PNAS
www.pnas.org

Supplementary Information for

Functional recovery of secondary tropical forests

Authors: Lourens Poorter, Danaë M.A. Rozendaal, Frans Bongers, Jarcilene S. de Almeida-Cortez, Francisco S. Álvarez, José Luís Andrade, Luis Felipe Arreola Villa, Justin M. Becknell, Radika Bhaskar, Vanessa Boukili, Pedro H.S. Brancalion, Ricardo G. César, Jerome Chave, Robin L. Chazdon, Gabriel Dalla Colletta, Dylan Craven, Ben H.J. de Jong, Julie S. Denslow, Daisy H. Dent, Saara J. DeWalt, Elisa Díaz García, Juan Manuel Dupuy, Sandra M. Durán, Mário M. Espírito Santo, Geraldo Wilson Fernandes, Bryan Finegan, Vanessa Granda Moser, Jefferson S. Hall, José Luis Hernández-Stefanoni, Catarina C. Jakovac, Deborah Kennard, Edwin Lebrija-Trejos, Susan G. Letcher, Madelon Lohbeck, Omar R. Lopez, Erika Marín-Spiotta, Miguel Martínez-Ramos, Jorge A. Meave, Francisco Mora, Vanessa de Souza Moreno, Sandra C. Müller, Rodrigo Muñoz, Robert Muscarella, Yule R.F. Nunes, Susana Ochoa-Gaona, Rafael S. Oliveira, Horacio Paz, Arturo Sanchez-Azofeifa, Lucía Sanaphre-Villanueva, Marisol Toledo, Maria Uriarte, Luis P. Utrera, Michiel van Breugel, Masha T. van der Sande, Maria D.M. Veloso, S. Joseph Wright, Kátia J. Zanini, Jess K. Zimmerman, Mark Westoby

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

This PDF file includes:

- Supplementary text
- Figure S1
- Tables S1 to S3
- SI References

Supplementary Information Text

SI Methods 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 (1), 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 or zero, and sites with a CWA of 0 do not experience seasonal drought stress. Only three perhumid sites had a CWA of 0, so for these three sites CWA can not further discriminate whether they differ in water availability. We prefer to refer to this index as Climatic Water Availability rather than Climatic Water Deficit, as a high index value means high water availability rather than a high deficit.

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 database (2) for the rest of the sites. It should be said that CEC not only includes the base cations Ca^{2+}, Mg^{2+} and K^{+}, but also Na^{+} and $Al3^{+}$, 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. For 19 sites for which no local CEC data were available, CEC was obtained from the SoilGrids database from ISRIC. For the 11 sites for which we had local CEC data, the local and SoilGrids data were indeed strongly positively correlated ($r = 0.86$, $P<0.001$, $N = 11$), indicating that the SoilGrids data rank the sites well in terms of CEC. SoilGrids did not contain data on soil N and P. Across sites, CEC and CWA were not significantly correlated (Pearson $r=0.29$, $P=0.11$, $N=30$).

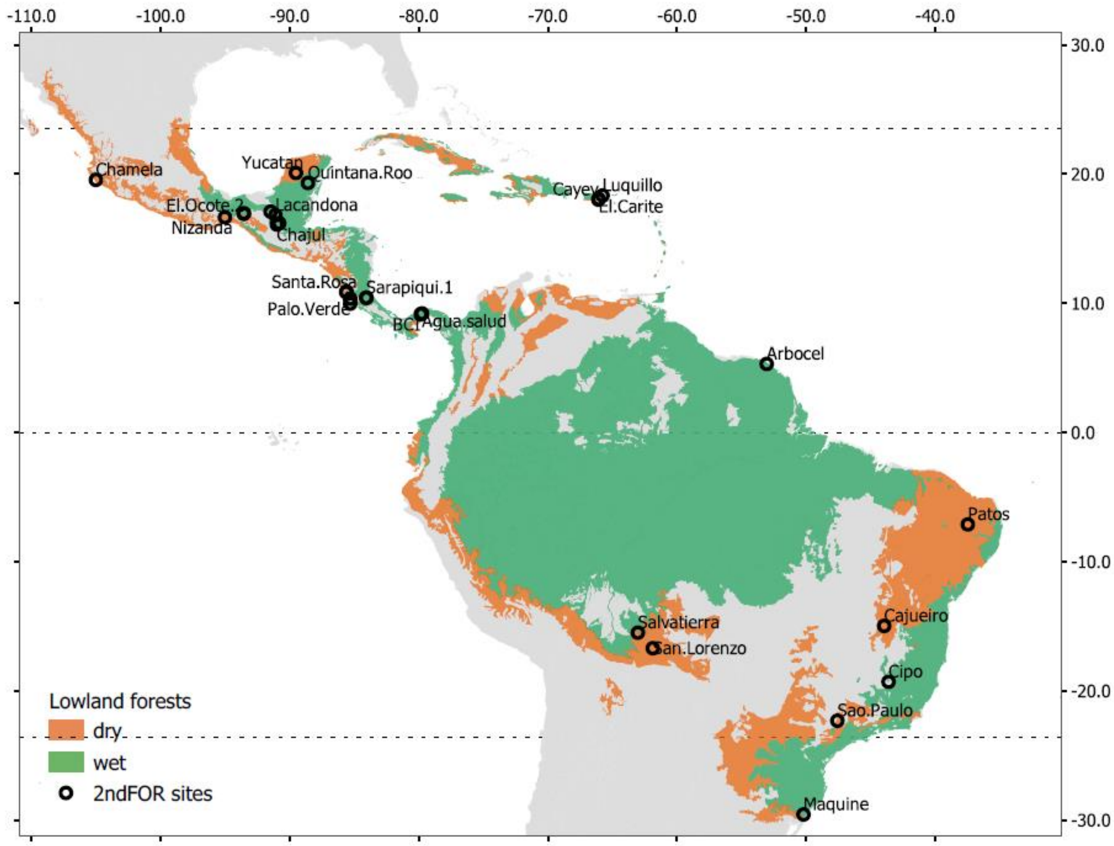

Fig. S1. Map of Neotropical lowland dry forest (brown) and moist and wet forests (green) with the chronosequence study sites (circles).

Table S1. Characteristics of the included Neotropical secondary forest sites (N=30). The name of the chronosequence site, country, forest type (dry=dry deciduous, wet= wet evergreen), 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. A reference (Ref.) is given for each site.

Site	Country	Forest	Lat.	Long.	Rainfall	CWA	CEC	FC	LU	Plots	Age	Ref.
			(°)	(°)	(mm/yr)	(mm/yr)	(cmol/kg)	(%)	(-)	(#)	(yr)	
Salvatierra	Bolivia	Dry	-15.50	-63.03	1200	-635	8.5	98.8	SA	28	(1-36)	1
San Lorenzo	Bolivia	Dry	-16.70	-61.87	1129	-719	9.3	94.5	SA	10	(5-50)	2
Cajueiro	Brazil	Dry	-14.98	-43.95	840	-906	10.5	73.9	PA	6	(14-27)	3
Serra do Cipo	Brazil	Dry	-19.30	-43.61	1519	-334	10.6	27.8	PA	9	(4-50)	4
Maquiné	Brazil	Wet	-29.57	-50.20	1720	0	32.7	94.6	SA	20	(6-45)	5
Patos	Brazil	Dry	-7.12	-37.47	750	-1201	13.2	34.2	SA&PA	15	(20-62)	6
Sao Paulo	Brazil	Dry	-22.32	-47.57	1367	-297	9.4	22.8	PA	18	(11-45)	
Nicoya Peninsula	Costa Rica	Dry	9.97	-85.30	2130	-619	27.4	69.9	SA&PA	53	(5-35)	
Santa Rosa (oak forest)	Costa Rica	Dry	10.89	-85.60	1765	-609	20.1	75.7	PA	22	(5-70)	7
Palo Verde	Costa Rica	Dry	10.36	-85.31	1444	-623	24.5	42.8	PA	19	(7-60)	7
Santa Rosa 1	Costa Rica	Dry	10.85	-85.61	1765	-626	21.7	74.1	PA	40	(6-70)	7
Sarapiquí 1	Costa Rica	Wet	10.43	-84.07	4000	0	22.8	89.1	PA	6	(10-41)	8
Sarapiquí 2	Costa Rica	Wet	10.42	-84.05	4000	0	22.9	88.3	PA	23	(10-42)	9
Arbocel	French Guiana	Wet	5.30	-53.05	3040	-176	12.5	99.9	SA	5	(3.5-28.5)	10
Chajul	Mexico	Wet	16.09	-90.99	3000	-272	23.3	88.6	SA	17	(0-27)	11
Chamela	Mexico	Dry	19.54	-105.00	788	-867	21.0	65.7	PA	8	(3-15)	12
Chinantla	Mexico	Wet	17.75	-96.65	1593	-546	10.1	99.5	SA	26	(5-50)	
El Ocote 1	Mexico	Dry	16.92	-93.54	1500	-563	26.3	91.7	SA	29	(2-75)	13
El Ocote 2	Mexico	Wet	16.97	-93.55	2000	-563	18.6	89.4	SA	63	(3-75)	13
Comunidad Lacandona	Mexico	Wet	16.81	-91.10	2500	-333	31.7	95.6	SA&PA	42	(1-30)	
Marqués de Comillas	Mexico	Wet	16.20	-90.80	2250	-302	26.9	87.2	SA&PA	74	(2-40)	
Nizanda	Mexico	Dry	16.65	-95.01	878	-1016	30.6	60.1	SA	12	(7-60)	14
JM Morelos	Mexico	Dry	19.31	-88.58	1250	-512	64.6	92.3	SA&PA	60	(2-80)	
Kaxil Kiuic	Mexico	Dry	20.08	-89.51	1100	-595	39.9	97.8	SA	274	(3-70)	15
Zona Norte of Selva Lacandona	Mexico	Wet	17.09	-91.47	2750	-243	25.2	85.7	SA&PA	39	(2-52)	
Agua Salud	Panama	Wet	9.21	-79.75	2700	-350	27.5	91.1	SA&PA	45	(2-31)	16
Barro Colorado Nature Monument	Panama	Wet	9.14	-79.85	2600	-328	23.3	54.1	SA&PA	8	(20-100)	17
Cayey	Puerto Rico	Wet	18.02	-66.08	2000	-251	33.8	71.4	PA	15	(10-80)	18
El Carite	Puerto Rico	Wet	18.08	-66.07	1822	-128	32.3	91.1	PA	28	(4-77)	19
Luquillo	Puerto Rico	Wet	18.34	-65.76	2660	-73	27.2	75.6	PA	12	(9-76)	19

1. 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).
2. 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).
3. Fonseca, M.B., O. Silva, J., Falcao, L.A.D . Dupin, M.G.V., Melo, G.A., & Espırito-Santo, M.M, Leaf damage and functional traits along a successional gradient in Brazilian tropical dry forests. Plant ecology 219, 403-415 (2018).
4. Silva, L. F., Souza, R. M., Solar, R. R., & de Siqueira Neves, F. (2017). Ant diversity in Brazilian tropical dry forests across multiple vegetation domains. Environmental Research Letters 12, 035002 (2017).
5. 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).

6. Cabral, G. A. L., de Sá Barreto-Sampaio, E. V. & de Almeida-Cortez, J. S. Estrutura espacial e biomassa da parte aérea em diferentes estádios successionais de caatinga, em Santa Terezinha, Paraíba. Rev. Bras. Geogr. Fís. 6, 566-574 (2013).
7. Powers, J. S., Becknell, J. M., Irving, J. & Perez-Aviles, D. Diversity and structure of regenerating tropical dry forests in Costa Rica: Geographic patterns and environmental drivers. For. Ecol. Manage. 258, 959-970, doi:10.1016/j.foreco.2008.10.036 (2009).
8. Chazdon, R. L., Brenes, A. R. & Alvarado, B. V. Effects of climate and stand age on annual tree dynamics in tropical second-growth rain forests. Ecology 86, 1808-1815, doi:10.1890/04-0572 (2005).
9. Letcher, S. G. & Chazdon, R. L. Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. Biotropica 41, 608-617, doi:10.1111/j.1744-7429.2009.00517.x (2009).
10. Maury-Lechon, G. Régénération forestière en Guyane Française: recrû sur 25 ha de coupe papetière de forêt dense humide (ARBOCEL). Revue Bois et Forêts des Tropiques 197, 3-21 (1982).
11. van Breugel, M., Martínez-Ramos, M. & Bongers, F. Community dynamics during early secondary succession in Mexican tropical rain forests. J. Trop. Ecol. 22, 663-674, doi:10.1017/s0266467406003452 (2006).
12. Mora, F. et al. Testing chronosequences through dynamic approaches: time and site effects on tropical dry forest succession. Biotropica, 38-48 (2015).
13. Orihuela-Belmonte, D. E. et al. Carbon stocks and accumulation rates in tropical secondary forests at the scale of community, landscape and forest type. Agric., Ecosyst. Environ. 171, 72-84, doi:10.1016/j.agee.2013.03.012 (2013).
14. Lebrija-Trejos, E., Bongers, F., Pérez-García, E. A. & Meave, J. A. Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. Biotropica 40, 422-431, doi:10.1111/j.1744-7429.2008.00398.x (2008).
15. Dupuy, J. M. et al. Patterns and correlates of tropical dry forest structure and composition in a highly replicated chronosequence in Yucatan, Mexico. Biotropica 44, 151-162, doi:10.1111/j.1744-7429.2011.00783.x (2012).
16. van Breugel, M. et al. Succession of ephemeral secondary forests and their limited role for the conservation of floristic diversity in a human-modified tropical landscape. PLoS One 8, doi:10.1371/journal.pone.0082433 (2013).
17. 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).
18. 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).
19. Aide, T. M., Zimmerman, J. K., Pascarella, J. B., Rivera, L. & Marcano-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).

Table S2. Predictions how mean trait values and trait variation (trait range) of plant communities will change with successional time for wet and dry forests, and how trait values of early-successional communities at 5 years is affected by variation in resource availability (rainfall, soil fertility) across sites. The functional value of traits are indicated. Traits are related to resource use (i.e., resource acquisition and conservation), water relations, light capture, and drought and heat avoidance. In the upper part of the cell it is indicated whether trait values are predicted to increase (+), remain constant (0) or decrease (-) over time, or with the resource gradient considered. Hypotheses on rainfall and soil fertility are based on closed forest systems only. In the upper part of the cell is in parentheses the observed relationship indicated. The observed changes with successional time are based on the Linear Mixed Model and whether there is a significant interaction between CWA and ln(forest age) or CEC and ln(forest age) (see effect size panels in Fig. 2) and the prediction slopes of the traits versus time (Fig. 1). Differences along environmental gradients are evaluated based on whether in the LMM there is a significant effected of rainfall (CWA) or soil fertility (CEC) (Fig. 2). Zero means a non-significant relationship. ? means an unclear relationship. Differences between observed and predicted trends along the resource gradients can be caused because the predictions were based on old-growth forest, but they were formally tested for secondary forest.

Trait	Abbr	Indicator of	Successional time		Environmental gradient	
			Wet Forest	Dry Forest	Rainfall	Fertility
Wood density	WD	Cavitation resistance, hydraulic capacity, capacitance, biomechanical strength and stability, defense, longevity, resource use	+ (+) Soft wooded fast growing ESS are replaced by dense-wooded persistent LSS.	- (0) Dense wooded cavitation resistant ESS are replaced by soft wooded LSS that can grow in a more benign environment.	- (-) Dense wooded cavitation resistant dry species are replaced by softer wooded wet species that can grow faster in a perhumid environment and compete for light.	- (0) Dense wooded persistent species that conserve nutrients in a resource poor environment are replaced by faster growing softer wooded species that can compete for light in a resource rich environment.
Deciduousness	Dec	Drought avoidance	- (-) Deciduous ESS that are fast-growing and light demanding are replaced by evergreen LSS that are more shade-tolerant because they benefit from a longer photosynthetic revenue stream from longer-lived leaves.	- (-) Deciduous drought-avoiding ESS are replaced by evergreen LSS that are more shade-tolerant because they benefit from a longer photosynthetic revenue stream from longer-lived leaves.	-(-) Deciduous drought-avoiding dry species are replaced by evergreen wet species that can benefit from a longer growing season and a longer photosynthetic revenue stream from leaves.	+ (0) Evergreen species that conserve leaf nutrients in a resource poor environment are replaced by faster growing deciduous species that can easily replace lost leaf nutrients in a resource rich environment.
Compoundness	Comp	Heat & drought avoidance, light capture	-? (0/-) ESS have large compound leaves with long rachae that function as cheap, throw-away branches, which allow species to postpone lateral branching and invest in fast height growth. They are replaced by simple leaved LSS that display their leaf lamina more efficiently and can better compete for light in a shaded environment. Alternatively ESS have large simple leaves to outshade competing neighbours and LSS canopy species with long hydraulic pathlengths and exposed crowns have compound leaves to deal with heat and drought stress.	- (0/-) Compound ESS that can sometimes close leaflets, release latent heat, avoid overheating and reduce transpirational water loss are replaced by simple leaved LSS that can better compete for light in a more benign and shaded environment.	-(-) Compound leaved dry species that can sometimes close leaflets, release latent heat, avoid overheating and reduce transpirational water loss are replaced by simple leaved wet species that can better compete for light in a more benign environment with dense vegetation.	0 (0)
Leaf size	LS	Heat & drought avoidance, light capture	+ (+) Small-leaved ESS with thin boundary layer can better release latent heat in hot early-successional environments. They are replaced by large-leaved LSS that have less self-shading and capture more light in a shaded environment.	+ (0) Small-leaved ESS with thin boundary layer can better release latent heat and reduce transpirational water loss in a hot and dry early-successional environment are replaced by large-leaved LSS that have less self-shading and capture more light in a shaded environment. Small-leaved species have also more leaves and lateral buds, and can resprout more profusely after drought or fire.	+ (-) Small-leaved dry species with thin boundary layer can better release latent heat and reduce transpirational water loss in a hot and dry environment are replaced by large-leaved wet species that have less self-shading and capture more light in a dense and shaded vegetation.	+ (0) Small-leaved coriaceous species that conserve leaf nutrients in a resource poor environment are replaced by faster growing large-leaved species that can better compete for light in a dense vegetation in a resource rich environment.
Specific leaf area	SLA	Biomass efficiency of leaf display, defense, longevity, resource use	- (0) ESS with high SLA and efficient light capture can attain fast growth rate in a high light environment. They are replaced by LSS with low SLA and well-protected leaves that can survive well in the shade.	+ (0) ESS with relatively low SLA have tougher leaves that better can resist drought. They are replaced by LSS with high SLA that can better compete for light in more benign, cooler, and humid closed-forest environments.	-(0) In closed forest systems, drought-avoiding deciduous species with high SLA are replaced by wet evergreen species with low SLA and longer leaf lifespan, that better can persist in the shade.	+ (0) In a nutrient poor environment, species with thick, dense, low SLA leaves can better conserve nutrients. In a productive, nutrient-rich environment they are replaced by species with high SLA that can grow faster and compete better in dense stands.
Leaf nitrogen conc.	LNC	Photosynthetic capacity, resource use	- (0) ESS have large LNC to invest in photosynthetic pigments and Rubisco which increases photosynthetic capacity and growth. LSS are more shade tolerant conservative leaves with low LNC, and hence, low maintenance and respiration costs.	- (-) ESS are dominated by nitrogen fixing Fabaceae (that have high LNC) and by species with high leaf nitrogen concentrations. High nitrogen investment in Rubisco allows to draw down the internal CO_2 concentration, which creates a steeper CO_2 diffusion gradient and requires smaller stomatal aperture, resulting in less water loss. LSS are dominated by more conservative species with low LNC.	-(-) Dry forest species with high leaf nitrogen concentration may draw down the internal CO_2 concentration and use water more efficiently. They are replaced by wet species that are more shade tolerant, and have slower growth rates and nutrient requirements	+ (0) Species with low nutrient requirement (i.e., low leaf nitrogen concentration) can better persist on nutrient poor soils. They are replaced nu species with high leaf nitrogen concentration, photosynthetic capacity, and fast growth, that can better compete in productive forests on nutrient rich soils.
			- (+)	- (-)	- (-)	-?+? (0)

Perc. N fix	NF	Nitrogen fixation potential	N fixers dominate in dry, hot, and sometimes nutrient poor early successional environment because their nitrogen fixing ability gives them an advantage on nutrient depleted soils. As nitrogen fixation is an energetically costly process and requires high light, they are replaced by non-N fixing species later in succession, in a more shaded environment (Gei et al. 2018, Batterman et al.)	N fixers dominate in dry, hot, and sometimes nutrient poor early successional environment because their nitrogen fixing ability gives them an advantage on nutrient depleted soils. As nitrogen fixation is an energetically costly process and requires high light, they are replaced by non-N fixing species later in succession, in a more shaded environment (Gei et al. 2018, Batterman et al.)	N fixers are especially dominant in arid areas because of their nitrogen fixing ability they have high leaf nitrogen concentrations that allow for reduced stomatal conductance.	N fixers fix atmospheric nitrogen and may therefore have an advantage and be dominant on nitrogen poor soils. With an increase in nitrogen fertility N fixers may decrease in abundance because there is no benefit in acquiring additional nitrogen while it is an energetically costly process. Alternatively, relative abundance of N fixers increases with soil phosphorus fertility, as they need phosphorus to form nitrogen fixing nodules.
			+ (+)	+(+)	+?-? (0/+)	+? (0)
Trait range		Niche complementarity, resistance to and recovery after environmental change	During succession, the trait range increases over time due to 1) accumulation of new species with more extreme trait values, 2) more niches, and 3) limiting similarity.	During succession, the trait range increases over time due to 1) accumulation of new species with more extreme trait values, 2) more niches, and 3) limiting similarity.	Wetter forests are taller and more species and niches, and are therefore likely to have a larger trait range. Alternatively, drier forests have a larger trait range because temporal fluctuation in water availability leads to a larger number of trait strategies to deal with drought	Forests on nutrient-rich soils are taller, and may therefore have more forest layers and niches and a larger trait range.

Table S3. Successional responses in abundance-weighted CWM trait properties. For two forest types and 7 functional traits it is shown for how many chronosequences the regression slope of CWM trait values against time is significantly negative (-), positive (+), or significant independent of the direction (sign). The frequency of significance is presented as a percentage of the number of chronosequences evaluated. Dry forests are here defined as forest with precipitation < 1500 mm/yr, moist and wet forest as forests with precipitation >1500 mm/yr). Also the values for dry, moist and wet forests combined (all) are shown. The number of chronosequences evaluated can vary with the trait considered. Grey cells indicate for each trait the most common successional pathway in each forest type.

	Dry				Moist and Wet				All			
Trait	- (%)	+ (%)	sign (%)	N (#)	- (%)	+ (%)	sign (%)	N (#)	- (%)	+ (%)	sign (%)	N (#)
Wood density	18	36	55	11	11	26	37	19	13	30	43	30
Deciduousness	36	9	45	11	33	7	40	15	35	8	42	26
Compoundness	55	9	64	11	6	17	22	18	24	14	38	29
Leaf size	25	13	38	8	0	25	25	8	13	19	31	16
Specific leaf area	36	9	45	11	32	26	58	19	33	20	53	30
Leaf nitrogen conc.	29	14	43	7	16	16	32	19	19	15	35	26
Perc. Fabaceae	45	0	45	11	5	21	26	19	20	13	33	30
All traits combined			49				35				40	

SI References

1. H. ter Steege *et al.*, Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* **443**, 444-447 (2006).
2. T. Hengl *et al.*, SoilGrids250m: global gridded soil information based on Machine Learning. *PLOS ONE* (2017).