1   **Legume Abundance Along Successional And Rainfall Gradients In Neotropical Forests**

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105   **The nutrient demands of regrowing tropical forests are partly satisfied by nitrogen (N)-**

106   **fixing legume trees, but our understanding of the abundance of those species is biased**

107   **towards wet tropical regions. Here we show how the abundance of Leguminosae is affected**

108   **by both recovery from disturbance and large-scale rainfall gradients through a synthesis of**

109   **forest-inventory plots from a network of 42 Neotropical forest chronosequences. During the**

110   **first three decades of natural forest regeneration, legume basal area is twice as high in dry**

111   **compared to wet secondary forests. The tremendous ecological success of legumes in**

112   **recently disturbed, water-limited forests is likely related to both their reduced leaflet size**

113   **and ability to fix N_2, which together enhance legume drought tolerance and water-use**

114   **efficiency. Earth system models should incorporate these large-scale successional and**

115   **climatic patterns of legume dominance to provide more accurate estimates of the maximum**

116   **potential for natural N fixation across tropical forests.**

117   More than half of the tropical forest area worldwide is made up of secondary forests,

118   which regrow after canopy removal due to natural or anthropogenic disturbances[1]. Second-

119   growth forests are important globally because they supply firewood and timber, regulate the

120   hydrological cycle, benefit biodiversity, and provide carbon storage as above- and below-ground

121   biomass[2,3], but their growth can be constrained by nitrogen (N) availability[4]. Symbiotic fixation

122   is thought to provide the largest natural input of N to tropical forests[5], and part of the N demand

123   of regrowing tropical forests is satisfied by legume trees (Leguminosae) that have the capacity to

124   fix atmospheric N_2 through interactions with rhizobia bacteria[6]. The abundance of N-fixing

125   legumes is not always strictly proportional to the rates of rhizobial activity, as some legumes

126   down-regulate fixation when the costs outweigh the benefits[7]. Nevertheless, legume abundance

127   as represented by total basal area may provide a good estimate of the maximum potential N

128   fixation in an ecosystem, with the advantage that this metric can be extracted from standard

129   forest inventory surveys. Spatially explicit estimates of legume abundance through time could

130   help to reduce uncertainties in Earth system models that include coupled carbon and N

131   biogeochemistry[8], but assessments of legume abundance have not yet been synthesized across

132   the successional and climatic gradients that characterize tropical forests.

133   The abundance of N-fixing legumes relative to non-fixing trees has been closely

134   examined in undisturbed tropical forests[9,10] and savannas[11,12]. But studies of legume abundance

135   in regenerating forests are rare and have been restricted to the wet tropics[6,13–16], so are likely not

136   representative of tropical secondary succession globally. Due to environmental filtering[17],

137   systematic variations in legume abundance should occur along both rainfall and successional

138   gradients. Wet and (seasonally) dry tropical forests[10,18] experience substantial differences in

139   water and nutrient availability, which in turn may influence the competitive success of legumes

140   in both biomes[19]. Nitrogen-fixing legumes should possess particular advantages in drier

141   conditions; they can access N when mineralization rates decline due to low soil moisture[20], and

142   use their high foliar N content to maintain high growth rates and use water more efficiently

143   relative to non-fixers[21]. Because young tropical forests are often N-limited[4], trees that are able to

144   fix may be favored during the earliest stages of forest regrowth after disturbance[22,23]. Some

145   studies indeed show that legumes are more abundant in young compared to old wet Neotropical

146   forests[6,14], but others report successional trends in the opposite direction, with the relative

147   abundance of these species instead increasing with stand age[13,15]. Characterizing these macro-

148   ecological patterns of legume abundance across climate space and through successional time,

149   along with variations in their functional traits, is crucial to determine whether our current

150   knowledge of legume distributions can be generalized across the tropics and to achieve a more

151 complete understanding of the role of this exceptionally diverse plant family within secondary

152 Neotropical forest ecosystems.

153   Here we evaluate how the abundance of legumes (as measured by absolute and relative

154 basal area) varies through secondary succession using data from 42 chronosequence sites[24]

155 (Supplementary Fig. 1; Supplementary Table 1) that span a large gradient in mean annual rainfall

156 (from 750 to 4000 mm yr^{-1}) and explain legume success based on N fixation potential and two

157 functional traits related to drought tolerance (leaf size and leaf type). We primarily focused our

158 climate analysis on mean annual rainfall ("rainfall" hereafter), but also tested the effect of

159 rainfall seasonality[25] (the rainfall coefficient of variation from WorldClim) and climatic water

160 deficit[26] ("CWD"; which tracks water losses during the months where evapotranspiration

161 exceeds rainfall) as alternative predictors. Because leaf habit or leafing phenology is a better

162 indicator of seasonal moisture stress than total annual precipitation[27], we used this parameter to

163 classify study sites as "dry" forests if the vegetation was mostly drought-deciduous (sensu *10*), or

164 as "wet" forests in all other instances (i.e., mostly evergreen; Supplementary Table 1). As such,

165 the terms "dry" and "wet" forests refer to two ecologically distinct tropical biomes with floristic

166 compositions that differ in phylogenetic, biogeographic, functional, and community ecological

167 patterns (see *28, 29, 30*). Therefore, although rainfall is used as the main (continuous) climatic

168 variable to model legume abundance, we did not use this variable to classify sites as either dry or

169 wet forests.

170   To understand the specific factors that enable legumes to thrive in particular tropical

171 environments, we also investigated how the abundance of these trees related to their capacity to

172 fix nitrogen and a pair of crucial leaf traits that reflect drought tolerance. For each of the 398

173 legume species present at our sites, we assessed potential to fix N_2 based on positive nodulation

174   reports and expert knowledge[31] (see Methods). Both of the leaf traits we examined – leaf size

175   and leaf type – reflect adaptations to limited water availability (Supplementary Tables 2 and 3).

176   Smaller leaves have reduced boundary layer resistance, which enables them to dissipate heat

177   through conductive or convective radiation[32–34]. Leaf type is considered to be associated with

178   drought severity and seasonality because plants with compound leaves (having either pinnate or

179   bipinnate divisions) are able to shed individual leaflets (rather than whole leaves) when faced

180   with severe moisture stress[35]. Our analysis demonstrates that the abundance of legumes indeed

181   varies substantially and systematically across Neotropical forests, and although the ecological

182   success (i.e., high relative abundance) of these species during the very earliest stages of

183   secondary succession is partly due to N fixation, other traits related to drought tolerance and

184   water-use efficiency likely also offer competitive advantages.

185

186   **Results**

187   During the first three decades of forest regeneration, the total abundance of all legume

188   trees as measured by their absolute basal area doubled in both dry and wet Neotropical forests

189   (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

190   legume biomass gradually built up through succession. Here we define legume relative

191   abundance (RA) as the basal area of Leguminosae trees divided by the total basal area of all trees

192   in each plot and interpret it as a measure of ecological success that reflects legume performance

193   relative to non-legume species. Overall, although absolute legume abundance increased with

194   succession, the RA of legumes declined with stand age in drier forests and declined with rainfall

195   in younger forests (Table 1, Fig. 1b). Despite these trends, site-to-site variation in successional

196   change in legume RA was substantial (Fig. 1b, Table 1). The fixed effects (stand age, rainfall,

197   and their interaction) accounted for 17% (marginal R^2) of the total variance explained by our

198   model of legume RA, while 45% was due to site-to-site variation (conditional $R^2 = 62\%$, Table

199   1). In the majority of dry forests, legume relative basal area decreased through time, which

200   indicates legumes were initially a dominant component of early successional communities and

201   then subsequently declined in abundance as other tree species became more common. By

202   contrast, legume RA in the wet forest chronosequences typically began lower but remained

203   constant through succession. The RA of legumes was much higher at the dry end of the rainfall

204   gradient (rainfall effect, Table 1) and this difference was most evident during the first three

205   decades of succession (0 to 30 years since abandonment, Fig. 1b). For example, in the youngest

206   dry forests (2 to 10 yr), legumes on average made up more than one third of the basal area of all

207   trees (37%, compared to 18% in wet forests; Fig. 2a), and in some plots in Mexico (Chamela,

208   Nizanda, Yucatán, and Quintana Roo) and Brazil (Cajueiro, Mata Seca, Patos), relative

209   abundance approached 100% (98% and greater). Although fewer chronosequences extend

210   beyond three decades, in later successional stages (30 to 100 years; Fig. 2d-f) legume abundance

211   was still high in dry forests. The greater overall abundance of legumes in dry forests (compared

212   to wet forests) may be partly a consequence of their higher initial recruitment, which is suggested

213   by the high RA of small diameter legume trees during the first two decades of forest regeneration

214   (Supplementary Fig. 2).

215   Mean annual rainfall was a strong determinant of legume RA over the entire Neotropical

216   network (Table 1). Alternative models of legume RA that used rainfall seasonality and CWD as

217   the main climatic predictor variable also explained a significant amount of variation in our data

218   (Supplementary Fig. 3 and 4), but the best-supported model was based on mean annual rainfall

219   ($R^2 = 0.62$, versus $R^2 = 0.49$ and $R^2 = 0.48$ for seasonality and CWD respectively; Supplementary

220   Table 4). The magnitude of legume RA and its relationship with rainfall differed strongly

221   between dry and wet secondary forests, most prominently during the first three decades of

222   secondary succession (Fig. 2). For the 26 chronosequences from wet forests, mean legume RA

223   was approximately 18% (± 16%), within the range reported previously for individual sites[6,13–16,]

224   and did not vary with rainfall. By contrast, legume RA in the 16 dry forest sites was much higher

225   (41% ± 27%) and was strongly and inversely related to annual rainfall. The transition between

226   these two patterns occurred at approximately 1500 mm yr^{-1} (Fig. 2).

227   The functional traits of legumes also varied across the large-scale environmental

228   gradients in our dataset. The spatial and successional patterns of legume abundance were largely

229   driven by N-fixing species (Fig. 1c). For nearly two-fifths of the plots in our network, fixers

230   were the only type of legumes present. At the plot level, the median percentage of total legume

231   basal area comprised by fixers was 93.5%. The proportion of N-fixer basal area to total legume

232   basal area did not vary with rainfall or stand age, and the RA of non-fixing legumes was much

233   lower in both dry and wet secondary forest sites (Supplementary Fig. 5). In contrast to the N-

234   fixers, the RA of non-fixing legumes remained constant throughout succession (Supplementary

235   Table 5). When we stratified our analyses by leaf type, it was evident that the extremely high

236   legume RA in young dry forests was largely due to the prevalence of species with bipinnate

237   leaves (Fig. 1d and 3; Table 1), which have significantly smaller leaflets than legumes with other

238   leaf types (Supplementary Table 3).

239

240   **Discussion**

241   Based on our survey of secondary forests across the Neotropics, we conclude the

242   ecological success of legume trees is markedly higher in seasonally dry forests than in wet

243   forests, especially during early stages of secondary succession. These findings agree with

244   analyses of other large datasets from Africa and the Americas that found higher abundance of N-

245   fixing legumes in arid conditions[12,36], although those studies were unable to examine the effect of

246   succession. We identified a threshold in mean annual rainfall at approximately 1500 mm yr^{-1}—

247   nearly identical to the threshold observed in forest inventories from North America[36]—below

248   this level, legume abundance was strongly and negatively correlated to water availability.

249   Because this relationship was driven mainly by species that are both able to fix N_2 and have

250   bipinnate leaves (Fig. 1), we suggest that the exceptional abundance of tropical legumes towards

251   the drier end of the rainfall spectrum during secondary succession is the combined product of (i)

252   small leaflet size, which allows for leaf temperature regulation and water conservation, and (ii) N

253   fixation, which contributes to photosynthetic acclimation, enhances water use efficiency, and

254   may satisfy the demand for nitrogen after the post-dry season leaf flush.

255   The availability of nitrogen is known to constrain biomass recovery in secondary

256   Neotropical forests[4,37] because it is often lost following disturbance, either through harvesting of

257   the canopy or crops, volatilization during burning, or leaching[37]. Our finding that Neotropical

258   legumes are proportionately more abundant in early succession throughout the Neotropics could

259   be due to the high demand for N in recently disturbed forests[6,37]. Under those circumstances,

260   fixation would allow legumes to overcome N limitation more easily than their competitors,

261   although the degree to which initial secondary forest regrowth is limited by N availability is

262   highly variable and influenced by local disturbance history and prior land use[38,39].

263   Besides providing legumes an advantage in young secondary forests in general, N

264   fixation could offer additional benefits to plants growing under seasonally dry conditions.

265   Forests that experience a pronounced annual dry season are affected by recurrent seasonal

266 declines in soil moisture and, due to the associated hiatus in transpiration, plants are not able to

267 access nutrients in the soil solution, including N (ref. *40*). Because many dry forest trees lose

268 their leaves each year and are required to grow an entirely new canopy, being able to obtain N

269 through symbiosis could allow legumes to more quickly rebuild their leaf canopy at the end of

270 the dry season compared to non-fixers[11,41], which may need to wait until soil water is sufficiently

271 recharged to acquire mineral N (ref. *40*). Towards the high end of the Neotropical rainfall

272 gradient, forests do not experience a strong seasonal moisture deficit, and as a result, are not

273 usually faced with the regular nutrient scarcity that consistently affects dry forests. In addition to

274 its role in satisfying seasonal nitrogen demands, fixation should also help legumes to further

275 acclimate to hot, dry conditions[21,42]. By investing part of their fixed N into the production of

276 photosynthetic enzymes, plants are able to draw down their internal concentrations of carbon

277 dioxide, thereby creating steeper diffusion gradients in their leaves[43]. This adjustment allows

278 photosynthesis to occur at lower stomatal conductance and reduced transpiration. These two

279 advantages offered by fixation could account for the extremely high abundance of legumes early

280 in dry forest succession, when air and soil temperatures are high, and soil water potential is at its

281 lowest[42], as well as their continued dominance in this ecosystem over evolutionary

282 timescales[10,11].

283   But N fixation is clearly not the only trait that is advantageous to legumes in Neotropical

284 dry forests. Because that biome is dominated by legumes that have bipinnate leaves particularly

285 during the early stages of succession, it is clear these species also benefit from their conservative

286 use of water. Reduced leaf size (and the accompanying thinner boundary layer) offers a

287 significant adaptive value in hot, dry environments[34] by enhancing heat dissipation and

288 regulating leaf temperature more efficiently[32]. Many legumes also have the ability to adjust the

289   angle of their laminae to regulate diurnal incident solar radiation[44], which further reduces heat

290   loading. Hence, having small leaflets could enable legumes at dry sites to benefit from high

291   irradiance while preventing excessively high leaf temperatures. The bipinnate leaf type is

292   confined exclusively to one subclade of legumes, the Caesalpinioideae[45], and half of all

293   caesalpinioid species in our dataset (mainly those that fix N_2 and were formerly classified as

294   Mimosoideae[46]) have bipinnate leaves. By contrast, only a quarter of all N-fixers have this trait,

295   which means a relatively small subset of taxa is extremely well represented in the secondary

296   forests of the dry Neotropics. This strong phylogenetic signal highlights the importance of

297   drought tolerance traits as an adaptation to seasonal dry forests[11,47], and demonstrates that leaf

298   traits enhancing moisture conservation are equally as important as the potential to fix N_2 when

299   explaining patterns of legume abundance. Nitrogen-fixing legumes that have small bipinnate

300   leaves thus hold a double advantage because those traits combine to minimize water loss during

301   C acquisition and lead to increased water use efficiency.

302   Across the Neotropics, a substantial amount of the variation in the relative abundance of

303   legumes in secondary forests (17%) can be predicted by rainfall, stand age, and their interaction.

304   The strong negative relationship between legume RA and water availability was not sensitive to

305   our choice of climate variable (either mean annual rainfall, rainfall seasonality, or CWD; Fig. 2

306   and Supplementary Fig. 3 and 4), which suggests that legumes have a competitive advantage in

307   dry climates that are characterized by recurrent seasonal droughts and strong water deficits

308   during the growing season. The climate transition near 1500 mm yr^{-1}, where the relationship

309   between legume RA and rainfall switched from strongly inverse to flat, coincides with a known

310   cross-over point in woody regeneration[48]. In regenerating dry forests, the canopy of established

311   plants serves to moderate the harsh microclimatic conditions, thus facilitating the establishment

312 of seedlings[48], while in some wet forests, N-fixing legumes act to inhibit the growth of

313 neighboring trees during secondary succession[49]. A large fraction (45%) of the variance in

314 legume abundance was associated with site identity (represented in our model as a random

315 factor), which could be related to site-specific factors such as resource limitation (phosphorus,

316 molybdenum, iron[50–52]) or biotic interactions (dispersal, herbivory) that influence fixation in

317 individual forest stands. More research is needed to determine how and to what extent these

318 factors influence legume dominance at finer spatial scales.

319   Nitrogen-fixing legume species attain their greatest levels of ecological success in

320 Neotropical dry forests, where the benefits of fixation and co-occurring traits related to water

321 conservation outweigh their costs throughout decades of succession. It is thus clear that insights

322 about legumes derived from studies conducted exclusively in wet forests (e.g., *6*) cannot be

323 extrapolated across all Neotropical forests, and in particular are not valid for dry forests. As an

324 alternative, future efforts to model the tropical N cycle must account for the strong heterogeneity

325 exhibited by this hyperdiverse family of plants. Incorporating these large-scale abundance trends

326 into Earth system models should allow for more accurate estimates of the potential for symbiotic

327 N fixation across tropical forests. Our study also demonstrates that, even though the potential to

328 fix N_2 through symbiosis is a crucial element of their success, it is not the only trait that accounts

329 for the exceptionally high abundance of legumes in Neotropical forests. Leaf traits related to

330 drought tolerance and water use efficiency are also key adaptive features possessed by dry forest

331 legumes. In conclusion, our results provide a deeper mechanistic explanation for the abundance

332 of Neotropical Leguminosae trees, which should be increasingly relevant to natural forest

333 regeneration and ecosystem functioning as global temperatures warm and dry conditions become

334 more widespread in the tropics[36,53].

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477   Statistical Computing, Vienna, 2015).

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479

508

509   **Author contributions:** M.G. and J.S.P. conceived the idea, all coauthors coordinated the data

510   compilations, M.G. and M.R.G. collected leaf traits data, M.G. analyzed the data,

511   D.M.A.R. contributed to the analytical approach, M.G. and J.S.P. wrote the paper, and all

512   co-authors collected field data, discussed the results, gave suggestions for further

513   analyses, and commented on the manuscript.

514

515 **Competing interests**

516   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 ($^{\dagger} P <$
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.

540   **Fig. 3 | Relative basal area of legumes for 5 and 20 year old forests as a function of mean**

541   **annual rainfall.** The exceptional ecological success of legumes in recently disturbed, water-

542   limited forests is mainly due to species that (i) are able to fix nitrogen and (ii) possess bipinnate

543   leaves. Fitted values were obtained using a linear mixed-effects model, with stand age and

544   rainfall as fixed effects and site as random effect (see Table 1c,d,e for full model results).

545   Relative basal area and stand age were arcsin and log-transformed, respectively, prior to analysis.

546   Models were computed separately for (**a**) N-fixing legume species, (**b**) legumes with bipinnate,

547   and (**c**) legumes with pinnate leaves.

548 **Table 1 | Effects of stand age and mean annual rainfall on legume abundance in**

549 **Neotropical secondary forests.** Across the Neotropics, the abundance of legumes in secondary

550 forests can be predicted by rainfall, stand age, and their interaction. Linear mixed-effects models

551 were run for absolute and relative basal area of all legume species (a and b) and for relative basal

552 area of N-fixing and bipinnate legumes separately (c and d). Stand age, mean annual rainfall

553 ("rainfall") and their interaction were included as fixed effects. Random site intercepts account

554 for between-site variation in initial legume basal area, and random slopes for the variation of the

555 effect of stand age on legume basal area among sites ($^{†}P < 0.05$; $^{*}P \leq 0.01$; $^{**}P \leq 0.001$; $^{***}P \leq$

556 0.001). The standardized regression coefficients compare the effect of the independent variables

557 on the dependent variable. Values of marginal (R^2 (m)) and conditional (R^2(c)) R^2 indicate the

558 proportion of the variance explained by the fixed effects of the model, and the fit of the whole

559 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	$0.29^{†}$	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	$-0.75^{†}$	6.83		

27

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	***		

560

561 **Methods**

562 **Chronosequence database.** We extracted plot-scale legume abundance (m^2 ha^{-1}, basal area; BA)

563 from 42 previously published chronosequence studies[24] (2ndFOR network; Supplementary Fig.

564 1, Supplementary Table 1). Our dataset includes lowland forests between 2 and 100 years old.

565 Plot size varied from 0.008 to 1.3 ha, and across all 1207 plots, mean plot area was 912 m^2. The

566 median number of plots per site was 14, ranging from 2 to 272. Prior land use in our sites

567 included cattle ranching, shifting cultivation, or a combination of the two. In each plot, all woody

568 trees, shrubs, and palms $\geq$ 5 cm in diameter were measured and identified, with the exception of

569 sites in Costa Rica (Santa Rosa and Palo Verde) and Puerto Rico (Cayey) for which a minimum

570 diameter at breast height of 10 cm was used. Across the network, mean annual rainfall varied

571 from 750 to 4000 mm yr^{-1}. Based on local site knowledge, study sites were classified as "dry"

572 forests when the vegetation is mostly drought deciduous, or "wet" forests (mostly evergreen) in

573 all other instances (sensu *10*; Supplementary Table 1). Because some tropical wet forests

574 experience annual rainfall averages that overlap with the range exhibited by dry forests

575 (particularly around 1500 mm yr^{-1}), we used seasonality in leaf habit (drought deciduous or

576 evergreen) to distinguish between the two main biome types. We also repeated our analysis using

577 two additional measures of water availability in the dry season, when water availability is a

578 stronger limiting factor for plant growth and functioning: the rainfall coefficient of variation

579 from WorldClim, which is an index of seasonality[25], and the climatic water deficit ("CWD", in

580 mm yr^{-1}, defined as months where evapotranspiration exceeds rainfall[26], http://chave.ups-

581 tlse.fr/pantropical_allometry.htm), which reflects the relative intensity of water loss during dry

582 months.

583

584 **Functional traits.** Across all sites, 398 legume species were present (Supplementary Table 2).

585 We classified the potential of each species to fix N_2 based on positive nodulation reports for each

586 species[31] (Dr. Janet Sprent determined the fixation potential of the species not included in this

587 reference). We determined leaf compoundness, which is considered an adaptation to severe

588 moisture stress as plants are able to shed individual leaflets (rather than whole leaves). Because

589 all legume species in our database had compound leaves, we also assessed the iteration of

590 divisions, which we refer to as "leaf type" (unifoliolate, pinnate, or bipinnate). Leaf size reflects

591 the thickness of the boundary layer and thus potential for heat dissipation, so we used

592 representative collection specimens to measure length and width of legume leaflets ($\pm$ 0.001 cm).

593 In total, we were able to quantify leaf size for 93% of all legume species within our dataset. To

594 accurately represent the morphological variation of leaflets, for each leaf we averaged

595 measurements made on leaflets from the bottom, middle, and top of the axis. Leaflet size was

596 measured on three leaves of each species ($N = 3$ individuals per species) using Neotropical

597 specimens from the University of Minnesota Herbarium (133 of 398 species) or from online

598 databases[54–58]. Leaflet length and width were highly correlated ($R^2 = 0.82$, $P < 0.0001$). Across

599 our dataset, intraspecific variation in leaflet size was small compared to the proportion of

600 variance explained by species (80% and 81% for leaf length and width, respectively), consistent

601 with (*34*) and (*59*, *60*). All N fixation potential and leaf size data for each species are provided in

602 Supplementary Table 3.

603

604 **Legume abundance.** We calculated (i) total legume basal area (m^2 ha^{-1}) to serve as an

605 approximate estimate of aboveground legume biomass, and (ii) relative basal area (%) which

606 summarizes the abundance of legumes compared to all species within each plot and is an

607   ecologically meaningful indication of community composition. We interpreted legume relative

608   basal area as a measure of legume ecological success because it reflects legume performance

609   relative to other species. In order to determine whether N fixation and leaf type influence legume

610   success, we also calculated relative basal area (%) for legume trees grouped by fixation potential

611   and by leaf type. Because the basal area of small diameter trees during early stages of forest

612   regeneration is an approximation of recruitment, we stratified legume basal area by tree diameter

613   classes. We focused our analysis on legume relative basal area as a measurement of legume

614   relative abundance ("RA") because it reflects biomass accumulation, but across our dataset, this

615   variable was positively and significantly correlated to relative stem density ($R^2 = 0.38$, $P <$

616   0.0001).

617

618   **Statistical analyses.** In order to evaluate how legume abundance changed over successional time

619   and along the rainfall gradient, we modeled legume RA as a function of stand age and mean

620   annual rainfall with a linear mixed model using the lme4 package (v. 1.1.11) in R. We applied an

621   arcsin and natural-logarithm transformation to improve the normality of RA and stand age,

622   respectively. We included random site intercepts, as we expected between-site variation in initial

623   legume abundance and random slopes to account for the variation of the effect of stand age on

624   legume abundance among sites (Fig. 1). P values for the effect of stand age were calculated from

625   the lmerTest package (v. 2.0.30), and random effect P values were estimated via the likelihood

626   ratio test. We obtained R^2 values for the effect of stand age (marginal R^2) and for the entire model

627   (conditional R^2) using the r.squaredGLMM function in the MuMIn package[61] (v. 1.15.6). In

628   order to determine whether other climatic variables also predicted legume abundance, we

629   repeated models for legume RA using rainfall seasonality or CWD as the main climatic predictor

630   variable. We compared the three models based on Akaike's information criterion adjusted for

631   small sample sizes (AIC_c) and selected the best-supported model with the lowest AIC_c. In order

632   to determine the effect of rainfall on legume abundance at different stand age categories (2 to 10,

633   11 to 20, 21 to 30, 31 to 40, 41 to 60 and 60 to 100 yrs of forest age), we performed a piecewise

634   linear regression using the Segmented package (v. 0.5.1.4). Lastly, to understand the

635   successional change in legume basal area of trees of different size classes (< 10 cm, 10 to 20 cm,

636   20 to 30 cm and > 30 cm), we performed a multiple regression on arcsin transformed RA with

637   stand age and forest type (dry or wet) as covariates. All analyses were performed in R version

638   3.2.2[62].

639

640   **Data availability**

641   Plot-level legume basal area data from the 42 Neotropical forest sites are available from the

642   Dryad Digital Repository: http://dx.doi.org/...
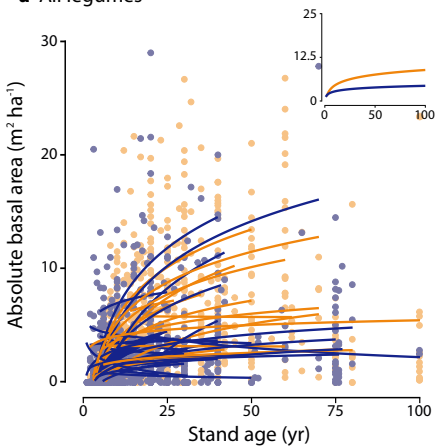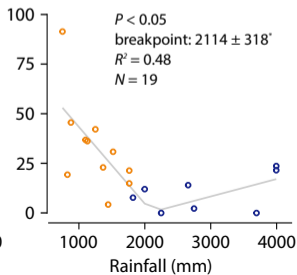
a All legumes

b All legumes
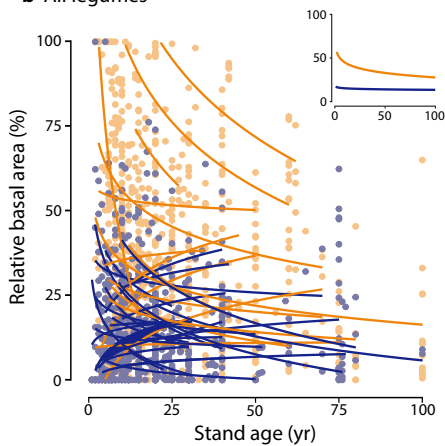
c Nitrogen-fixing legumes
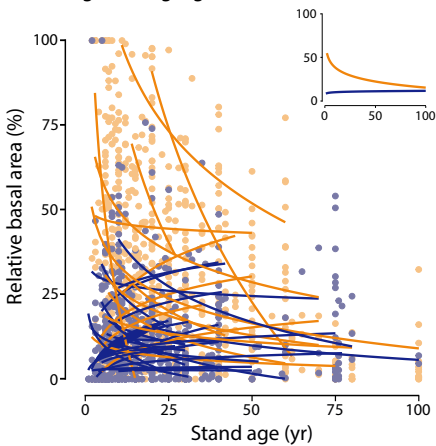
d Legumes with bipinnate leaves
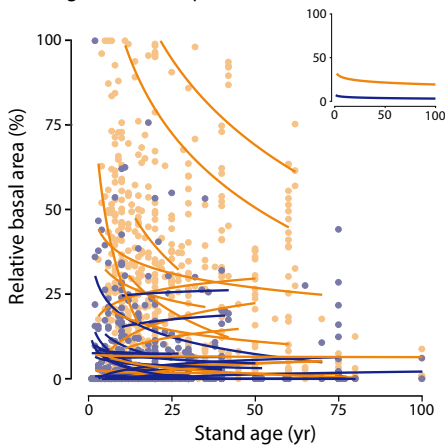
a Forests 2 to 10 yr
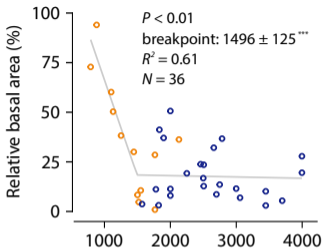
$P < 0.01$
breakpoint: 1496 ± 125 ***
$R^2 = 0.61$
$N = 36$

b Forests 11 to 20 yr
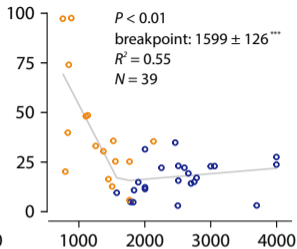
$P < 0.01$
breakpoint: 1599 ± 126 ***
$R^2 = 0.55$
$N = 39$

c Forests 21 to 30 yr

$P < 0.001$
breakpoint: 1500 ± 82 ***
$R^2 = 0.70$
$N = 34$

d Forests 31 to 40 yr

$N = 21$

e Forests 41 to 60 yr

$P < 0.05$
breakpoint: 2114 ± 318 *
$R^2 = 0.48$
$N = 19$

f Forests 61 to 100 yr

$N = 13$

Relative basal area (%)

Rainfall (mm)
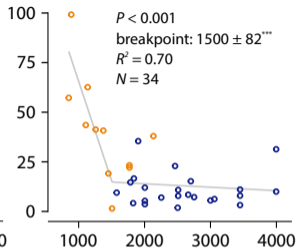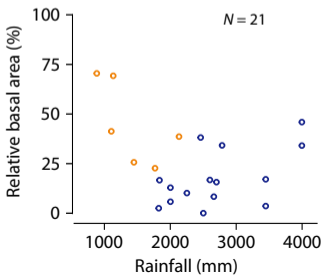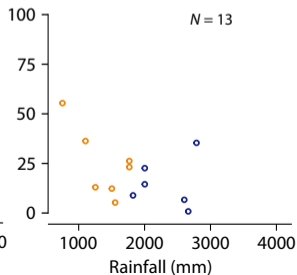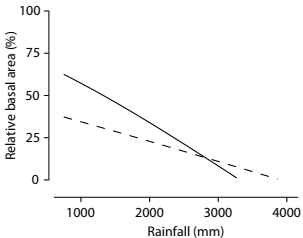
a N-fixing legumes
b Legumes with bipinnate leaves
c Legumes with pinnate leaves

Stand age
—— 5 yr
- - - 20 yr

Relative basal area (%)

Rainfall (mm)