Legume abundance along successional and rainfall gradients in Neotropical forests

Maga Gei1, Danaë M. A. Rozendaal2,3,4, Lourens Poorter3, Frans Bongers3, Janet I. Sprent5, Mira D. Garner6, T. Mitchell Aide7, José Luis Andrade8, Patricia Balvanera8,9, Justin M. Becknell10, Pedro H. S. Brancalion11, George A. L. Cabral12, Ricardo Gomes César11, Robin L. Chazdon13,14,15,16, Rebecca J. Cole17, Gabriel Dalla Colletta18, Ben de Jong19, Julie S. Denslow20, Daisy H. Dent21,22, Saara J. DeWalt23, Juan Manuel Dupuy8, Sandra M. Durán24, Mário Marcos do Espírito Santo25, G. Wilson Fernandes26, Yule Roberta Ferreira Nunes25, Bryan Finegan27, Vanessa Granda Moser28, Jefferson S. Hall29, José Luis Hernández-Stefanoni9, André B. Junqueira14,30,31, Deborah Kennard32, Edwin Lebrija-Trejos33, Susan G. Letcher34, Madelon Lohbeck3,35, Erika Marín-Spiotta36, Miguel Martínez-Ramos9, Jorge A. Meave37, Duncan N. L. Menge38, Francisco Mora9, Rodrigo Muñoz37, Robert Muscarella39, Susana Ochoa-Gaona19, Edith Orihuela-Belmonte40, Rebecca Ostertag41, Marielos Peña-Claro9, Eduardo A. Pérez-García37, Daniel Piotto42, Peter B. Reich43,44, Casandra Reyes-García8, Jorge Rodríguez-Velázquez9, I. Eunice Romero-Pérez37, Lucia Sanaphre-Villanueva45, Arturo Sanchez-Azofeifa24, Naomi B. Schwartz38, Arlete Silva de Almeida45, Jacilene S. Almeida-Cortez46, Whendee Silver47, Vanessa de Souza Moreno47, Benjamin W. Sullivan48, Nathan G. Swenson49, Maria Uriarte38, Michiel van Breugel49,50, Hans van der Wal51, Maria das Dores Magalhães Veloso25, Hans F. M. Vester52, Ima Célia Guimarães Vieira45, Jess K. Zimmerman54, Jennifer S. Powers1,21,*

The nutrient demands of regrowing tropical forests are partly satisfied by nitrogen-fixing legume trees, but our understanding of the abundance of those species is biased towards wet tropical regions. Here we show how the abundance of Leguminosae is affected by both recovery from disturbance and large-scale rainfall gradients through a synthesis of forest inventory plots from a network of 42 Neotropical forest chronosequences. During the first three decades of natural forest regeneration, legume basal area is twice as high in dry compared with wet secondary forests. The tremendous ecological success of legumes in recently disturbed, water-limited forests is likely to be related to both their reduced leaflet size and ability to fix N2, which together enhance legume drought tolerance and water-use efficiency. Earth system models should incorporate these large-scale successional and climatic patterns of legume dominance to provide more accurate estimates of the maximum potential for natural nitrogen fixation across tropical forests.

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

More than half of the tropical forest area worldwide is made up of secondary forests, which regrow after canopy removal due to natural or anthropogenic disturbances1. Secondary forests are important globally because they supply firewood and timber, regulate the hydrological cycle, benefit biodiversity, and provide carbon storage as above- and belowground biomass2,3, but their growth can be constrained by nitrogen (N) availability4. Symbiotic fixation is thought to provide the largest natural input of N to tropical forests5, and part of the N demand of regrowing tropical forests is satisfied by legume trees (Leguminosae) that have the capacity to fix atmospheric N2 through interactions with rhizobia bacteria6. The abundance of N-fixing legumes is not always strictly proportional to the rates of rhizobial activity, as some legumes downregulate fixation when the costs outweigh the benefits7. Nevertheless, legume abundance as represented by total basal area may provide a good estimate of the maximum potential N fixation in an ecosystem, with the advantage that this metric can be extracted from standard forest inventory surveys. Spatially explicit estimates of legume abundance through time could help to reduce uncertainties in Earth system models that include coupled carbon and N biogeochemistry6, but assessments of legume abundance have not yet been synthesized across the successional and climatic gradients that characterize tropical forests.

The abundance of N-fixing legumes relative to non-fixing trees has been closely examined in undisturbed tropical forests5,10 and savannahs1,12. However, studies of legume abundance in regenerating forests are rare and have been restricted to the wet tropics5,13–16, so are likely not representative of tropical
secondary succession globally. Due to environmental filtering, systematic variations in legume abundance should occur along both rainfall and successional gradients. Wet and (seasonally) dry tropical forests experience substantial differences in water and nutrient availability, which in turn may influence the competitive success of legumes in both biomes. N-fixing legumes should have particular advantages in drier conditions; they can access N when mineralization rates decline due to low soil moisture, and use their high foliar N content to maintain high growth rates and use water more efficiently relative to non-fixers. Because young tropical forests are often N limited, trees that are able to fix N may be favored during the earliest stages of forest regrowth after disturbance. Some studies indeed show that legumes are more abundant in young compared with old wet Neotropical forests, but others report successional trends in the opposite direction, with the relative abundance of these species instead increasing with stand age. Characterizing these macroecological patterns of legume abundance across climate space and through successional time, along with variations in their functional traits, is crucial to determine whether our current knowledge of legume distributions can be generalized across the tropics and to achieve a more complete understanding of the role of this exceptionally diverse plant family within secondary Neotropical forest ecosystems.

Here we evaluate how the abundance of legumes (as measured by absolute and relative basal area) varies through secondary succession using data from 42 chronosequence sites (Supplementary Fig. 1 and Supplementary Table 1) that span a large gradient in mean annual rainfall (from 750 to 4,000 mm yr\(^{-1}\)) and explain legume success based on N-fixation potential and two functional traits related to drought tolerance (leaf size and leaf type). We primarily focused our climate analysis on mean annual rainfall (‘rainfall’ hereafter), but also tested the effect of rainfall seasonality (the rainfall coefficient of variation from WorldClim) and climatic water deficit (CWD; which tracks water losses during the months where evapotranspiration exceeds rainfall) as alternative predictors. Because leaf habit or leafing phenology is a better indicator of seasonal moisture stress than total annual precipitation, we used this parameter to classify study sites as ‘dry’ forests if the vegetation was mostly drought deciduous (sensu ref. 10), or as ‘wet’ forests in all other instances (that is, mostly evergreen; Supplementary Table 1). As such, the terms ‘dry’ and ‘wet’ forests refer to two ecologically distinct tropical biomes with floristic compositions that differ in phylogenetic, biogeographic, functional and community ecological patterns (see refs 26–28). Therefore, although rainfall is used as the main (continuous) climatic variable to model legume abundance, we did not use this variable to classify sites as either dry or wet forests.

To understand the specific factors that enable legumes to thrive in particular tropical environments, we also investigated how the abundance of these trees related to their capacity to fix N\(_2\) and a pair of crucial leaf traits that reflect drought tolerance. For each of the 398 legume species present at our sites, we assessed potential to fix N\(_2\) based on positive nodulation reports and expert knowledge (see Methods). Both of the leaf traits we examined—leaf size and leaf type—reflect adaptations to limited water availability (Supplementary Tables 2 and 3). Smaller leaves have reduced boundary-layer resistance, which enables them to dissipate heat through conductive or convective radiation. Leaf type is considered to be associated with drought severity and seasonality because plants with compound leaves (having either pinnate or bipinnate divisions) are able to shed individual leaflets (rather than whole leaves) when faced with severe moisture stress. Our analysis demonstrates that the abundance of legumes indeed varies substantially and systematically across Neotropical forests, and although the ecological success (that is, high relative abundance) of these species during the very earliest stages of secondary succession is partly due to N fixation, other traits related to drought tolerance and water-use efficiency likely also offer competitive advantages.

**Results**

During the first three decades of forest regeneration, the total abundance of all legume trees as measured by their absolute basal area doubled in both dry and wet Neotropical forests (from 3 m\(^2\) ha\(^{-1}\) in 2- to 10-year-old forests to 6 m\(^2\) ha\(^{-1}\) in 21- to 30-year-old forests; Fig. 1a) as legume biomass gradually built up through succession. Here we define legume relative abundance (RA) as the basal area of Leguminosae trees divided by the total basal area of all trees in each plot and interpret it as a measure of ecological success that reflects legume performance relative to non-legume species. Overall, although absolute legume abundance increased with successional change in legume RA was substantial (Fig. 1b and Table 1). The fixed effects (stand age, rainfall and their interaction) accounted for 17% (marginal \(R^2\) of the total variance explained by our model of legume RA, while 45% was due to site-to-site variation (conditional \(R^2 = 62\%\), Table 1). In the majority of dry forests, legume relative basal area decreased through time, which indicates legumes were initially a dominant component of early successional communities and then subsequently declined in abundance as other tree species became more common. By contrast, legume RA in the wet forest chronosequences typically began lower but remained constant through succession. The RA of legumes was much higher at the dry end of the rainfall gradient (rainfall effect, Table 1) and this difference was most evident during the first three decades of succession (0 to 30 years since abandonment, Fig. 1b). For example, in the youngest dry forests (2 to 10 years old), legumes on average made up more than one-third of the basal area of all trees (37%, compared with 18% in wet forests; Fig. 2a), and in some plots in Mexico (Chamela, Nizanda, Yucatán, Quintana Roo) and Brazil (Cajueiro, Mata Seca, Patos), relative abundance approached 100% (98% and greater). Although fewer chronosequences extend beyond three decades, in later successional stages (30 to 100 years old; Fig. 2d–f) legume abundance was still high in dry forests. The greater overall abundance of legumes in dry forests (compared with wet forests) may be partly a consequence of their higher initial recruitment, which is suggested by the high RA of small diameter legume trees during the first two decades of forest regeneration (Supplementary Fig. 2).

Mean annual rainfall was a strong determinant of legume RA over the entire Neotropical network (Table 1). Alternative models of legume RA that used rainfall seasonality and CWD as the main climatic predictor variable also explained a significant amount of variation in our data (Supplementary Figs. 3 and 4), but the best-supported model was based on mean annual rainfall (\(R^2 = 0.62\), versus \(R^2 = 0.49\) and \(R^2 = 0.48\) for seasonality and CWD respectively; Supplementary Table 4). The magnitude of legume RA and its relationship with rainfall differed strongly between dry and wet secondary forests, most prominently during the first three decades of secondary succession (Fig. 2). For the 26 chronosequences from wet forests, mean legume RA was approximately 15% (±16% s.d.), within the range reported previously for individual sites\(^{31–34}\), and did not vary with rainfall. By contrast, legume RA in the 16 dry forest sites was much higher (41% ±27% s.d.) and was strongly and inversely related to annual rainfall. The transition between these two patterns occurred at approximately 1,500 mm yr\(^{-1}\) (Fig. 2).

The functional traits of legumes also varied across the large-scale environmental gradients in our dataset. The spatial and successional patterns of legume abundance were largely driven by N-fixing species (Fig. 1c). For nearly two-fifths of the plots in our...
network, fixers were the only type of legumes present. At the plot level, the median percentage of total legume basal area comprised by fixers was 93.5%. The proportion of N-fixers basal area to total legume basal area did not vary with rainfall or stand age, and the RA of non-fixing legumes was much lower in both dry and wet secondary forest sites (Supplementary Fig. 5). In contrast to the N fixers, the RA of non-fixing legumes remained constant throughout succession (Supplementary Table 5). When we stratified our analyses by leaf type, it was evident that the extremely high legume RA in young dry forests was largely due to the prevalence of species with bipinnate leaves (Figs. 1d and 3 and Table 1), which have significantly smaller leaflets than legumes with other leaf types (Supplementary Table 3).

**Discussion**

Based on our survey of secondary forests across the Neotropics, we conclude the ecological success of legume trees is markedly higher in seasonally dry forests than in wet forests, especially during early stages of secondary succession. These findings agree with analyses of other large datasets from Africa and the Americas that found higher abundance of N-fixing legumes in arid conditions\textsuperscript{12,36}, although those studies were unable to examine the effect of succession. We identified a threshold in mean annual rainfall at approximately 1,500 mm yr\textsuperscript{-1}—nearly identical to the threshold observed in forest inventories from North America\textsuperscript{37}. Below this level, legume abundance was strongly and negatively correlated to water availability. Because this relationship was driven mainly by species that are both able to fix $N_2$ and have bipinnate leaves (Fig. 1), we suggest that the exceptional abundance of tropical legumes towards the drier end of the rainfall spectrum during secondary succession is the combined product of (1) small leaflet size, which allows for leaf temperature regulation and water conservation, and (2) N fixation, which contributes to photosynthetic acclimation, enhances water-use efficiency, and may satisfy the demand for nitrogen after the post-dry season leaf flush.

The availability of nitrogen is known to constrain biomass recovery in secondary Neotropical forests\textsuperscript{4,37} because it is often lost following disturbance, either through harvesting of the canopy or crops, volatilization during burning or leaching\textsuperscript{37}. Our finding that Neotropical legumes are proportionately more abundant in early succession throughout the Neotropics could be due to the high demand for N in recently disturbed forests\textsuperscript{4,37}. Under those conditions,
circumstances, fixation would allow legumes to overcome N limitation more easily than their competitors, although the degree to which initial secondary forest regrowth is limited by N availability is highly variable and influenced by local disturbance history and prior land use.\textsuperscript{36,39}

Besides providing legumes with an advantage in young secondary forests in general, N fixation could offer additional benefits to plants growing under seasonally dry conditions. Forests that experience a pronounced annual dry season are affected by recurrent seasonal declines in soil moisture and, due to the associated hysteresis in transpiration, plants are not able to access nutrients in the soil solution, including N (ref. \textsuperscript{40}). Because many dry forest trees lose their leaves each year and are required to grow an entirely new canopy, being able to obtain N through symbiosis could allow legumes to more quickly rebuild their leaf canopy at the end of the dry season compared with non-fixers\textsuperscript{31,32}, which may need to wait until soil water is sufficiently recharged to acquire mineral N (ref. \textsuperscript{40}). Towards the high end of the Neotropical rainfall gradient, forests do not experience a strong seasonal moisture deficit, and as a result, are not usually faced with the regular nutrient scarcity that consistently affects dry forests. In addition to its role in satisfying seasonal nitrogen demands, fixation should also help legumes to further acclimate to hot, dry conditions\textsuperscript{33,34}. By investing part of their fixed N into the production of photosynthetic enzymes, plants are able to draw down their internal concentrations of carbon dioxide, thereby creating steeper diffusion gradients in their leaves\textsuperscript{35}. This adjustment allows photosynthesis to occur at lower stomatal conductance and reduced transpiration. These two advantages offered by fixation could account for the extremely high abundance of legumes early in dry forest succession, when air and soil temperatures are high, and soil water potential is at its lowest\textsuperscript{42}, as well as their continued dominance in this ecosystem over evolutionary timescales\textsuperscript{43,44}.

But N fixation is clearly not the only trait that is advantageous to legumes in Neotropical dry forests. Because this biomass is dominated by legumes that have bipinnate leaves particularly during the early stages of succession, it is clear that these species also benefit from their conservative use of water. Reduced leaf size (and the accompanying thinner boundary layer) offers a significant adaptive value in hot, dry environments\textsuperscript{45} by enhancing heat dissipation and regulating leaf temperature more efficiently\textsuperscript{46,47}. Many legumes also have the ability to adjust the angle of their laminae to regulate diurnal incident solar radiation\textsuperscript{48}, which further reduces heat loading. Hence, having small leaflets could enable legumes at dry sites to benefit from high irradiance while preventing excessively high leaf temperatures. The bipinnate leaf type is confined exclusively to one subclade of legumes, the Caesalpinioideae\textsuperscript{45}, and half of all species found in our dataset (mainly those that fix N) were formerly classified as Mimosoideae\textsuperscript{46}.

### Table 1 | Effects of stand age and mean annual rainfall on legume abundance in Neotropical secondary forests

| Dependent variable | Parameter | Standardized coefficients | F value | $R^2$ (m) | $R^2$ (c) |
|--------------------|-----------|---------------------------|---------|-----------|-----------|
| (1) Absolute basal area—all legumes | Stand age | 0.29* | 4.21 | 0.08 | 0.33 |
| | Rainfall | -0.03 | 0.04 | 0.08 | 0.33 |
| | Stand age x Rainfall | -0.04 | 0.04 | 0.08 | 0.33 |
| | Stand age | **** | **** | 0.08 | 0.33 |
| (2) Relative basal area—all legumes | Stand age | -0.61*** | 21.15 | 0.17 | 0.62 |
| | Rainfall | -0.95*** | 16.23 | 0.17 | 0.62 |
| | Stand age x Rainfall | 0.62** | 12.01 | 0.17 | 0.63 |
| | Stand age | **** | **** | 0.17 | 0.63 |
| (3) Relative basal area—N-fixing legumes | Stand age | -0.83**** | 22.09 | 0.17 | 0.63 |
| | Rainfall | -1.11*** | 15.05 | 0.17 | 0.63 |
| | Stand age x Rainfall | 0.88*** | 13.72 | 0.17 | 0.63 |
| | Stand age | **** | **** | 0.17 | 0.63 |
| (4) Relative basal area—bipinnate legumes | Stand age | -0.42** | 8.39 | 0.12 | 0.73 |
| | Rainfall | -0.75* | 6.83 | 0.12 | 0.73 |
| | Stand age x Rainfall | 0.40 | 4.09 | 0.12 | 0.73 |
| | Stand age | **** | **** | 0.12 | 0.73 |
| (5) Relative basal area—pinnate legumes | Stand age | -0.36** | 9.31 | 0.03 | 0.15 |
| | Rainfall | -0.45* | 6.74 | 0.03 | 0.15 |
| | Stand age x Rainfall | 0.41* | 6.08 | 0.03 | 0.15 |
| | Stand age | **** | **** | 0.03 | 0.15 |

Across the Neotropics, the abundance of legumes in secondary forests can be predicted by rainfall, stand age and their interaction. Linear mixed-effects models were run for absolute and relative basal area of all legume species ((1) and (2)), and for relative basal area of N-fixing and bipinnate legumes separately ((3) and (4)). Stand age, mean annual rainfall (‘rainfall’) and their interaction were included as fixed effects. Random site intercepts account for between-site variation in initial legume basal area, and random slopes for the variation of the effect of stand age on legume basal area among sites (\(P < 0.05; \cdot \cdot \cdot P < 0.01; \cdot \cdot \cdot \cdot P < 0.001; \cdot \cdot \cdot \cdot \cdot \cdot P < 0.0001\)). The standardized regression coefficients compare the effect of the independent variables on the dependent variable. Values of marginal ($R^2$ (m)) and conditional ($R^2$ (c)) $R^2$ indicate the proportion of the variance explained by the fixed effects of the model, and the fit of the whole model with fixed and random effects, respectively. For all models, N = 42 chronosequence sites.
Forests 31–40 yr

4,000

Forests 2–10 yr

N-fixing legumes

1,000 2,000 3,000 4,000

Fig. 2 | Legume relative basal area across a rainfall gradient in the Neotropics. For forests in the wet Neotropics, the RA of legume trees is not influenced by variations in mean annual rainfall. However, below a threshold at approximately 1,500 mm yr\(^{-1}\), legume RA increases as total rainfall diminishes. Results are stratified by stand age: a, 2- to 10-year-old forests; b, 11- to 20-year-old forests; c, 21- to 30-year-old forests; d, 31- to 40-year-old forests; e, 41- to 60-year-old forests; f, 61- to 100-year-old forests. Results of a segmented linear fit are shown in each panel (**P < 0.01; ****P < 0.0001); N indicates the number of chronosequence sites with plots in each age category. Grey lines represent fitted values obtained using segmented regression models. Each circle represents site-level legume relative basal area averaged for each stand age category. Dry forest sites (with dominant deciduous vegetation) are indicated in orange, and wet forests in blue. Some dry forest sites receive higher average annual rainfall than some wet forest sites, but these sites are classified as ‘dry’ or ‘wet’ because of their functional composition (evergreen or deciduousness), not their mean climatology.

Fig. 3 | Relative basal area of legumes for 5- and 20-year-old forests as a function of mean annual rainfall. a-c. The exceptional ecological success of legumes in recently disturbed, water-limited forests is mainly due to species that (1) are able to fix nitrogen and (2) have bipinnate leaves. Fitted values were obtained using a linear mixed-effects model, with stand age and rainfall as fixed effects and site as random effect (see (3)–(5) in Table 1 for full model results). Relative basal area and stand age were arcsin and log-transformed, respectively, before analysis. Models were computed separately for N-fixing legume species (a), legumes with bipinnate leaves (b) and legumes with pinnate leaves (c).

in the secondary forests of the dry Neotropics. This strong phylogenetic signal highlights the importance of drought tolerance traits as an adaptation to seasonal dry forests\(^{1,47}\), and demonstrates that leaf traits enhancing moisture conservation are equally as important as the potential to fix N\(_2\) when explaining patterns of legume abundance. N-fixing legumes that have small bipinnate leaves thus hold a double advantage because those traits combine to minimize water loss during C acquisition and lead to increased water-use efficiency.

Across the Neotropics, a substantial amount of the variation in the relative abundance of legumes in secondary forests (17%) can be predicted by rainfall, stand age and their interaction. The strong negative relationship between legume RA and water availability was not sensitive to our choice of climate variable (either mean annual rainfall, rainfall seasonality or CWD; Fig. 2 and Supplementary Figs. 3 and 4), which suggests that legumes have a competitive advantage in dry climates that are characterized by recurrent seasonal droughts and strong water deficits during the growing season. The climate transition near 1,500 mm yr\(^{-1}\), where the relationship between legume RA and rainfall switched from strongly inverse to flat, coincides with a known cross-over point in woody regeneration\(^{48}\). In regenerating dry forests, the canopy of established plants serves to moderate the harsh microclimatic conditions, thus facilitating the establishment of seedlings\(^{49}\), while in some wet forests, N-fixing legumes act to inhibit the growth of neighbouring trees.
during secondary succession. A large fraction (45%) of the variance in legume abundance was associated with site identity (represented in our model as a random factor), which could be related to site-specific factors such as resource limitation (phosphorus, molybdenum, iron) or biotic interactions (dispersal, herbivory) that influence fixation in individual forest stands. More research is needed to determine how and to what extent these factors influence legume dominance at finer spatial scales.

N-fixing legume species attain their greatest levels of ecological success in Neotropical dry forests, where the benefits of fixation and co-occurring traits related to water conservation outweigh their costs throughout decades of succession. It is thus clear that insights about legumes derived from studies conducted exclusively in wet forests (for example, ref. 34) cannot be extrapolated across all Neotropical forests, and in particular are not valid for dry forests. As an alternative, future efforts to model the tropical N cycle must account for the strong heterogeneity exhibited by this hyperdiverse family of plants. Incorporating these large-scale abundance trends into Earth system models should allow for more accurate estimates of the potential for symbiotic N fixation across tropical forests. Our study also demonstrates that, even though the potential to fix N2 through symbiosis is a crucial element of their success, it is not the only trait that accounts for the exceptionally high abundance of legumes in Neotropical forests. Leaf traits related to drought tolerance and water-use efficiency are also key adaptive features of dry forest legumes. In conclusion, our results provide a deeper mechanistic explanation for the abundance of Neotropical Leguminosae trees, which should be increasingly relevant to natural forest regeneration and ecosystem functioning as global temperatures warm and dry conditions become more widespread in the tropics.

Methods

Chronosequence database. We extracted plot-scale legume abundance (m² ha⁻¹), basal area from 42 previously published chronosequence studies (2ndFOR network; Supplementary Fig. 1 and Supplementary Table 1). Our dataset includes lowland forests between 2 and 100 years old. Plot size varied from 0.008 to 1.3 ha, and across all 1,207 plots, mean plot area was 912 m². The median number of plots network; Supplementary Fig. 1 and Supplementary Table 1). Our dataset includes network, mean annual rainfall varied from 750 to 4,000 mm yr⁻¹, an exception of sites in Costa Rica (Santa Rosa and Palo Verde) and Puerto Rico (Cayey) ranching, shifting cultivation or a combination of the two. In each plot, all woody trees, shrubs and palms >5 cm in diameter were measured and identified, with the exception of sites in Costa Rica (Santa Rosa and Palo Verde) and Puerto Rico (Cayey) for which a minimum diameter at breast height of 10 cm was used. Across the network, annual rainfall varied from 750 to 4,000 mm yr⁻¹. Based on local site knowledge, study sites were classified as ‘dry’ forests when the vegetation is mostly drought deciduous, or ‘wet’ forests (mostly evergreen) in all other instances (sensu ref. 35; Supplementary Table 1). Because some tropical wet forests experience annual rainfall averages that overlap with the range exhibited by dry forests (particularly around 1,500 mm yr⁻¹), for legume abundance at different stand age categories (2 to 10, 11 to 20, 21 to 30, 31 to 40, 41 to 60 and 60 to 100 years of forest age), we performed a piecewise linear regression using the Segmented package (v. 0.5.1.4). Lastly, to understand the successional change in legume basal area of trees of different size classes (<10 cm, 10 to 20 cm, 20 to 30 cm and >30 cm), we performed a multiple regression on arsin transformed legume RA with stand age and forest type (dry or wet) as covariates. All analyses were performed in R version 3.2.2 (ref. 36).

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

Data availability. Plot-level legume basal area data from the 42 Neotropical forest sites are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.3p1k5d2.

Received: 7 September 2017; Accepted: 18 April 2018; Published online: 28 May 2018

References

1. Global Forest Resources Assessment 2015: How Are the World’s Forests Changing? (FAO, Rome, 2015).
2. Pan, Y. et al. A large and persistent carbon sink in the world’s forests. Science 333, 988–993 (2011).
3. Chazdon, R. L. et al. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. Sci. Adv. 2, e1501639 (2017).
4. Davidson, E. A. et al. Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. Ecol. Appl. 14, S50–S163 (2004).
5. Cleveland, C. C. et al. Patterns of new versus recycled primary production in the terrestrial biosphere. Proc. Natl Acad. Sci. USA 110, 12733–12737 (2013).
6. Battenman, S. A. et al. Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. Nature 502, 224–227 (2013).
7. Barrow, A. R., Purvis, W. D. & O. Facultative nitrogen fixation by canopies in a lowland tropical forest. Oecologia 165, 511–520 (2010).
8. Wieder, W. R., Cleveland, C. C., Lawrence, D. M. & Bonan, G. B. Effects of model structural uncertainty on carbon cycle projections: biological nitrogen fixation as a case study. Environ. Res. Lett. 10, 1–9 (2015).
9. Small, R. H. et al. Continental-scale dryness affects tree composition and function across Amazonia. Nature 443, 444–447 (2006).
10. DRYFLOR Plant diversity patterns in neotropical dry forests and their conservation implications. Science 353, 1383–1387 (2016).
Author contributions
M.G. and J.S.P. conceived the idea, all co-authors coordinated the data compilations, M.G. and M.D.G. collected leaf traits data, M.G. analysed the data, D.M.A.R. contributed to the analytical approach, M.G. and J.S.P. wrote the paper, and all co-authors collected field data, discussed the results, gave suggestions for 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/s41559-018-0559-6.
Reprints and permissions information is available at www.nature.com/reprints.
Correspondence and requests for materials should be addressed to J.S.P.
Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN, USA. *Department of Biology, University of Regina, Regina, Saskatchewan, Canada. 2Forest Ecology and Forest Management Group, Wageningen University and Research, Wageningen, The Netherlands. 3Laboratory of Geo-Information Science and Remote Sensing, Wageningen University and Research, Wageningen, The Netherlands. 4Royal Botanic Gardens Edinburgh, Edinburgh, UK. 5College of Biological Sciences, University of Minnesota, St. Paul, MN, USA. 6Department of Biology, University of Puerto Rico-Rio Piedras, San Juan, Puerto Rico. 7Centro de Investigación Científica de Yucatán, Unidad de Recursos Naturales, Mérida, Yucatán, Mexico. 8Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Mexico. 9Environmental Studies Program, Colby College, Waterville, ME, USA. 10Department of Forest Sciences, Luiz de Queiroz College of Agriculture, University of São Paulo, Piracicaba, Brazil. 11Departamento de Genética, Universidad Federal de Pernambuco, Recife, Brazil. 12Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA. 13International Institute for Tropical Agriculture, Si Río de Janeiro, Brazil. 14Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA. 15Tropical Forests and People Research Centre, University of the Sunshine Coast, Sippy Downs, Queensland, Australia. 16Department of Natural Resources and Environmental Management, University of Hawaii at Manoa, Honolulu, HI, USA. 17Programa de Pós-graduação em Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, Brazil. 18Department of Sustainability Science, El Colegio de la Frontera Sur, Campeche, Mexico. 19Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA, USA. 20Smithsonian Tropical Research Institute, Panamá, Republic of Panama. 21Biological and Environmental Sciences, University of Stirling, Stirling, UK. 22Department of Biological Sciences, Clemson University, Clemson, SC, USA. 23Earth and Atmospheric Sciences Department, University of Alberta, Edmonton, Alberta, Canada. 24Department of Biología Geral, Universidade Estadual de Montes Claros, Montes Claros, Brazil. 25Ecologia Evolutiva y Biodiversidad, ICB, Universidad Federal de Minas Gerais, Belo Horizonte, Brazil. 26Forests, Biodiversity and Climate Change Programme, Tropical Agricultural Centre for Research and Higher Education (CATIE), Turrialba, Costa Rica. 27Graduate School, Tropical Agricultural Centre for Research and Higher Education (CATIE), Turrialba, Costa Rica. 28ForestGEO, Smithsonian Tropical Research Institute, Panamá, Republic of Panama. 29Department of Soil Quality, Wageningen University, Wageningen, The Netherlands. 30Centre for Conservation and Sustainability Science (CSRio), Department of Geography and the Environment, Pontifical Catholic University of Rio de Janeiro, Rio de Janeiro, Brazil. 31Department of Biological and Environment, Faculty of Natural Sciences, University of Haifa-Oranim, Tivon, Israel. 32Department of Plant Biology, College of the Atlantic, Bar Harbor, ME, USA. 33World Agroforestry Centre (ICRAF), Nairobi, Kenya. 34Department of Geography, University of Wisconsin–Madison, Madison, WI, USA. 35Department of Ecology and Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México, Mexico. 36Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY, USA. 37Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Aarhus, Denmark. 38National Institute of Ecology and Climate Change, Delegación Coyoacán, Mexico. 39Department of Biology, University of Hawaii at Hilo, Hilo, HI, USA. 40Centro de Formação em Ciências Agroflorestares, Universidade Federal do Sul da Bahia, Itabuna, Brazil. 41Department of Forest Resources, University of Minnesota, St. Paul, MN, USA. 42Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia. 43Museu Paraense Emilio Goeldi, Belém, Brazil. 44Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Brazil. 45Department of Environmental Science, Policy and Management, University of California, Berkeley, CA, USA. 46Department of Natural Resources and Environmental Science, University of Nevada, Reno, NV, USA. 47Department of Biology, College Park, MD, USA. 48Department of Biology, University of Maryland, College Park, MD, USA. 49Department of Biology, University of California, Berkeley, CA, USA. 50Department of Soil Resource and Environmental Science, University of Nevada, Reno, NV, USA. 51Department of Biology, University of Maryland, College Park, MD, USA. 52Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, Amsterdam, The Netherlands. 53Department of Environmental Sciences, University of Puerto Rico–Río Piedras, San Juan, Puerto Rico. 54Department of Plant Biology and Microbial Biology, University of Minnesota, St. Paul, MN, USA. *e-mail: powers@umn.edu
Life Sciences Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form is intended for publication with all accepted life science papers and provides structure for consistency and transparency in reporting. Every life science submission will use this form; some list items might not apply to an individual manuscript, but all fields must be completed for clarity.

For further information on the points included in this form, see Reporting Life Sciences Research. For further information on Nature Research policies, including our data availability policy, see Authors & Referees and the Editorial Policy Checklist.

Experimental design

1. Sample size
   - Describe how sample size was determined.
   - Sample sizes were determined by the number of plots that individual research teams contributed to the pooled dataset.

2. Data exclusions
   - Describe any data exclusions.
   - The only data exclusions were sites for which the minimum threshold tree diameters were insufficient.

3. Replication
   - Describe whether the experimental findings were reliably reproduced.
   - Our study relied on pooling data from many individual chronosequence studies. As such, we can consider each chronosequence a replicated site.

4. Randomization
   - Describe how samples/organisms/participants were allocated into experimental groups.
   - This does not apply to our dataset.

5. Blinding
   - Describe whether the investigators were blinded to group allocation during data collection and/or analysis.
   - Not applicable.
   - Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters
   - For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).
   - n/a Confirmed

     □ [X] The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
     □ □ A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
     □ □ A statement indicating how many times each experiment was replicated
     □ [X] The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
     □ □ A description of any assumptions or corrections, such as an adjustment for multiple comparisons
     □ □ The test results (e.g. P values) given as exact values whenever possible and with confidence intervals noted
     □ [X] A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
     □ □ Clearly defined error bars

See the web collection on statistics for biologists for further resources and guidance.
7. Software

Describe the software used to analyze the data in this study.

All statistical analyses were performed in R.

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). Nature Methods guidance for providing algorithms and software for publication provides further information on this topic.

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

Not applicable.

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

Not applicable.

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

b. Describe the method of cell line authentication used.

c. Report whether the cell lines were tested for mycoplasma contamination.

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.

Not applicable.

Provide a rationale for the use of commonly misidentified cell lines OR state that no commonly misidentified cell lines were used.

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.

None used.

Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

None used.