

LETTERS

Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest

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The accumulation of species-specific enemies around adults is hypothesized to maintain plant diversity by limiting the recruitment of conspecific seedlings relative to heterospecific seedlings^{1–6}. Although previous studies in forested ecosystems have documented patterns consistent with the process of negative feedback^{7–16}, these studies are unable to address which classes of enemies (for example, pathogens, invertebrates, mammals) exhibit species-specific effects strong enough to generate negative feedback¹⁷, and whether negative feedback at the level of the individual tree is sufficient to influence community-wide forest composition. Here we use fully reciprocal shade-house and field experiments to test whether the performance of conspecific tree seedlings (relative to heterospecific seedlings) is reduced when grown in the presence of enemies associated with adult trees. Both experiments provide strong evidence for negative plant–soil feedback mediated by soil biota. In contrast, above-ground enemies (mammals, foliar herbivores and foliar pathogens) contributed little to negative feedback observed in the field. In both experiments, we found that tree species that showed stronger negative feedback were less common as adults in the forest community, indicating that susceptibility to soil biota may determine species relative abundance in these tropical forests. Finally, our simulation models confirm that the strength of local negative feedback that we measured is sufficient to produce the observed community-wide patterns in tree-species relative abundance. Our findings indicate that plant–soil feedback is an important mechanism that can maintain species diversity and explain patterns of tree-species relative abundance in tropical forests.

Negative feedbacks occur when detrimental effects of enemies that accumulate in the vicinity of a given adult are expressed more strongly on conspecific relative to heterospecific juveniles. As a result, enemy-mediated reduction of growth and survival of conspecific juveniles near a given adult can provide a localized recruitment advantage for juveniles of other species^{1–3}. This process can maintain species richness by preventing any one species from dominating the plant community^{18–20}.

In forests, the strongest evidence that negative feedback processes influence plant species composition comes from demographic analyses of spatial and temporal patterns of tree growth and survival. These demographic studies often reveal that seedlings and saplings perform more poorly when in high densities or near conspecific adults^{7–12}. Such patterns of density and distance dependence are expected to emerge if the process of enemy-mediated negative feedback is operating in the plant community. Demographic analyses, however, are not able to identify the principal classes of enemies (for example, pathogens, invertebrates, mammals) that drive negative feedbacks, nor are they able to distinguish between enemy-mediated

feedback and other possible mechanisms that could lead to similar demographic patterns, such as higher intraspecific competition for abiotic resources near parent trees.

Experimental studies in both temperate and tropical forests have attempted to demonstrate the process of negative feedback and to identify the causal agents. These studies often find that detrimental effects of enemies on seed or seedlings are greater near than away from conspecific trees^{13–16}. However, with few exceptions²¹, these studies restrict their analyses to within single tree species, and thus fail to examine whether the effects of enemies are species-specific, which is an essential requirement to provide a recruitment advantage to heterospecific seedlings. Instead, experimental studies that examine performance of conspecific relative to heterospecific juveniles near a host tree are necessary¹⁷. Furthermore, simulation models are needed to determine whether empirically based estimates of negative feedback occurring at the local scale of the tree are sufficient to influence community-wide patterns in species diversity and relative abundances.

We first conducted a shade-house experiment designed to assess the importance of soil biota (for example, fungi, bacteria, fauna) in generating negative feedback, while controlling for nutrients and light. We chose six shade-tolerant tree species, the adult relative abundances of which in the 50-ha plot on Barro Colorado Island (BCI) ranged over roughly two orders of magnitude, which allowed us to examine whether variation in the strength of feedback among species was correlated with their adult abundance. We filled all pots with an identical mixture (3:1) of sterilized field soil and sand. To each pot, we added a single seedling along with a small quantity (6% total volume) of either live or sterilized soil inoculum collected from under either conspecific or heterospecific adult trees in a fully reciprocal design. This experimental design allowed us to control for abiotic soil effects, while introducing soil biota. We measured total seedling biomass after 5 months.

We found strong evidence for negative plant–soil feedback based on growth when averaged across all species, with four of the six being significant (Fig. 1a). For these four species, seedling growth was reduced relative to heterospecific seedlings when grown with conspecific versus heterospecific inoculum (see Supplementary Fig. 1). Overall seedling growth (averaged across species) did not differ across sterilized inocula from the different adult species; however, growth did differ significantly across different sources of inocula containing live biota (Fig. 1b). This finding confirms that differences in seedling response were due to differences in live soil biota and not due to differences in abiotic properties of the soil. Furthermore, the strength of negative feedback was correlated with the relative abundance of those adult trees found on the BCI 50-ha plot ($P = 0.058$). Tree species showing strong negative feedback were less

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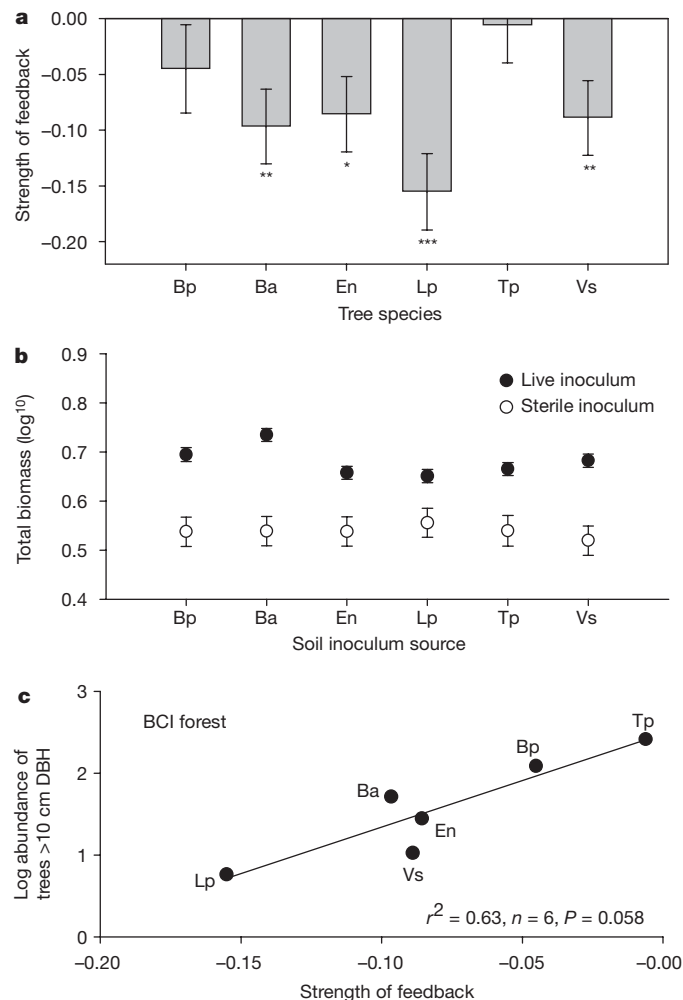


Figure 1 | Strengths of negative plant–soil feedback measured in the shade-house experiment are correlated with adult tree species abundance of the BCI forest. **a**, Variation in the strength of negative feedback mediated by soil biota among the six seedling species. Ba, *Brosimum alicastrum*; Bp, *Beilschmiedia pendula*; En, *Eugenia nesiotica*; Lp, *Lacmellea panamensis*; Tp, *Tetragastris panamensis*; Vs, *Virola surinamensis*. Bars indicate standard errors, and means that differ from zero are indicated by asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Number of seedlings analysed = 349. **b**, Seedling response (averaged across seedling species) varied across live inocula (ANCOVA: $F_{5,408} = 5.31, P < 0.0001$) but not across sterile inocula (ANCOVA: $F_{5,408} = 0.15, P = 0.981$). Bars indicate standard errors. **c**, Tree species that exhibited stronger negative feedback were less common as adults in the BCI 50-ha plot. DBH, diameter at breast height.

common as adults than were species exhibiting weaker or no significant negative feedback (Fig. 1c).

We then conducted a reciprocal field experiment in a mainland forest (Gigante Peninsula, Panama) located adjacent to BCI to determine whether patterns of negative plant–soil feedback observed in the shade-house experiment were also found in the forest in the presence of above-ground enemies and other potentially confounding processes. We selected five tree species that differed in adult relative abundance (three of which were used in the shade-house experiment). We grew seedlings in sterilized soil for 1 month and then transplanted them into plots containing all five species in July 2008. A single mixed-species seedling plot was established under each replicate adult tree of each species. We measured growth and survival at the end of the first wet season (January 2009) and survival at both the end of the first dry season (May 2009) and after 16 months, near the end of the second wet season (November 2009).

We found that of the 1,270 seedlings planted into the forest, 945 (74%) survived after 6 months in the forest. All five species exhibited

significant negative feedback based on growth of surviving seedlings (Fig. 2a). Consistent with the shade-house experiment, tree species exhibiting strong negative feedback were less common as adults in this mainland forest than those species exhibiting weaker negative feedback (Fig. 2b). Foliar enemies contributed little to the strength of feedback. Leaf damage caused by insect herbivores and foliar pathogens explained an average of only 14% of the overall strength of negative feedback (averaged across all species), with the maximum contribution (28%) occurring in *Beilschmiedia pendula* due to foliar fungi (Fig. 2c and Supplementary Fig. 2). These findings, combined with the strong effect of soil biota and no effect of nutrients on feedback in the shade-house experiment, indicate that below-ground biota contributed to the majority of growth-based negative feedback measured in the forest (see Supplementary Discussion).

Mortality during the first 6 months was primarily due to above-ground enemies (uprooting by vertebrates or clipping of stems by vertebrates or insects) and occurred shortly after we transplanted the seedlings. Seedling death caused by these above-ground enemies did not lead to mortality-based feedback when measured in January

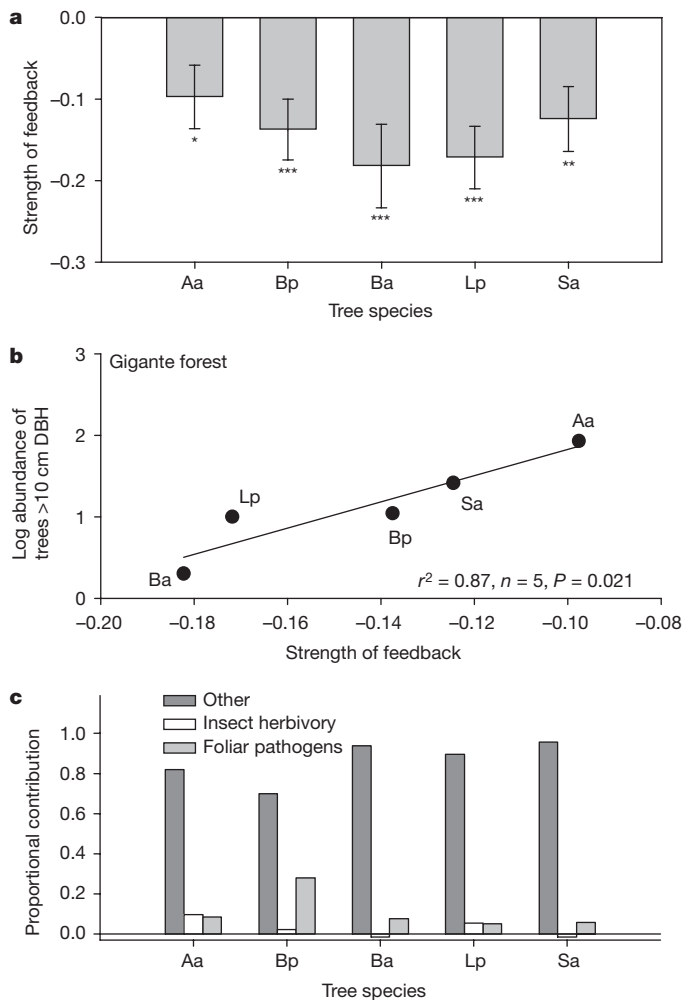


Figure 2 | Strengths of negative feedback measured in the field experiment are correlated with adult tree species abundance of the Gigante forest. **a**, Variation in the strength of negative feedback among the five seedling species. Species abbreviations are the same as those in Fig. 1, except for: Aa, *Apeiba aspera*; Sa, *Simarouba amara*. Bars indicate standard errors, and means that differ from zero are indicated by asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Number of seedlings analysed = 945. **b**, Tree species that exhibited stronger negative feedback were less common as adults in the forest of the Gigante Peninsula than those species exhibiting weaker negative feedback. **c**, Proportional contribution of foliar insect herbivory, foliar pathogens and other causes to observed patterns of negative feedback.

2009. However, in a subsequent mortality census conducted in May 2009, faster growing seedlings (as measured in January 2009) had a higher probability of surviving the first dry season than did slower growing seedlings (Supplementary Table 2). By November 2009, estimates of feedback through mortality became increasingly negative (Supplementary Table 3), demonstrating that growth differences among seedlings emerge quickly and develop into mortality-based negative feedback over longer periods of time, as slower growing seedlings are increasingly likely to die.

Analytical models and simulations indicate that negative feedback can maintain plant diversity^{18–20}; however, theory on the expected response in tree relative abundance to variation in feedback strength is lacking. In addition, it has been argued that localized processes such as negative feedback may not be sufficient to influence community-wide patterns in tree composition²². We addressed these issues by simulating community dynamics using a stochastic spatially explicit cellular automata model. We found that simulations that included the strength of plant–soil feedback between species pairs measured in our experiments generated community-wide species abundances of similar rank order as those found on BCI and the mainland forest (Fig. 3a, b). Moreover, this pattern holds for simulations of more species-rich communities (Fig. 3c). The correlation between abundance and average feedback was robust when we relaxed the assumption that species had equivalent growth and mortality rates ($t = 17.19$,

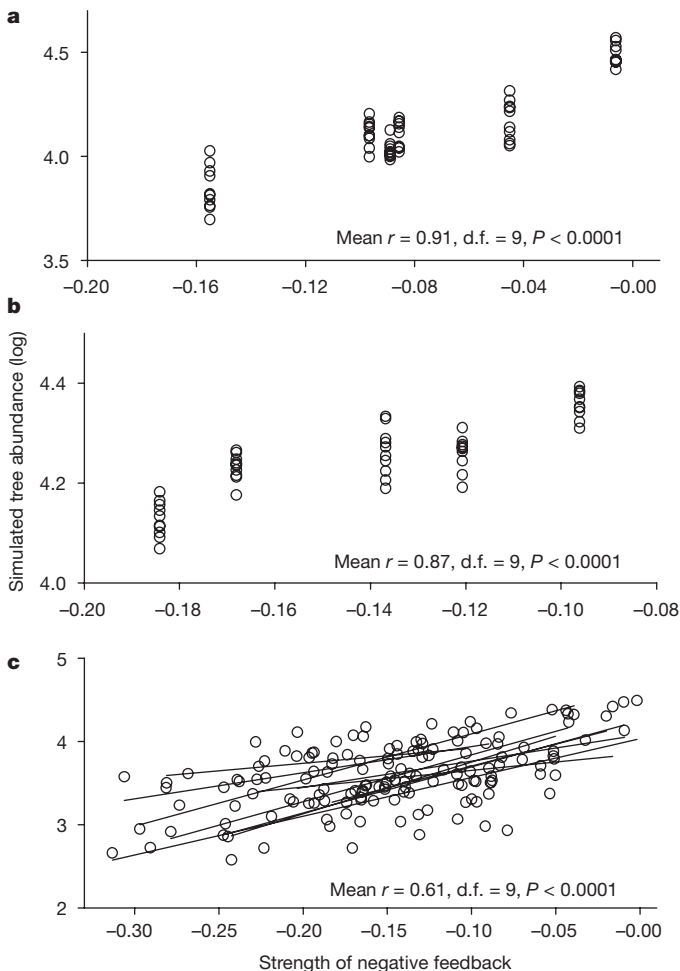


Figure 3 | Simulations indicate that variation in feedback strength predicts tree species abundance. **a–c**, Species abundance generated using simulations including shade-house plant response data (**a**), field-collected plant response data (**b**) and randomly generated feedback data (**c**). All simulations demonstrate that stronger negative feedback leads to lower species abundance. Each circle falling at the same location of the x axis in panels **a** and **b** indicates simulated abundance for each of 10 runs. Regression lines per run are plotted in panel **c**.

$P < 0.0001$; see Supplementary Methods). When we included variation in species-specific life history traits, a single highly competitive species dominated the simulations in the absence of feedback. Species coexistence occurred only when we also included the empirically measured feedback responses. These simulations demonstrate that the relationship between feedback and abundance is expected only when negative plant–soil feedback is the major force driving plant species coexistence.

Our study is consistent with other findings that soil biota (for example, soil-borne fungi, bacteria, fauna) mediate negative plant–soil feedback in temperate grasslands^{3,4,23–26}. In a greenhouse experiment, rare temperate grassland species exhibited stronger negative plant–soil feedback due to soil pathogens than more common plant species⁴. Notably, our field experiment suggests that the correlation between the strength of negative feedback among species and their relative abundance occurs even in the presence of plant competition and other naturally occurring processes in tropical forests. Furthermore, this relationship does not seem to be restricted to just those tree species that we examined. A recent, demographic analysis found a positive correlation between patterns of density-dependent seedling mortality and abundance when 180 tree species on BCI were examined²⁷. Our simulations confirm theoretically that variation in the strength of plant–soil feedback can drive this relationship.

For decades, resource partitioning, above-ground herbivory⁶ and neutral processes²⁸ have received considerable attention as mechanisms for the maintenance of plant species diversity. However, much of this work has overlooked the effects of soil biota, particularly in species-rich tropical forests. Soil communities are characterized by a great diversity of microbes and fauna^{26,29}, but the extent to which these organisms contribute to the functioning of plant communities is only now beginning to be discovered. By using fully reciprocal experiments, we were able to demonstrate that species-specific interactions between tropical trees and their soil biota are sufficiently strong to maintain tree diversity through negative feedback. Self-limiting processes such as negative plant–soil feedback have been assumed previously to occur more strongly in tree species of high abundance³⁰. However, empirically we found the opposite result: more abundant tree species exhibited the weakest negative feedback. Our simulations reinforce the conclusion that trees are abundant because they are less susceptible to the detrimental effects of their associated soil communities than are rarer tree species. Thus, localized negative plant–soil feedback occurring between plants and below-ground organisms may be a general mechanism for the maintenance of plant species diversity and patterns of relative abundance across ecosystems ranging from temperate grasslands to tropical forests.

METHODS SUMMARY

Study species. We selected shade-tolerant tree species from different families that produced sufficient amounts of seeds at the onset of each experiment. We used *Beilschmiedia pendula*, *Brosimum alicastrum* and *Lacmellea panamensis* in both experiments; *Eugenia nesiotica*, *Tetragastris panamensis* and *Virola surinamensis* in the shade-house experiment; and *Apeiba aspera* and *Simarouba amara* in the field experiment. We were unable to use identical species sets for each experiment because seed availability varied between the two years in which each experiment was conducted. For each experiment, we collected seeds of all species from their respective forests (shade-house experiment: Barro Colorado Island; field experiment: Gigante Peninsula, Panama), surface sterilized the seeds, and germinated them in sterile soil (see Methods).

Feedback measure. For each experiment, feedback was measured using a priori contrasts within the ‘seedling species \times soil-biota source’ interaction term in our mixed-model analysis of covariance (ANCOVA) tests (see Methods). These contrasts isolated the strength and direction of the interaction between seedling species and adult biota source for each possible species pair (that is, pairwise feedbacks¹⁸). The strength of average feedback per species was determined by averaging all pairwise feedbacks involving that species¹⁸ (see Supplementary Fig. 1).

Stochastic cellular automata simulation. Initially, all cells were occupied and each species was equally represented. A cell was then chosen at random and the species identity was reassigned based on the pairwise plant–soil responses measured in each experiment. Simulations in Fig. 3 assumed species equivalence in

growth and mortality. This assumption was then relaxed for subsequent runs of the model (see Methods and Supplementary Equations). The abundance of each species after 20 million replacements was recorded and the correlation with the average strength of feedback per species was tested.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions S.A.M. designed and conducted the experiments, analysed the data and wrote the first draft. S.A.S., E.A.H. and J.D.B. provided important revisions. J.D.B. and K.M.L.M. developed the simulation. M.C.V. and E.I.S. provided essential field support.

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METHODS

Reciprocal shade-house experiment. We collected seeds from three adults of *Beilschmiedia pendula*, *Brosimum alicastrum*, *Eugenia nesiotica*, *Lacmellea panamensis*, *Tetragastris panamensis* and *Virola surinamensis* located near the 50-ha plot on Barro Colorado Island (BCI). For each adult, we collected and homogenized soil samples from three locations 2 m away from the base of the tree to be used as inoculum. To separate the effects of soil biota from that of potential variation in abiotic properties, we filled all 4-l pots with an identical steam-pasteurized 3:1 sand–field soil mixture. To each pot, we also added a small quantity of live soil inoculum (6% total soil volume) collected from one of the six target species. We planted a single one-month-old seedling of each tree species into pots containing their own live inoculum (conspecific combinations) and pots containing inoculum from each of the five other species (heterospecific combinations). For each tree species, we replicated the conspecific plant–biota combination fifteen times and each heterospecific combination eight times. To confirm that our dilution technique adequately controlled for potential variation in abiotic properties introduced by the small volume of soil inoculum, we assessed seedling growth in the same plant–inoculum combinations, but using sterilized inoculum. Each plant–sterile inoculum combination was replicated twice. We divided all treatment combinations equally across four shade-houses, which were included in the analysis as blocks. Seedlings were well watered and allowed to grow for 5 months, after which seedlings were harvested and total dry weight was determined.

We used mixed-model ANCOVA to examine the main effects of seedling species and soil biota source and their interaction on log-transformed seedling biomass using the SAS procedure PROC MIXED. In this model, we included seedling species and block (and all interactions with block) as random effects, with log-transformed initial biomass as a covariate. We estimated initial biomass per species using regression equations obtained from extra harvested seedlings at the onset of the experiment, where the product of leaf area and stem height was regressed with total seedling dry weights. Within the ‘seedlings species \times soil-biota source’ interaction, we used a priori contrasts that isolated the strength and direction of the interaction between seedling species and adult biota source for each possible species pair (that is, pairwise feedbacks¹⁸). These contrasts compared the relative growth response of seedlings when associated with soil biota from their own adults versus from under heterospecific adults, relative to how heterospecific seedlings responded across these same soil biota sources (see Supplementary Fig. 1).

Reciprocal field experiment. In July 2008, we transplanted ten seedlings of the same species as the adult (conspecifics) and five seedlings of each of the heterospecific species (30 seedlings total) into a single 1 \times 0.8 m grid \sim 2.5 m from the base of each adult. Seedlings were randomized and planted 20 cm apart. Ten adult trees of *Apeiba aspera*, *Brosimum alicastrum* and *Lacmellea panamensis*, nine of *Simarouba amara* and four of *Beilschmiedia pendula* were haphazardly located in the forest of the mainland Gigante Peninsula, adjacent to BCI. We monitored seedling survival and estimated levels of visible damage (for example, insect herbivory, stem clipping, foliar pathogen infection) biweekly for the first four months, and monthly until the final census. In January 2009, we measured stem height and leaf lengths and widths, and estimated total above-ground biomass using regression equations. These equations were obtained per species by regressing the product of the growth measurements with total above-ground biomass of extra harvested seedlings (4 of 5 species: $r^2 > 0.91$; *B. alicastrum*:

$r^2 = 0.84$). Initial seedling above-ground biomass was obtained in the same manner. The percentage of herbivory or foliar pathogen damage was estimated per leaf for each surviving seedling. We also assessed seedling survival in May 2009 and November 2009.

We analysed survival after 6 months using the SAS procedure PROC GLIMMIX for binomial distributions and log-transformed above-ground biomass using PROC MIXED. Each model included seedling and adult species and their interaction as main effects, and log-transformed initial above-ground biomass (per seedling) as a covariate. The growth model also included number of days between the initial and final census (per seedling) as a covariate. We included ‘site \times adult species’ and ‘site \times adult species \times seedling species’ as random effects, with site defined as a single adult tree (43 ‘sites’ in total). We determined the average feedback per species using methods identical to the shade-house experiment. To investigate the contribution of leaf herbivory and foliar fungal damage to the strength of feedback, we computed the per cent decrease in strength of feedback per species when each damage type was included as a covariate in two additional growth models (see Supplementary Table 2 and Supplementary Fig. 2).

Simulation. We used stochastic spatially explicit cellular automata computer simulations. Each cell on a 300 \times 300 torus grid was randomly assigned a species identity. The initial grid contained an equal number of cells per species. Focal cells were then chosen at random and replaced. After 20 million replacements, we examined the abundance of cells representing each species. For all simulations, seeds of each species were assumed to disperse evenly over their 25 surrounding cells. The identity of the new occupant of a replaced focal cell was determined by the establishment probability of each species occurring within the local neighbourhood (25 surrounding cells) of the focal cell. Establishment probabilities were determined by the species-specific response to soil biotic compositions created by both the species previously occupying the focal cell and the suite of species occurring immediately adjacent to the focal cell (surrounding 8 cells). The strength of this response was scaled so that it would be highest immediately adjacent to an adult and taper in strength with increasing distance (see Supplementary Equations). We parameterized two separate simulations where plant response to soil biota (that is, establishment probability) was based on pairwise growth responses measured in either the field or the shade-house experiment. In addition, we simulated a community containing 15 species by assigning the conspecific plant response as a value between 0.1 and 0.2 and the base of the heterospecific pairwise plant response as a value between 0.2 and 0.6, with the individual heterospecific responses being chosen from a uniform distribution within 0.1 of that base value. In this simulation, a new random establishment matrix was generated for each replication. For simulations described thus far, all cells had an equal probability of being selected for replacement (that is, adult mortality rates were assumed to be equal across species). We ran an additional simulation where we relaxed the assumption of species equivalence in mortality by weighting the probability of replacement by estimates of species-specific difference in tree mortality. We also relaxed the assumption that establishment was determined only by plant response to soil biota by weighting this measure by species-specific seedling growth rates (see Supplementary Equations). For all simulations, we replicated each simulation ten times and averaged the correlation coefficients that examined the relationship between the average strength of feedback and tree abundance. Simulations were run in MATLAB.

SUPPLEMENTARY INFORMATION

Supplementary Table 1. Analysis of covariance (ANCOVA) examining the effect of species identity of seedlings and target adults on aboveground biomass of six-month old seedlings grown in the understory of the mainland forest, either near a conspecific adult, or near adults of each of the other species. Two additional ANCOVAs were constructed that either controlled for foliar damage caused by herbivores or pathogens. Because F-values of average negative feedback were not significantly reduced by inclusion of foliar herbivore or pathogen damage (and see Supplementary Fig. 2), these antagonists are not likely drivers of negative feedback.

Effect	d.f.	Not controlling	Herbivore	Pathogen
		for damage	damage	damage
		F ratio	F ratio	F ratio
Seedling species	4, 147	56.38^{***}	53.18^{***}	64.84^{***}
Adult species	4, 38	0.81	0.85	0.88
Seedling species × adult species	16, 147	2.64^{**}	2.52^{**}	2.36^{**}
Average <i>Apeiba</i> feedback	1, 147	6.28[*]	5.39[*]	5.47[*]
Average <i>Beilschmiedia</i> feedback	1, 147	13.57^{***}	13.61^{***}	6.92^{**}
Average <i>Brosimum</i> feedback	1, 147	12.74^{***}	13.70^{***}	10.91^{**}
Average <i>Lacmellea</i> feedback	1, 147	20.11^{***}	18.35^{***}	18.41^{***}
Average <i>Simbaruba</i> feedback	1, 147	9.79^{**}	10.40^{**}	8.85^{**}
Initial seedling mass (log ¹⁰)	1, 706 [†]	228.74^{***}	251.04^{***}	193.81^{***}
Days between initial and final census	1, 706 [†]	6.05[*]	5.51[*]	4.98[*]
Proportion herbivory damage	1, 706	---	57.81^{***}	---
Proportion foliar-fungal damage	1, 706	---	---	40.33^{***}

All models (SAS procedure MIXED) included ‘site × adult species’ and ‘site × seedlings species × adult species’ as random effects, with site defined as a single adult tree. †: denominator d.f. = 707 for the model not including herbivory or foliar-fungal damage as a covariate. *P < 0.05; ** P < 0.01; *** P < 0.001

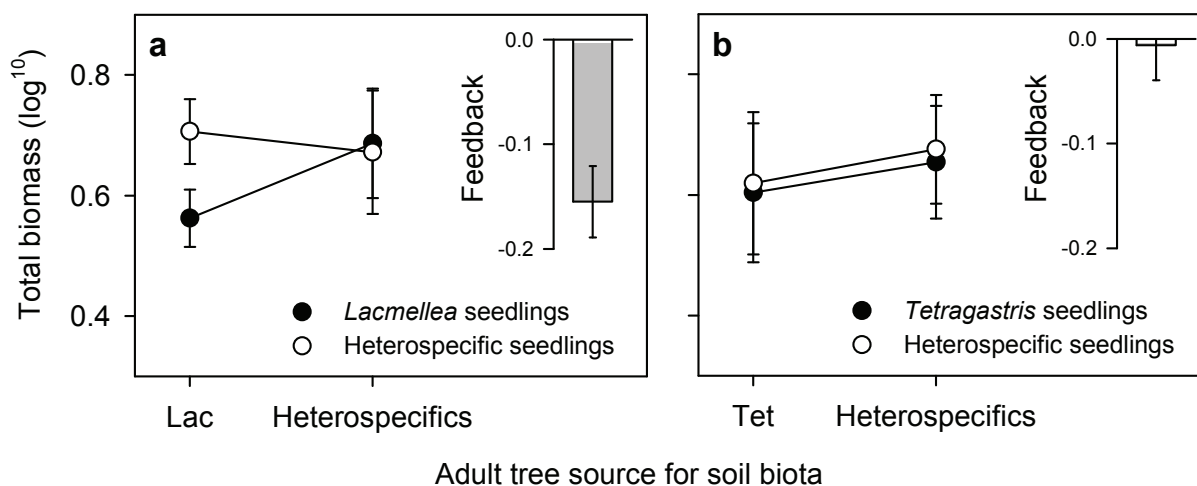
Supplementary Table 2. Logistic regression examining the relationship between estimated above ground biomass of seedlings measured at the end of the wet season (January 2009) and survival at the end of the subsequent dry season (May 2009). Proportion of seedlings surviving in each census is indicated in parentheses. Consistent across tree species, larger seedlings measured in January 2009 had a higher probability of surviving through the first dry season when measured in (May 2009) than did smaller seedlings.

Species	Estimate	S.E.	Chi-square	Initial number of seedlings planted in July 08	Number of seedlings surviving in Jan. 09	Number of seedlings surviving in May 2009
<i>Apeiba aspera</i>	4.441	0.790	31.61***	265	174 (0.66)	81 (0.31)
<i>Beilschmiedia pendula</i>	0.266	0.067	15.78***	265	201 (0.76)	156 (0.59)
<i>Brosimum alicastrum</i>	0.894	0.236	14.40***	215	167 (0.78)	157 (0.73)
<i>Lacmellea panamensis</i>	2.310	0.424	29.64***	265	217 (0.82)	176 (0.66)
<i>Simbarouba amara</i>	1.048	0.320	10.70***	260	186 (0.72)	156 (0.60)

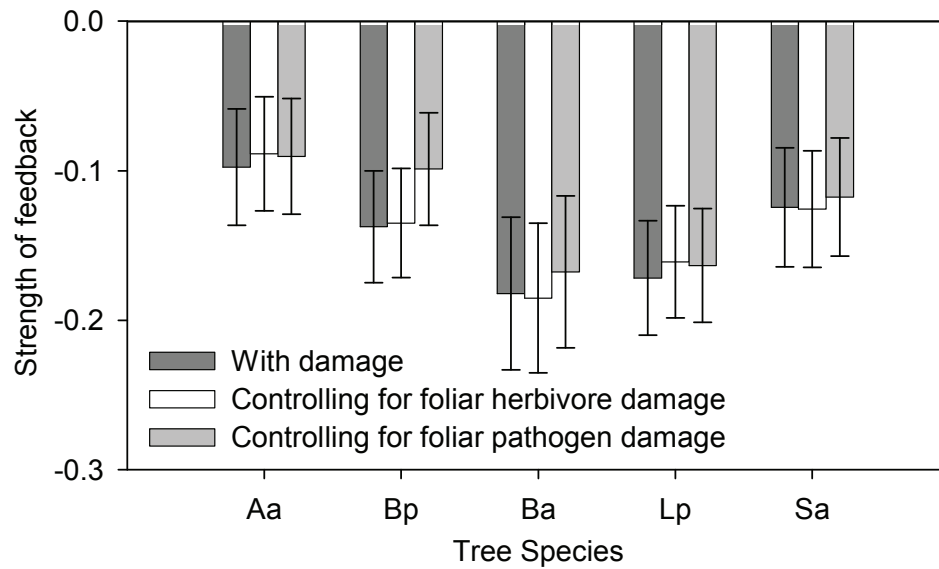
*** P < 0.001

Supplementary Table 3. Contrasts examining the strength of average feedback based on mortality per tree species at the end of the first wet season (January 2009), after the first dry season (May 2009) and near the end of the second wet season (November 2009). Each model (SAS procedure GLIMMIX) included seedlings species and adult species (and their interaction) as fixed effects, and ‘site × adult species’ and ‘site × seedlings species × adult species’ as random effects, with site defined as a single adult tree. Mortality-based feedbacks become more negative over time.

Species	Feedback based on mortality January 2009				Feedback based on mortality May 2009				Feedback based on mortality November 2009			
	Estimate	S.E.	<i>F</i>	P	Estimate	S.E.	<i>F</i>	P	Estimate	S.E.	<i>F</i>	P
<i>A. aspera</i>	0.2107	0.4960	0.18	0.6716	-0.9197	0.5259	3.06	0.0823	-1.4453	0.6768	4.56	0.0343
<i>B. pendula</i>	0.5021	0.5571	0.81	0.3689	-0.4993	0.5060	0.97	0.3254	-1.0242	0.4656	4.84	0.0293
<i>B. alicastrum</i>	0.5419	0.7341	0.54	0.4615	-0.5419	0.7083	0.59	0.4443	-0.9182	0.6495	2.00	0.1595
<i>L. panamensis</i>	0.3541	0.5215	0.46	0.4982	-1.0664	0.5013	4.53	0.0350	-1.4467	0.4643	9.71	0.0022
<i>S. amara</i>	0.5272	0.5218	1.02	0.3140	-0.4756	0.5145	0.85	0.3568	-0.3850	0.5314	0.52	0.4698



Supplementary Figure 1. Performance of seedlings of both the target species and heterospecific seedlings when grown with soil biota collected from conspecific adults versus from heterospecific adults. The resulting interaction between seedling species and adult biota source was used to define the strength and direction of feedback. For example, **a**) *Lacmellea* in the shadehouse experiment exhibited strong negative feedback (insert) because their seedlings performed more poorly with biota from their own adults relative to with heterospecific biota, whereas heterospecific seedlings performed better with *Lacmellea* biota relative to with their own biota (i.e., significant interaction). **b**) Although *Tetragastris* tended to perform more poorly with soil biota from their own adults than with soil biota from adults of other species, no feedback occurred because seedling response of heterospecifics mirrored that of *Tetragastris* (i.e., no interaction).



Supplementary Figure 2. Comparison between strengths of negative feedback when no damage was controlled for (same as presented in Fig. 2a of the text), when percent herbivore damage was included as a covariate in the model, or when percent foliar pathogen damage was included as a covariate in the model. Total number of seedlings analyzed = 749.

Supplementary Discussion

When compared across both experiments, *L. panamensis* and *B. alicastrum* changed rank in both their strengths of growth-based negative feedback and their relative abundances (see Figures 1c and 2b). Such shifts may have been caused by variation in the composition of soil biota between the two forests. To confirm this hypothesis, further studies are required that characterize soil biota and their contribution to feedbacks at the seedling stage (and other developmental stages) across larger geographical scales.

Supplementary Equations

The probability of mortality (m) for species i was determined by the following:

$$m_i = (P_i M_i) / \sum_{i=1}^S P_i M_i$$

where S is the number of species in the population, P_i is the proportion of that species in the population, and M_i is its estimated per capita adult mortality rate. In simulations where species were assumed to be equivalent, M for all species was set to 1. In the simulation where this assumption was relaxed, M_i differed among species and was estimated as the inverse of adult longevity (L_i). Species-specific adult longevities were estimated using the equation $L_i = -233.45 \times \ln(g_i) + 452.98$, where g was the growth rate of that species (Laurance et al. 2004).

The probability of establishment (e) for species i was determined by the following:

$$e_i = (p_i F_i E_i) / \sum_{i=1}^S p_i F_i E_i$$

where p_i is the proportion of that species in the dispersal neighborhood, F_i is the contribution of feedback, and E_i is the relative growth rate of that species. The contribution of feedback was determined by:

$$F_i = \left(\sum_{d=1}^D \overline{f_i^d} \right) / D$$

where D is the radius that contains cells that influence the composition of soil biota. In this term, dividing by D inversely scales the individual adult effects with distance from the focal cell. In all simulations, this “interaction neighborhood” was assumed to contain the focal cell and the eight cells surrounding the focal cell. For each distance d from the focal cell, the average effects of plants within this neighborhood on growth of species i ($\overline{f_i^d}$) was determined by:

$$\overline{f_i^d} = \sum_{j=1}^S (P_j^d f_{ij})$$

where f_{ij} is the influence of soil biota associated with species j on the growth of species i and P_j^d is the proportion of soil biota influenced by species j at distance d . In simulations where all species were assumed to be equivalent, E for all species was set to 1. In the simulations allowing species-specific variation in life-history parameters, species specific E_i was estimated from the average growth rates in the shadehouse experiments.

31. Laurance, W. F., et al. Inferred longevity of Amazonian rainforest trees based on a long-term demographic study. *Forest Ecol. Manag.* **190**,131-143 (2004).