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Legume Abundance Along Successional And Rainfall Gradients In Neotropical Forests

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The nutrient demands of regrowing tropical forests are partly satisfied by nitrogen (N)-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 to wet secondary forests. The tremendous ecological success of legumes in recently disturbed, water-limited forests is likely related to both their reduced leaflet size and ability to fix N_2, 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 N fixation across tropical forests.

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 disturbances[1]. Second-growth forests are important globally because they supply firewood and timber, regulate the hydrological cycle, benefit biodiversity, and provide carbon storage as above- and below-ground biomass[2,3], but their growth can be constrained by nitrogen (N) availability[4]. Symbiotic fixation is thought to provide the largest natural input of N to tropical forests[5], and part of the N demand of regrowing tropical forests is satisfied by legume trees (Leguminosae) that have the capacity to fix atmospheric N_2 through interactions with rhizobia bacteria[6]. The abundance of N-fixing legumes is not always strictly proportional to the rates of rhizobial activity, as some legumes down-regulate fixation when the costs outweigh the benefits[7]. 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 biogeochemistry[8], 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 forests[9,10] and savannas[11,12]. But studies of legume abundance in regenerating forests are rare and have been restricted to the wet tropics[6,13–16], so are likely not representative of tropical secondary succession globally. Due to environmental filtering[17], systematic variations in legume abundance should occur along both rainfall and successional gradients. Wet and (seasonally) dry tropical forests[10,18] experience substantial differences in water and nutrient availability, which in turn may influence the competitive success of legumes in both biomes[19]. Nitrogen-fixing legumes should possess particular advantages in drier conditions; they can access N when mineralization rates decline due to low soil moisture[20], and use their high foliar N content to maintain high growth rates and use water more efficiently relative to non-fixers[21]. Because young tropical forests are often N-limited[4], trees that are able to fix may be favored during the earliest stages of forest regrowth after disturbance[22,23]. Some studies indeed show that legumes are more abundant in young compared to old wet Neotropical forests[6,14], but others report successional trends in the opposite direction, with the relative abundance of these species instead increasing with stand age[13,15]. Characterizing these macro-ecological 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[24] (Supplementary Fig. 1; Supplementary Table 1) that span a large gradient in mean annual rainfall (from 750 to 4000 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[25] (the rainfall coefficient of variation from WorldClim) and climatic water deficit[26] ("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[27], we used this parameter to classify study sites as "dry" forests if the vegetation was mostly drought-deciduous (sensu *10*), or as "wet" forests in all other instances (i.e., 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 *28*, *29*, *30*). 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 nitrogen 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[31] (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[32–34]. 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[35]. Our analysis demonstrates that the abundance of legumes indeed varies substantially and systematically across Neotropical forests, and although the ecological success (i.e., 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 succession, the RA of legumes declined with stand age in drier forests and declined with rainfall in younger forests (Table 1, Fig. 1b). Despite these trends, site-to-site variation in successional change in legume RA was substantial (Fig. 1b, 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 yr), legumes on average made up more than one third of the basal area of all trees (37%, compared to 18% in wet forests; Fig. 2a), and in some plots in Mexico (Chamela, Nizanda, Yucatán, and 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; Fig. 2d-f) legume abundance was still high in dry forests. The greater overall abundance of legumes in dry forests (compared to 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 Fig. 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 18% (± 16%), within the range reported previously for individual sites[6,13–16,] and did not vary with rainfall. By contrast, legume RA in the 16 dry forest sites was much higher (41% ± 27%) and was strongly and inversely related to annual rainfall. The transition between these two patterns occurred at approximately 1500 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-fixer 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 (Fig. 1d and 3; 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[12,36], although those studies were unable to examine the effect of succession. We identified a threshold in mean annual rainfall at approximately 1500 mm yr^{-1}—nearly identical to the threshold observed in forest inventories from North America[36]—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 (i) small leaflet size, which allows for leaf temperature regulation and water conservation, and (ii) 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[4,37] because it is often lost following disturbance, either through harvesting of the canopy or crops, volatilization during burning, or leaching[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[6,37]. Under those 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[38,39].

Besides providing legumes 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 hiatus in transpiration, plants are not able to access nutrients in the soil solution, including N (ref. *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 to non-fixers[11,41], which may need to wait until soil water is sufficiently recharged to acquire mineral N (ref. *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[21,42]. 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[43]. 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[42], as well as their continued dominance in this ecosystem over evolutionary timescales[10,11].

But N fixation is clearly not the only trait that is advantageous to legumes in Neotropical dry forests. Because that biome is dominated by legumes that have bipinnate leaves particularly during the early stages of succession, it is clear 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[34] by enhancing heat dissipation and regulating leaf temperature more efficiently[32]. Many legumes also have the ability to adjust the angle of their laminae to regulate diurnal incident solar radiation[44], 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[45], and half of all caesalpinioid species in our dataset (mainly those that fix N_2 and were formerly classified as Mimosoideae[46]) have bipinnate leaves. By contrast, only a quarter of all N-fixers have this trait, which means a relatively small subset of taxa is extremely well represented 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[11,47], 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. Nitrogen-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 Fig. 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 1500 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[48], while in some wet forests, N-fixing legumes act to inhibit the growth of neighboring trees during secondary succession[49]. 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[50–52]) 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.

Nitrogen-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 (e.g., *6*) 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 N_2 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 possessed by 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[36,53].

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Competing interests

The authors declare no competing financial interests.

Fig. 1 | Absolute and relative basal area of legume species in Neotropical secondary forests. The relative abundance of legume trees goes down during forest regeneration, but is markedly higher in seasonally dry forests than in wet forests, especially during the earliest stages of secondary succession. (**a**) Plot-level total basal area of all legume species; (**b**) relative basal area of all legume species; (**c**) relative basal area of N-fixing legumes; and (**d**) relative basal area of legumes with bipinnate leaves. Each circle represents one plot. Regression lines were drawn to highlight the successional trajectory of each of our 42 chronosequences. Dry forest sites (with dominant deciduous vegetation) are indicated in orange, and wet forests in blue. Insets show the average of all fits for absolute (a) or relative (b,c,d) basal area of legumes in dry and wet forests.

Fig. 2 | Legume relative basal area stratified by stand age across a rainfall gradient in the Neotropics. For forests in the wet Neotropics, the relative abundance (RA) of legume trees is not influenced by variations in mean annual rainfall. But below a threshold at approximately 1500 mm yr^{-1}, legume RA increases as total rainfall diminishes. (**a**) 2 to 10 yr old forests; (**b**) 11 to 20 yr old forests; (**c**) 21 to 30 yr old forests; (**d**) 31 to 40 yr old forests; (**e**) 41 to 60 yr old forests; and (**f**) 61 to 100 yr old forests. Results of a segmented linear fit are shown in each panel († $P <$ 0.05; * $P < 0.01$; ** $P < 0.001$; *** $P < 0.0001$); *N* indicates the number of chronosequence sites with plots in each age category. 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. The exceptional ecological success of legumes in recently disturbed, water-limited forests is mainly due to species that (i) are able to fix nitrogen and (ii) possess 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 Table 1c,d,e for full model results). Relative basal area and stand age were arcsin and log-transformed, respectively, prior to analysis. Models were computed separately for (**a**) N-fixing legume species, (**b**) legumes with bipinnate, and (**c**) legumes with pinnate leaves.

Table 1 | Effects of stand age and mean annual rainfall on legume abundance in Neotropical secondary forests. 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 (a and b) and for relative basal area of N-fixing and bipinnate legumes separately (c and d). 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 ($^{\dagger}P < 0.05$; $^{*}P \leq 0.01$; $^{**}P \leq 0.001$; $^{***}P \leq 0.001$). 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.

Dependent variable	**Parameter**	**Standardized coefficients**	**F-value**	**R^2 (m)**	**R^2 (c)**
a. Absolute basal area – all legumes				0.08	0.33
	Stand age	$0.29^{\dagger}$	4.21		
	Rainfall	-0.03	0.04		
	Stand age × Rainfall	-0.04	0.04		
	Stand age | Site	***			
b. Relative basal area – all legumes				0.17	0.62
	Stand age	-0.61^{**}	21.15		
	Rainfall	-0.95^{**}	16.23		
	Stand age × Rainfall	0.62^{*}	12.01		
	Stand age | Site	***			
c. Relative basal area – N-fixing legumes				0.17	0.63
	Stand age	-0.83^{***}	22.09		
	Rainfall	-1.11^{**}	15.05		
	Stand age × Rainfall	0.88^{**}	13.72		
	Stand age | Site	***			
d. Relative basal area – Bipinnate legumes				0.12	0.73
	Stand age	-0.42^{*}	8.39		
	Rainfall	$-0.75^{\dagger}$	6.83		

	Stand age × Rainfall	0.40	4.09		
	Stand age | Site	***			
e. Relative basal area – Pinnate legumes				0.03	0.15
	Stand age	-0.36*	9.31		
	Rainfall	-0.45†	6.74		
	Stand age × Rainfall	0.41†	6.08		
	Stand age | Site	***			

Methods

Chronosequence database. We extracted plot-scale legume abundance (m^2 ha^{-1}, basal area; BA) from 42 previously published chronosequence studies[24] (2ndFOR network; Supplementary Fig. 1, 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 1207 plots, mean plot area was 912 m^2. The median number of plots per site was 14, ranging from 2 to 272. Prior land use in our sites included cattle 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, mean annual rainfall varied from 750 to 4000 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 *10*; Supplementary Table 1). Because some tropical wet forests experience annual rainfall averages that overlap with the range exhibited by dry forests (particularly around 1500 mm yr^{-1}), we used seasonality in leaf habit (drought deciduous or evergreen) to distinguish between the two main biome types. We also repeated our analysis using two additional measures of water availability in the dry season, when water availability is a stronger limiting factor for plant growth and functioning: the rainfall coefficient of variation from WorldClim, which is an index of seasonality[25], and the climatic water deficit ("CWD", in mm yr^{-1}, defined as months where evapotranspiration exceeds rainfall[26], http://chave.ups-tlse.fr/pantropical_allometry.htm), which reflects the relative intensity of water loss during dry months.

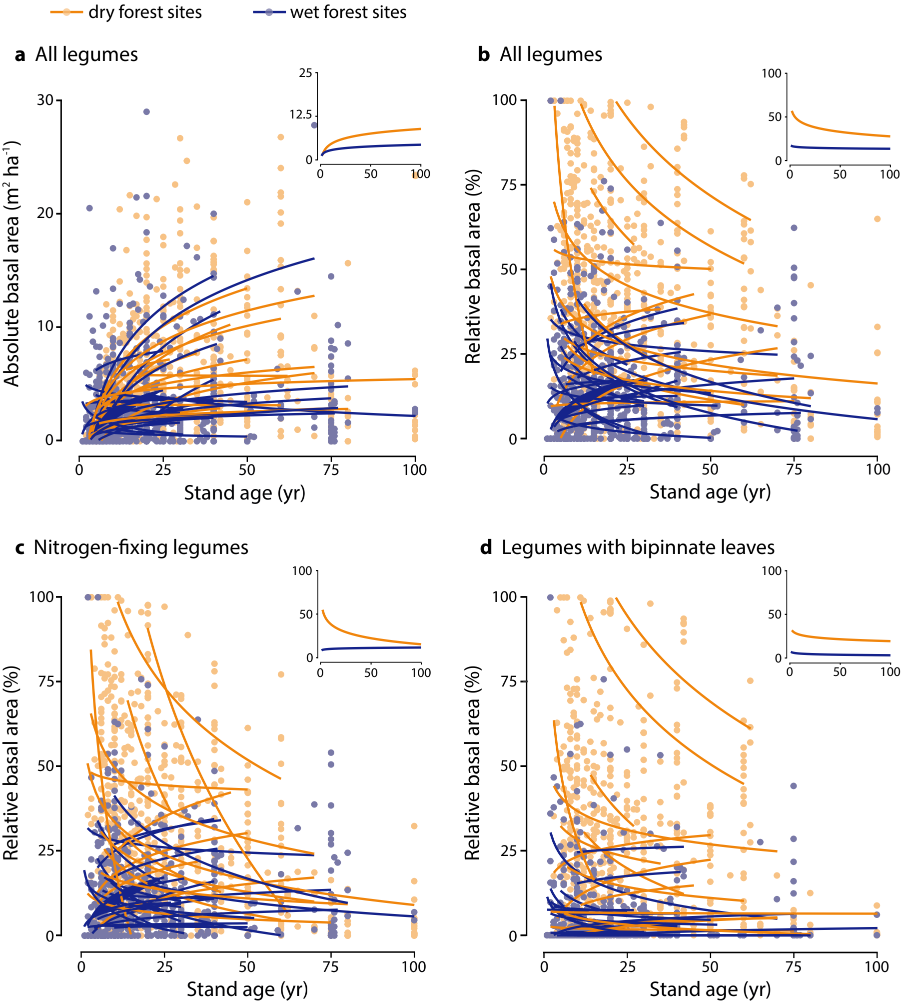
Functional traits. Across all sites, 398 legume species were present (Supplementary Table 2). We classified the potential of each species to fix N_2 based on positive nodulation reports for each species[31] (Dr. Janet Sprent determined the fixation potential of the species not included in this reference). We determined leaf compoundness, which is considered an adaptation to severe moisture stress as plants are able to shed individual leaflets (rather than whole leaves). Because all legume species in our database had compound leaves, we also assessed the iteration of divisions, which we refer to as "leaf type" (unifoliolate, pinnate, or bipinnate). Leaf size reflects the thickness of the boundary layer and thus potential for heat dissipation, so we used representative collection specimens to measure length and width of legume leaflets (± 0.001 cm). In total, we were able to quantify leaf size for 93% of all legume species within our dataset. To accurately represent the morphological variation of leaflets, for each leaf we averaged measurements made on leaflets from the bottom, middle, and top of the axis. Leaflet size was measured on three leaves of each species ($N = 3$ individuals per species) using Neotropical specimens from the University of Minnesota Herbarium (133 of 398 species) or from online databases[54–58]. Leaflet length and width were highly correlated ($R^2 = 0.82$, $P < 0.0001$). Across our dataset, intraspecific variation in leaflet size was small compared to the proportion of variance explained by species (80% and 81% for leaf length and width, respectively), consistent with (*34*) and (*59*, *60*). All N fixation potential and leaf size data for each species are provided in Supplementary Table 3.

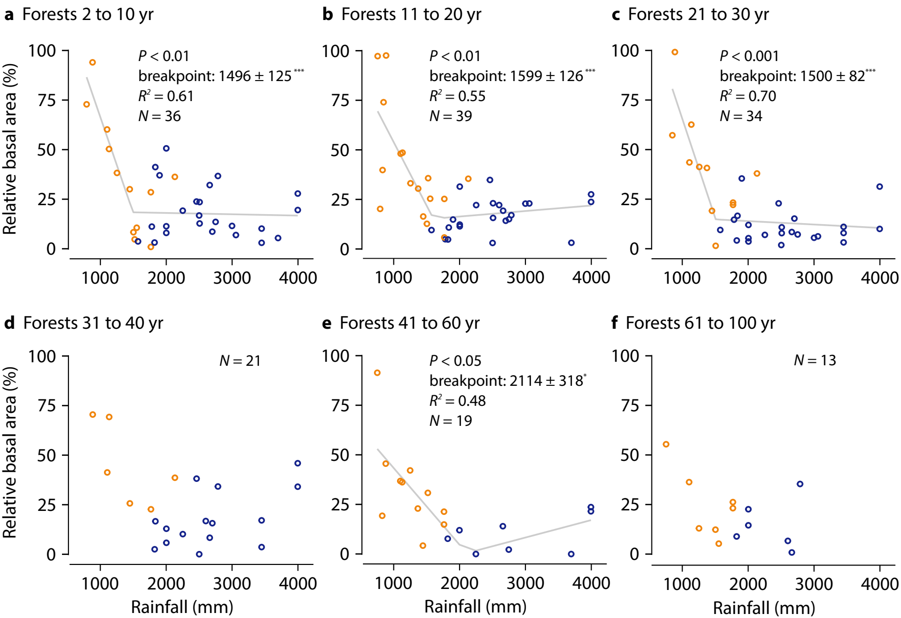
Legume abundance. We calculated (i) total legume basal area (m^2 ha^{-1}) to serve as an approximate estimate of aboveground legume biomass, and (ii) relative basal area (%) which summarizes the abundance of legumes compared to all species within each plot and is an ecologically meaningful indication of community composition. We interpreted legume relative basal area as a measure of legume ecological success because it reflects legume performance relative to other species. In order to determine whether N fixation and leaf type influence legume success, we also calculated relative basal area (%) for legume trees grouped by fixation potential and by leaf type. Because the basal area of small diameter trees during early stages of forest regeneration is an approximation of recruitment, we stratified legume basal area by tree diameter classes. We focused our analysis on legume relative basal area as a measurement of legume relative abundance ("RA") because it reflects biomass accumulation, but across our dataset, this variable was positively and significantly correlated to relative stem density ($R^2 = 0.38$, $P < 0.0001$).

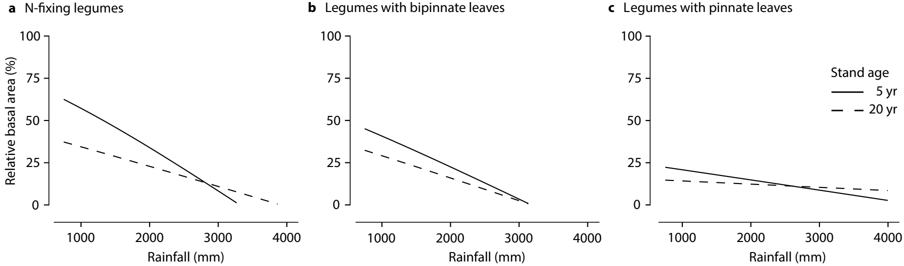
Statistical analyses. In order to evaluate how legume abundance changed over successional time and along the rainfall gradient, we modeled legume RA as a function of stand age and mean annual rainfall with a linear mixed model using the lme4 package (v. 1.1.11) in R. We applied an arcsin and natural-logarithm transformation to improve the normality of RA and stand age, respectively. We included random site intercepts, as we expected between-site variation in initial legume abundance and random slopes to account for the variation of the effect of stand age on legume abundance among sites (Fig. 1). P values for the effect of stand age were calculated from the lmerTest package (v. 2.0.30), and random effect P values were estimated via the likelihood ratio test. We obtained R^2 values for the effect of stand age (marginal R^2) and for the entire model (conditional R^2) using the r.squaredGLMM function in the MuMIn package[61] (v. 1.15.6). In order to determine whether other climatic variables also predicted legume abundance, we repeated models for legume RA using rainfall seasonality or CWD as the main climatic predictor variable. We compared the three models based on Akaike's information criterion adjusted for small sample sizes (AIC_C) and selected the best-supported model with the lowest AIC_C. In order to determine the effect of rainfall on 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 yrs 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 arcsin transformed RA with stand age and forest type (dry or wet) as covariates. All analyses were performed in R version 3.2.2[62].

Data availability

Plot-level legume basal area data from the 42 Neotropical forest sites are available from the Dryad Digital Repository: http://dx.doi.org/...


dry forest sites
wet forest sites
a All legumes
Absolute basal area (m^2 ha^{-1})
0
10
20
30
0
12.5
25
0
50
100
Stand age (yr)
0
25
50
75
100
b All legumes
Relative basal area (%)
0
25
50
75
100
0
50
100
Stand age (yr)
c Nitrogen-fixing legumes
Relative basal area (%)
Stand age (yr)
d Legumes with bipinnate leaves
Relative basal area (%)
Stand age (yr)


a Forests 2 to 10 yr
P < 0.01
breakpoint: 1496 ± 125***
R² = 0.61
N = 36
b Forests 11 to 20 yr
P < 0.01
breakpoint: 1599 ± 126***
R² = 0.55
N = 39
c Forests 21 to 30 yr
P < 0.001
breakpoint: 1500 ± 82***
R² = 0.70
N = 34
d Forests 31 to 40 yr
N = 21
e Forests 41 to 60 yr
P < 0.05
breakpoint: 2114 ± 318*
R² = 0.48
N = 19
f Forests 61 to 100 yr
N = 13
Relative basal area (%)
0
25
50
75
100
1000
2000
3000
4000
Rainfall (mm)


a N-fixing legumes
b Legumes with bipinnate leaves
c Legumes with pinnate leaves
Relative basal area (%)
100
75
50
25
0
1000
2000
3000
4000
Rainfall (mm)
Stand age
5 yr
20 yr