Nitrogen-fixing trees inhibit growth of regenerating Costa Rican rainforests

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Edited by Christopher B. Field, Stanford University, Stanford, CA, and approved June 30, 2017 (received for review April 28, 2017)

More than half of the world's tropical forests are currently recovering from human land use, and this regenerating biomass now represents the largest carbon (C)-capturing potential on Earth. How quickly these forests regenerate is now a central concern for both conservation and global climate-modeling efforts. Symbiotic nitrogen-fixing trees are thought to provide much of the nitrogen (N) required to fuel tropical secondary regrowth and therefore to drive the rate of forest regeneration, yet we have a poor understanding of how these N fixers influence the trees around them. Do they promote forest growth, as expected if the new N they fix facilitates neighboring trees? Or do they suppress growth, as expected if competitive inhibition of their neighbors is strong? Using 17 consecutive years of data from tropical rainforest plots in Costa Rica that range from 10 y since abandonment to old-growth forest, we assessed how N fixers influenced the growth of forest stands and the demographic rates of neighboring trees. Surprisingly, we found no evidence that N fixers facilitate biomass regeneration in these forests. At the hectare scale, plots with more N-fixing trees grew slower. At the individual scale, N fixers inhibited their neighbors even more strongly than did nonfixing trees. These results provide strong evidence that N-fixing trees do not always serve the facilitative role to neighboring trees during tropical forest regeneration that is expected given their N inputs into these systems.

nitrogen fixation | neighborhood crowding | growth | succession | tropical forest

The past two decades have seen a dramatic increase in the appreciation for the role that tropical secondary forests play in local economies (1), species conservation (2), and climate change mitigation (3). As this interest has spurred new research into the dynamics of tropical forest regeneration, we are beginning to recognize the wide range of regeneration rates and trajectories that tropical secondary forests can exhibit (4). In addition to climatic drivers (4), soil N availability can regulate tropical forest regrowth (5, 6) and dictate how these forests respond to changing climatic conditions (7–10). The largest potential source of new N into tropical secondary forests is from symbiotic N-fixing plants (11, 12), which form specialized root nodules to house symbiotic bacteria that convert atmospheric N_2 gas into plant-available forms of N. These "N fixers" can fix up to 150 kg $N\cdot ha^{-1}\cdot y^{-1}$ (12), which becomes available to the surrounding ecosystem as N-fixer tissues return to the soil and the N in those tissues is mineralized. These N inputs from N fixers are thought to meet most of the external N demands of rapidly regenerating forests (13). However, the effect that these N fixers have on tropical forest regrowth depends on both their N inputs and how they influence the demographic rates of the neighboring trees around them.

The unique potential for N fixers to bring newly fixed N into the surrounding ecosystem (14) means that they might fertilize neighboring trees, but N fixers also compete with their neighbors for light and other resources. N fixers have, on average, higher tissue N content in their foliage than nonfixers (15–18). Litterfall and decomposition of this N-rich leaf tissue is the primary means by which N fixers fertilize the surrounding ecosystem. However, high N content can also fuel rapid growth of the N fixer itself (11, 13, 19), potentially increasing the N fixer's competitive influence on its surrounding neighbors. If the fertilization effect is strong, N fixers might facilitate neighbors or at least inhibit neighbors less than nonfixers (hereafter, "weak inhibition"; Fig. 1 *A* and *B*). Alternatively, if their competitive effect outweighs their fertilization effect, N fixers might inhibit neighbors more than nonfixers do (20) ("strong inhibition"; Fig. 1 *C* and *D*).

How N fixers affect neighboring trees is especially important in Neotropical secondary forests, which have great capacity for carbon storage (3, 4), are often thought to be N limited (5, 6), and have high relative abundances of N fixers. In Neotropical forests, N fixers typically comprise ~10% of all trees (compared with <1% at higher latitudes in North America) (21–23), and commonly make up 30–55% of the forest basal area at some sites (19, 24) (Fig. 2 and Table 1), making their impact on neighboring trees critical to the growth of these forests.

Do N fixers promote or inhibit growth in regenerating tropical forests? We addressed this question at multiple spatial scales using 10–17 y of census data from eight 1-ha moist tropical rainforest plots in Northeastern Costa Rica—six regenerating forests ranging in stand age from 10 to 42 y old and two old-growth forests (19, 25, 26) (Table 1). First, we asked whether the abundance of N fixers affects forest growth at the 1-ha forest plot and 10 × 10 m subplot levels. Next, we analyzed the effects of N fixers on their neighbors at the individual scale—the scale where competition and facilitation interactions likely occur. Specifically, we asked how the makeup of a tree's neighborhood—the

Significance

Regrowing tropical forests are critical for global biodiversity conservation and carbon capture. Nitrogen availability often controls how fast these forests can regrow. Because nitrogen-fixing plants are the primary source of new nitrogen into these forests, one might expect that more nitrogen fixers lead to faster forest regrowth. However, here we show that nitrogen fixers actually slow forest regrowth. Their competitive influence on neighboring trees outweighs any growth enhancement from their nitrogen inputs at this site. Our results call for a more critical evaluation of how nitrogen fixers influence the surrounding forest, especially given the large uncertainty in global climate projections that hinges on the role of nitrogen fixers during tropical forest regeneration.

Author contributions: B.N.T. and D.N.L.M. designed research; B.N.T. and R.L.C. performed research; B.N.T. and B.B. analyzed data; and B.N.T., R.L.C., B.B., and D.N.L.M. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Data deposition: Data used in this study are available in the figshare data repository at https://figshare.com/articles/Supplement_1_Data_on_tree_dynamics_during_secondary_succession_and_wood_specific_gravity_in_northeastern_Costa_Rica_/3520553/1.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1707094114/-/DCSupplemental.

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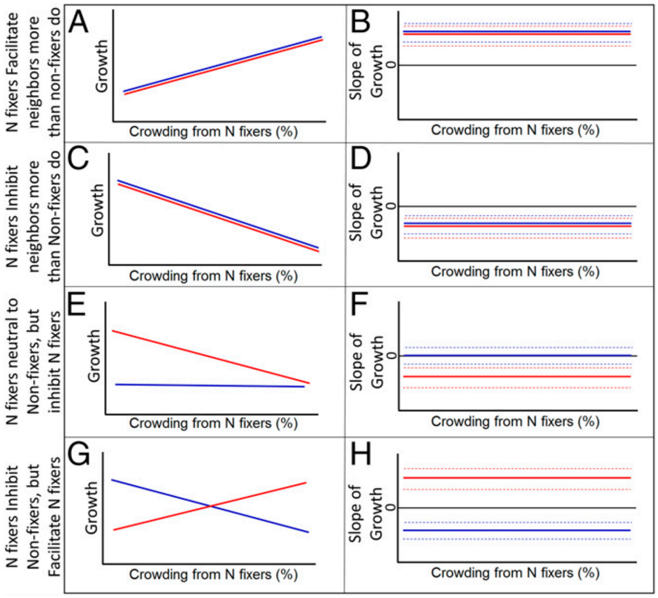

Fig. 1. Conceptual diagram illustrating potential effects of N fixers on neighboring trees. Potential effects of N fixers on neighbor growth (also applies to recruitment or survival) are shown (*A*, *C*, *E*, and *G*) along with the slopes of these relationships (*B*, *D*, *F*, and *H*). Red and blue lines indicate the response of neighboring N fixers and neighboring nonfixers, respectively. A positive slope (*A* and *B*) indicates that N fixers either facilitate or weakly inhibit their neighbors. A negative slope (*C* and *D*) indicates that N fixers strongly inhibit their neighbors. A zero slope (blue line in *E* and *F*) indicates that N fixers and nonfixers affect their neighbors equally.

percent of its crowding that comes from neighboring N fixers rather than from nonfixers—affects its growth, recruitment, and survival.

Results

If N fixers promote forest growth at the 1-ha plot level, we would expect a positive relationship between the abundance of N fixers and the annual increase in tree basal area of a plot. However, we found that plots with more N fixers had lower overall growth ($P < 0.0001$; Fig. 2*A*) and lower nonfixer growth ($P < 0.0001$; Fig. 2*C*), even after accounting for variation in total plot basal area. A change in N-fixer prevalence from 10 to 35% of the plot's basal area corresponded to a reduction of total annual growth from 2.2 to 0.6% and reduced nonfixer growth from 2.0 to 0.06%. To overcome potential confounding correlations between plot age, N-fixer abundance, and growth, we also assessed growth at the 10 × 10 m subplot scale within each plot. We found a nonsignificant negative trend between total growth and N-fixer prevalence ($P = 0.12$; Fig. 2*B*) and a significant negative correlation between nonfixer growth and N-fixer prevalence ($P < 0.0001$; Fig. 2*D*). These results suggest that N fixers are inhibiting, not facilitating, overall growth and growth of local nonfixers in our study region.

To gain a more mechanistic understanding of how individual N fixers drive plot-level growth patterns, we assessed how N fixers affect individual neighboring trees. This requires spatially explicit data on the demographic rates of individual trees over relatively long timescales. We estimated the degree of neighbor crowding that each individual experienced using a Neighborhood Crowding Index (NCI). A larger NCI (more crowding) could come from any combination of more neighbors, bigger neighbors, and closer neighbors. To estimate crowding from N fixers, we calculated the percent of each tree's NCI coming from neighboring N fixers—a continuous scale from 0 (all of an individual's neighbors are nonfixers) to 100% (all of an individual's neighbors are N fixers). We then used hierarchical Bayesian models to examine how crowding from N fixers affected the growth, survival, and recruitment of each tree (both N fixers and nonfixers), after accounting for overall crowding and tree size (27). Based on established changes in tree demographic rates at this site (19), we ran our models independently for forest stands ≤25 y old ("young forests") and >25 y old ("old forests").

If N fixers facilitate or weakly inhibit their neighbors, we would expect tree demographic rates to increase with crowding from N fixers (Fig. 1 *A* and *B*). Our results showed the opposite trend. N fixers strongly inhibited their neighbors—exhibiting greater negative effects on their neighbors than nonfixers did (Figs. 3 and 4 and *SI Appendix*, Figs. S2–S4, resembling Fig. 1 *C* and *D*). In young forests, crowding from N fixers strongly inhibited all demographic rates of neighboring nonfixers and strongly inhibited the growth rates of neighboring N fixers (Fig. 3). In old forests, N fixers strongly inhibited both the growth and survival of neighboring N fixers (Fig. 4). This N-fixer inhibition effect was stronger on the growth of neighboring N fixers than neighboring nonfixers regardless of forest age (Figs. 3*B* and 4*B*) and on the survival of neighboring N fixers in old forests (Fig. 4*F*). However, N fixers more strongly inhibited the recruitment of neighboring nonfixers than neighboring N fixers in young forests (Fig. 3*D*).

Discussion

Together, our individual-scale results and our 1-ha plot-scale findings show that N fixers in these forests inhibit their neighbors more than do nonfixers. It is important to note that the strong inhibition of N fixers we report is independent of the overall level of crowding and tree size. For example, an average-sized nonfixing tree (diameter at breast height [DBH] ~ 13 cm) with an average amount of crowding (NCI ~ 1,900) in a young forest stand would have a 43% lower expected growth rate if its neighbors were all N fixers than if its neighbors were all nonfixers. If this "average tree" is an N fixer itself, a neighborhood with all N fixers reduces its expected growth rate by over 60% compared with a neighborhood with all nonfixers.

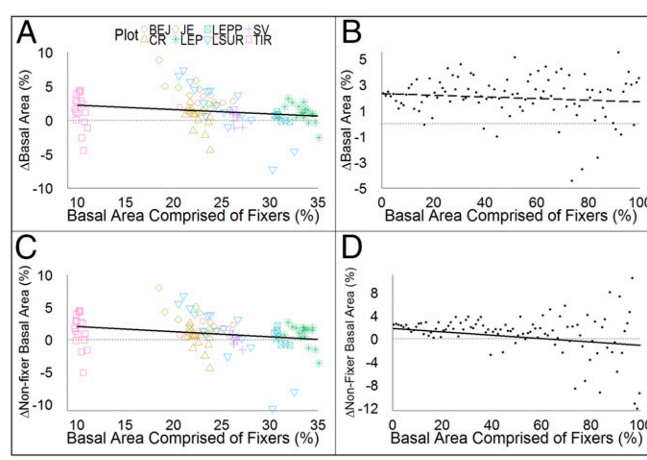

Fig. 2. Effects of N fixers on plot- and subplot-level basal area growth. At the plot level, changes in (*A*) total and (*C*) nonfixer basal area were negatively correlated with the proportion of the plot's basal area comprised of N fixers. Each point represents an individual plot over a single census period. At the subplot level, changes in (*B*) total and (*D*) nonfixer basal area were also negatively related to N-fixer prevalence, but this relationship was not significant for total basal area change (*B*). Points represent means of basal area change for all subplots within 1% bins of N-fixer prevalence. *A* and *C* represent 104 individual data points (plots in individual census years), and *B* and *D* represent 7,030 individual data points (subplots in individual census years).

Table 1. Characteristics of eight tropical forest study plots in the Bosques project

Plot	Age range, y	Basal area (±SE), m^2/ha	Fixer proportion of basal area (±SE)	Fixer proportion of stems (±SE)	Δ basal area (±SE), $m^2 \cdot ha^{-1} \cdot y^{-1}$
Bejuco (BEJ)	10–20	24.36 (±0.61)	0.23 (±0.007)	0.26 (±0.012)	0.60 (±0.069)
Juan Enrique (JE)	10–20	17.10 (±0.71)	0.21 (±0.007)	0.17 (±0.004)	0.74 (±0.100)
Lindero Sur (LSUR)	12–29	23.82 (±0.70)	0.25 (±0.008)	0.21 (±0.007)	0.42 (±0.211)
TIR	15–32	22.54 (±0.47)	0.10 (±0.001)	0.13 (±0.001)	0.31 (±0.133)
Lindero El Peje Secondary (LEPS)	20–37	29.48 (±0.42)	0.33 (±0.003)	0.19 (±0.004)	0.31 (±0.095)
Cuatro Rios (CR)	25–42	33.25 (±0.28)	0.22 (±0.002)	0.14 (±0.002)	0.12 (±0.136)
Lindero El Peje Primary (LEPP)	300+	30.40 (±0.17)	0.31 (±0.002)	0.11 (±0.001)	0.15 (±0.050)
Selva Verde (SV)	300+	33.26 (±0.12)	0.26 (±0.001)	0.09 (±0.001)	0.10 (±0.097)

Each plot name corresponds to an acronym used in Fig. 2. For each plot, the range of stand ages (years since agricultural abandonment) during the study period, mean total basal area, mean proportion of basal area comprised of N fixers, mean proportion of stems comprised of N fixers, and the mean annual change in basal area are presented along with SEs.

The negative influence that N fixers have on their neighboring trees in our study region is likely due to two factors. First, high growth and survival rates of N fixers in these plots (19), and the high nutrient demand of N fixers (15–17, 28), mean that N fixers likely cast more shade and take up more soil nutrients and water than do nonfixers. Second, the presumed facilitation of N fixation might not occur because nonfixers are not limited by N availability. It is also possible that facilitation might not occur because N fixers are not fixing much N, but we find this possibility less likely. The lower cost of acquiring N from the soil than from fixation (29) suggests that N fixers down-regulate fixation when soil N is available, and a number of recent studies are consistent with this idea (13, 24, 30). However, our observations from preliminary soil cores indicate that the N fixers in our plots commonly have active nodules, and theory suggests that even small amounts of N fixation can enhance the growth of neighboring nonfixers if they are N limited (31). This suggests that the N fixers in our study are not merely operating ecologically as nonfixers—they are bringing new N into these ecosystems—but rather that nonfixers in our study do not respond to this greater N availability.

Our results come from a single region with high annual rainfall, so they may not be ubiquitous across tropical forests. However, because ours is one of the few studies to assess the effect of N fixers on the growth of neighboring trees, statistical sampling suggests that our results are likely not rare. Beyond this sampling argument, several lines of evidence indicate that our findings might be common in moist tropical forests. First, the climate and soil type of our study area are commonly found in other moist tropical forest sites (32). Second, although we do not have rigorous soil N data from our plots, litterfall N and N transformation rates in our broad study area (La Selva Biological Station) are similar to those in many rainforests in the African, Asian, American, and Australian tropics (33, 34), indicating that N cycling at our site is representative of many moist tropical forests worldwide. Finally, the most likely mechanism for the strong competitive effects of N fixers that we found is high N-fixer growth rates, which are also common at other moist tropical forest sites (11, 13, 35).

Despite the similarities between our study site and many moist tropical forests, the heterogeneity in this biome (36) means that differences in local features, such as soil nutrient availability, may drive N fixers to have different effects on their neighbors in some sites. Although no other studies have assessed the effects of N fixers on the demographic rates of their neighbors in regenerating tropical forests, two previous studies have investigated how N fixers influence ecosystem-scale biomass accumulation in other regenerating moist tropical forests in Brazil and Panama (11, 13). Contrary to our 1-ha plot-scale findings, both of those studies showed that N fixers were correlated with total biomass accumulation, primarily due to N fixers' own high growth rates. Although N fixers also grow faster than nonfixers at our study sites (19), we found that N-fixing trees inhibit biomass accumulation at the plot scale (Fig. 2*A*) because their inhibition of neighbors outweighs their own rapid growth.

Why might N-fixers inhibit their neighbors more in our sites than in sites in Brazil (11) and Panama (13)? The three studies differ in the primary N-fixing taxa (*Pentaclethra macroloba* here vs. *Inga* spp. in ref. 13 and a diverse group of legumes in ref. 11) and the age range of succession studied (our youngest sites are 10 y vs. 5 y in ref. 13 and 2 y in ref. 11). One of our study plots, Tirimbina (TIR), was dominated by *Inga* rather than *P. macroloba* N fixers yet still demonstrated the same patterns as our other

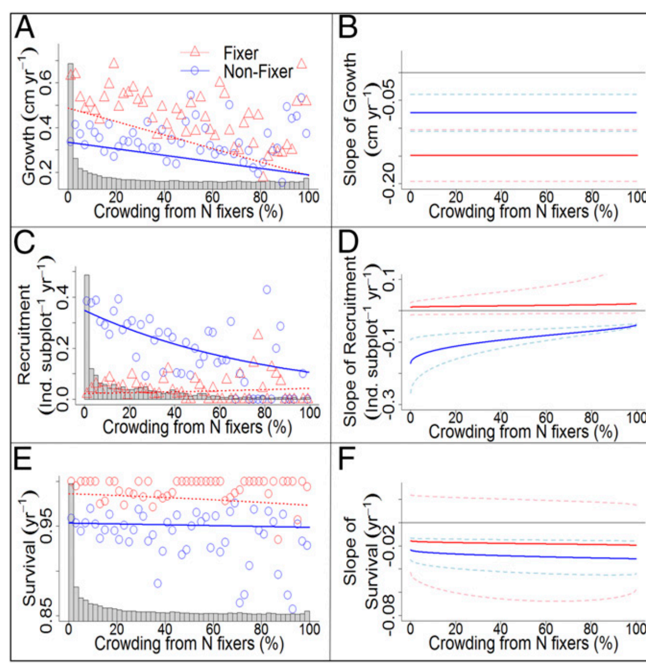

Fig. 3. Effects of N-fixer crowding on neighboring trees in young (≤25 y) forests. Growth (*A*), recruitment (*C*), and survival (*E*) of N fixers (red) and nonfixers (blue) are plotted as a function of the proportion of a tree's crowding coming from N fixers. Each symbol represents a binned average of trees. Gray histograms represent the relative data density in each proportion bin. Median slopes (solid curves) and their 95% credible intervals (CIs; dashed curves) are shown for growth (*B*), recruitment (*D*), and survival (*F*). Nonoverlapping 95% CIs indicate significant differences. These plots show the effects of N fixers on neighboring trees, independent of overall tree crowding and tree size. Growth and survival models (*A*, *B*, *E*, and *F*) represent 20,586 data points (individual trees), and recruitment models (*C* and *D*) represent 2,770 individual data points (subplots).

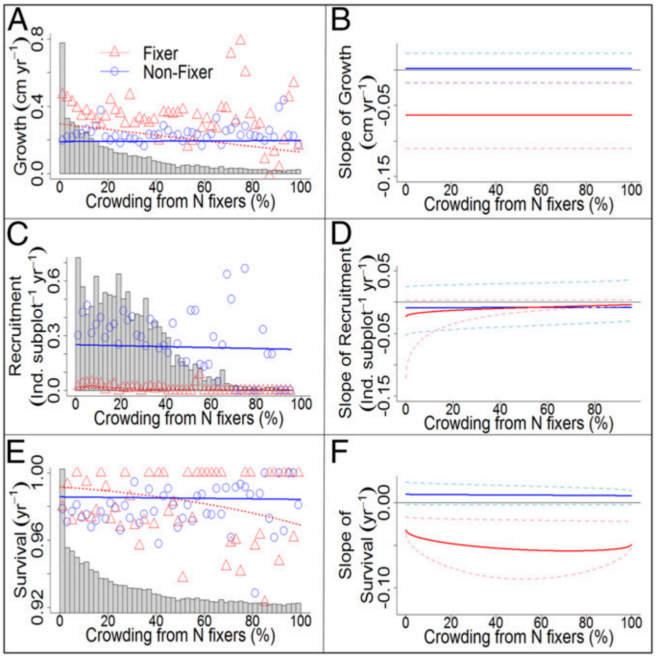

Fig. 4. Effects of N-fixer crowding on neighboring trees in old (>25 y) forests. Growth (*A*), recruitment (*C*), and survival (*E*) as well as the slopes of growth (*B*), recruitment (*D*), and survival (*F*) are plotted as a function of the proportion of a tree's crowding coming from N fixers. All colors and symbols are as in Fig. 3. Growth and survival models (*A*, *B*, *E*, and *F*) represent 27,065 data points (individual trees), and recruitment models (*C* and *D*) represent 3,259 individual data points (subplots).

plots—N fixers inhibited neighbors more than did nonfixers (*SI Appendix*, Fig. S7)—suggesting that species identity is not the primary driver of our results. Could the age range explain the discrepancy? In a site near ours, Gilman et al. (37) experimentally planted a diverse set of N fixers in fallow cattle pasture and found no positive influence of these N fixers on the recruitment and growth of neighboring trees during the first 5 y of succession. Their study suggests that N fixers do not facilitate their neighbors at earlier ages in these forests, but given the substantial differences between studies (e.g., naturally regenerating forest in ours vs. experimental planting in theirs), we cannot rule out the possibility that N fixers might have facilitated or weakly inhibited neighbors in earlier years in our plots. More likely, however, other site-specific factors like soil water, nitrogen, phosphorus, and molybdenum availability explain the discrepancy between inhibitory versus facilitative effects of N fixers in our region versus other sites. More broadly, N fixers may play different roles in the dynamics of dry forests (38), which cover 523 million hectares of the world's tropics (39).

Current modeling efforts allow for high C-capturing potential in tropical secondary forests, but only if *N*-fixing trees relieve N limitation (8, 10). Based on the N inputs of N fixers into these systems, modelers may be tempted to use high N-fixer abundances in forests as an indicator of high growth and C-capturing potential, especially given that advances in remote sensing of tropical N fixers (40) may soon make abundance data much more readily available than direct data on N inputs. Our findings suggest that these modeling results might be misleading for some or even many moist tropical forest sites and that a more critical evaluation of N fixers' effect on forest growth is needed to accurately predict the regeneration dynamics and future C sink of the world's secondary tropical forests.

Conclusions

The influence that N fixers have on the surrounding forest is a balance between their negative competitive interactions with neighboring plants and the facilitative effects of their N inputs into the surrounding ecosystem. Because their ability to bring N into ecosystems is both important and rare within the plant kingdom, it is easy to focus on the potential facilitative effects of N fixers. However, our results demonstrate that the competitive effects of N fixers on their neighbors can be sufficiently strong that N fixers inhibit tropical forest growth. Many Earth System models now incorporate dynamic N cycles (including N fixation) into estimates of future tropical forest carbon capture. As we refine how N fixers are incorporated into these models, our results highlight that we must consider that N fixers may have a negative influence on tropical forests' ability to capture and store C in some sites. Given the large potential for C capture in regenerating tropical forests, improving our understanding of how N fixers influence this C-capturing potential is vital to our ability to predict future climate scenarios.

Methods

Plot and Census Data Description. We studied eight 1-ha plots in a humid tropical rainforest in the Caribbean lowlands of northeastern Costa Rica, in and around La Selva Biological Station (10.4233°N, 84.022°W). All plots are within 15 km of each other, are similar in elevation (5–220 m), have similar topography and soil type, and experience similar climatic conditions. Similar sets of species dominate all of the plots, but species-relative abundances change with stand age throughout succession in our plots (25). *P. macroloba*, an N fixer, was the most common species across all plots, and *Inga cocleensis* and *Inga pezizifera* were the second and third most abundant N fixers in our dataset (*SI Appendix*, Table S4). The three most common nonfixing species across all of our plots were *Miconia affinis*, *Casearia arborea*, and the palm *Socratea exorrhiza*. Detailed descriptions of plot design and census methods are available elsewhere (19, 26, 41).

Each plot is 50 × 200 m, for a total area of 1 ha. Plots are broken up into 100 square subplots with 10 m sides. Six plots are located in naturally regenerating secondary forests that ranged in age from 10 to 25 y at the time of establishment. The remaining two plots are located in primary, old-growth forest that has remained undisturbed for at least 200 y. Within each plot, all adult trees ≥5 cm DBH were tagged, identified to species, measured for diameter at breast height (1.3 m above ground level), and mapped onto a plot-level *x,y* coordinate system using the subplot corners as reference points. Based on species identification, each tree was categorized as a putative N fixer or nonfixer based on methods in ref. 19. This designation followed a three-tiered approach in which species identifications were first checked for reports of nodulation in ref. 42 and the US Forest Service's GRIN database. After these two N-fixer lists were exhausted, we assigned species as N fixers if they were in a genus with ≥60% congeners that were confirmed N fixers, as fixation is thought to be a trait primarily conserved at the genus level.

Plot-Scale Effects of N Fixers. To determine the effect of N fixers on plot- and subplot-level growth, we calculated the percent change in tree basal area (ΔBA) as the change in tree basal area divided by the total tree basal area for each plot or subplot over each census period and multiplied by 100. Changes in nonfixer basal area were scaled by total nonfixer basal area in the same fashion. We used generalized mixed linear regression to model changes in total basal area and nonfixer basal area in response to the proportion of a plot or subplot comprised of N fixers accounting for variation in total basal area and including a random plot effect.

Individual-Scale Effects of N Fixers. At the individual scale, we calculated absolute growth rate and survival of each tree over each annual census period. For recruitment, we calculated the frequency of recruits into each 10 × 10 m subplot over each annual census period. NCI was calculated as the squared DBH of each neighbor divided by the squared distance of that neighbor to the focal individual, summed for all neighbors within 10 m. We modeled the response of individual growth and survival, and subplot recruitment, to the NCI and proportion of NCI comprised of N fixers that each individual or subplot experienced using a hierarchical Bayesian approach. Each demographic process (growth, recruitment, and survival) was individually modeled as a response to the effects of NCI, the proportion of NCI made up of N-fixers, DBH (for growth and survival), and the interactions between these variables, as well as the plant's fixer type (N fixer or nonfixer) and plot. We interpreted 95% credible intervals that did not overlap 0 as statistically significant.

For each tree in each census year, we indicated whether that individual had recruited into the adult dataset or suffered a mortality event. We calculated growth since the previous census for each tree that was present in consecutive census years. Recruitment and mortality were treated as binary variables for each individual in each census year. Growth rate was calculated as $G_{i,c} = (DBH_{i,c} - DBH_{i,c-1})/t$, where $G_{i,c}$ is the growth rate of tree i in census c, $DBH_{i,c}$ is the DBH of tree i in census c, and t is the time interval between censuses. Because census intervals varied slightly from year to year, t was calculated as the time between measurements of an individual tree in days. The NCI of each tree was calculated to represent the crowding that each individual experienced within a set radius around the individual's stem. We calculated NCI as $NCI_i = \sum_{j=1, j\neq i}^{n} DBH_j^2/d_{j,i}^2$, where NCI of individual i is the sum of the squared DBH of all neighbors j divided by the squared distance of each neighbor j to individual i of which there are n number of neighbors within a set radius of 10 m. Using a radius of 10 m meant that all trees ≤10 m from the plot edge were excluded as focal trees from neighborhood-scale analyses as NCI could not be accurately calculated along the plot edge.

Model Description. We used a set of three Bayesian models to determine how tree size, fixation status, and neighborhood crowding influence the growth and survival of an individual tree, and the recruitment of individuals into 10 × 10 m subplots, in a given census year. Data for DBH and NCI were natural log-transformed, and data for the proportion of NCI comprised of N fixers were arcsine-square root transformed before analysis. Each demographic model estimated the effect of each covariate—ln(DBH), ln(NCI), the proportion of NCI comprised of N fixers (arcsin[$\sqrt{Neigh\_Fix}$]), ln(DBH) × ln(NCI), ln(NCI)^2, and ln(NCI) × (arcsin[$\sqrt{Neigh\_Fix}$])—on the demographic response variable (growth, recruitment, or survival). Random intercepts were included in the growth and survival models for each species, individual, and plot, and in the recruitment model for each plot and stem. To allow for comparison between variables in different units, data for growth, DBH, NCI, and Neigh_Fix were z-transformed by subtracting the mean value for that variable and dividing by the SD. Within the model, each of these parameter estimates could vary based on whether the individual was an N fixer or nonfixer. We modeled each parameter estimate as a normal distribution with uninformative priors (mean and SD of 0 and 100, respectively), and all error terms associated with random effects (plot, species, and individual random effects) were modeled as gamma distributions with uninformative priors (shape and scale of 100 and 100, respectively). All models were run in the stan package of R version 3.2.2 (43).

Standardized absolute growth rate data (change in the DBH of a tree over the census period; $G_{i,c}$ in cm·d^{-1}) were modeled as a function of each of the six transformed covariates listed above along with random intercept effects for individual tree ID, species ID, and plot. Each parameter estimate could vary based on the N fixation status of the individual tree. The structure of the growth model was as follows:

$$G_{i,j,p,f} \sim Normal\left(E\left(G_{i,j,p,f}\right), \sigma^2\right)$$

$$\begin{aligned} E\left(G_{i,j,p,f}\right) = {} & \mu_{j,f} + (\sigma_i) + (\sigma_p) + (Plot_p) + (\beta_{1,f} * DBH_i) + (\beta_{2,f} * NCI_i) \\ & + (\beta_{3,f} * Neigh\_Fix_i) + \left(\beta_{4,f} * NCI_i^2\right) + (\beta_{5,f} * (DBH_i * NCI_i)) \\ & + (\beta_{6,f} * (NCI_i * Neigh\_Fix_i)), \end{aligned}$$

where G and $E(G)$ are the standardized growth rate of individual i of species j in plot p with fixation status f and its expected value, respectively. The intercept ($\mu_{j,f}$) is species-specific and fixation-specific, and the error terms represent the random effects of individual stem (σ_i) and plot (σ_p) to account for repeated measurements. Parameter estimates β_1–β_6 were modeled for each covariate (described above) and allowed to vary based on the fixation status (f) of the individual.

Survival was modeled as a binary variable using a logit link, which could vary as a function of the six covariates used in the growth model with random species-specific and fixation-species intercepts ($\mu_{j,f}$), and random effects for individual i and plot p (σ_i, σ_p). Again, each parameter estimate could vary based on the fixation status of the individual. The structure of the survival model was:

$$S_{i,j,p,f} \sim Bernouli\left(s_{i,j,p,f}\right)$$

$$\begin{aligned} s_{i,j,p,f} \sim {} & logit^{-1}\left[\mu_{j,f} + (\sigma_i) + (\sigma_p) + (\beta_{1,f} * DBH_i) + (\beta_{2,f} * NCI_i)\right. \\ & + (\beta_{3,f} * Neigh\_Fix_i) + \left(\beta_{4,f} * NCI_i^2\right) + (\beta_{5,f} * (DBH_i * NCI_i)) \\ & \left. + (\beta_{6,f} * (NCI_i * Neigh\_Fix_i))\right]^t, \end{aligned}$$

where S and s represent the survival and the probability of survival, respectively, of an individual (i) in a given time interval (t) with all subscripts the same as the growth and model above.

Recruitment was modeled as the frequency of individual trees recruiting into each 10 × 10 m subplot, that varied as a function of the standardized, transformed covariates: average NCI of trees in that subplot [ln(NCI)], the average proportion of NCI comprised of N fixers for all trees in the subplot [arcsin($\sqrt{Neigh\_Fix}$)], ln(NCI)^2, and ln(NCI) × the proportion of NCI comprised of N fixers [arcsin($\sqrt{Neigh\_Fix}$)], with random intercepts for plot and subplot. For our recruitment model, we did not include any covariates corresponding to the DBH of recruiting trees as all recruits had DBHs at or very close to the minimum size classified in the dataset (5 cm). As with the growth model above, each parameter estimate could vary based on the fixation status of the individual. Because recruitment into a subplot within a year was often 0, we used an adjusting model structure, which used both Bernoulli and Poisson distributions to model the 0-inflated subplot recruitment data as follows:

$$Rec_{i,j,p,f} \sim \begin{cases} Bernouli\left(logit^{-1}\left(r_{i,j,p,f}\right)^t\right) & with\ probability\ \alpha \\ Poisson\left(r_{i,j,p,f}\right) & with\ probability\ 1-\alpha \end{cases}$$

$$\begin{aligned} r_{i,j,p,f} \sim {} & \mu_{j,f} + (\sigma_i) + (\sigma_{sp}) + (\beta_{1,f} * NCI_i) + (\beta_{2,f} * Neigh\_Fix_i) \\ & + \left(\beta_{3,f} * NCI_i^2\right) + \left(\beta_{4,f} * (NCI_i * Neigh\_Fix)_i\right), \end{aligned}$$

where Rec is the recruitment of an individual in a given census year with all subscripts the same as in the growth and survival equations above except for σ_{sp}, which represents the random effect of subplot.

ACKNOWLEDGMENTS. We thank J. Paniagua, B. Paniagua, and E. Salicetti for their work collecting field data and M. Uriarte, N. Schwartz, and A. Quebbeman for statistical advice. This work was supported by NSF Grants DEB-0424767, DEB-0639393, and DEB-1147429; the Andrew W. Mellon Foundation; the NASA Terrestrial Ecology Program; and the University of Connecticut Research Foundation (to R.L.C.).

1. Brown S, Lugo AE (1990) Tropical secondary forests. *J Trop Ecol* 6:1–32.
2. Chazdon RL, et al. (2009) The potential for species conservation in tropical secondary forests. *Conserv Biol* 23:1406–1417.
3. Pan Y, et al. (2011) A large and persistent carbon sink in the world's forests. *Science* 333:988–993.
4. Poorter L, et al. (2016) Biomass resilience of Neotropical secondary forests. *Nature* 530:211–214.
5. Davidson E, et al. (2004) Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. *Ecol Appl* 14:150–163.
6. Davidson EA, et al. (2007) Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. *Nature* 447:995–998.
7. Hungate BA, Dukes JS, Shaw MR, Luo Y, Field CB (2003) Atmospheric science. Nitrogen and climate change. *Science* 302:1512–1513.
8. Gerber S, Hedin LO, Keel SG, Pacala SW, Shevliakova E (2013) Land use change and nitrogen feedbacks constrain the trajectory of the land carbon sink. *Geophys Res Lett* 40:5218–5222.
9. Gerber S, Hedin LO, Oppenheimer M, Pacala SW, Shevliakova E (2010) Nitrogen cycling and feedbacks in a global dynamic land model. *Global Biogeochem Cycles* 24:1–15.
10. Wårlind D, Smith B, Hickler T, Arneth A (2014) Nitrogen feedbacks increase future terrestrial ecosystem carbon uptake in an individual-based dynamic vegetation model. *Biogeosciences* 11:151–185.
11. Gehring C, Vlek PLG, de Souza LAG, Denich M (2005) Biological nitrogen fixation in secondary regrowth and mature rainforest of central Amazonia. *Agric Ecosyst Environ* 111:237–252.
12. Binkley D, Giardina C (1997) Nitrogen fixation in tropical forest plantations. *ACIAR Monogr Ser* 43:297–337.
13. Batterman SA, et al. (2013) Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. *Nature* 502:224–227.
14. Chapin F, Walker L, Fastie C, Sharman L (1994) Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecol Monogr* 64:149–175.
15. Adams MA, Turnbull TL, Sprent JI, Buchmann N (2016) Legumes are different: Leaf nitrogen, photosynthesis, and water use efficiency. *Proc Natl Acad Sci USA* 113: 4098–4103.
16. Nasto MK, et al. (2014) Interactions among nitrogen fixation and soil phosphorus acquisition strategies in lowland tropical rain forests. *Ecol Lett* 17:1282–1289.
17. Fyllas NM, et al. (2009) Basin-wide variations in foliar properties of Amazonian forest: Phylogeny, soils and climate. *Biogeosciences* 6:2677–2708.
18. Townsend AR, Cleveland CC, Asner GP, Bustamante MMC (2007) Controls over foliar N:P ratios in tropical rain forests. *Ecology* 88:107–118.
19. Menge DNL, Chazdon RL (2016) Higher survival drives the success of nitrogen-fixing trees through succession in Costa Rican rainforests. *New Phytol* 209:965–977.

20. Boyden S, Binkley D, Senock R (2005) Competition and facilitation between *Eucalyptus* and nitrogen-fixing *Falcataria* in relation to soil fertility. *Ecology* 86:992–1001.
21. ter Steege H, et al. (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* 443:444–447.
22. Menge DN, Lichstein JW, Angeles-Pérez G (2014) Nitrogen fixation strategies can explain the latitudinal shift in nitrogen-fixing tree abundance. *Ecology* 95:2236–2245.
23. Menge DNL, et al. (2017) Nitrogen-fixing tree abundance in higher-latitude North America is not constrained by diversity. *Ecol Lett* 20:842–851.
24. Sullivan BW, et al. (2014) Spatially robust estimates of biological nitrogen (N) fixation imply substantial human alteration of the tropical N cycle. *Proc Natl Acad Sci USA* 111: 8101–8106, and erratum (2015) 112:E4157.
25. Chazdon RL, et al. (2007) Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philos Trans R Soc Lond B Biol Sci* 362: 273–289.
26. Lasky JR, Uriarte M, Boukili VK, Chazdon RL (2014) Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. *Proc Natl Acad Sci USA* 111:5616–5621.
27. Canham CD, LePage PT, Coates KD (2004) A neighborhood analysis of canopy tree competition: Effects of shading versus crowding. *Can J For Res* 34:778–787.
28. McKey D (1994) Legumes and nitrogen: The evolutionary ecology of a nitrogen-demanding lifestyle. *Advances in Legume Systematics 5: The Nitrogen Factor*, eds Sprent J, McKey D (Royal Botanic Gardens, Kew, UK), pp 211–228.
29. Gutschick V (1981) Evolved strategies in nitrogen acquisition by plants. *Am Nat* 118: 607–637.
30. Barron AR, Purves DW, Hedin LO (2011) Facultative nitrogen fixation by canopy legumes in a lowland tropical forest. *Oecologia* 165:511–520.
31. Menge DNL, Wolf AA, Funk JL (2015) Diversity of nitrogen fixation strategies in Mediterranean legumes. *Nat Plants* 1:15064.
32. McDade L, Hartshorn G (1994) *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (University of Chicago, Chicago).
33. Brookshire ENJ, Gerber S, Menge DNL, Hedin LO (2012) Large losses of inorganic nitrogen from tropical rainforests suggest a lack of nitrogen limitation. *Ecol Lett* 15: 9–16.
34. Vitousek PM, Matson PA (1988) Nitrogen transformations in a range of tropical forest soils. *Soil Biol Biochem* 20:361–367.
35. Pearson H, Vitousek P (2001) Stand dynamics, nitrogen accumulation, and symbiotic nitrogen fixation in regenerating stands of *Acacia koa*. *Ecol Appl* 11:1381–1394.
36. Townsend AR, Asner GP, Cleveland CC (2008) The biogeochemical heterogeneity of tropical forests. *Trends Ecol Evol* 23:424–431.
37. Gilman A, et al. (2016) Recovery of floristic diversity and basal area in natural forest regeneration and planted plots in a Costa Rican wet forest. *Biotropica* 48:798–808.
38. Ferreira da Silva A, et al. (2017) Biological nitrogen fixation in tropical dry forests with different legume diversity and abundance. *Nutr Cycl Agroecosyst* 107:321–334.
39. Bastin J-F, et al. (2017) The extent of forest in dryland biomes. *Science* 356:635–638.
40. Asner GP, Jones MO, Martin RE, Knapp DE, Hughes RF (2008) Remote sensing of native and invasive species in Hawaiian forests. *Remote Sens Environ* 112:1912–1926.
41. Chazdon R, Brenes AR, Alvarado BV (2005) Effects of climate and stand age on annual tree dynamics in tropical second-growth rain forests. *Ecology* 86:1808–1815.
42. Sprent JI (2009) *Legume Nodulation: A Global Perspective* (Wiley-Blackwell, Oxford, UK).
43. R Core Team (2015) *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna), Version 3.2.2.

Supplemental Appendix

Figure S1. a) Summed basal area of each plot in each census year. b) The proportional change in the total basal area of a plot (change in basal area divided by the total basal area for each plot in each census period) averaged across the entire study duration for each plot plotted against the mean proportion of the plot's basal area comprised of N fixers.

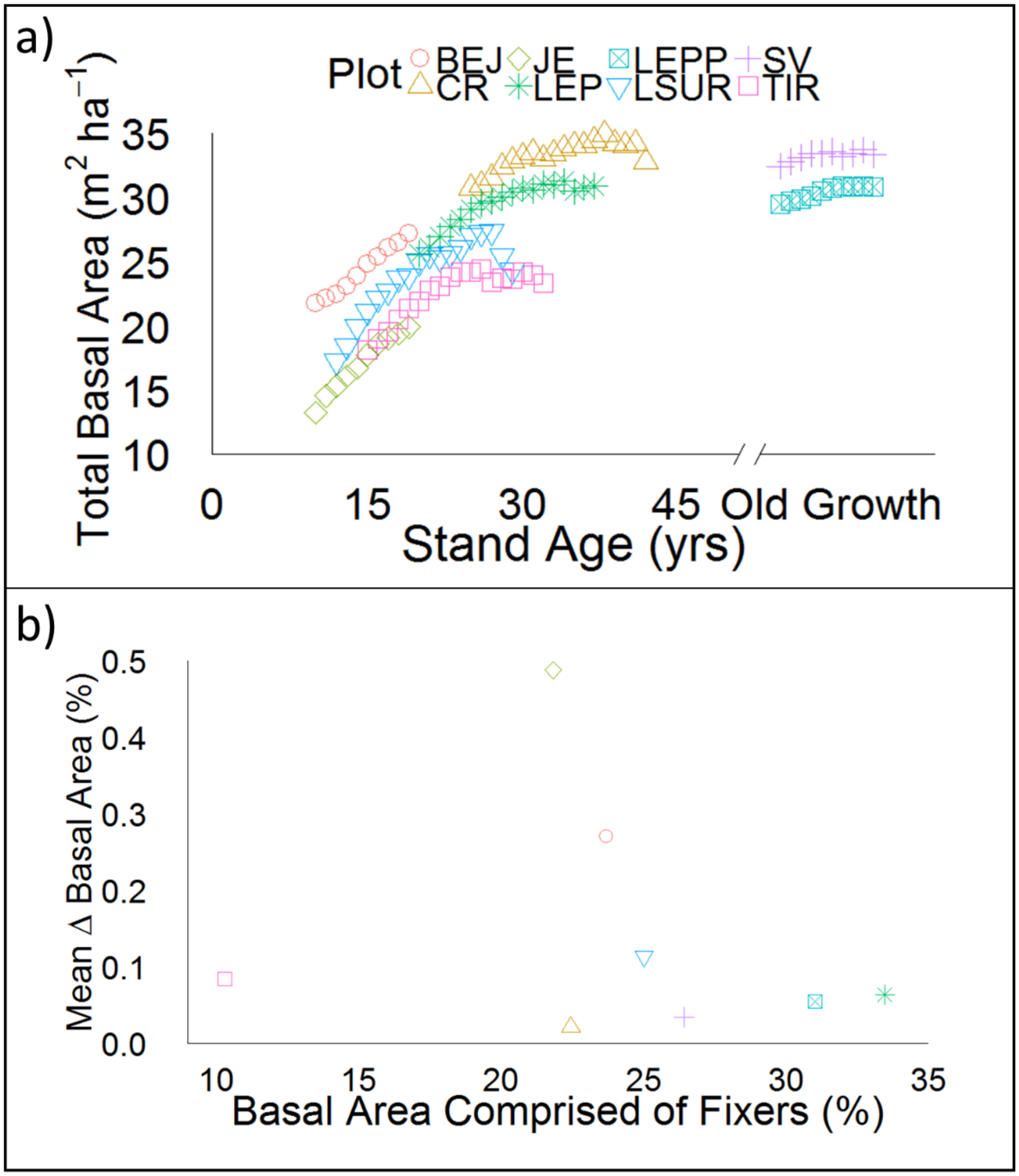

Figure S2. Parameter estimate plot for the effect of each model covariate (left axis) on the relative growth rate of N fixers and non-fixers (right axis) in forests a) ≤ 25 yrs, and b) > 25 yrs since disturbance. Covariates from bottom to top are NCI, DBH, the proportion of NCI comprised of N fixers (NEIGHfix), NCI^2, NCI x DBH, and NCI x the proportion of NCI comprised of N fixers. Dots represent the parameter estimate for each covariate with the 95% credible interval (CI) represented by solid lines on either side of the dot. Solid dots represent covariates for which the 95% CI does not overlap 0 (which we interpret as statistical significance), and open circles represent those covariates for which the 95% CI does overlap 0.

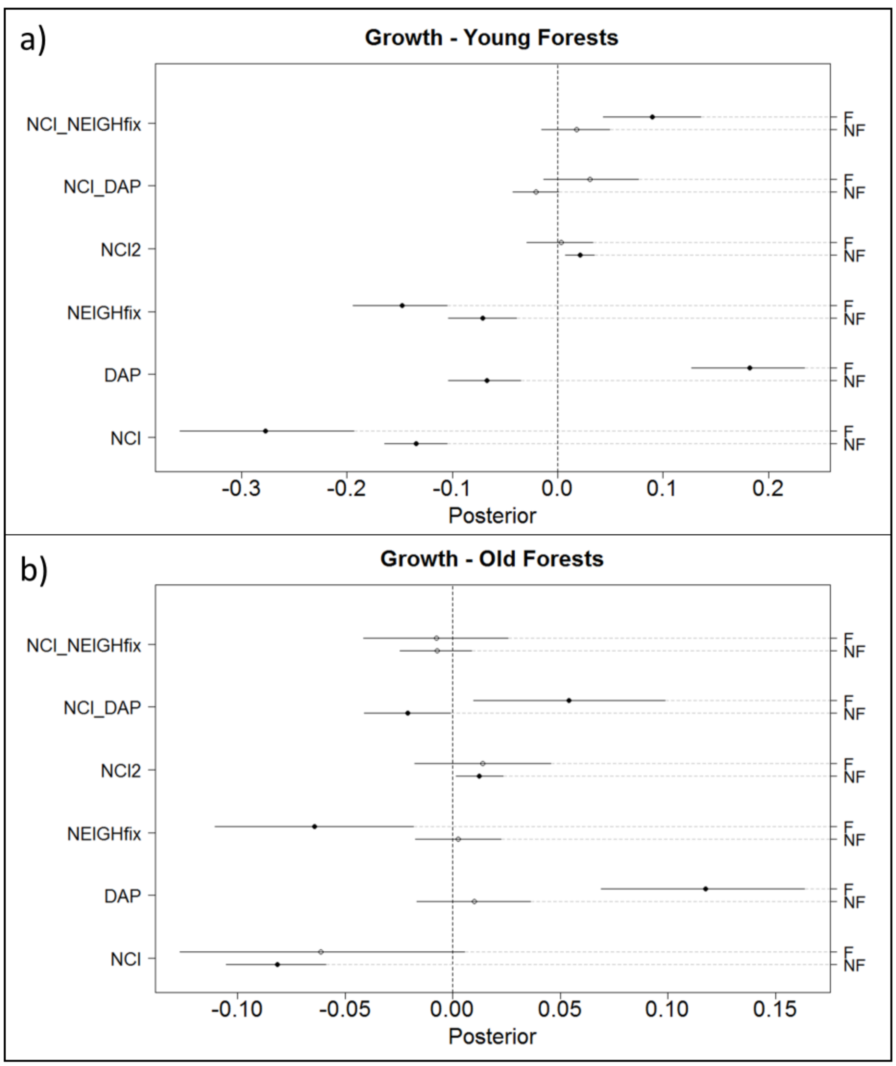

Figure S3. Parameter estimate plot for the effect of each model covariate (left axis) on the recruitment of N fixers and non-fixers (right axis) in forests a) ≤ 25 yrs, and b) > 25 yrs since disturbance. All covariates and symbols correspond to the description above in the caption for Figure S2.

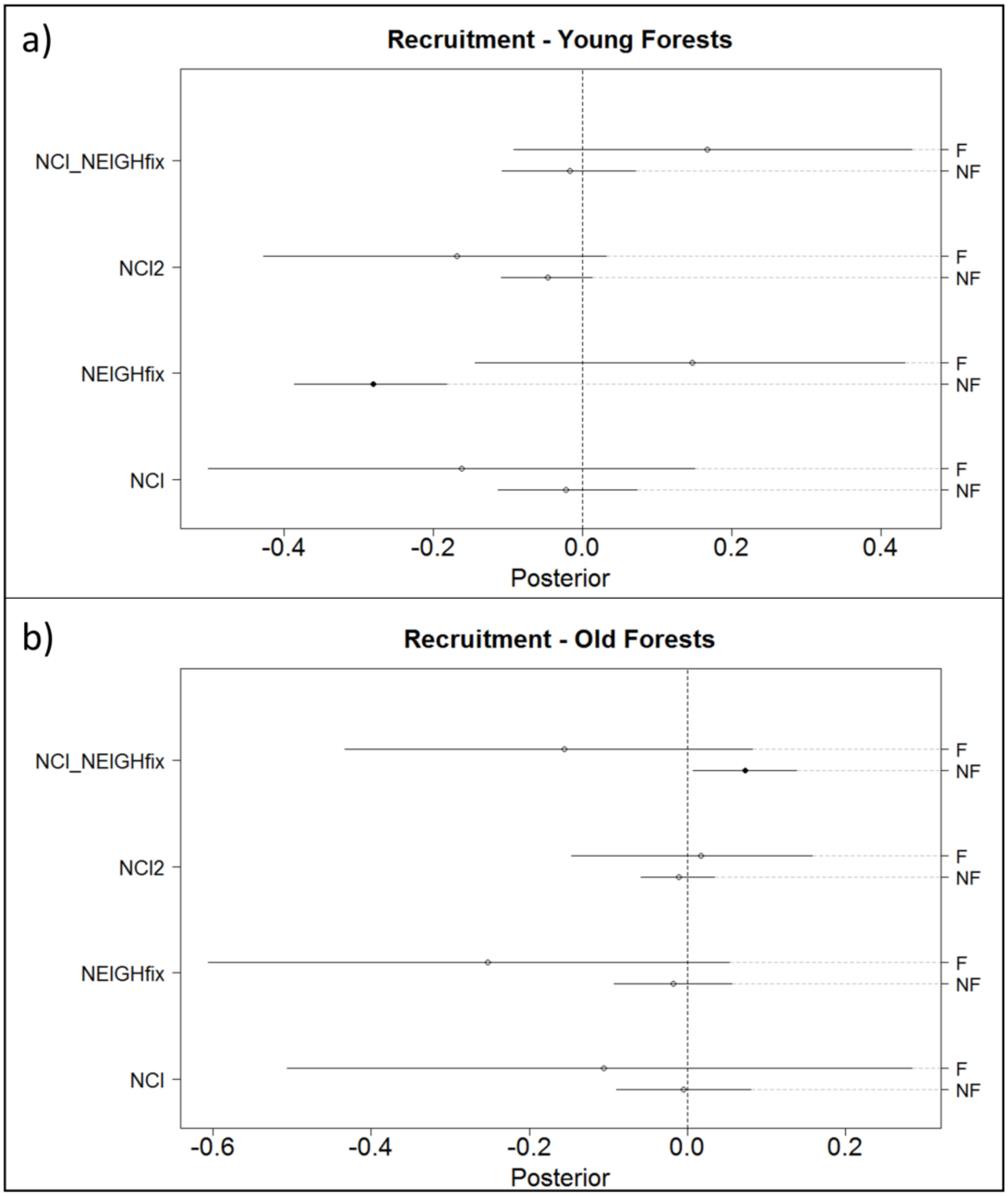

Figure S4. Parameter estimate plot for the effect of each model covariate (left axis) on the survival of N fixers and non-fixers (right axis) in forests a) ≤ 25 yrs, and b) > 25 yrs since disturbance. All covariates and symbols correspond to the description above in the caption for Figure S2.

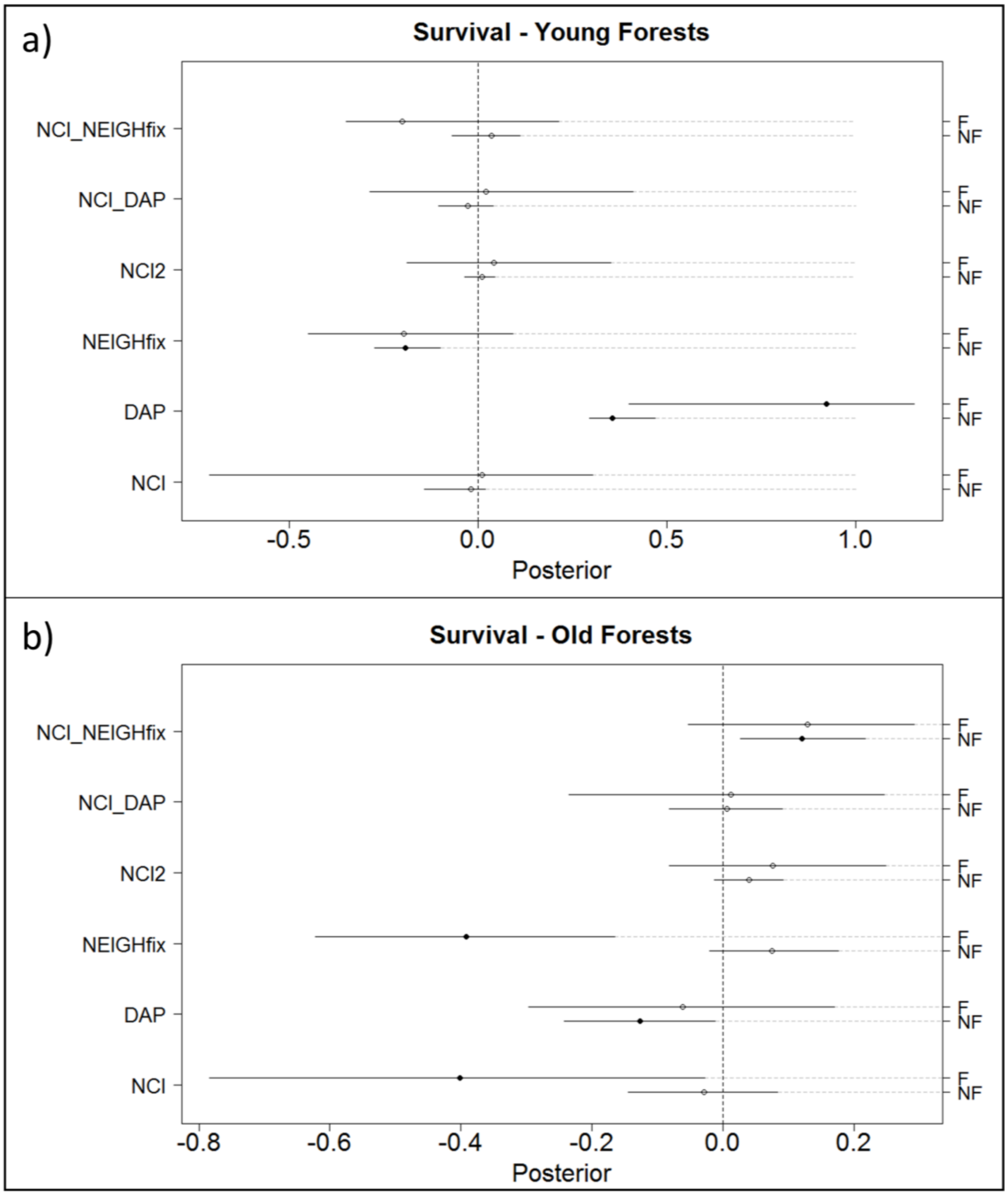

Figure S5. Effects of NCI on N fixers and non-fixers in young (≤ 25 yr) forests. Growth (a), recruitment (c), and survival (e) of N fixers (red) and non-fixers (blue) are plotted as a function of crowding (NCI). Each symbol represents an average of trees binned across 50 NCI units. Curves represent model fit means as a function of NCI, for an average DBH and proportion of NCI coming from N fixers. Histograms represent the relative data density in each proportion bin. Median slopes are shown for growth (b), recruitment (d), and survival (f) from posterior distributions of our individual-scale models. Dashed lines show 95% credible intervals (CI's) around the median. Where 95% CI's do not overlap 0 indicates that negative or positive effects of NCI are significant. Where 95% CI's for N fixers and non-fixers do not overlap each other indicates that NCI has significantly different effects on N fixers and non-fixers.

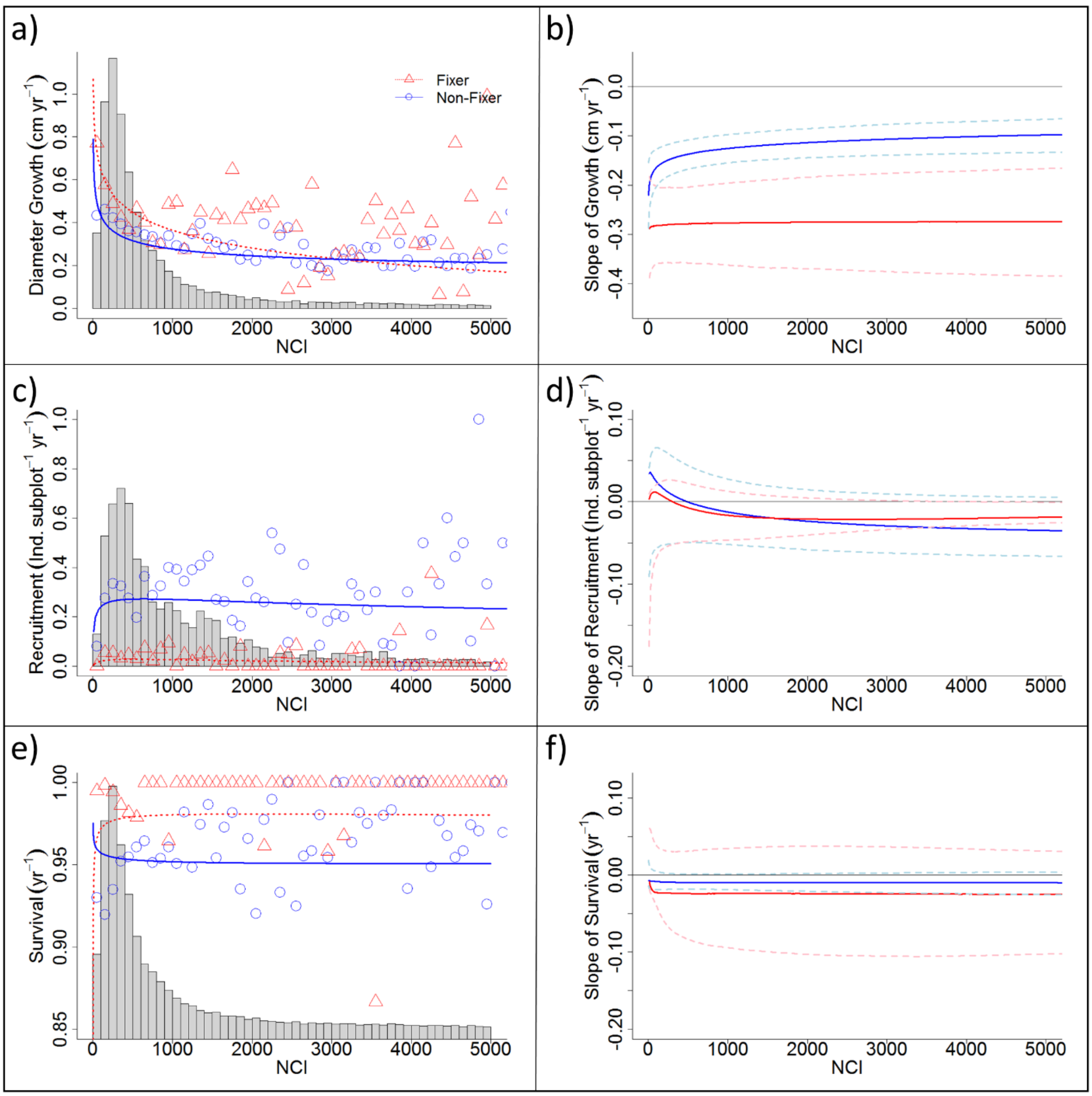

Figure S6. Effects of NCI on N fixers and non-fixers in old (> 25 yr) forests. Growth (a), recruitment (c), and survival (e) of N fixers (red) and non-fixers (blue) are plotted as a function of crowding (NCI). Each symbol represents an average of trees binned across 50 NCI units. Curves represent model fit means as a function of NCI, for an average DBH and proportion of NCI coming from N fixers. Histograms represent the relative data density in each proportion bin. Median slopes are shown for growth (b), recruitment (d), and survival (f) from posterior distributions of our individual-scale models. Colors and symbols are as in Fig S5.

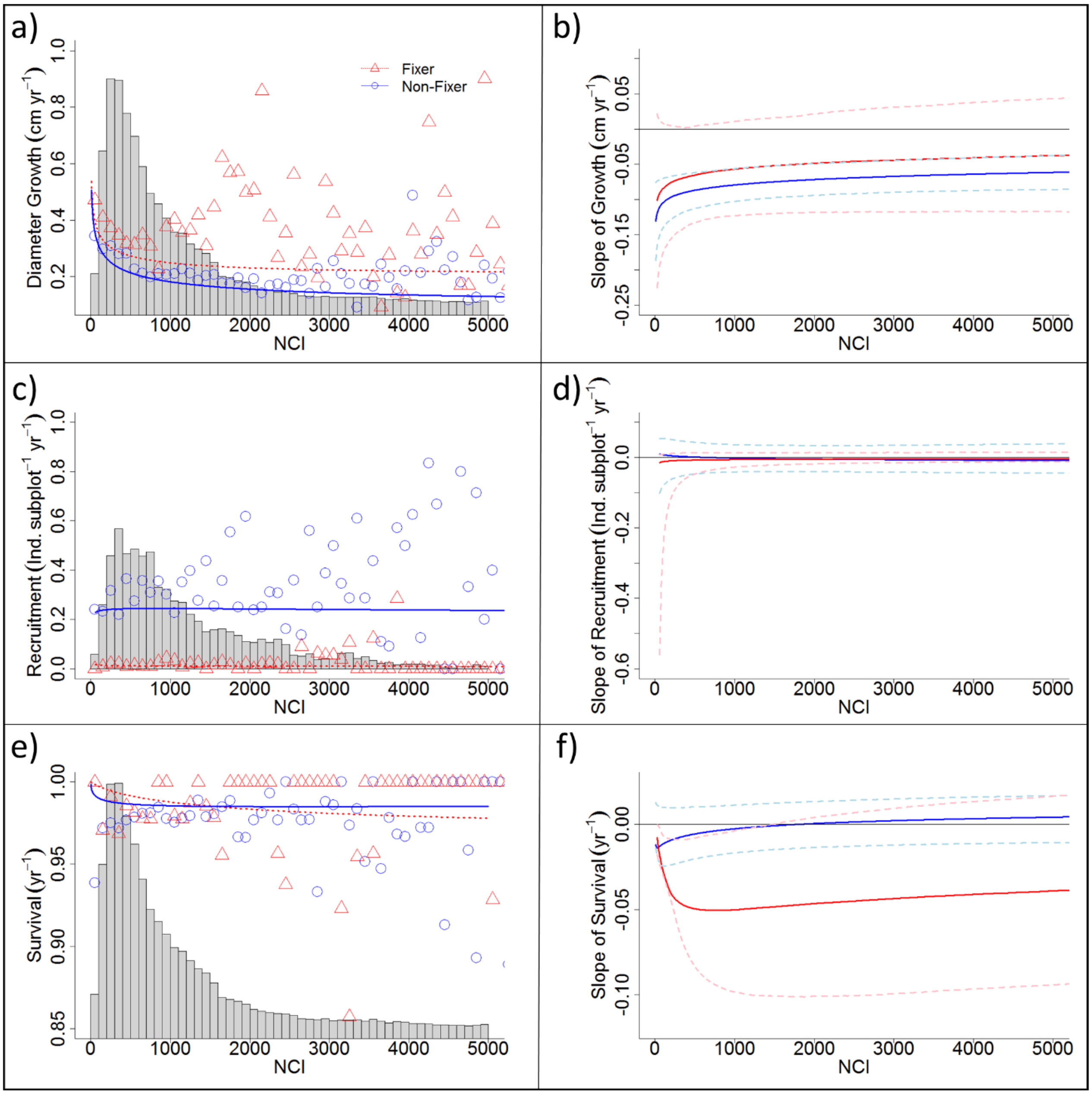

Figure S7. The effect of N fixers on plot- and individual-level growth in study plot TIR, which does not contain *Pentaclethra macroloba*, the dominant N fixer in the other 7 plots. At the plot level, the prevalence of N fixers was marginally negatively correlated with the change in basal area of a) all trees ($P = 0.08$), and b) non-fixers ($P = 0.06$). C) Effect of crowding by N fixers on the growth of individual N fixers (red; $P < 0.001$) and non-fixers (blue; $P < 0.001$). Lines represent linear regression models, and all colors and symbols for c) are as in Fig S5.

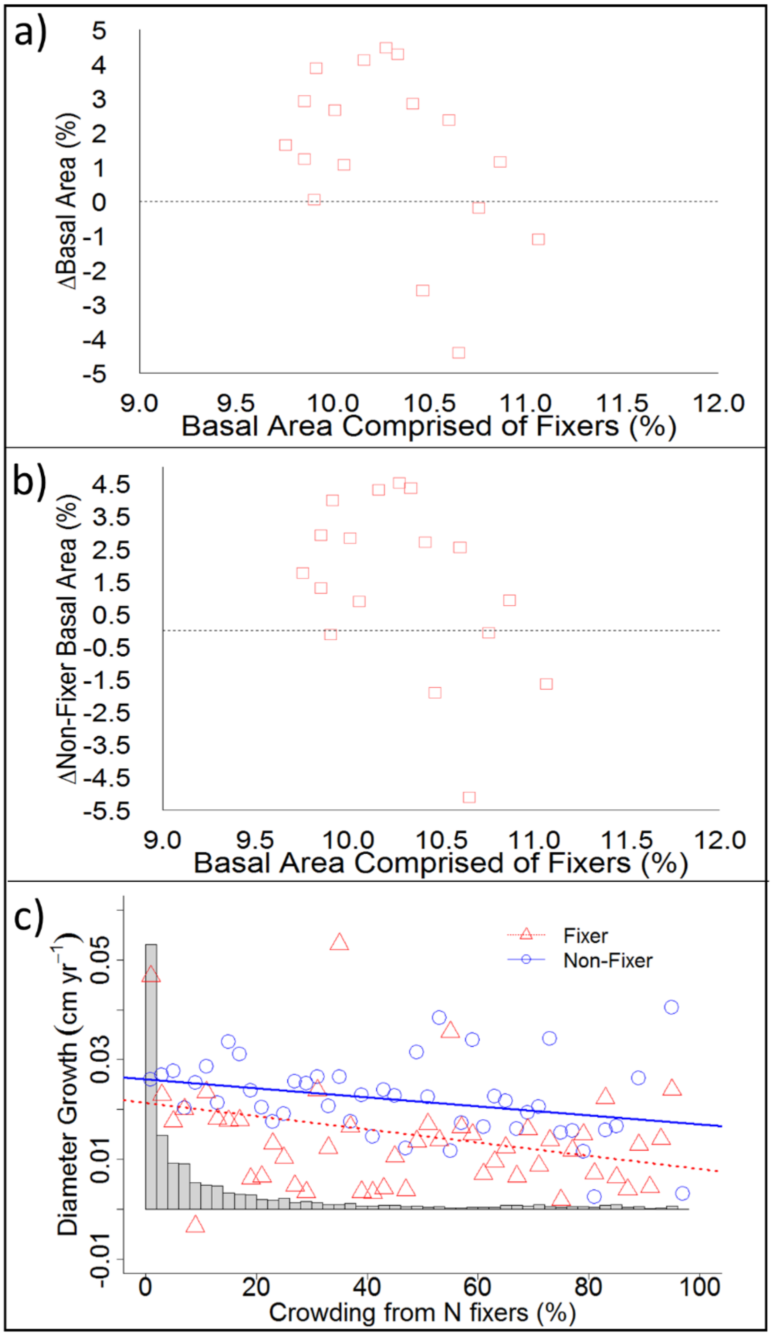

Table S1. Table of model coefficient values for growth model of assessing the impact of neighbor crowding (NCI), the proportion of crowding due to N fixers (neigh_fix), DBH, and the interactions between these variables on the growth of individual N fixers and non-fixers. Values are the parameter estimate (50%) and lower (2.5%) and upper (97.5) bounds of the credible interval in the model output for each covariate's effect on the growth of individuals based on their fixation status. Values are presented for the separate models run for young (≤ 25 years stand age) and old (> 25 years stand age) forests. These values correspond to those presented in Figure S2.

Growth in Young Forests				
Model Covariate	**Fixation Status**	**2.50%**	**50%**	**97.50%**
NCI	Non-Fixer	-0.16418094	-0.134102662	-0.104257413
DBH	Non-Fixer	-0.103423634	-0.067419913	-0.034675755
neigh_fix	Non-Fixer	-0.103728397	-0.071454147	-0.038667516
NCI^2	Non-Fixer	0.007321601	0.021485471	0.035561224
NCI x DBH	Non-Fixer	-0.042379625	-0.020651502	0.001210065
NCI x neigh_fix	Non-Fixer	-0.015345086	0.017714527	0.050194316
NCI	Fixer	-0.358381355	-0.277450844	-0.192622521
DBH	Fixer	0.127240105	0.182198306	0.234983854
neigh_fix	Fixer	-0.194316016	-0.147636904	-0.10453367
NCI^2	Fixer	-0.02908105	0.003046833	0.034010012
NCI x DBH	Fixer	-0.013363898	0.030953798	0.077401146
NCI x neigh_fix	Fixer	0.043517734	0.089533507	0.136421931

Growth in Old Forests				
Model Covariate	**Fixation Status**	**2.50%**	**50%**	**97.50%**
NCI	Non-Fixer	-0.105249342	-0.081489878	-0.058621957
DBH	Non-Fixer	-0.016836474	0.009990375	0.03638741
neigh_fix	Non-Fixer	-0.01727689	0.002397728	0.022621499
NCI^2	Non-Fixer	0.001435007	0.012393082	0.023654503
NCI x DBH	Non-Fixer	-0.041167616	-0.021043018	-0.000755745
NCI x neigh_fix	Non-Fixer	-0.024536377	-0.007380389	0.009079975
NCI	Fixer	-0.126736741	-0.061206613	0.005860932
DBH	Fixer	0.069044509	0.117456514	0.163885657
neigh_fix	Fixer	-0.110517166	-0.064197328	-0.017969619
NCI^2	Fixer	-0.017591095	0.014016779	0.045857013
NCI x DBH	Fixer	0.00967944	0.05404792	0.098911931
NCI x neigh_fix	Fixer	-0.041376023	-0.007438615	0.025897038

Table S2. Table of model coefficient values for recruitment model of assessing the impact of neighbor crowding (NCI), the proportion of crowding due to N fixers (neigh_fix), and the interactions between these variables on the frequency of individual N-fixer and non-fixer recruitment into individual 10 x 10 m subplots. Values are the parameter estimate (50%) and lower (2.5%) and upper (97.5) bounds of the credible interval in the model output for each covariate's effect on the frequency of N-fixer and non-fixer recruits. Values are presented for the separate models run for young (≤ 25 years stand age) and old (> 25 years stand age) forests. These values correspond to those presented in Figure S3.

Recruitment in Young Forests				
Model Covariate	**Fixation Status**	**2.50%**	**50%**	**97.50%**
NCI	Non-Fixer	-0.113898176	-0.0224169	0.07398544
neigh_fix	Non-Fixer	-0.386787044	-0.280389413	-0.181315198
NCI^2	Non-Fixer	-0.109266161	-0.046608219	0.013765278
NCI x neigh_fix	Non-Fixer	-0.108672516	-0.017124927	0.071095037
NCI	Fixer	-0.501886647	-0.162055515	0.151130145
neigh_fix	Fixer	-0.144741257	0.146970515	0.433011194
NCI^2	Fixer	-0.427513366	-0.168821451	0.032282261
NCI x neigh_fix	Fixer	-0.092806729	0.167381842	0.442299601
Recruitment in Old Forests				
Model Covariate	**Fixation Status**	**2.50%**	**50%**	**97.50%**
NCI	Non-Fixer	-0.089887787	-0.004677652	0.080639129
neigh_fix	Non-Fixer	-0.092932231	-0.018160485	0.056816558
NCI^2	Non-Fixer	-0.059063451	-0.010470275	0.034575821
NCI x neigh_fix	Non-Fixer	0.007322807	0.07277068	0.139009277
NCI	Fixer	-0.506362899	-0.105380147	0.284810064
neigh_fix	Fixer	-0.605860659	-0.252632135	0.054128547
NCI^2	Fixer	-0.146281631	0.016602165	0.158914944
NCI x neigh_fix	Fixer	-0.433279658	-0.156137697	0.082861559

Table S3. Table of model coefficient values for survival model of assessing the impact of neighbor crowding (NCI), the proportion of crowding due to N fixers (neigh_fix), DBH, and the interactions between these variables on the survival of individual N fixers and non-fixers. Values are the parameter estimate (50%) and lower (2.5%) and upper (97.5) bounds of the credible interval in the model output for each covariate's effect on the survival of individuals based on their fixation status. Values are presented for the separate models run for young (≤ 25 years stand age) and old (> 25 years stand age) forests. These values correspond to those presented in Figure S4.

Survival in Young Forests				
Model Covariate	**Fixation Status**	**2.50%**	**50%**	**97.50%**
NCI	Non-Fixer	-0.020836856	0.019010394	0.141736029
DBH	Non-Fixer	-0.470285359	-0.35583688	-0.29499912
neigh_fix	Non-Fixer	0.09977168	0.192149015	0.274575392
NCI^2	Non-Fixer	-0.045635487	-0.009900515	0.035112159
NCI x DBH	Non-Fixer	-0.041118099	0.027606086	0.104739243
NCI x neigh_fix	Non-Fixer	-0.111492709	-0.034132167	0.069400179
NCI	Fixer	-0.302547946	-0.010808257	0.71128891
DBH	Fixer	-1.154464216	-0.922759952	-0.399401099
neigh_fix	Fixer	-0.091861221	0.197977736	0.449237138
NCI^2	Fixer	-0.351842072	-0.041930587	0.188479978
NCI x DBH	Fixer	-0.409102606	-0.021330851	0.286060579
NCI x neigh_fix	Fixer	-0.211824753	0.200588751	0.349449829
Survival in Old Forests				
Model Covariate	**Fixation Status**	**2.50%**	**50%**	**97.50%**
NCI	Non-Fixer	-0.084042625	0.029387412	0.144510804
DBH	Non-Fixer	0.011358366	0.126916717	0.243061532
neigh_fix	Non-Fixer	-0.176862724	-0.073848598	0.021254437
NCI^2	Non-Fixer	-0.092670035	-0.03939129	0.01366022
NCI x DBH	Non-Fixer	-0.091697314	-0.005506539	0.08217381
NCI x neigh_fix	Non-Fixer	-0.217975717	-0.120630146	-0.025872088
NCI	Fixer	0.027934381	0.401842926	0.783572587
DBH	Fixer	-0.169199369	0.062252245	0.296572807
neigh_fix	Fixer	0.164908907	0.392357934	0.622249847
NCI^2	Fixer	-0.248014146	-0.075279998	0.082372637
NCI x DBH	Fixer	-0.24534621	-0.012076941	0.234946439
NCI x neigh_fix	Fixer	-0.291619738	-0.128485222	0.053620839

Table S4. Species represented in our dataset. Each of the 366 species and its putative fixation status is listed in order of the frequency of stems represented in our full dataset. The relative abundance (percent of stems) of each species for each plot is presented as the average over the census period for that plot.

Species	**Fixer Status**	**Frequency**	**CR Relative Abundance**	**LSUR Relative Abundance**	**BEJ Relative Abundance**	**TIR Relative Abundance**	**JE Relative Abundance**	**LEPP Relative Abundance**	**SV Relative Abundance**
Pentaclethra macroloba	Fixer	14024	11.49	18.76	24.61	0.00	14.73	5.75	6.49
Miconia affinis	Non-Fixer	7495	0.08	18.88	14.53	5.16	10.67	0.22	0.00
Casearia arborea	Non-Fixer	6897	8.13	7.24	2.67	2.76	2.93	1.04	0.51
Socratea exorrhiza	Non-Fixer	4338	1.32	3.64	1.42	0.08	0.16	1.99	0.34
Goethalsia meiantha	Non-Fixer	4134	1.09	10.34	0.48	0.25	0.61	0.73	0.00
Euterpe precatoria var. longevaginata	Non-Fixer	4099	8.24	5.82	0.15	0.01	0.08	4.41	4.03
Anaxagorea crassipetala	Non-Fixer	3932	15.76	0.22	0.00	0.00	0.00	0.11	0.00
Virola sebifera	Non-Fixer	3414	2.27	4.89	1.07	1.94	4.06	1.47	0.45
Vochysia ferruginea	Non-Fixer	3316	1.45	1.06	3.52	10.08	4.05	0.31	0.45
Laetia procera	Non-Fixer	3110	6.46	0.36	0.68	0.40	0.29	0.45	0.26
Iriartea deltoidea	Non-Fixer	2806	0.63	1.03	0.10	0.00	0.00	4.79	3.50
Dendropanax arboreus	Non-Fixer	2787	2.05	1.03	1.48	5.52	2.16	2.24	2.40
Simarouba amara	Non-Fixer	2702	0.31	1.23	4.02	5.84	6.00	0.62	0.13
Warszewiczia coccinea	Non-Fixer	2701	5.49	0.06	2.17	1.41	0.09	1.57	0.90
Miconia elata	Non-Fixer	2692	0.00	0.65	12.33	2.38	8.05	0.17	0.04
Cordia bicolor	Non-Fixer	2023	2.16	0.03	0.20	2.12	0.97	0.00	0.00
Piper colonense	Non-Fixer	1910	4.16	2.29	0.20	1.89	0.20	0.02	0.25

Species	Fixer Status	Frequency	CR Relative Abundance	LSUR Relative Abundance	BEJ Relative Abundance	TIR Relative Abundance	JE Relative Abundance	LEPP Relative Abundance	SV Relative Abundance
Inga cocleensis	Fixer	1775	0.07	0.09	0.40	8.68	0.38	0.00	0.09
Xylopia sericophylla	Non-Fixer	1561	2.67	2.48	1.82	0.11	1.75	0.10	0.09
Welfia regia	Non-Fixer	1503	0.41	0.00	0.00	0.00	0.09	5.19	7.71
Miconia prasina	Non-Fixer	1331	0.00	0.00	7.67	0.00	5.26	0.00	0.00
Cespedesia spathulata	Non-Fixer	1225	0.49	0.21	1.16	3.25	1.33	0.48	0.76
Miconia multispicata	Non-Fixer	1144	0.32	0.15	0.04	4.02	0.11	0.22	0.39
Hampea appendiculata	Non-Fixer	919	0.18	0.70	0.20	1.42	4.02	0.00	0.00
Guatteria amplifolia	Non-Fixer	874	0.18	2.10	0.16	0.89	0.52	0.33	0.62
Hernandia didymantha	Non-Fixer	825	0.37	0.33	0.15	1.50	0.41	0.00	0.17
Cryosophila warscewiczii	Non-Fixer	812	0.00	0.00	0.00	0.00	0.00	4.20	0.00
Annona papilionella	Non-Fixer	799	1.09	1.24	0.40	0.40	1.82	0.00	0.00
Protium confusum	Non-Fixer	781	0.18	0.01	0.00	2.23	0.08	1.07	1.60
Protium ravenii	Non-Fixer	754	0.31	0.16	0.02	0.03	0.00	0.87	4.15
Handroanthus chrysanthus	Non-Fixer	752	0.16	0.00	1.57	1.56	2.44	0.00	0.00
Virola koschnyi	Non-Fixer	737	0.24	0.69	1.44	0.70	1.40	0.61	0.23
Ryania speciosa	Non-Fixer	736	0.00	0.00	0.46	0.00	0.18	4.19	0.00
Capparis pittieri	Non-Fixer	679	1.06	0.34	0.00	0.00	0.00	2.61	0.09
Guatteria aeruginosa	Non-Fixer	670	0.51	1.04	0.09	0.99	0.05	0.43	0.10
Apeiba membranacea	Non-Fixer	667	0.75	0.03	0.00	1.26	0.10	0.10	0.09
Faramea parvibractea	Non-Fixer	656	0.00	0.00	0.00	0.00	0.00	1.80	4.14
Jacaranda copaia	Non-Fixer	608	0.00	2.71	0.17	0.16	0.26	0.00	0.00
Inga pezizifera	Fixer	581	0.36	0.09	0.14	0.17	0.08	0.21	0.00
Brosimum lactescens	Non-Fixer	558	0.19	0.15	0.10	0.00	0.18	2.18	1.67
Cupania glabra	Non-Fixer	557	0.13	0.00	0.01	1.99	0.04	0.00	1.24
Inga alba	Fixer	554	0.44	0.00	0.00	0.09	0.09	0.24	0.64

Species	Fixer Status	Frequency	CR Relative Abundance	LSUR Relative Abundance	BEJ Relative Abundance	TIR Relative Abundance	JE Relative Abundance	LEPP Relative Abundance	SV Relative Abundance
Vochysia guatemalensis	Non-Fixer	552	0.00	0.00	0.00	2.83	0.15	0.00	0.00
Ocotea leucoxylon	Non-Fixer	545	0.54	0.83	0.00	0.12	0.03	0.48	0.30
Casearia commersoniana	Non-Fixer	544	0.36	0.00	0.00	2.07	0.00	0.10	0.17
Pourouma bicolor	Non-Fixer	540	0.88	0.00	0.24	0.00	0.06	0.87	0.70
Inga thibaudiana	Fixer	533	0.04	0.44	0.12	0.42	0.47	0.10	0.00
Protium pittieri	Non-Fixer	525	0.37	0.41	0.00	0.01	0.00	2.57	0.27
Minquartia guianensis	Non-Fixer	516	0.80	0.06	0.36	0.30	0.10	0.86	0.96
Byrsonima crassifolia	Non-Fixer	458	0.40	0.12	0.10	0.00	0.00	0.10	0.43
Pausandra trianae	Non-Fixer	428	0.00	0.00	0.00	0.00	0.00	0.00	3.67
Psychotria elata	Non-Fixer	419	0.00	0.18	1.03	0.03	1.40	0.00	0.16
Psychotria panamensis	Non-Fixer	415	0.52	0.59	0.00	0.01	0.00	0.30	0.00
Tetragastris panamensis	Non-Fixer	415	0.34	0.00	0.20	0.30	0.00	0.10	2.06
Miconia punctata	Non-Fixer	409	0.08	0.00	0.68	0.00	0.44	0.00	2.36
Alibertia atlantica	Non-Fixer	404	0.08	0.00	0.00	0.04	0.00	0.60	2.75
Carapa nicaraguensis	Non-Fixer	388	0.08	0.00	1.21	0.00	0.72	0.83	0.79
Quararibea ochrocalyx	Non-Fixer	387	0.00	0.00	0.00	0.00	0.00	2.70	1.08
Alchorneopsis floribunda	Non-Fixer	368	0.16	1.05	0.19	0.04	0.56	0.20	0.00
Protium panamense	Non-Fixer	366	0.54	0.08	0.00	0.43	0.00	0.91	0.17
Guarea guidonia	Non-Fixer	350	0.22	0.09	0.00	0.05	0.00	2.09	0.45
Stryphnodendron microstachyum	Fixer	343	0.03	0.87	0.00	0.01	0.00	0.00	0.00
Zanthoxylum panamense	Non-Fixer	342	0.07	0.00	1.44	0.47	0.74	0.00	0.00
Croton smithianus	Non-Fixer	341	0.00	0.00	0.57	0.43	1.21	0.00	0.61
Pterocarpus rohrii	Fixer	341	0.14	0.00	0.00	0.02	0.00	0.21	0.09
Alchornea latifolia	Non-Fixer	336	0.23	0.00	0.00	1.44	0.01	0.00	0.07

Species	Fixer Status	Frequency	CR Relative Abundance	LSUR Relative Abundance	BEJ Relative Abundance	TIR Relative Abundance	JE Relative Abundance	LEPP Relative Abundance	SV Relative Abundance
Brosimum guianensis	Non-Fixer	332	0.15	0.00	0.10	0.14	0.09	0.60	1.13
Tapirira guianensis	Non-Fixer	332	0.22	0.00	0.00	0.00	0.00	0.75	1.38
Cordia alliodora	Non-Fixer	321	0.00	0.00	0.90	0.00	2.14	0.00	0.00
Rauvolfia purpurascens	Non-Fixer	319	0.07	0.00	0.00	0.38	0.00	0.41	0.04
Euterpe oleracea	Non-Fixer	301	0.00	0.00	0.63	1.05	0.35	0.00	0.00
Vitex cooperi	Non-Fixer	301	0.16	0.00	0.10	0.89	0.00	0.21	0.00
Vismia baccifera	Non-Fixer	297	0.00	0.04	0.04	0.79	1.27	0.00	0.00
Conceveiba pleiostemona	Non-Fixer	283	0.86	0.06	0.00	0.00	0.00	0.00	0.00
Zanthoxylum ekmanii	Non-Fixer	275	1.21	0.00	0.00	0.00	0.00	0.00	0.00
Erythroxylum macrophyllum	Non-Fixer	262	0.09	0.11	0.00	1.12	0.00	0.00	0.00
Ocotea laetevirens	Non-Fixer	259	0.10	0.00	0.00	0.02	0.00	0.80	0.35
Inga acuminata	Fixer	254	0.00	0.00	0.00	1.05	0.00	0.01	0.00
Ocotea cernua	Non-Fixer	249	0.00	0.12	0.00	0.60	0.00	0.00	0.00
Inga leiocalycina	Fixer	244	0.49	0.01	0.00	0.10	0.06	0.00	0.00
Licaria sarapiquensis	Non-Fixer	230	0.04	0.00	0.10	0.50	0.00	0.35	0.61
Vismia macrophylla	Non-Fixer	222	0.00	0.17	0.10	0.72	0.40	0.00	0.00
Prestoea decurrens	Non-Fixer	217	0.59	0.02	0.00	0.00	0.00	0.56	0.21
Byrsonima arthropoda	Non-Fixer	216	0.00	0.00	0.06	0.00	1.94	0.00	0.00
Cecropia insignis	Non-Fixer	212	0.07	0.42	0.00	0.04	0.09	0.00	0.02
Clethra costaricensis	Non-Fixer	207	0.24	0.00	0.00	0.00	0.18	0.00	0.09
Pouteria calistophylla	Non-Fixer	206	0.07	0.00	0.00	0.03	0.00	1.00	0.75
Vismia billbergiana	Non-Fixer	206	0.05	0.00	0.01	0.04	1.73	0.00	0.00
Calophyllum brasiliense	Non-Fixer	205	0.00	0.00	0.00	0.09	0.13	0.29	1.24
Pourouma minor	Non-Fixer	205	0.49	0.09	0.00	0.03	0.00	0.66	0.06
Guarea bullata	Non-Fixer	196	0.00	0.05	0.00	0.04	0.00	1.39	0.35

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Naucleopsis naga	Non-Fixer	194	0.08	0.00	0.00	0.00	0.00	0.92	0.75
Neea laetevirens	Non-Fixer	194	0.08	0.00	0.10	0.77	0.09	0.00	0.09
Cupania pseudostipularis	Non-Fixer	189	0.00	0.55	0.00	0.00	0.00	0.31	0.00
Guarea rhopalocarpa	Non-Fixer	189	0.13	0.10	0.00	0.45	0.00	0.44	0.11
Inga umbellifera	Fixer	187	0.08	0.00	0.00	0.03	0.00	0.00	0.17
Colubrina spinosa	Non-Fixer	182	0.11	0.00	0.00	0.16	0.00	0.31	0.40
Rhodostemonodaphne kunthiana	Non-Fixer	180	0.00	0.26	0.06	0.18	0.52	0.00	0.00
Hirtella racemosa	Non-Fixer	175	0.00	0.00	0.00	0.00	0.00	0.00	1.50
Swartzia ochnea	Fixer	173	0.00	0.00	0.00	0.05	0.00	1.50	0.00
Neea popenoei	Non-Fixer	172	0.16	0.00	0.00	0.66	0.00	0.00	0.09
Siparuna cuspidata	Non-Fixer	163	0.30	0.00	0.00	0.11	0.00	0.00	0.52
Casearia sylvestris	Non-Fixer	158	0.00	0.00	0.00	0.78	0.00	0.00	0.09
Aspidosperma desmanthum	Non-Fixer	157	0.08	0.00	0.10	0.00	0.00	0.00	1.11
Ormosia velutina	Fixer	153	0.00	0.00	0.00	0.65	0.00	0.00	0.26
Ocotea macropoda	Non-Fixer	150	0.18	0.00	0.02	0.24	0.31	0.29	0.00
Pseudolmedia spuria	Non-Fixer	150	0.08	0.00	0.00	0.34	0.00	0.10	0.38
Ferdinandusa panamensis	Non-Fixer	149	0.00	0.00	0.00	0.00	0.00	1.54	0.00
Lacunaria panamensis	Non-Fixer	149	0.03	0.00	0.00	0.08	0.00	0.18	0.85
Miconia stevensiana	Non-Fixer	149	0.00	0.00	0.00	0.02	0.06	0.54	0.75
Lacmellea panamensis	Non-Fixer	146	0.08	0.00	0.01	0.25	0.00	0.10	0.21
Psychotria luxurians	Non-Fixer	146	0.00	0.01	0.15	0.40	0.13	0.11	0.00
Cordia dwyeri	Non-Fixer	142	0.00	0.00	0.00	0.00	0.00	0.41	0.42
Ampelocera macrocarpa	Non-Fixer	141	0.00	0.00	0.00	0.05	0.00	0.10	1.05

Species	Fixer Status	Frequency	CR Relative Abundance	LSUR Relative Abundance	BEJ Relative Abundance	TIR Relative Abundance	JE Relative Abundance	LEPP Relative Abundance	SV Relative Abundance
Ilex skutchii	Non-Fixer	141	0.13	0.18	0.00	0.31	0.00	0.00	0.00
Rinorea deflexiflora	Non-Fixer	141	0.00	0.00	0.00	0.01	0.00	0.00	0.72
Trichilia septentrionalis	Non-Fixer	141	0.00	0.08	0.02	0.00	0.03	1.00	0.21
Hieronyma alchorneoides	Non-Fixer	139	0.13	0.01	0.00	0.41	0.00	0.00	0.26
Coccoloba tuerckheimii	Non-Fixer	137	0.00	0.00	0.00	0.72	0.00	0.00	0.00
Faramea multiflora	Non-Fixer	137	0.00	0.00	0.00	0.00	0.00	1.01	0.33
Compsoneura mexicana	Non-Fixer	135	0.08	0.00	0.00	0.00	0.00	0.31	0.75
Pouteria durlandii	Non-Fixer	130	0.00	0.00	0.00	0.00	0.00	0.93	0.34
Pera arborea	Non-Fixer	128	0.00	0.00	0.50	0.00	0.72	0.00	0.00
Pouteria sp1	Non-Fixer	128	0.04	0.00	0.10	0.00	0.00	0.21	0.76
Annona amazonica	Non-Fixer	124	0.05	0.24	0.00	0.35	0.00	0.00	0.00
Maranthes panamensis	Non-Fixer	124	0.08	0.00	0.00	0.19	0.00	0.21	0.43
Inga sertulifera	Fixer	121	0.00	0.00	0.00	0.32	0.00	0.10	0.27
Dussia macroprophyllata	Fixer	119	0.08	0.00	0.00	0.10	0.00	0.00	0.15
Ocotea hartshorniana	Non-Fixer	119	0.19	0.19	0.00	0.03	0.00	0.25	0.00
Posoqueria maxima	Non-Fixer	119	0.00	0.00	0.00	0.00	0.00	0.62	0.51
Balizia elegans	Fixer	118	0.00	0.00	0.40	0.00	0.00	0.21	0.26
Unonopsis pittieri	Non-Fixer	116	0.00	0.00	0.00	0.02	0.00	0.41	0.62
Quararibea bracteolosa	Non-Fixer	115	0.07	0.00	0.00	0.00	0.00	0.30	0.45
Bactris gasipaes	Non-Fixer	112	0.00	0.00	0.31	0.00	0.75	0.00	0.00
Inga spectabilis	Fixer	109	0.00	0.00	0.00	0.00	1.01	0.00	0.00
Hirtella media	Non-Fixer	107	0.00	0.00	0.12	0.04	0.12	0.21	0.46

Species	Fixer Status	Frequency	CR Relative Abundance	LSUR Relative Abundance	BEJ Relative Abundance	TIR Relative Abundance	JE Relative Abundance	LEPP Relative Abundance	SV Relative Abundance
Nectandra umbrosa	Non-Fixer	105	0.00	0.00	0.18	0.10	0.05	0.00	0.54
Licaria misantlae	Non-Fixer	104	0.00	0.00	0.00	0.36	0.00	0.20	0.15
Talisia nervosa	Non-Fixer	104	0.00	0.27	0.00	0.02	0.00	0.00	0.26
Chrysophyllum colombianum	Non-Fixer	103	0.00	0.00	0.10	0.00	0.00	0.13	0.69
Persea americana	Non-Fixer	103	0.00	0.00	0.00	0.00	0.00	0.75	0.26
Beilschmiedia sp.A	Non-Fixer	102	0.08	0.08	0.00	0.00	0.00	0.12	0.19
Inga venusta	Fixer	102	0.00	0.00	0.00	0.00	0.00	0.52	0.29
Ocotea insularis	Non-Fixer	102	0.05	0.41	0.00	0.00	0.00	0.10	0.00
Richeria dressleri	Non-Fixer	102	0.00	0.00	0.00	0.00	0.00	0.50	0.09
Sacoglottis trichogyna	Non-Fixer	102	0.16	0.00	0.00	0.14	0.00	0.31	0.09
Nephelium mutabile	Non-Fixer	98	0.00	0.00	0.40	0.00	0.54	0.00	0.00
Lozania pittieri	Non-Fixer	97	0.12	0.00	0.06	0.12	0.00	0.21	0.17
Marila pluricostata	Non-Fixer	97	0.07	0.00	0.00	0.11	0.00	0.00	0.52
Ossaea brenesii	Non-Fixer	95	0.00	0.00	0.00	0.50	0.00	0.00	0.00
Loreya mespiloides	Non-Fixer	94	0.00	0.00	0.00	0.00	0.87	0.00	0.00
Callicarpa acuminata	Non-Fixer	93	0.33	0.00	0.10	0.00	0.06	0.00	0.00
Cinnamomum chavarrianum	Non-Fixer	92	0.21	0.00	0.00	0.00	0.00	0.09	0.00
Meliosma donnellsmithii	Non-Fixer	92	0.00	0.00	0.00	0.28	0.07	0.10	0.17
Terminalia amazonia	Non-Fixer	91	0.08	0.00	0.00	0.28	0.00	0.00	0.17
Eugenia hammelii	Non-Fixer	90	0.00	0.00	0.00	0.00	0.00	0.00	0.77
Phyllanthus skutchii	Non-Fixer	90	0.24	0.19	0.00	0.00	0.00	0.00	0.00
Qualea polychroma	Non-Fixer	88	0.00	0.00	0.10	0.00	0.00	0.00	0.67
Andira inermis	Fixer	86	0.00	0.05	0.20	0.19	0.00	0.21	0.00
Ardisia fimbrillifera	Non-Fixer	84	0.14	0.00	0.00	0.00	0.00	0.17	0.00
Maquira guianensis	Non-Fixer	83	0.00	0.03	0.00	0.02	0.00	0.29	0.15

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Cecropia obtusifolia	Non-Fixer	82	0.00	0.00	0.15	0.01	0.61	0.00	0.00
Hieronyma oblonga	Non-Fixer	82	0.08	0.00	0.00	0.00	0.00	0.00	0.09
Virola multiflora	Non-Fixer	81	0.04	0.00	0.00	0.00	0.01	0.00	0.62
Zygia gigantifoliola	Fixer	80	0.00	0.00	0.00	0.28	0.00	0.24	0.00
Vouarana anomala	Non-Fixer	78	0.16	0.00	0.00	0.00	0.00	0.00	0.09
Chrysophyllum venezuelanense	Non-Fixer	77	0.08	0.00	0.00	0.26	0.00	0.10	0.00
Senna papillosa	Non-Fixer	75	0.00	0.11	0.00	0.13	0.26	0.00	0.00
Abarema adenophora	Fixer	74	0.24	0.00	0.00	0.00	0.00	0.00	0.17
Eugenia sp	Non-Fixer	71	0.00	0.00	0.00	0.00	0.00	0.00	0.17
Coussarea hondensis	Non-Fixer	70	0.00	0.04	0.00	0.00	0.00	0.28	0.00
Dystovomita paniculata	Non-Fixer	70	0.00	0.00	0.00	0.00	0.00	0.31	0.34
Ocotea mollifolia	Non-Fixer	70	0.17	0.00	0.00	0.00	0.00	0.00	0.00
Psidium guajava	Non-Fixer	70	0.00	0.00	0.10	0.04	0.49	0.00	0.00
Licania sp. A	Non-Fixer	69	0.00	0.00	0.00	0.00	0.00	0.51	0.17
Mabea occidentalis	Non-Fixer	69	0.00	0.00	0.00	0.00	0.00	0.00	0.15
Psychotria calidicola	Non-Fixer	69	0.00	0.00	0.00	0.00	0.00	0.71	0.00
Sorocea pubivena	Non-Fixer	69	0.00	0.00	0.08	0.13	0.00	0.00	0.00
Pouteria campechiana	Non-Fixer	67	0.00	0.00	0.04	0.07	0.00	0.31	0.17
Dipteryx panamensis	Non-Fixer	66	0.00	0.00	0.10	0.00	0.33	0.00	0.17
Perebea hispidula	Non-Fixer	66	0.00	0.00	0.00	0.04	0.00	0.01	0.50
Pouteria torta	Non-Fixer	65	0.08	0.00	0.00	0.00	0.00	0.21	0.17
Hirtella lemsii	Non-Fixer	64	0.16	0.00	0.00	0.00	0.00	0.21	0.00
Swartzia nicaraguensis	Fixer	64	0.16	0.00	0.00	0.09	0.00	0.10	0.00
Quiina macrophylla	Non-Fixer	63	0.04	0.00	0.00	0.08	0.00	0.18	0.17
Ocotea sp1	Non-Fixer	58	0.00	0.00	0.00	0.00	0.00	0.08	0.43
Pouteria reticulata	Non-Fixer	58	0.08	0.00	0.00	0.00	0.00	0.10	0.26

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Psychotria cooperi	Non-Fixer	58	0.00	0.00	0.00	0.00	0.54	0.00	0.00
Syzygium jambos	Non-Fixer	58	0.00	0.00	0.58	0.00	0.00	0.00	0.00
Inga chocoensis	Fixer	57	0.24	0.00	0.00	0.02	0.00	0.00	0.00
Hippotis panamensis	Non-Fixer	56	0.10	0.00	0.00	0.00	0.00	0.00	0.28
Lecythis ampla	Non-Fixer	56	0.00	0.00	0.00	0.09	0.00	0.00	0.17
Lacistema aggregatum	Non-Fixer	55	0.00	0.00	0.00	0.00	0.00	0.10	0.00
Hymenolobium mesoamericanum	Fixer	54	0.00	0.00	0.00	0.09	0.00	0.10	0.00
Ocotea pentagona	Non-Fixer	54	0.08	0.00	0.00	0.00	0.00	0.00	0.31
Hedyosmum scaberrimum	Non-Fixer	52	0.07	0.04	0.00	0.02	0.10	0.13	0.00
Chrysophyllum hirsutum	Non-Fixer	51	0.22	0.00	0.00	0.00	0.00	0.00	0.00
Croton schiedeanus	Non-Fixer	51	0.07	0.00	0.00	0.00	0.00	0.06	0.26
Guatteria recurvisepala	Non-Fixer	51	0.00	0.00	0.30	0.05	0.10	0.00	0.00
Talauma gloriensis	Non-Fixer	51	0.00	0.00	0.10	0.00	0.06	0.00	0.30
Humiriastrum diguense	Non-Fixer	50	0.00	0.00	0.00	0.00	0.00	0.00	0.43
Xylosma chlorantha	Non-Fixer	50	0.00	0.00	0.10	0.00	0.09	0.10	0.17
Chrysochlamys silvicola	Non-Fixer	49	0.07	0.00	0.00	0.00	0.00	0.00	0.28
Ocotea floribunda	Non-Fixer	49	0.00	0.00	0.00	0.26	0.00	0.00	0.00
Astrocaryum confertum	Non-Fixer	48	0.08	0.00	0.00	0.02	0.08	0.03	0.00
Cedrela odorata	Non-Fixer	48	0.00	0.13	0.10	0.03	0.06	0.00	0.00
Casearia coronata	Non-Fixer	47	0.01	0.23	0.00	0.00	0.00	0.00	0.00
Heisteria concinna	Non-Fixer	47	0.00	0.02	0.00	0.02	0.00	0.41	0.00
Jacaratia dolichaula	Non-Fixer	47	0.00	0.14	0.00	0.00	0.00	0.10	0.00
Mollinedia costaricensis	Non-Fixer	46	0.16	0.00	0.00	0.00	0.00	0.00	0.09
Pholidostachys pulchra	Non-Fixer	46	0.00	0.00	0.00	0.00	0.00	0.48	0.00
Swartzia costaricensis	Fixer	46	0.00	0.00	0.00	0.00	0.00	0.48	0.00

Species	Fixer Status	Frequency	CR Relative Abundance	LSUR Relative Abundance	BEJ Relative Abundance	TIR Relative Abundance	JE Relative Abundance	LEPP Relative Abundance	SV Relative Abundance
Myrcia splendens	Non-Fixer	43	0.00	0.00	0.00	0.03	0.00	0.18	0.00
Gmelina arborea	Non-Fixer	42	0.00	0.00	0.00	0.22	0.00	0.00	0.00
Pachira aquatica	Non-Fixer	42	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tachigali costaricensis	Fixer	41	0.00	0.06	0.05	0.00	0.04	0.00	0.18
Annona subnubila	Non-Fixer	40	0.00	0.00	0.00	0.00	0.00	0.21	0.17
Couepia polyandra	Non-Fixer	40	0.00	0.00	0.00	0.00	0.00	0.21	0.17
Mabea klugii	Non-Fixer	40	0.00	0.00	0.00	0.00	0.00	0.00	0.34
Vantanea occidentalis	Non-Fixer	40	0.00	0.00	0.20	0.00	0.00	0.00	0.17
Garcinia intermedia	Non-Fixer	37	0.00	0.00	0.00	0.00	0.00	0.10	0.23
Bunchosia macrophylla	Non-Fixer	36	0.08	0.09	0.00	0.00	0.00	0.00	0.00
Psychotria chagrensis	Non-Fixer	36	0.00	0.00	0.00	0.19	0.00	0.00	0.00
Trophis involucrata	Non-Fixer	35	0.00	0.00	0.00	0.00	0.00	0.27	0.08
Faramea glandulosa	Non-Fixer	34	0.00	0.00	0.00	0.00	0.00	0.35	0.00
Sapium glandulosum	Non-Fixer	34	0.07	0.00	0.00	0.09	0.00	0.00	0.00
Cestrum racemosum	Non-Fixer	33	0.02	0.05	0.00	0.09	0.00	0.00	0.00
Inga oerstediana	Fixer	33	0.00	0.00	0.20	0.07	0.00	0.00	0.00
Inga sapindoides	Fixer	33	0.00	0.08	0.00	0.04	0.00	0.00	0.00
Conostegia montana	Non-Fixer	32	0.00	0.00	0.00	0.09	0.00	0.06	0.08
Sclerolobium costaricense	Fixer	32	0.00	0.17	0.00	0.00	0.00	0.00	0.00
Symphonia globulifera	Non-Fixer	32	0.00	0.00	0.00	0.00	0.00	0.26	0.00
Unonopsis hammelii	Non-Fixer	32	0.05	0.00	0.00	0.00	0.00	0.11	0.09
Graffenrieda galeottii	Non-Fixer	31	0.08	0.00	0.00	0.07	0.00	0.00	0.00
Pouteria bracteata	Non-Fixer	30	0.00	0.00	0.00	0.00	0.00	0.00	0.26
Sloanea guianensis	Non-Fixer	30	0.00	0.00	0.00	0.00	0.00	0.00	0.26
Allophylus psilospermus	Non-Fixer	29	0.00	0.00	0.00	0.15	0.00	0.00	0.00
Eschweilera longirachis	Non-Fixer	29	0.00	0.00	0.00	0.00	0.00	0.30	0.00

Species	Fixer Status	Frequency	CR Relative Abundance	LSUR Relative Abundance	BEJ Relative Abundance	TIR Relative Abundance	JE Relative Abundance	LEPP Relative Abundance	SV Relative Abundance
Ardisia standleyana	Non-Fixer	28	0.00	0.00	0.00	0.15	0.00	0.00	0.00
Neea amplifolia	Non-Fixer	28	0.00	0.00	0.00	0.09	0.00	0.10	0.00
Parathesis trichogyne	Non-Fixer	28	0.08	0.00	0.00	0.00	0.00	0.10	0.00
Persea laevifolia	Non-Fixer	28	0.00	0.00	0.00	0.00	0.00	0.00	0.24
Sterculia recordiana	Non-Fixer	28	0.00	0.00	0.00	0.09	0.00	0.00	0.09
Lonchocarpus latisiliquus	Fixer	27	0.00	0.00	0.00	0.00	0.00	0.28	0.00
Neea delicatula	Non-Fixer	27	0.00	0.00	0.00	0.00	0.00	0.28	0.00
Unonopsis sp	Non-Fixer	27	0.00	0.00	0.00	0.00	0.00	0.00	0.17
Clusia croatii	Non-Fixer	25	0.00	0.00	0.00	0.00	0.23	0.00	0.00
Cordia porcata	Non-Fixer	24	0.00	0.00	0.00	0.00	0.00	0.25	0.00
Ficus colubrinae	Non-Fixer	24	0.00	0.00	0.00	0.13	0.00	0.00	0.00
Palicourea guianensis	Non-Fixer	24	0.00	0.00	0.00	0.00	0.22	0.00	0.00
Eugenia sp1	Non-Fixer	23	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Miconia appendiculata	Non-Fixer	23	0.00	0.00	0.00	0.00	0.21	0.00	0.00
Syzygium malaccensis	Non-Fixer	23	0.00	0.00	0.23	0.00	0.00	0.00	0.00
Ceiba pentandra	Non-Fixer	21	0.06	0.00	0.00	0.00	0.00	0.00	0.06
Licaria sp	Non-Fixer	21	0.01	0.00	0.00	0.03	0.00	0.00	0.09
Alchornea costaricensis	Non-Fixer	20	0.00	0.00	0.00	0.00	0.18	0.00	0.00
Aniba venezuelana	Non-Fixer	20	0.00	0.00	0.00	0.00	0.00	0.00	0.17
Cocos nucifera	Non-Fixer	20	0.00	0.00	0.00	0.00	0.18	0.00	0.00
Coussarea psychotrioides	Non-Fixer	20	0.00	0.00	0.00	0.00	0.00	0.10	0.09
Eschweilera collinsii	Non-Fixer	20	0.00	0.00	0.00	0.00	0.00	0.00	0.17
Eugenia glandulosopunctata	Non-Fixer	20	0.00	0.00	0.00	0.00	0.00	0.21	0.00
Guarea ciliata	Non-Fixer	20	0.00	0.00	0.00	0.00	0.00	0.21	0.00

Species	Fixer Status	Frequency	CR Relative Abundance	LSUR Relative Abundance	BEJ Relative Abundance	TIR Relative Abundance	JE Relative Abundance	LEPP Relative Abundance	SV Relative Abundance
Inga marginata	Fixer	20	0.00	0.00	0.00	0.11	0.00	0.00	0.00
Ossaea macrophylla	Non-Fixer	20	0.00	0.00	0.00	0.04	0.00	0.12	0.00
Pouteria glomerata	Non-Fixer	20	0.00	0.00	0.00	0.00	0.00	0.21	0.00
Ruptiliocarpon caracolito	Non-Fixer	20	0.00	0.00	0.00	0.00	0.00	0.00	0.17
Xylopia bocatorena	Non-Fixer	20	0.00	0.00	0.00	0.00	0.00	0.00	0.17
Dussia sp. A	Fixer	19	0.00	0.00	0.00	0.05	0.00	0.10	0.00
Inga ruiziana	Fixer	19	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nectandra reticulata	Non-Fixer	19	0.00	0.00	0.00	0.00	0.18	0.00	0.00
Calatola costaricensis	Non-Fixer	18	0.08	0.00	0.00	0.00	0.00	0.00	0.00
Casearia tacanensis	Non-Fixer	18	0.08	0.00	0.00	0.00	0.00	0.00	0.00
Chimarrhis parviflora	Non-Fixer	18	0.08	0.00	0.00	0.00	0.00	0.00	0.00
Chrysophyllum brenesii	Non-Fixer	18	0.08	0.00	0.00	0.00	0.00	0.00	0.00
Cinnamomum sp1	Non-Fixer	18	0.08	0.00	0.00	0.00	0.00	0.00	0.00
Cordia correae	Non-Fixer	18	0.08	0.00	0.00	0.00	0.00	0.00	0.00
Freziera grisebachii	Non-Fixer	18	0.00	0.00	0.00	0.09	0.00	0.00	0.00
Guarea chiricana	Non-Fixer	18	0.00	0.09	0.00	0.00	0.00	0.00	0.00
Henrietella tuberculosa	Non-Fixer	18	0.00	0.00	0.00	0.00	0.00	0.19	0.00
Herrania purpurea	Non-Fixer	18	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Maquira costaricana	Non-Fixer	18	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nectandra belizensis	Non-Fixer	18	0.08	0.00	0.00	0.00	0.00	0.00	0.00
Ormosia subsimplex	Fixer	18	0.00	0.00	0.00	0.09	0.00	0.00	0.00
Piper auritifolium	Non-Fixer	18	0.00	0.00	0.00	0.00	0.00	0.07	0.00
Symplocos striata	Non-Fixer	18	0.08	0.00	0.00	0.00	0.00	0.00	0.00
Vochysia allenii	Non-Fixer	18	0.08	0.00	0.00	0.00	0.00	0.00	0.00
Vernonia patens	Non-Fixer	17	0.00	0.00	0.00	0.00	0.16	0.00	0.00
Conostegia lasiopoda	Non-Fixer	16	0.03	0.00	0.00	0.00	0.00	0.10	0.00

Species	Fixer Status	Frequency	CR Relative Abundance	LSUR Relative Abundance	BEJ Relative Abundance	TIR Relative Abundance	JE Relative Abundance	LEPP Relative Abundance	SV Relative Abundance
Hirtella triandra	Non-Fixer	16	0.07	0.00	0.00	0.00	0.00	0.00	0.00
Miconia trinervia	Non-Fixer	16	0.05	0.00	0.00	0.02	0.00	0.00	0.00
Nectandra membranacea	Non-Fixer	16	0.00	0.00	0.00	0.08	0.00	0.00	0.00
Protium glabrum	Non-Fixer	16	0.00	0.00	0.00	0.08	0.00	0.00	0.00
Stephanopodium costaricense	Non-Fixer	16	0.00	0.00	0.00	0.00	0.00	0.00	0.14
Coussarea nigrescens	Non-Fixer	15	0.03	0.00	0.00	0.00	0.00	0.08	0.00
Ficus tonduzii	Non-Fixer	15	0.04	0.00	0.00	0.00	0.00	0.00	0.00
Miconia dorsiloba	Non-Fixer	15	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Ocotea dendrodaphne	Non-Fixer	15	0.03	0.00	0.00	0.00	0.00	0.00	0.08
Chrysochlamys nicaraguensis	Non-Fixer	14	0.00	0.00	0.00	0.04	0.00	0.03	0.03
Miconia ligulata	Non-Fixer	14	0.02	0.00	0.00	0.03	0.00	0.02	0.02
Inga tonduzii	Fixer	13	0.00	0.00	0.00	0.00	0.12	0.00	0.00
Simira maxonii	Non-Fixer	12	0.05	0.00	0.00	0.00	0.00	0.00	0.00
Citrus sinensis	Non-Fixer	11	0.00	0.00	0.00	0.00	0.10	0.00	0.00
Psychotria suerrensis	Non-Fixer	11	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tabernaemontana amygdalifolia	Non-Fixer	11	0.00	0.00	0.00	0.00	0.00	0.11	0.00
Ardisia sp	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.10	0.00
Bactris gracilior	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Bactris sp	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Castilla elastica	Non-Fixer	10	0.00	0.00	0.10	0.00	0.00	0.00	0.00
Chione venosa	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Clusia uvitana	Non-Fixer	10	0.00	0.00	0.10	0.00	0.00	0.00	0.00
Coussarea impetiolaris	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09

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Cymbopetalum costaricense	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Drypetes standleyi	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Elaeoluma glabrescens	Non-Fixer	10	0.00	0.00	0.10	0.00	0.00	0.00	0.00
Garcinia sp1	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Genipa americana	Non-Fixer	10	0.00	0.00	0.00	0.00	0.09	0.00	0.00
Geonoma interrupta	Non-Fixer	10	0.00	0.00	0.10	0.00	0.00	0.00	0.00
Guarea grandiflora	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.10	0.00
Guarea pilosa	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.10	0.00
Licania hypoleuca	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.10	0.00
Licania kallunkiae	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Maytenus guyanensis	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Miconia bubalina	Non-Fixer	10	0.00	0.00	0.00	0.05	0.00	0.00	0.00
Miconia sparrei	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.07	0.03
Mouriri gleasoniana	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Myrcia aliena	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Ocotea bijuga	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.10	0.00
Persea silvatica	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.10	0.00
Posoqueria latifolia	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Randia mira	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Spachea correae	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Spondias mombin	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Tabernaemontana arborea	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.10	0.00

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Tetrorchidium gorgonae	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Theobroma simiarum	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Zanthoxylum sp	Non-Fixer	10	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Luehea seemannii	Non-Fixer	9	0.00	0.00	0.00	0.05	0.00	0.00	0.00
Ouratea valerioi	Non-Fixer	9	0.00	0.00	0.00	0.00	0.00	0.00	0.08
Pradosia atroviolacea	Non-Fixer	9	0.00	0.00	0.00	0.05	0.00	0.00	0.00
Tetrorchidium euryphyllum	Non-Fixer	9	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Neea urophylla	Non-Fixer	8	0.00	0.00	0.00	0.00	0.00	0.08	0.00
Hirtella sp	Non-Fixer	7	0.00	0.00	0.00	0.00	0.00	0.00	0.06
Mangifera indica	Non-Fixer	7	0.00	0.00	0.07	0.00	0.00	0.00	0.00
Miconia minutiflora	Non-Fixer	7	0.00	0.00	0.07	0.00	0.00	0.00	0.00
Psychotria poeppigiana	Non-Fixer	7	0.00	0.00	0.00	0.00	0.05	0.00	0.00
Quararibea parvifolia	Non-Fixer	7	0.00	0.00	0.00	0.00	0.00	0.00	0.06
Theobroma mammosum	Non-Fixer	7	0.00	0.00	0.00	0.00	0.00	0.07	0.00
Cestrum microcalyx	Non-Fixer	6	0.01	0.02	0.00	0.00	0.00	0.00	0.00
Clusia flava	Non-Fixer	6	0.00	0.00	0.00	0.00	0.06	0.00	0.00
Ficus insipida	Non-Fixer	6	0.00	0.00	0.06	0.00	0.00	0.00	0.00
Inga densiflora	Fixer	6	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Siparuna pauciflora	Non-Fixer	6	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Inga edulis	Fixer	5	0.00	0.00	0.00	0.00	0.05	0.00	0.00
Miconia nervosa	Non-Fixer	5	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Crescentia cujete	Non-Fixer	4	0.00	0.00	0.04	0.00	0.00	0.00	0.00
Trophis racemosa	Non-Fixer	4	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Eschweilera costaricensis	Non-Fixer	3	0.01	0.00	0.00	0.00	0.00	0.00	0.00

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Macrolobium costaricense	Non-Fixer	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ocotea atirrensis	Non-Fixer	3	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Persea sp	Non-Fixer	3	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Peschiera arborea	Non-Fixer	3	0.00	0.00	0.00	0.00	0.00	0.03	0.00
Psychotria sp1	Non-Fixer	3	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Spondias radlkoferi	Non-Fixer	3	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Zygia longifolia	Fixer	3	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Cassipourea elliptica	Non-Fixer	2	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Solanum novo-granatense	Non-Fixer	2	0.00	0.01	0.00	0.00	0.00	0.00	0.00