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Title: **The importance of *Ficus* (Moraceae) trees for tropical forest restoration**

Short running title: *Ficus* led restoration

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The importance of *Ficus* (Moraceae) trees for tropical forest restoration

Abstract

Forest restoration is an increasingly important tool to offset and indeed reverse global deforestation rates. One low cost strategy to accelerate forest recovery is conserving scattered native trees that persist across disturbed landscapes and which may act as seedling recruitment foci. *Ficus* trees, which are considered to be critically important components of tropical ecosystems, may be particularly attractive to seed dispersers in that they produce large and nutritionally rewarding fruit crops. Here we evaluate the effectiveness of remnant *Ficus* trees in inducing forest recovery compared to other common trees. We studied the sapling communities growing under 207 scattered trees, and collected data on seed rain at 55 trees in a modified landscape in Assam, India. We found *Ficus* trees have more sapling species around them (species richness=140.1±9.9) than non-*Ficus* trees (79.5±12.9), and significantly more saplings of shrub and large tree species. Sapling densities were twice as high under *Ficus* trees (median=0.06/m^2) compared to non-*Ficus* (0.03/m^2), and seed rain densities of non-parent trees were significantly higher under *Ficus* trees (mean=12.73±3/m^2/week) than other fruit or non-zoochorous trees (2.19±0.97/m^2/week). However, our regression model found that canopy area, used as a proxy for tree size, was the primary predictor of sapling density, followed by remnant tree type. These results suggest that large trees, and in particular large *Ficus* trees, may be more effective forest restoration agents than other remnant trees in disturbed landscapes, and therefore the conservation of these trees should be prioritized.

Key words: Assam; focal trees; forest restoration; India; sapling recruitment; scattered trees; seed dispersal

RESTORING DEGRADED LANDS TO FOREST cover is an increasingly important conservation priority in the tropics (Chazdon *et al*. 2009). Several methods can be used to restore forests, including large-scale sapling replanting, commercial plantations, tree islands, focal trees, and passive succession (Holl 2012, Singh *et al.* 2012, Zahawi *et al.* 2013). In areas where remnant trees have survived deforestation, these structures can play an important role in forest recovery (Guevara & Laborde 1993, McIntyre 2002, Holl *et al.* 2013). Remnant trees attract frugivores across disturbed landscapes, thereby facilitating seed dispersal (Guevara *et al.* 1992, Galindo-González *et al.* 2000, Holl *et al.* 2000). They also stabilise local microclimatic conditions and provide nutrients under their canopies, both of which improve seedling recruitment rates (Guevara *et al*. 1992, Zahawi & Augspruger 1999, Holl *et al.* 2000, Loik & Holl 2001, Zahawi & Augspruger 2006). Therefore, by improving dispersal and recruitment in disturbed habitats, remnant trees may act as regeneration foci, helping to develop a nucleated pattern of succession (Guevara *et al.* 1986, Elmqvist *et al.* 2002, Lindenmayer & Franklin 2002, Manning *et al.* 2006, Schlawin & Zahawi 2008).

The effectiveness of remnant trees has been demonstrated in Neotropical pasture (Guevara *et al.* 1992, Guevara & Laborde 1993, Slocum 2001), Australian savannahs (Dorrough & Moxham 2005), and temperate field landscapes (McDonnell & Stiles 1983). However, the characteristics of remnant trees which best serve restoration remain poorly understood. For example, how do isolation and tree size influence seed immigration and survival in the immediate vicinity of a remnant tree (cf. MacArthur & Wilson 1967, Whittaker & Fernández-Palacios 2007)? A handful of studies have found remnant tree size to increase seed deposition (Slocum & Horvitz 2000, Slocum 2001), while no consistent relationship has been found between the distance to forest edge and either seed rain or sapling density (Slocum 2001, Zahawi

& Augspurger 2006; but see Robinson & Handel 1993 and Schlawin & Zahawi 2008). Another important concept of remnant tree-led restoration is the ability of woody vegetation to expand beyond the perimeter of a tree's canopy, yet little evidence for this process has been documented (Zahawi & Augspurger 2006, Cole *et al.* 2010). And finally, the effectiveness of different remnant tree species in encouraging faster restoration, or directing restoration towards a particular community composition, remains poorly known (Slocum 2001).

Seed dispersal has often been cited as a limiting factor in forest restoration studies (Cole *et al.* 2010, Holl *et al.* 2013, Zahawi *et al.* 2013). Fleshy-fruited trees are believed to be the most effective species at attracting frugivores over disturbed habitats and thus prove to be more effective restoration nuclei than other species (Slocum 2001). *Ficus* in particular is believed to be a very important genus of fleshy-fruited tree for a wide range of frugivores (Leighton & Leighton 1983, Terborgh 1986, Janzen 1988, Lambert & Marshall 1991, Shanahan *et al.* 2001, Kinnaird & O'Brien 2005). Within intact forests, the unusual asynchronous fruiting cycle, large crop sizes, and pan-tropical availability of *Ficus* means that over 1,200 tropical birds and mammals have been recorded consuming *Ficus* fruit (Shanahan *et al.* 2001). Beyond the forest edge in Neotropical pastures, Guevara and Laborde (1993) recorded 47 species of frugivorous bird feeding in four isolated *Ficus* trees over 247 hours of observation, and Slocum (2001) found *Ficus* trees to have higher seed rain, greater density of saplings, and higher sapling diversity than three other tree genera. If sufficient evidence of the importance of *Ficus* trees as regeneration nuclei can be gathered, policy makers may be encouraged to more actively conserve remnant *Ficus* trees, as well as devise strategies to include *Ficus* trees in new plantings.

We sought to test hypotheses on the importance of remnant *Ficus* trees as restoration nuclei in an agricultural mosaic landscape beyond the Neotropics. In particular, we aimed to test

92 the following hypotheses: (1) that isolated *Ficus* trees harbour a greater diversity and density of
93 saplings than other common remnant trees (Slocum 2001); (2) that isolation, tree size, and local
94 grazing intensity influence the density of saplings growing under remnant trees (Guevara *et al*.
95 2004); and (3) that sapling densities differ between the area under the crown and in a 5 m radius
96 beyond the immediate vicinity of the crown (Guevara *et al.* 1992).

97 **METHODS**

98 The study was conducted between October 2012 and June 2013 in the Golaghat District of
99 Assam, North-East India. The study site is a ≈250 km^2 area bounded by the Western Range of
100 Kaziranga National Park at 26°34’23” N, 93°15’25” E, the city of Jorhat at 26°46’11” N,
101 94°12’40” E, and the town of Golaghat at 26°27’4” N, 93°54’58” E. The elevation of the study
102 area ranges between 30–100 m asl, and the mean annual rainfall for the region is 1,500–2,500
103 mm, most of which falls in the May to August monsoon (Barua & Sharma 1999, Shrivastava &
104 Heinen 2007). The annual temperature range varies from an average minimum of 5°C to an
105 average maximum of 35°C (Barua & Sharma 1999).

106 The original habitat of moist subtropical deciduous forest was largely cleared following
107 the local commercialisation of tea production in 1840 (Shrivastava & Heinen 2007). Remnants of
108 the original forest remain in the 7.65 km^2 Panbari Forest Reserve on the edge of the Karbi Hills,
109 and in the 430 km^2 Kaziranga National Park (Barua & Sharma 1999). The landscape is an
110 agricultural mosaic, with a heterogeneous assortment of small-holder rice cultivation, tea estates,
111 and village home gardens. The area has a population density of 302 people per square kilometre
112 (GOI 2011).

113 REMNANT TREE SELECTION. – We randomly selected 103 mature isolated *Ficus* trees, and another
114 104 mature non-*Ficus* trees that were commonly found in the anthropogenic landscape. The

115 *Ficus* focal trees were large, hemi-epiphytic species, comprising of 26 *F. benghalensis*, which
116 has large fruit (mean diameter=182 mm, n=62), with the rest small-fruited species (mean
117 diameter=131 mm, n=47), comprising 57 *F. religiosa*, 13 *F. rumphii*, 5 *F. microcarpa*, and 3 *F.*
118 *benjamina*. Non-*Ficus* trees comprised of 28 species, the most common of which were
119 *Mangifera indica* (12 individuals) and *Albizia saman* (11 individuals). A species list of non-
120 *Ficus* trees, and the number of each used in this study, is provided in Table S1.

121 We recorded the species of each of these 207 focal trees and measured the diameter at
122 breast height, height, and canopy diameter along two axes. Canopy area was later calculated
123 using the formula for an ellipse. We also recorded the grazing intensity of the area under the
124 canopy using a three point rank scale (where 0 is very little evidence of grazing; 1 is some
125 livestock occasionally graze the site; and 2 is large numbers of livestock frequently graze the
126 site). The human land use of the area under the canopy was also recorded using a similar three-
127 point scale (where 0 is very little human land use; 1 is some human land use, such as cultivation;
128 and 2 is intense human land use, in cases where a road, house, or paddy field are present under
129 the canopy).

130 SAPLING SAMPLING. – At each focal tree, we identified all saplings growing under the canopy,
131 and then all the saplings growing in a 5 m radius around the edge of the canopy. A sapling was
132 defined as a woody-stemmed plant 20–200 cm tall. Several sources were used to establish the
133 saplings' taxonomy (Kanjilal *et al.* 1934–1940, Bora & Kumar 2003, Sarma *et al.* 2010).

134 SEED RAIN SAMPLING. – Seed rain was measured under 35 fruiting *Ficus* trees, 10 fruiting non-
135 *Ficus* trees, and 10 non-fleshy fruit bearing trees. Seed traps were constructed out of a fine
136 (0.5×0.5 mm) mesh net, with square sides measuring 50 cm (making the total area of a trap 0.25
137 m^2). They were erected one metre above the ground to avoid seed predation, and a small stone

was placed in the centre to prevent wind inverting the net. Seed traps were placed 4 m away from the trunk of each tree. In the case of large *Ficus* trees, a second seed trap was placed at 8 m from the trunk. In 8 cases, seed traps were also placed 4 m beyond the edge of the crown to quantify the amount of seed rain falling just beyond the crown perimeter. We used one seed trap per distance category. For fruiting *Ficus* trees, the material caught in seed traps was collected once every 2–3 days, for other trees it was collected once a week over a three-month period. Leaf litter and twigs that fell into the traps were carefully brushed to collect seeds before being discarded. The material was dried in plastic bottles over several days, and then sorted by species and counted using a hand-held 10× magnifying lens. Seeds were classed as being either zoochorous or anemochorous by morphology. Traps that were damaged by humans, livestock, or, in one case, wild elephants (*Elephas maximus* L.), were excluded from analysis.

STATISTICAL ANALYSIS. – We estimated sapling species richness under *Ficus* and non-*Ficus* focal trees using a bias-corrected Chao 1 estimator (Chao 1984). Significant differences in the density of saplings under *Ficus* and non-*Ficus* focal trees were determined using a Mann-Whitney U test, and we used a t-test for sapling densities in a 5 m radius beyond the canopy of the two focal tree types. A factorial ANOVA was used to identify any interaction effects between tree type and the change in sapling density between the area under the canopy, and the 5 m radius beyond the canopy.

Sapling species were classified into groups depending on their dispersal syndrome (animal, wind, or gravity) and life history (large tree, small tree, or shrub). A threshold of 20 m height at maturity was used to differentiate large trees from small trees, following the local botanical literature (Kanjilal *et al.* 1934–1940, Bora & Kumar 2003, Sarma *et al.* 2010). These data were square root transformed, before differences in the densities of these groups under

Ficus and non-*Ficus* focal trees were analysed with MANOVA using Pillai's trace as the test statistic and follow-up ANOVAs.

We calculated diversity, dominance, and similarity measures for the sapling communities recorded under and within 5 m of *Ficus* and non-*Ficus* focal trees. For diversity, we used the Shannon diversity index with bias-corrected maximum likelihood ratio. We used a Simpson dominance index with maximum likelihood estimator for dominance, and to compare community similarity we used Sørensen's abundance index, adjusted for unseen species, with 200 simulations. All formulae followed Chao and Shen (2012) and the analyses were computed in the SPADE software package (Chao & Shen 2010).

We conducted a regression analysis to test the influence of focal tree type, distance from the nearest forest, focal tree canopy area, and grazing intensity on sapling density. Sapling density was logarithmically transformed to meet the assumptions of the model, and was used as the response variable. Tree type, distance from the nearest forest, canopy area (logarithmically transformed), and grazing intensity were entered as the predictor variables.

To analyse total seed rain densities and dispersed seed rain densities, we compared the density of seed rain falling per metre squared per week across the five net positions: (i) under non-zoochorous trees, (ii) under fruiting non-*Ficus* trees, (iii) 4 m from the trunk of *Ficus* trees, (iv) 8 m from the trunk of *Ficus* trees, and (v) 4 m beyond the canopy of *Ficus* trees. We performed a Kruskal-Wallis test, with a Jonckheere-Terpstra test to determine any trends in the data, followed by four Mann-Whitney U tests with a new critical value of 0.0125 to identify specific differences between dependent variables. Finally, to investigate the relationship between distance from the nearest forest and seed rain densities, we ran a linear regression with logarithmically transformed dispersed seed rain densities per metre squared per week for 4 m

Ficus nets as the dependent variable, and distance from the nearest forest as the predictor variable. Other than where specified, all analyses were conducted using IBM SPSS Statistics 21 (IBM 2012).

RESULTS

A total of 7,078 saplings, comprising 117 species, were recorded under or in a 5 m vicinity of the 207 focal trees. While *Ficus* canopies (mean=424.11 m^2, SE=35.31) had a larger area than non-*Ficus* trees (mean=130.79 m^2, SE=16.98), sapling densities under *Ficus* tree canopies (median=0.06/m^2) were still significantly higher than under non-*Ficus* trees (median=0.03/m^2; U=4446, z=-2.12, $P<0.05$), although the effect size was small ($r=-0.15$).

Excluding the area under the canopy, the density of saplings growing in a 5 m radius of *Ficus* tree canopies (mean=0.036/m^2, SE=0.006) was significantly higher than the density of saplings growing in a 5 m radius of the canopies of non-*Ficus* trees (mean=0.016/m^2, SE=0.004; $t_{(180)}=-2.86$, $P<0.05$, $r=0.21$). However, there was no significant interaction effect between the type of tree and the area under the canopy versus the 5 m radius ($F_{(1,410)}=0.57$, $P>0.05$, $r=0.04$). This suggests that while sapling densities differed significantly, the drop in densities from beneath the canopy to immediately beyond the canopy perimeter was not significantly different according to the type of tree (for means and standard errors, see Table 1).

Focal tree type had a significant effect on the densities of saplings when classified into groups according to their dispersal ecology (V=0.09, $F_{(3,203)}=6.6$, $P<0.05$). Separate univariate analyses on the outcome variables revealed higher mean densities of animal dispersed ($F_{(1,205)}=14.43$, $P<0.05$) and wind dispersed saplings ($F_{(1,205)}=7.68$, $P<0.05$) under *Ficus* trees, but no difference in the mean density of gravity dispersed saplings according to focal tree type ($F_{(1,205)}=3.31$, $P>0.05$). The type of focal tree also had a significant effect on the densities of

saplings according to their life histories (V=0.08, $F_{(3,203)}$=5.97, P<0.05). Follow-up univariate contrasts found significant differences between the density of large tree saplings (*Ficus* tree mean=0.03±0.005/m^2 versus 0.01±0.002/m^2 for non-*Ficus* trees; $F_{(1,205)}$=15.64, P<0.05) and shrubs (0.02±0.004/m^2 versus 0.01±0.002/m^2; $F_{(1,205)}$=8.05, P<0.05), but not for the density of small trees ($F_{(1,205)}$=3.01, P>0.05).

The sapling communities growing under and around *Ficus* trees were richer than non-*Ficus* trees (Table 2). However, the Shannon diversity index and Simpson dominance index were similar for both focal tree types, and the Sørensen's index score suggested very high homogeneity in community composition.

Our regression analysis determined that *Ficus* trees held higher sapling densities than non-*Ficus* trees, while higher grazing intensity was linked to lower sapling densities, larger canopy areas were associated with higher sapling densities, and distance from the nearest forest had no discernable influence ($F_{(4,202)}$=26.98, P<0.05, R^2=0.34; Table 3).

Overall seed rain results, which include seeds of the same species as the tree under which a trap was situated, were significantly different across the five experiment types ($H_{(4)}$=10.32, P<0.05; Table 4). The group of particular interest, the dispersed seeds, also returned a significant result ($H_{(4)}$=18.76, P<0.05). An upward trend in dispersed seed rain densities was detected from non-zoochorous, to fruit, and then to *Ficus* trees with nets at 4 m from the trunk (z=2.97, P<0.05, r=0.31). The Mann Whitney U tests found no significant difference between fruit and non-zoochorous trees (U=187, z=-0.43, P>0.0125), or between *Ficus* tree nets at 4 m and *Ficus* tree nets at 8 m (U=683, z=-0.74, P>0.0125). However, the tests did find a significant difference between non-zoochorous trees and *Ficus* trees at 4 m (U=339, z=-2.58, P<0.0125), and fruit trees and *Ficus* trees with nets at 4 m (U=326.5, z=-2.76, P<0.0125). Finally, the distance from the

nearest forest had no effect on dispersed seed rain densities in *Ficus* trees ($F_{(1,27)}$=0.07, P>0.05, R^2=0.002).

DISCUSSION

Our results demonstrate the important role isolated *Ficus* trees can play in ecological restoration. The density of saplings growing under *Ficus* trees in the study was twice as high as the density of saplings growing under other non-*Ficus* trees, while the species richness of these saplings was also significantly higher. This indicates that *Ficus* trees are more effective restoration nuclei than other remnant tree types. With regards to the communities developing around *Ficus* trees, the diversity and dominance index scores were comparable to non-*Ficus* trees, while the Sørensen's index found *Ficus* and non-*Ficus* trees to support very similar communities. This suggests that *Ficus* trees are supporting the regeneration of plant communities that are representative of the general landscape, and not simply favouring frugivore-dispersed species, which would still restore forests, but which would likely produce assemblages of novel compositional structure (Corbin & Holl 2012).

However, our regression analysis also indicated that tree size has a major influence on sapling densities. Indeed, canopy area (0.36) was the primary effect on sapling density, while focal tree type was a secondary effect (-0.21). This result suggests that conserving large trees, whether *Ficus* or not, would be a prudent first order conservation priority in modified landscapes, and that *Ficus* trees should be prioritized within that subset. The importance of remnant tree size in facilitating restoration may reflect the attractiveness of larger trees to frugivores, perhaps because they provide larger food resources, or better cover from predators (Murray *et al.* 2008). It is worth noting, though, that *Ficus* trees were on average considerably larger than non-*Ficus* trees (which may reflect the strangling life-strategies of several species in

253 the study area), and rather than treating tree size as a confounding factor, we consider the size of
254 *Ficus* trees to be an integral characteristic when comparing them to other trees.

255 In examining sapling communities, our pattern of higher densities but equivalent
256 diversity concurs with Slocum's (2001) Neotropical results, where he found high community
257 similarity in sapling assemblages around remnant trees in open and closed pasture types, but
258 twice as many sapling recruits in the enclosed system. While the driver in Slocum's case was
259 grazing pressure, in this system it appears that propagule dispersal may have had some role in
260 creating the lower sapling densities found in non-*Ficus* communities. Dispersal limitation has
261 been cited as a major constraint on ecological restoration in a range of environments (Holl *et al.*
262 2000, Slocum 2001, Albornoz *et al.* 2013). However, in this study, *Ficus* trees had significantly
263 higher rates of non-parent seed rain than random trees or other fruiting trees, and significantly
264 higher densities of zoochorous plant species growing under and around them. This suggests that
265 frugivores are either preferentially visiting *Ficus* trees, or for some other reason are dispersing
266 seeds under *Ficus* trees more effectively than other tree types, which corresponds with the
267 findings of several studies that found a high abundance and richness of frugivorous birds and
268 bats at isolated *Ficus* trees (Guevara & Laborde 1993, Galindo-González *et al.* 2000,
269 Eshiamwata *et al.* 2006).

270 Other reasons for higher sapling densities under *Ficus* trees may include the abiotic
271 environment. The large size and dense canopies of *Ficus* species analysed in this study provided
272 a high amount of shade (Slocum 2001, Guevara *et al.* 2004, Dhanya *et al.* 2013a), which may
273 facilitate seed germination and growth (Loik & Holl 2001). Soil nutrient levels under *Ficus* trees
274 may also differ from non-*Ficus* trees, with a higher biomass of leaf fall and high levels of
275 minerals such as calcium and potassium from decomposing *Ficus* fruit (O'Brien *et al.* 1998,

Wendeln *et al.* 2000, Dhanya *et al.* 2013b). Therefore the microclimate and soil nutrient balance under *Ficus* trees may also be more conducive to seed germination and sapling growth than other tree types. In practice, an interaction between these factors is likely to be at play (Vieira *et al.* 1994). Indeed, in Slocum's study of four focal tree species in Neotropical pastures, the high amount of shade under *Ficus* trees, along with good incoming seed dispersal (*Ficus* trees received the highest rate and richness of seed rain; Slocum & Horvitz 2000), resulted in *Ficus* trees having the most diverse and dense sapling assemblages (Slocum 2001).

For restoration nuclei to be successful, saplings must establish and mature beyond the perimeter of the nucleus itself. Our results indicate that *Ficus* trees have denser sapling communities in a 5 m perimeter of the canopy edge than non-*Ficus* trees, but that the rate of decline in sapling densities away from the canopy is comparable in both tree types. This is consistent with findings for isolated Mexican *Ficus* trees, where sapling densities decreased around the perimeter of focal trees (Guevara *et al.* 1992), along with findings around remnant trees in Costa Rica (Sclawin & Zahawi 2008), and tree islands in Honduras (Zahawi & Augspurger 2006).

There was also no decline in seed rain with distance to the nearest forest. This result has previously been explained by the small range and absolute distances between the seed trap and the nearest forest (usually of 20–50 m; Holl 1999, Cubiña & Aide 2001, Zahawi & Augspurger 2006, Pejchar *et al.* 2008, Cole *et al.* 2010), which would provide only a minor barrier to dispersal. However, the present study was carried out at a much larger scale, with a range of 0.01–32.06 km, and an average of 16.81 km from the seed trap to the nearest forest. Although there were differences in matrix quality across the landscape, our results suggest that the frugivores acting as dispersal vectors were not sensitive to isolation, and therefore may have

299 been matrix generalists rather than forest specialists (Devictor *et al*. 2008, Cottee-Jones *et al.*
300 2015). This is supported by studies of remnant trees and tree islands in Neotropical pastures,
301 where most of the frugivores recorded were open habitat species (Guevara & Laborde 1993,
302 Zahawi & Augspruger 2006).

303 We found isolated *Ficus* trees in human landscapes to support richer and denser sapling
304 communities than non-*Ficus* trees. However, canopy area was the primary predictor of sapling
305 density, underlining the importance of conserving large remnant trees in modified landscapes.
306 While the abiotic conditions under *Ficus* trees may play a role, our findings suggest that seed
307 dispersal, which is often a major limiting factor in ecological restoration, is higher under *Ficus*
308 trees than other tree types. Promisingly, seed rain rates under *Ficus* trees did not deteriorate with
309 distance from the nearest forest, suggesting that they are robust to increasing isolation, perhaps
310 because parent trees were growing in the agricultural landscape (Aldrich & Hamrick 1998,
311 Murray *et al.* 2008). Further good news is the similarity of communities developing under and
312 around *Ficus* trees and non-*Ficus* trees. We found no evidence to suggest *Ficus* trees are
313 generating non-analogue forest assemblages, dominated by a small suite of species ecologically
314 compatible with *Ficus* life-histories. We therefore recommend that, wherever possible,
315 conservation practitioners and land managers attempt to conserve large remnant trees, and within
316 that subset, prioritize *Ficus* trees and the area around their canopies to facilitate effective
317 ecological restoration in degraded landscapes.

318 However, there are numerous situations where remnant *Ficus* trees do not survive in the
319 landscape at all. In these scenarios, further work will be required to see whether preferentially
320 planting *Ficus* trees, some of which grow very well in poor soil conditions (Fredericksen *et al.*
321 1999), may be a useful strategy for encouraging regeneration. In time, we hope long-term studies

322 that evaluate the effectiveness of restoration treatments in the second or even third generation of
323 regrowth will provide some guidance on this topic.

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Tables

Table 1. SAPLING characteristics at non-*Ficus* and *Ficus* focal trees in Assam, India. Sapling densities are m^2, values are means ± SE with range beneath. The column reporting sapling density in a 5 m radius encompasses a 5 m radius from the edge of the canopy, and excludes the area under the canopy. Different letters in each column denote significantly different means (see text for test types).

Focal tree type	n	Sapling density under the canopy	Sapling density in a 5 m radius	Animal dispersed sapling density
Non-*Ficus* tree	104	0.07±0.01[a]	0.016±0.004[a]	0.02±0.0002[a]
		0–1.06	0–0.33	0–0.11
Ficus tree	103	0.11±0.02[b]	0.036±0.006[b]	0.04±0.0008[b]
		0–1.32	0–0.44	00.72

Table 2. RICHNESS, diversity, dominance, and community similarity indices for different focal tree types in Assam, India. *estimated with bias-corrected Chao 1 (Chao 1984), 200 simulations. **estimated with Sørensen's Abundance Index, adjusted for unseen species (Chao *et al.* 2005), 200 simulations. Scores are Maximum Likelihood Estimators ± Standard Error. H' and DI were not significantly different between focal tree types (P>0.05).

Focal tree type	n	Sapling richness*	Shannon index (H')	Simpson index (DI)	Sørensen 's index**
Non-*Ficus* tree	104	79.5±12.9	3.07±0.13	0.08±0.01	0.97±0.01
Ficus tree	103	140.1±9.9	3.02±0.24	0.11±0.03	

488 **Table 3.** REGRESSION model coefficients for sapling density under remnant trees, as predicted
489 by focal tree type, canopy area, grazing intensity, and the distance to the nearest forest in Assam,
490 India. Sapling density and canopy area were logarithmically transformed prior to analysis.
491 Number of remnant focal trees=207. R^2=0.35, adjusted R^2=0.34.
492

Dependent variable	**Unstandardised coefficients ± SE**	**Standardised coefficients**	**t**	***P***
Constant	0.85±0.45	-	1.89	0.06
Focal tree type	-0.29±0.10	-0.21	-2.81	>0.01
Canopy area	0.58±0.12	0.36	4.72	>0.001
Grazing intensity	-0.34±0.07	-0.29	-5.00	>0.001
Distance to nearest forest	-0.001±0.01	-0.01	-0.22	0.82

493
494

Table 4. SEED rain densities at different net types placed under or close to different Assamese focal trees. Seed rain densities are m^2/week, values are means ± SE. Different letters denote significantly different means in each column, according to Mann-Whitney tests with a critical value of 0.0125. Overall seed rain results include seeds of the same species as the tree under which a trap was situated. No tests were performed on *Ficus* 4 m beyond as no seeds were recorded in this category.

Net type	n	Overall seed rain	Dispersed seed rain
Non-zoochorous tree	20	4.42±2.16[a]	2.19±0.97[x]
Fruit tree	20	155.65±71.1[a]	3.5±1.87[x]
Ficus tree (4 m)	54	18,492.14±2,768.66[b]	12.73±3[y]
Ficus tree (8 m)	28	12,297.75±2,184.67[b]	18.82±10.93[y]
Ficus tree (4 m beyond the canopy)	8	98.41±34.79[a]	-

503 **Supporting information**

504 **Table S1:** A list of the non-*Ficus* focal trees analysed in this study, with the number of
505 individual trees analysed recorded in the second column.

Species	Number studied
Adenanthera pavonina L.	1
Albizia lucidior (Steud.) I.C.Nielsen	1
Albizia procera (Roxb.) Benth.	4
Albizia saman (Jacq.) Merr.	11
Alstonia scholaris (L.) R. Br.	6
Artocarpus heterophyllus Lam.	6
Artocarpus lakoocha Roxb.	7
Bombax ceiba L.	2
Carallia brachiata (Lour.) Merr.	1
Cassia fistula L.	7
Dillenia indica L.	3
Dysoxylum binectariferum Hook f. ex. Bedd.	2
Gmelina arborea Roxb.	6
Heliotropium indicum L.	1
Lagerstroemia speciosa (L.) Pers.	4
Litsea monopetala (Roxb.) Pers.	1
Magnolia mannii (King) Figlar	2
Mangifera indica L.	12
Mesua ferrea L.	1
Murraya koenigii (L.) Spreng.	1
Neolamarckia cadamba (Roxb.) Bosser	3
Pongamia pinnata (L.) Pierre	5
Premna bengalensis C.B.Clarke	3

Spondias mombin L.	1
Spondias pinnata (L. f.) Kurz	2
Syzygium cumini (L.) Skeels	5
Tetrameles nudiflora R. Br.	3
Toona ciliata M.Roem.	3

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