginally better than a model without CEC, Extended Data Table 2). High WD of early-successional communities on fertile soils is surprising, as studies in Amazonian old-growth forest have found that community WD is highest on infertile soils⁵⁴. High WD may protect trees against insects and pathogens, increase nutrient residence time in the plant, and enhance tree longevity in low resource environments. Perhaps our results are different compared to the Amazonian study, because (1) we studied a larger rainfall- and soil fertility gradient, and (2) early-successional communities show different responses to soil fertility than old-growth communities. Community WD increased with time for infertile sites, which is in line with successional hypotheses, but hardly changed over time for fertile sites (Extended Data Figure 2, although again, a model with CEC was only marginally better than a model without CEC, Extended Data Table 2). In some fertile, hurricane prone areas such as Puerto Rico, WD of the “old-growth” forests may be low, as these forests have been frequently disturbed by hurricanes, and are characterized by many light demanding species. However, this is not a likely explanation for other sites. **Alternatively, fertile soils increase the success of soft-wooded fast growing, light demanding gap specialists, that can be very abundant in the canopy.**