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

Poorter, Lourens; Rozendaal, Danaë M.A.; Bongers, Frans; Almeida-Cortez, Jarcilene S.; Almeyda Zambrano, Angélica María et al

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

Lourens Poorter [1]*, Danaë M. A. Rozendaal[1,2,3,4], Frans Bongers [1], Jarcilene S. de Almeida-Cortez[5],
Angélica María Almeyda Zambrano[6], Francisco S. Álvarez [7], José Luís Andrade [8],
Luis Felipe Arreola Villa[9], Patricia Balvanera [9], Justin M. Becknell[10], Tony V. Bentos[11],
Radika Bhaskar[12], Vanessa Boukili[13], Pedro H. S. Brancalion [14], Eben N. Broadbent[6],
Ricardo G. César[14], Jerome Chave [15], Robin L. Chazdon[16,17], Gabriel Dalla Colletta[18], Dylan Craven[19],
Ben H. J. de Jong[20], Julie S. Denslow[21], Daisy H. Dent[22,23], Saara J. DeWalt[24], Elisa Díaz García[14],
Juan Manuel Dupuy [8], Sandra M. Durán[25,26], Mário M. Espírito Santo[27], María C. Fandiño[28],
Geraldo Wilson Fernandes[29], Bryan Finegan [7], Vanessa Granda Moser[7], Jefferson S. Hall [30],
José Luis Hernández-Stefanoni [8], Catarina C. Jakovac [1,11,31,32], André B. Junqueira [11,31,32,33],
Deborah Kennard[34], Edwin Lebrija-Trejos[35], Susan G. Letcher [36], Madelon Lohbeck [1,37],
Omar R. Lopez[22,38], Erika Marín-Spiotta[39], Miguel Martínez-Ramos[9], Sebastião V. Martins[40],
Paulo E. S. Massoca [11], Jorge A. Meave [41], Rita Mesquita[11], Francisco Mora [9],
Vanessa de Souza Moreno[14], Sandra C. Müller [42], Rodrigo Muñoz [41], Robert Muscarella [43,44],
Silvio Nolasco de Oliveira Neto[45], Yule R. F. Nunes[46], Susana Ochoa-Gaona [20], Horacio Paz[9],
Marielos Peña-Claros[1], Daniel Piotto [47], Jorge Ruíz [48], Lucía Sanaphre-Villanueva [8,49],
Arturo Sanchez-Azofeifa[25], Naomi B. Schwartz[50], Marc K. Steininger[51], William Wayt Thomas [52],
Marisol Toledo[53], Maria Uriarte [54], Luis P. Utrera [7], Michiel van Breugel [30,55,56],
Masha T. van der Sande [1,57,58,59,60], Hans van der Wal[61], Maria D. M. Veloso[27], Hans F. M. Vester[62],
Ima C. G. Vieira[63], Pedro Manuel Villa [40,64], G. Bruce Williamson[11,65], S. Joseph Wright [22],
Kátia J. Zanini[42], Jess K. Zimmerman[66] and Mark Westoby [67]

Tropical forests are converted at an alarming rate for agricultural use and pastureland, but also regrow naturally through secondary succession. 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 1,403 plots that differ in age since agricultural abandonment from 50 sites across the Neotropics. We analyse changes in community composition using species-specific stem wood 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. However, in dry forest, succession proceeds from high towards low community WD (conservative towards acquisitive trait values), 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 the community WD over time as vegetation cover builds up. These ecological insights can be used to improve species selection for reforestation. Reforestation species selected to establish a first protective canopy layer should, among other criteria, ideally have a similar WD to the early successional communities that dominate under the prevailing macroclimatic conditions.

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 site[1]. Although the study of succession has a long history[2], we currently lack tests of successional hypotheses across broad biogeographic scales because biogeographically distinct areas have

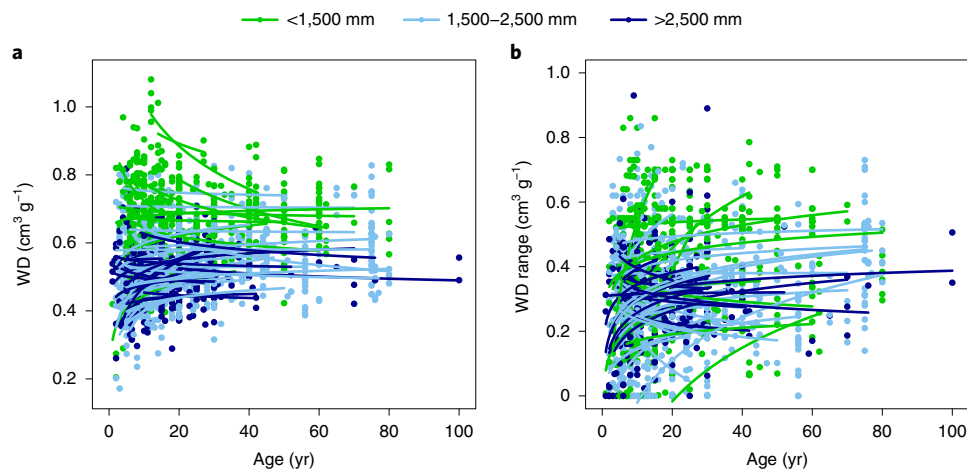A full list of affiliations appears at the end of the paper.

Fig. 1 | Recovery of WD values and WD variation with time since abandonment in Neotropical secondary forest sites. a, CWM WD. **b**, WD range within each community (that is, plot). Each line represents a different site ($n = 50$). Significant changes ($P \leq 0.05$) over time are indicated by continuous lines. Non-significant changes are indicated by broken lines. Lines and dots (individual plots; $n = 1,403$) are colour coded according to forest type: dry forest (700–1,500 mm yr⁻¹, green); moist forest (1,500–2,500 mm yr⁻¹, light blue); and wet forest (>2,500 mm yr⁻¹, dark blue). The range is calculated per plot as the trait value of the 90th percentile minus the trait value of the 10th percentile of trait values in a plot.

different taxonomic species compositions. 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 provide important insights not only into the mechanisms of succession and community assembly, but also into 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[3,4]. 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[5,6]. Late successional species are expected to have conservative trait values that allow them to conserve limiting resources and survive under low-resource conditions[4,7]. These ideas have been confirmed in mesic forests, where succession is driven by changes in light availability[8–10]. Yet, a recent study[11] 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 dry forests and that we should reconsider one of the successional paradigms. However, the question is to what extent these results can be generalized. Here, we report recovery in wood density (WD) 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 WD recovery at an unprecedented spatial scale, using original data from 50 sites, 1,403 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 (hereafter referred to as 'sites') where plots that differ in time since agricultural abandonment (0–100 years) were compared. We focused on stem WD because it is a key trait that 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[12], carbon gain and growth[13], whereas high WD is associated with increased physiological drought tolerance[14], biomechanical stability[15], nutrient retention, defense against herbivores, fungi and pathogens[16], and increased plant survival. For these reasons, WD is an important component of global plant strategies[17] and the global wood economics spectrum[18]. Moreover, WD has been measured across many sites, making cross-site comparisons possible. For each plot, the average (that is, community-weighted mean (CWM)) 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 five years) and direction (slope of the fitted time course) of succession were then related to climatic water availability (CWA) and cation exchange capacity (CEC) as an indicator of soil fertility.

Results

The CWM WD varied widely across all plots early in succession and more narrowly later in succession (Fig. 1a). There is a funnel shape 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 CWA and, to a lesser extent, soil fertility (Table 1). The community WD at 5 years (WD$_{5y}$) varied from 0.32–1.14 g cm⁻³ across sites (Table 1) covering nearly the whole natural range in WD, with drier sites having significantly higher initial WD values than wetter sites (Table 1 and Fig. 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 showed an increase (Fig. 2b), so that overall, WD values converged over time for wet and dry forests towards more similar values (Fig. 1a). The same results were found after a randomization test (Supplementary Fig. 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 differed considerably in early succession and converged later in succession (that is, a funnel-shaped relationship is observed).

Table 1 | Environmental predictors of community WD and range across Neotropical forest sites

Trait	Variable	CWA		CWA^2		CEC		R^2
		β	P	β	P	β	P	
WD	5 years	0.0002	0.251	5.8×10^{-7}	0.001	0.0030	0.035	0.58
WD	Slope	−0.0001	0.178	-1.9×10^{-7}	0.001	−0.0013	0.012	0.52
WD range	5 years	−0.0007	<0.001	-8.7×10^{-7}	<0.001	–	–	0.38
WD range	Slope	0.0002	0.177	3.4×10^{-7}	0.007	–	–	0.31

The CWM WD_{5y} and CWM WD change over time (slope), as well as the range in WD_{5y} and the change in range of WD over time (slope), were evaluated for 50 sites. All possible combinations of predictors (CWA, its squared value (CWA^2) and CEC) were compared, and the best-supported model with the lowest AICc value was selected (Supplementary Table 2). The parameter estimate (β), P value and explained variation (R^2) are shown. See Supplementary Fig. 2 for bivariate relationships.
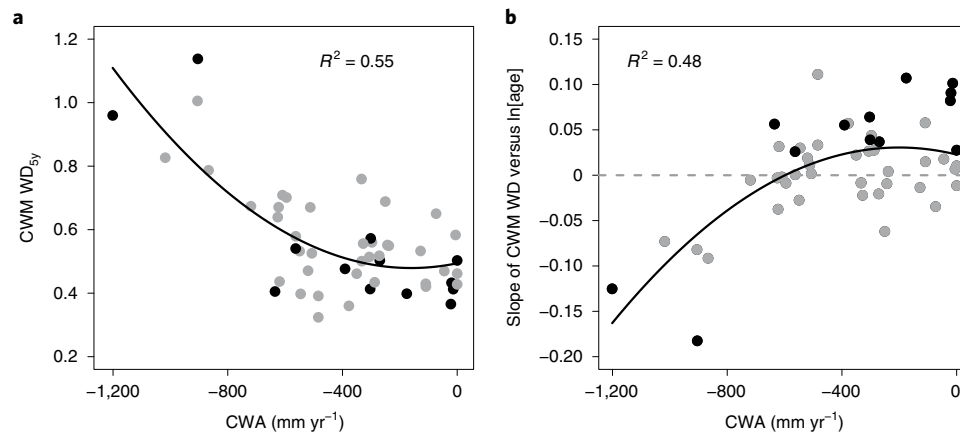

Fig. 2 | CWM WD_{5y} and successional changes in CWM WD as a function of CWA. a, CWM WD_{5y} versus CWA. **b**, Successional changes in CWM WD (slope) versus CWA for 50 Neotropical sites. Black symbols indicate sites with significant slopes. CWA refers to the water deficit during the dry season, with zero meaning no water deficit.

Some sites showed a significant increase in WD over time, while others showed a significant decrease or no net change (Fig. 1a). Such contrasting results can contribute to the idea that succession is highly unpredictable, stochastic and context dependent[19]. However, we show at the continental scale that this seemingly idiosyncratic behaviour is partly caused by opposite patterns in the start (that is, initial state) and direction (that is, trajectory) of succession, largely due to climate. Species with high WD values 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 the recovery of forest functioning during natural regeneration and restoration.

The strong differences in starting values among sites may be caused by strong functional constraints imposed by climatic filtering (Fig. 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[14,20] and fire[21]. In dry forests, resprouting from stumps and roots is an important regeneration mechanism after fire and drought disturbance[22]. WD increases the survival of resprouts, and hence the plant, possibly because it increases resistance to fungi and pathogens and reduces stem decay[23]. 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 conditions[12]. Variation in plot WD is large at the start of succession (Fig. 1a), not only because of climatic filtering across sites, but also because of large trait variation within sites caused by dispersal limitation (colonizing

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 (Fig. 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 time[8]. In dry forests, the situation for early successional species is characterized by low water availability and high heat load[11,24,25]. As vegetation regrows, the understory becomes cooler and more humid[25], 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 (Fig. 1a).

Across sites, the start and direction of succession were driven by CWA and, to a lesser extent, CEC (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)[26]. 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 nitrogen and especially phosphorus[27].

For most sites, within-plot variation in WD increased over time (Fig. 1b), which may have been 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 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 still being present in the older successional plots, thus extending the WD range. This is partly in line with recent experimental[28] and theoretical[29] 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 (Fig. 1b and Table 1), perhaps because drier forests start with fewer species, or because of a rapid accumulation of different drought-coping strategies during succession.

Successional shifts in WD 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 leaves[30], and may accelerate nutrient cycling through faster decomposition of soft stem litter[31]. In wet forests, succession proceeds from acquisitive to conservative trait values (increasing the community WD with time), which may slow down biogeochemical cycling and partly offset the positive effects of increased aboveground biomass. Increased trait variation during succession in many forests (Fig. 1b) may lead to greater niche complementarity, more efficient resource use and higher productivity[32]. It may also buffer ecosystem functioning to environmental change and enhance ecosystem resilience[33].

Insight into the mechanisms of succession can facilitate the design of effective forest restoration strategies adapted to local site conditions. The need for efficient reforestation is urgent given global ambitions to restore an area of 3.5 million km[2] by 2030 (of which 1.7 million has been pledged so far)[34], to enhance biodiversity[35], site productivity, water quality and flows, and carbon storage[36]. Rapid establishment of an initial vegetation layer is of paramount importance because it ameliorates local microclimate and soil, suppresses weeds and facilitates the establishment of late successional species[9,37]. Succession is governed by various processes, such as dispersal, facilitation[38], competition and tolerance[39]. In areas with sufficient high surrounding forest cover, natural regeneration is often an appropriate and economically efficient forest restoration strategy. However, in fragmented or degraded areas that suffer dispersal limitation, direct seeding or planting can accelerate the establishment of an initial layer[40]. Species selected for initial planting should fulfil many criteria (such as economic and cultural values, being native or attracting frugivore dispersers[41]), 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 in the long term. Early successional forests in Latin America show tremendous variation in community-weighted mean (CWM) WD, and the relationship between CWM WD_{5y} and CWA (Fig. 2a) can be used to optimize species selection for restoration. Additionally, in climatically harsh environments, land managers may use nurse shrubs to facilitate and increase the survival of planted target trees[42], as their canopy improves the microclimate and may protect target plants against grazing, while hydraulic lift and litter accumulation may increase water and nutrient availability[43].

In summary: (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 WD of long-lived stems also apply to traits of shorter-lived leaves, as some studies show that stem and leaf traits are strongly coupled[44], whereas others show that they are uncoupled[45]. 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.

Methods

Study sites. We compiled site data for 50 Neotropical lowland forest sites[26] covering the entire latitudinal gradient in the Neotropics (Supplementary Fig. 1 and Supplementary Table 1). We focused on the Neotropics (that is, tropical South America and Mesoamerica) because shifting cultivation is an important land-use type there, and many chronosequence studies have been established in the area. Annual rainfall varied from 750–4,000 mm yr^{−1} across sites, topsoil CEC varied from 1.7–64.6 centimoles of positive charge per kilogram of soil (cmol(+) kg^{−1}), and percentage forest cover in the landscape matrix ranged from 9–100% (Supplementary Table 1).

Plots. On average, 28 plots (range 5–251) were established per site, with the age of the youngest plot ranging from 0–20 years in the time since abandonment. The age range covered by site plots varied from 9–80 years across sites (Supplementary Table 1) and plot sizes ranged from 0.01–1.00 ha, with an average of 0.10 ha across all plots. Per site, plots were of the same size. For trees, palms and shrubs, all stems with a stem diameter at breast height of ≥5 were measured and identified to species level, except at six sites where the minimum stem diameter at breast height was 10 cm. Across sites, on average, 94.5% of stems were identified to species level (range 71–100%), and 99.5% (range 94–100%) were identified to family, genus, species or morphospecies level.

WD. We focused on stem WD 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). 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 due to 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[44,46]. 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 the community functional composition based on species-specific WD values. Traits can be plastic and respond to environmental gradients. To take trait acclimatization 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 the successional stage could not be accounted for, although within-species variation in WD tends to be small, with an average coefficient of variation of 5–9%[47]. Successional changes in community WD as reported here are due only to species turnover and not plasticity.

Species-specific WD data were collected for 22 sites and taken from a WD database for the remaining sites[48]. When local species data were not available, we used the average local site data at the genus or family level, as WD values of tropical trees are strongly phylogenetically conserved[49], although WD can also vary substantially within coexisting genera or families, due to adaptive radiation[50]. For an average of 23.0% of the trees, we used average site-specific genus-level data; for 8.7% of the trees, we used 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 a small effect on the calculated community-weighted WD; plot CWM WD values with and without imputed data are strongly correlated (Pearson's $r = 0.88$; $P < 0.0001$). The remaining species without trait values were excluded from the analysis.

For each plot, we calculated 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 the 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

rainfall[51], we obtained 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 (that is, the sum of (evapotranspiration minus rainfall) over the course of the dry season). It therefore reflects the dry season intensity. CWA is by definition negative, and sites with a CWA value of zero 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 sites (CWA = −949 + 0.279 × rainfall; $n = 49$; $P < 0.0001$; coefficient of determination (R^2) = 0.53).

Topsoil 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. Also, data were available for some of the sites and could be obtained from the global SoilGrids database of the International Soil Reference and Information Centre[52] for the remaining sites. It should be noted that CEC not only includes the base cations Ca, Mg and K, but also Na and Al, which can impair plant growth. However, in general, 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 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 nitrogen or phosphorus might be stronger drivers of forest recovery, as nitrogen especially might be limiting in the early stages of succession and phosphorus 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 they allow us to rank the sites based on their potential soil fertility; in this respect, they are consistent with date from the SoilGrids database, which for these tropical areas also mostly include soil characteristics associated with mature forest. For 34 sites for which no local CEC data were available, CEC values were obtained from the SoilGrids database[52]. SoilGrids does not contain data on soil nitrogen and phosphorus. Across sites, CEC and CWA were not significantly correlated (Pearson's $r = −0.09$; $n = 50$; $P = 0.548$).

Statistical analyses. Successional changes in functional composition were assessed for each site using secondary forest plots only. We related the functional properties of the plot (CWM WD and WD range) to the time since abandonment using linear regressions. Time since abandonment was natural log-transformed before analysis because forest structure, environmental conditions and species composition typically change nonlinearly over time with rapid initial changes and slow changes afterwards. The regression slope (WD$_\beta$) indicates the direction and pace of functional change during succession. We used the site-specific regression equations to predict CWM WD$_{5y}$, reflecting the early successional community that is filtered out by the macroenvironment. WD$_{5y}$ and WD$_\beta$ were then related to CWA (as an indicator of water availability), CWA^2 (to account for nonlinear 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 the lowest AICc given the number of predictors was selected. All statistical tests were two-sided, and all analyses were performed in R 3.3.2. CWM WD was calculated using the FD package[53]. In our results we observed a convergence of WD values from different forests over time. Convergence over time may also arise from a sampling effect, as at our sites, species richness increases logarithmically over time[35], and 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 (that is, the number of species and their abundances) but randomized the species names and, hence, WD values within a site, based on the species pool occurring in the plots within a site. We performed 999 iterations per site, and in each iteration calculated the CWM WD for all of the plots at that site. After each iteration, we calculated for the site the slope of CWM WD versus ln[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: (observed slope − the average of random slopes) / the standard deviation of random slopes. We then plotted the standardized slopes against CWA.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability
The dataset on CWM WD values and WD ranges for the plots from 49 sites (Fig. 1) is available from the Data Archiving and Networked Services repository at https://

doi.org/10.17026/dans-z3s-3d7t. For one other site, data are available on request. The data used to produce Fig. 2 can be found in Supplementary Table 1.

References
1. Shipley, B., Vile, D. & Garnier, É. From plant traits to plant communities: a statistical mechanistic approach to biodiversity. *Science* **314**, 812–814 (2006).
2. Clements, F. E. *Plant Succession: an Analysis of the Development of Vegetation* (Carnegie Institution of Washington, 1916).
3. Bazzaz, F. A. Physiological ecology of plant succession. *Annu. Rev. Ecol. Syst.* **10**, 351–371 (1979).
4. Wright, I. J. et al. The worldwide leaf economics spectrum. *Nature* **428**, 821–827 (2004).
5. Pianka, E. On *r* and *K* selection. *Am. Nat.* **104**, 592–597 (1970).
6. Tilman, D. *Plant Strategies and the Dynamics and Structure of Plant Communities* (Princeton Univ. Press, 1988).
7. 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).
8. Finegan, B. Pattern and process in Neotropical secondary rain forests: the first 100 years of succession. *Trends Ecol. Evol.* **11**, 119–124 (1996).
9. Chazdon, R. L. *Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation* (Univ. Chicago Press, 2014).
10. Peterson, C. & Carson, W. in *Tropical Forest Community Ecology* 367–383 (Wiley-Blackwell, 2008).
11. Lohbeck, M. et al. Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology* **94**, 1211–1216 (2013).
12. Santiago, L. et al. Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia* **140**, 543–550 (2004).
13. 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 Phytol.* **185**, 481–492 (2010).
14. 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 Environ.* **36**, 405–418 (2013).
15. Van Gelder, H. A., Poorter, L. & Sterck, F. J. Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. *New Phytol.* **171**, 367–378 (2006).
16. Loehle, C. Tree life history strategies: the role of defenses. *Can. J. For. Res.* **18**, 209–222 (1988).
17. Díaz, S. et al. The global spectrum of plant form and function. *Nature* **529**, 167–171 (2016).
18. Chave, J. et al. Towards a worldwide wood economics spectrum. *Ecol. Lett.* **12**, 351–366 (2009).
19. Norden, N. et al. Successional dynamics in Neotropical forests are as uncertain as they are predictable. *Proc. Natl Acad. Sci. USA* **112**, 8013–8018 (2015).
20. 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 Environ.* **34**, 137–148 (2011).
21. 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. *Glob. Change Biol.* **18**, 630–641 (2012).
22. Vieira, D. L. & Scariot, A. Principles of natural regeneration of tropical dry forests for restoration. *Restor. Ecol.* **14**, 11–20 (2006).
23. Poorter, L. et al. Resprouting as a persistence strategy of tropical forest trees: relations with carbohydrate storage and shade tolerance. *Ecology* **91**, 2613–2627 (2010).
24. 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. *Pers. Plant Ecol. Evol. Syst.* **12**, 267–275 (2010).
25. 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. *J. Trop. Ecol.* **27**, 477–489 (2011).
26. Poorter, L. et al. Biomass resilience of Neotropical secondary forests. *Nature* **530**, 211–214 (2016).
27. Fyllas, N. M. et al. Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. *Biogeosciences* **6**, 2677–2708 (2009).
28. Chase, J. M. Drought mediates the importance of stochastic community assembly. *Proc. Natl Acad. Sci. USA* **104**, 17430–17434 (2007).
29. Fukami, T. Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annu. Rev. Ecol. Evol. Syst.* **46**, 1–23 (2015).

30. Finegan, B. et al. Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *J. Ecol.* **103**, 191–201 (2015).

31. Cornwell, W. K. et al. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol. Lett.* **11**, 1065–1071 (2008).

32. Sande, M. T. et al. Biodiversity in species, traits, and structure determines carbon stocks and uptake in tropical forests. *Biotropica* **49**, 593–603 (2017).

33. Sakschewski, B. et al. Resilience of Amazon forests emerges from plant trait diversity. *Nat. Clim. Change* **6**, 1032–1036 (2016).

34. Holl, K. D. Restoring tropical forests from the bottom up. *Science* **355**, 455–456 (2017).

35. Rozendaal, D. M. A. et al. Biodiversity recovery of Neotropical secondary forests. *Sci. Adv.* **5**, eaau3114 (2019).

36. Chazdon, R. L. et al. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Sci. Adv.* **2**, e1501639 (2016).

37. Van Breugel, M., Bongers, F. & Martínez-Ramos, M. Species dynamics during early secondary forest succession: recruitment, mortality and species turnover. *Biotropica* **39**, 610–619 (2007).

38. Gei, M. et al. Legume abundance along successional and rainfall gradients in Neotropical forests. *Nat. Ecol. Evol.* **2**, 1104–1111 (2018).

39. Connell, J. H. & Slatyer, R. O. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* **111**, 1119–1144 (1977).

40. Chazdon, R. L. Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science* **320**, 1458–1460 (2008).

41. Quesada, M. et al. Succession and management of tropical dry forests in the Americas: review and new perspectives. *For. Ecol. Manag.* **258**, 1014–1024 (2009).

42. Gómez-Aparicio, L. et al. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecol. Appl.* **14**, 1128–1138 (2004).

43. Padilla, F. M. & Pugnaire, F. I. The role of nurse plants in the restoration of degraded environments. *Front. Ecol. Environ.* **4**, 196–202 (2006).

44. Reich, P. B. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *J. Ecol.* **102**, 275–301 (2014).

45. Baraloto, C. et al. Decoupled leaf and stem economics in rain forest trees. *Ecol. Lett.* **13**, 1338–1347 (2010).

46. Lambers, H. & Poorter, H. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Adv. Ecol. Res.* **23**, 187–261 (1992).

47. Pérez-Harguindeguy, N. et al. New handbook for standardised measurement of plant functional traits worldwide. *Aus. J. Bot.* **61**, 167–234 (2013).

48. Zanne, A. E. et al. *Data from: Towards a Worldwide Wood Economics Spectrum* (Dryad Digital Repository, 2009); https://doi.org/10.5061/dryad.234

49. Coelho de Souza, F. et al. Evolutionary heritage influences Amazon tree ecology. *Proc. R. Soc. B* **283**, 20161587 (2016).

50. Thomas, S. C. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. *Am. J. Bot.* **83**, 556–566 (1996).

51. Ter Steege, H. et al. Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* **443**, 444–447 (2006).

52. Hengl, T. et al. SoilGrids250m: global gridded soil information based on machine learning. *PLoS ONE* **12**, e0169748 (2017).

53. 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).

Author contributions

L.P. and M.W. conceived the idea. L.P. and D.M.A.R. coordinated the data compilations. D.M.A.R. carried out the data analysis. L.P., D.M.A.R., F.B. and M.W. contributed to the analytical tools used in the analysis. E.N.B. and A.M.A.Z. made the map. L.P. wrote the paper. All co-authors collected field data, discussed the results, suggested further analyses and commented on the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-019-0882-6.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to L.P.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

¹Forest Ecology and Forest Management Group, Wageningen University and Research, Wageningen, the Netherlands. ²Laboratory of Geo-Information Science and Remote Sensing, Wageningen University and Research, Wageningen, the Netherlands. ³Plant Production Systems Group, Wageningen University and Research, Wageningen, the Netherlands. ⁴Centre for Crop Systems Analysis, Wageningen University and Research, Wageningen, the Netherlands. ⁵Departamento de Botânica, CCB, Universidade Federal de Pernambuco, Recife, Brazil. ⁶School of Forest Resources and Conservation, University of Florida, Gainesville, FL, USA. ⁷Centro Agronómico Tropical de Investigación y Enseñanza, Turrialba, Costa Rica. ⁸Centro de Investigación Científica de Yucatán, Unidad de Recursos Naturales, Mérida, Mexico. ⁹Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Mexico. ¹⁰Environmental Studies Program, Colby College, Waterville, ME, USA. ¹¹Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil. ¹²College of Design, Engineering, and Commerce, Thomas Jefferson University, Philadelphia, PA, USA. ¹³Somerville City Hall, Somerville, MA, USA. ¹⁴Department of Forest Sciences, Luiz de Queiroz College of Agriculture, University of São Paulo, Piracicaba, Brazil. ¹⁵Laboratoire Evolution et Diversité Biologique, UMR5174, CNRS/Université Paul Sabatier, Toulouse, France. ¹⁶Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA. ¹⁷Tropical Forests and People Research Centre, University of the Sunshine Coast, Sippy Downs, Queensland, Australia. ¹⁸Institute of Biology, University of Campinas, Campinas, Brazil. ¹⁹Biodiversity, Macroecology and Biogeography, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Göttingen, Germany. ²⁰Department of Sustainability Science, El Colegio de la Frontera Sur, Lerma, Mexico. ²¹Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA, USA. ²²Smithsonian Tropical Research Institute, Panama City, Panama. ²³Biological and Environmental Sciences, University of Stirling, Stirling, UK. ²⁴Department of Biological Sciences, Clemson University, Clemson, SC, USA. ²⁵Earth and Atmospheric Sciences Department, University of Alberta, Edmonton, Alberta, Canada. ²⁶Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA. ²⁷Departamento de Biologia Geral, Universidade Estadual de Montes Claros, Montes Claros, Brazil.

[28]Fondo Patrimonio Natural, Bogotá, Colombia. [29]Ecologia Evolutiva e Biodiversidade/DBG, ICB, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil. [30]ForestGEO, Smithsonian Tropical Research Institute, Panama City, Panama. [31]International Institute for Sustainability, Rio de Janeiro, Brazil. [32]Centre for Conservation and Sustainability Science (CSRio), Department of Geography and the Environment, Pontifical Catholic University of Rio de Janeiro, Rio de Janeiro, Brazil. [33]Institut de Ciència i Tecnologia Ambientals, Universitat Autònoma de Barcelona, Barcelona, Spain. [34]Department of Physical and Environmental Sciences, Colorado Mesa University, Grand Junction, CO, USA. [35]Department of Biology and the Environment, Faculty of Natural Sciences, University of Haifa-Oranim, Tivon, Israel. [36]College of the Atlantic, Bar Harbor, ME, USA. [37]World Agroforestry (ICRAF), Nairobi, Kenya. [38]Instituto de Investigaciones Científicas y Servicios de Alta Tecnología, Panama City, Panama. [39]Department of Geography, University of Wisconsin-Madison, Madison, WI, USA. [40]Departamento de Engenharia Florestal, Universidade Federal de Viçosa, Viçosa, Brazil. [41]Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City, Mexico. [42]Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil. [43]Department of Plant Ecology and Evolution, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden. [44]Section of Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Aarhus, Denmark. [45]Departamento de Engenharia Florestal, Universidade Federal de Viçosa, Viçosa, Brazil. [46]Departamento de Biologia Geral, Universidade Estadual de Montes Claros, Montes Claros, Brazil. [47]Centro de Formação em Ciências Agroflorestais, Universidade Federal do Sul da Bahia, Itabuna, Brazil. [48]School of Social Sciences, Geography Area, Universidad Pedagogica y Tecnologica de Colombia, Tunja, Colombia. [49]Consejo Nacional de Ciencia y Tecnologia, Centro del Cambio Global y la Sustentabilidad, Villahermosa, Mexico. [50]Department of Geography, University of British Columbia, Vancouver, British Columbia, Canada. [51]Department of Geographical Sciences, University of Maryland, College Park, MD, USA. [52]Institute of Systematic Botany, The New York Botanical Garden, New York, NY, USA. [53]FCA-UAGRM, Santa Cruz de la Sierra, Bolivia. [54]Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY, USA. [55]Yale-NUS College, Singapore, Singapore. [56]Department of Biological Sciences, National University of Singapore, Singapore, Singapore. [57]Department of Community Ecology, Helmholtz Centre for Environmental Research - UFZ, Halle, Germany. [58]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany. [59]Department of Biological Sciences, Florida Institute of Technology, Melbourne, FL, USA. [60]Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, the Netherlands. [61]Departamento de Agricultura, Sociedad y Ambiente, El Colegio de la Frontera Sur, Unidad Villahermosa, Centro, Mexico. [62]Bonhoeffer College, Enschede, the Netherlands. [63]Museu Paraense Emilio Goeldi, Belém, Brazil. [64]Fundación para la Conservación de la Biodiversidad, Mérida, Venezuela. [65]Department of Biological Sciences, Louisiana State University, Baton Rouge, LA, USA. [66]Department of Environmental Sciences, University of Puerto Rico, San Juan, Puerto Rico, USA. [67]Department of Biological Sciences, Macquarie University, Sydney, New South Wales, Australia. *e-mail: lourens.poorter@wur.nl

Corresponding author(s):   L. Poorter

Last updated by author(s):   Mar 13, 2019

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see Authors & Referees and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Plot-level data and, where possible, species-specific wood density data were collected by the data owners, and provided using excel sheets. Other wood density data was downloaded from the global wood density database.
Data analysis	All analyses were performed in R 3.3.2

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

The dataset on community weighted mean wood density and wood density range for plots from 49 sites (Fig. 1) is available from the DANS repository, http://doi.org/XX.XXXXX/dans-XXX-XXXX (46), and for one site it is available upon request. The data of Fig. 2 can be found in Extended Table 1. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to L.P. (lourens.poorter@wur.nl).

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences   ☐ Behavioural & social sciences   ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We compiled chronosequence data for 50 Neotropical lowland forest sites covering the entire latitudinal gradient in the Neotropics (Extended Data Fig 1, 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. 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).
Research sample	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.
Sampling strategy	Plots were established in different areas, to cover different time since abandonment. The exact location of the plots depended therefore on the ages known and available. The number of replicate plots varied per site, as this is a compilation of different studies that were establsihed for different purposes. It depended, amongst others, on financial and logistic opportunities, and the amount of secondary forest of different ages available in the area.
Data collection	All 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.
Timing and spatial scale	This is a compilation of 50 studies. We have provided the references of the original studies, so that you can know when they were established
Data exclusions	No data was excluded.
Reproducibility	This is a field study and not an experiment.
Randomization	Not relevant (it is a field study without treatments (the "treatment" was time since abandonment).
Blinding	Not applicable.

Did the study involve field work?   ☒ Yes   ☐ No

Field work, collection and transport

Field conditions	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).
Location	See the Extended table 1 in the manuscript with the locations.
Access and import/export	See the original 50 studies.
Disturbance	The only disturbance was sometimes collection of plant vouchers for species identification.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	Antibodies
☒	Eukaryotic cell lines
☒	Palaeontology
☒	Animals and other organisms
☒	Human research participants
☒	Clinical data

Methods

n/a	Involved in the study
☒	ChIP-seq
☒	Flow cytometry
☒	MRI-based neuroimaging