Successional status, seed dispersal mode and overstorey species influence tree regeneration in tropical rain-forest fragments in Western Ghats, India

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Abstract: The effects of fragmentation and overstorey tree diversity on tree regeneration were assessed in tropical rain forests of the Western Ghats, India. Ninety plots were sampled for saplings (1–5 cm diameter at breast height (dbh); 5×5-m plots) and overstorey trees (>9.55 cm dbh; 20×20-m plots) within two fragments (32 ha and 18 ha) and two continuous forests. We tested the hypotheses that fragmentation and expected seed-dispersal declines (1) reduce sapling densities and species richness of all species and old-growth species, and increase recruitment of early-successional species, (2) reduce the prevalence of dispersed recruits and (3) increase influence of local overstorey on sapling densities and richness. Continuous forests and fragments had similar sapling densities and species richness overall, but density and richness of old-growth species declined by 62% and 48%, respectively, in fragments. Fragments had 39% lower densities and 24% lower richness of immigrant saplings (presumed dispersed into sites as conspecific adults were absent nearby), and immigrant densities of old-growth bird-dispersed species declined by 79%. Sapling species richness (overall and old-growth) increased with overstorey species richness in fragments, but was unrelated to overstorey richness in continuous forests. Our results show that while forest fragments retain significant sapling diversity, losses of immigrant recruits and increased overstorey influence strengthen barriers to natural regeneration of old-growth tropical rain forests.

Key Words: fragmentation, old-growth tree species, regeneration, seed dispersal, tropical forests, Western Ghats

INTRODUCTION

Tropical forests are the greatest reservoirs of terrestrial biodiversity with tree diversity comprising at least 40 000 to 53 000 species (Slik *et al.* 2015). Due to historical and ongoing deforestation across the biome, most remaining tropical forests exist as small fragments interspersed among agriculture, plantations and other non-forest human land uses (Haddad *et al.* 2015, Lewis *et al.* 2015, Newbold *et al.* 2014). With anthropogenic pressures predicted to further intensify forest fragmentation in most regions (Haddad *et al.* 2015, Lewis *et al.* 2015), understanding how fragmentation alters the structure and composition of tropical forest tree communities has gained importance globally.

The effects of forest fragmentation on plant communities are driven by a combination of abiotic and biotic factors affecting different life stages and operating across a range of temporal scales (Hobbs & Yates 2003, Kolb & Diekmann 2005). While forest dynamics in the initial decades following fragmentation are characterized by elevated mortality of large, old-growth trees (Laurance 1997), in the longer term fragmentation is known to impose strong biotic and abiotic filters on tree regeneration (Laurance *et al.* 1998, Santo-Silva *et al.* 2013). Abiotic changes, such as increased light in forest understoreys due to the presence of nearby edges, are known to favour regeneration of shade-intolerant early-successional tree species over more shade-tolerant

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old-growth species (Laurance *et al.* 2006a, Tabarelli *et al.* 2008). Regeneration dynamics of fragments are also influenced by shifts in faunal communities, with reduced seed removal and dispersal distances decreasing recruitment of old-growth tree species having large, animal-dispersed seeds (Cordeiro & Howe 2003, Cramer *et al.* 2007, Melo *et al.* 2010).

Our understanding of abiotic factors and seed dispersal limitation leads to two hypotheses regarding fragmentation effects on the composition of regenerating classes (i.e. seedlings and saplings). First, fragmentation would be expected to decrease density and diversity of old-growth species, while early-successional tree species would be expected to increase in density and diversity in fragments, compared with continuous forests (Tabarelli *et al.* 2008). Previous studies, mostly from the Neotropics, have reported reductions in overall seedling densities and species richness in fragments (Benítez-Malvido 1998, Benítez-Malvido & Martínez-Ramos 2003), with declines of old-growth tree species underlying shifts in seedling community composition (Melo *et al.* 2010, Santo-Silva *et al.* 2013). However, our understanding of fragmentation effects on regeneration of Palaeotropical tree communities – which differ markedly in taxonomy and function and have been geologically separate for tens of millions of years (Corlett 2007, Corlett & Primack 2006) – remains limited.

A second hypothesis relating to tree regeneration in fragments is that by reducing seed dispersal (Cordeiro & Howe 2003, Cramer *et al.* 2007), fragmentation would increase the influence of overstorey trees on the structure and composition of regenerating stands locally (Melo *et al.* 2010). Previous research has shown that understoreys of tropical forest fragments have fewer old-growth immigrant recruits (i.e. inferred as having emerged from dispersed seeds due to the absence of conspecific adults nearby, following Martínez-Ramos & Soto-Castro 1993) than larger forest patches (Melo *et al.* 2010). However, no studies to our knowledge have examined relationships of regeneration density and diversity with overstorey tree diversity in tropical forest fragments, nor asked how these understorey–overstorey relationships differ between continuous forests and fragments.

In this study, we compare tree sapling communities of relatively undisturbed continuous tropical rain forests and rain-forest fragments in the Western Ghats of peninsular India, and ask how sapling density and species composition vary in relation to fragmentation and overstorey tree species richness. The specific hypotheses tested are that (1) fragments have lower sapling densities and species richness overall and of old-growth tree species, and higher densities and richness of early-successional species than continuous forests; (2) fragments have lower densities and species richness of immigrant saplings – as an index of seed dispersal (Martínez-Ramos & Soto-Castro 1993, Melo *et al.* 2010) – than continuous forests, especially of old-growth tree species which depend on large birds and mammals for seed dispersal; and (3) as a consequence of seed-dispersal limitation, sapling density and species richness are more strongly correlated with overstorey tree species richness in fragments than in continuous forests.

METHODS

Study area

The study was conducted on the Valparai plateau in the Anamalai Hills (22 000 ha, 10°15′–10°22′N, 76°52′–76°59′E) of the Western Ghats (Figure 1), a global biodiversity hotspot (Kumar *et al.* 2004). The Valparai plateau has an undulating terrain and ranges between 600 m and 1400 m asl. The annual rainfall averages about 3500 mm, with 70% of the precipitation occurring during the south-west monsoon between June and September (data from Injipara estate, 1989–1998). The natural vegetation of the area has been classified as mid-elevation tropical evergreen rain-forest of the *Cullenia exarillata–Mesua ferrea–Palaquium ellipticum* type (Pascal 1988, Pascal *et al.* 2004). The most abundant trees in the forests are *Palaquium ellipticum* (Sapotaceae), *Vateria indica* (Dipterocarpaceae), *Cullenia exarillata* (Malvaceae), *Reinwardtiodendron anamallayanum* (Meliaceae), *Drypetes malabarica* (Putranjivaceae) and *Oreocnide integrifolia* (Urticaceae) (Muthuramkumar *et al.* 2006).

Rain forests on the Valparai plateau have been cleared for establishing plantations – mainly of tea, shade coffee and cardamom – since the late 1800s (Mudappa & Raman 2007). The rapid expansion of plantations to over 13 000 ha by the 1940s was the main cause of rain-forest fragmentation (Mudappa & Raman 2007). At present, the plateau has a landscape matrix dominated by plantations of tea, followed by shade coffee, and small areas of cardamom and *Eucalyptus* (c. 15 000 ha in total). There are also over 40 remnant rain-forest fragments (1–300 ha in area) nestled within these plantations and abutting or extending into the surrounding wildlife reserves. The surrounding reserves – chiefly Anamalai Tiger Reserve in Tamil Nadu (95 800 ha, 10°12′–10°35′N, 76°49′–77°24′E) and Parambikulam Tiger Reserve (63 400 ha, 10°20′–10°32′14″N, 76°35′–76°50′E) and Vazhachal Reserved Forest in Kerala (41 395 ha, 10°31′–10°33′N, 76.70′–76.81′E) – also contain extensive continuous rain forests extending to over 30 000 ha alongside other vegetation types.

The Valparai landscape matrix allows us to compare rain-forest fragments to contiguous forests and examine changes in tree species assemblages. In this study, we compare tree sapling communities of two relatively
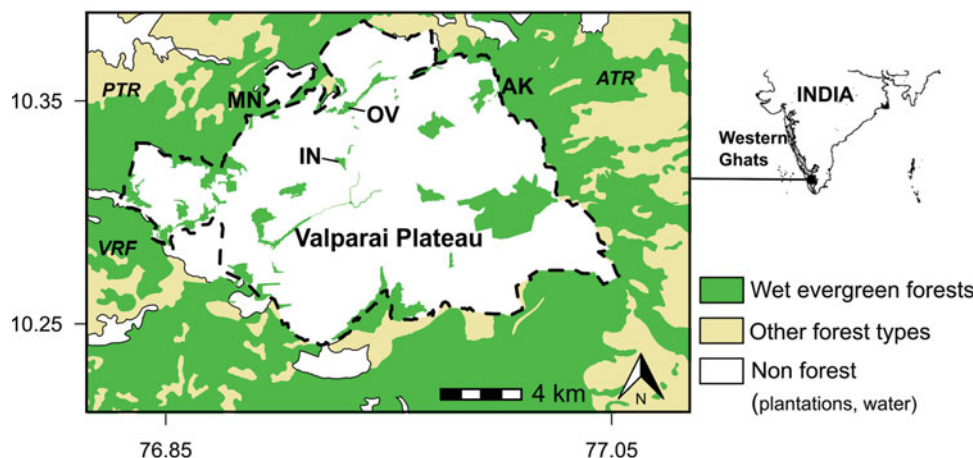
Figure 1. Map of Valparai plateau and adjoining protected areas in southern India showing wet evergreen forests (rain forests), other forest types and non-forest areas. Locations of continuous forest sites Akkamalai (AK) and Manamboli (MN) and forest fragment sites Old Valparai (OV) and Injipara (IN) are marked. General locations of Anamalai Tiger Reserve (ATR), Parambikulam Tiger Reserve (PTR) and Vazhachal Reserved Forest (VRF) are also indicated. Forest and land cover maps were derived from layers generated by French Institute of Pondicherry, available at http://indiabiodiversity.org/, and from digitized rain-forest fragment boundaries available with Nature Conservation Foundation.

undisturbed continuous tropical rain forests, Akkamalai (AK, 2600 ha) and Manamboli (MN, 100 ha), with two rain-forest fragments, Injipara (IN, 18 ha) and Old Valparai (OV, 32 ha; earlier known as Tata Finlay, TF, in Muthuramkumar *et al.* 2006). While AK and MN are within the Anamalai Tiger Reserve, IN and OV are located in the plantation-dominated part of the Valparai plateau. IN is surrounded by privately owned tea and *Eucalyptus* plantations, while OV adjoins traditional shade coffee plantations under a canopy of native tree species, and *Eucalyptus* plantations. Both forest fragments face a moderate amount of human disturbance, with non-native *Spathodea campanulata* (Bignoniaceae) and *Maesopsis eminii* (Rhamnaceae) trees present in IN, which were planted as plantation shade trees in the past, while AK and MN are relatively undisturbed except for some understorey invasion by robusta coffee *Coffea canephora* (Rubiaceae) from adjoining plantations in MN (Joshi *et al.* 2009).

Vegetation sampling

The sampling design for assessing tree regeneration in this study was nested within and carried out concurrently with vegetation sampling plots surveyed in 2003 for a larger study examining plant community structure in the same rain-forest fragments and continuous forests (Muthuramkumar *et al.* 2006). Each sampling unit consisted of a 20 × 20-m (0.04 ha) plot for sampling adult tree communities (hereafter, overstorey trees and species). All plots were randomly placed, maintaining a minimum distance of 50 m between plots. They were also located at least 20 m away from roads, major trails and

habitat edges. Each plot was then divided into four 10 × 10-m quarters. The regeneration sampling was done in a 5 × 5-m plot (0.0025 ha) placed at the outer corner of the first (south-west) quarter. Within each regeneration plot, we identified, counted and measured all tree saplings >1 cm diameter at breast height (dbh, at 1.3 m) and <9.55 cm dbh (equivalent to <30 cm girth at breast height, gbh). Woody shrubs of 1–9.55 cm dbh were also recorded in the regeneration plots, but were not included in the present analysis. All stems ≥9.55 cm dbh within the 20 × 20-m plot were identified and counted as overstorey plot trees. In addition, trees (dbh ≥ 9.55 cm) outside the tree plot but whose canopy extended directly overhead the 5 × 5-m regeneration plot area were identified and counted as overhanging trees. Plant species were identified using Gamble & Fischer (1935) and herbarium collections from previous studies in the region kept at the Salim Ali School of Ecology, Pondicherry University (Annaselvam & Parthasarathy 1999, Ayyappan & Parthasarathy 2001, Muthuramkumar & Parthasarathy 2000, Parthasarathy 1999, 2001). Species names were updated with reference to The Plant List (Version 1.1, http://theplantlist.org). A total of 90 regeneration plots were sampled including 25 each in the two continuous forest sites and 20 each in the two fragments.

Tree species groups

All the tree species in the regeneration dataset were divided into groups of ecologically similar species based on successional status and seed dispersal mode. First, all native species were classified as either old-growth (climax) species, which are shade-tolerant

Maximum adult heights, wood densities and percentage of species having large or medium-sized seeds among old-growth and early-successional tree species in rain forests of the Anamalai Hills, Western Ghats.

Trait	Old-growth species (91 species)	Early-successional species (31 species)
Maximum adult height (m) (Mean $\pm$ 1 SE)	18.1 $\pm$ 1.3	12.7 $\pm$ 1.5
Wood density (g cm^{-3}) (Mean $\pm$ 1 SE)	0.63 $\pm$ 0.03	0.51 $\pm$ 0.03
Large/medium seed size (%)	43	6

and closely associated with interiors of mature and undisturbed rain forests, or early-successional (pioneer) species, which are less shade-tolerant and more closely associated with clearings, habitat edges and disturbed areas (Swaine & Whitmore 1988). We based our classification of old-growth and early-successional species groups on published species descriptions in online databases containing information on trees of the Western Ghats such as Biodiversity Informatics and co-Operation in Taxonomy for Interactive shared Knowledge base (http://www.biotik.org/), India Biodiversity Portal (http://indiabiodiversity.org/) and the Kerala Forest Research Institute Herbarium (http://kfriherbarium.org), and on previous studies that provided information on the successional status of rain-forest species in the Western Ghats (Chetana 2013, Pascal 1988, Raman *et al.* 2009, Sreejith 2005).

Information on other species traits such as seed size (length: small $\leq$ 1 cm; medium = 1–3 cm; large $\geq$ 3 cm), wood density and maximum adult height, collated from secondary sources, were also used to corroborate our species classifications (Appendix 1 gives a species list, traits-based groups and information sources). Consistent with expectations based on known ecological differences between old-growth and early-successional species (Laurance *et al.* 2006a, b; Tabarelli *et al.* 2008), old-growth species have 43% greater maximum adult heights and 24% higher wood densities, on average, than early-successional species, and a greater proportion of old-growth species have large- or medium-sized seeds (43%) than early-successional species (6%; Table 1). Apart from old-growth and early-successional species, two non-native tree species that are grown in plantations and woodlots in the surrounding matrix, namely *Spathodea campanulata* and *Maesopsis eminii*, were found regenerating in one of the fragments and were classified as introduced species.

Next, each tree species was assigned to one of four seed-dispersal categories, namely: (1) bird, (2) mammal, (3) bird and mammal, and (4) abiotic – including wind, water, gravity and explosive dehiscence. Dispersal mode classifications were based on published information on seed-dispersal mechanisms of Western Ghats tree species (Appendix 1), combined with unpublished notes and observations recorded by DM and TRSR over the last 20 y in the study area. Species that could not be placed with certainty into any seed-dispersal group were assigned to an unknown dispersal-mode group.

Immigrant saplings

Tree saplings in the regeneration plots were classified based on dispersal history as either immigrant or local saplings. Saplings within regeneration plots belonging to species that were not present in corresponding 20× 20-m overstorey tree plots were classified as immigrants – their presence in the regeneration plot is most likely an outcome of seed-dispersal events because no adults of those species were recorded in the immediate vicinity (Martínez-Ramos & Soto-Castro 1993, Melo *et al.* 2010). Immigrant densities therefore provide a conservative estimate of the amount of regeneration that has arisen from dispersed seeds in continuous forests and forest fragments (Melo *et al.* 2010). On the other hand, saplings establishing under or close to conspecific adults could have arisen from seeds that simply fell – rather than having been dispersed – from nearby parent trees, and are therefore classified as local. All small tree species (maximum adult height ≤5 m) were placed in a third category – unknown – because even as adults these trees rarely attain sizes needed (>10 cm dbh) to be recorded in overstorey tree plots.

Data analysis

The regeneration-plot data, which contained individuals ranging in size from 1–9.55 cm dbh, was filtered to retain only tree saplings (1–5 cm dbh). We then counted the numbers of individuals (density) and species (richness) of saplings in the regeneration plots, taken overall and as separate subsets of species grouped by successional status (old-growth and early-successional) and seed-dispersal mode (bird, mammal, bird and mammal, and abiotic). As species richness was also expressed per unit area of the plot (0.0025 ha), it is equivalent to species density as defined by Gotelli & Colwell (2001).

We used generalized linear mixed models (GLMMs) to first examine variation in plot-level sapling densities and species richness of all, old-growth and early-successional species in relation to fragmentation status (hypothesis 1) and, second, to examine how regeneration density and richness vary with respect to overstorey species richness in continuous forests and fragments (hypothesis 3). Sapling responses at the plot level were modelled with

fragmentation status, overstorey species richness and a two-way interaction between fragmentation status and overstorey richness as fixed predictors, while site was included as the random grouping variable. We compared model intercepts to ask whether sapling density and richness differed between continuous forests and fragments. Model slope estimates for continuous forests and fragments were compared to ask whether relationships between sapling responses and overstorey species richness differed between the two habitats. Model parameters (intercept and slope) were considered to differ significantly between continuous forests and fragments when the 95% confidence interval (95% CI) of the estimated difference between the two habitats spanned a range that did not include zero (Nakagawa & Cuthill 2007).

We also examined sapling species-richness patterns at the site level after controlling for differences in sampling effort across sites using rarefaction. As the number of plots sampled per site varied from 20 (IN and OV) to 25 (AK and MN), species richness of 15 plots, averaged across 500 random 15-plot samples, was assessed for each site.

Next, we used GLMMs to test for differences in the densities and species richness of immigrant saplings between continuous forests and fragments, and asked whether responses differed across seed-dispersal modes and successional status groups (hypothesis 2). We modelled immigrant densities and richness of bird-, mammal-, bird-and-mammal-, and abiotically dispersed species as well as immigrant densities and richness of old-growth species and early-successional species belonging to different dispersal groups as response variables, with fragmentation status as a fixed predictor and site as a random grouping variable.

The placement of regeneration plots at the corners, rather than centres, of the respective overstorey tree plots, which was done to simplify plot marking and data collection at the time of sampling, could introduce a bias by inflating the numbers of saplings classified as immigrants. We tested for this bias by repeating the immigrant classification and analysis by defining the overstorey species pool as the list of species from within the 20 × 20-m plots combined with overhanging trees that were located outside the plots. Immigrant densities and richness estimated using the latter (20 × 20-m plots plus overhanging trees) and former (20 × 20-m plots only) classifications were virtually identical (average differences: density = 1%, species richness = 0.7%), suggesting that including overstorey trees beyond the corner of the 20 × 20-m plot does not strongly modify immigrant responses. Hereafter, only the former set of immigrant results (overstorey trees in 20 × 20-m plots only) is presented.

As all response variables assessed were in the form of counts, GLMMs were specified using a Poisson error distribution. As the GLMMs comprised multiple predictors, values of numerical predictors (overstorey tree species richness) were scaled and centred on zero prior to the analysis. All data processing, statistical analyses and preparation of figures and other outputs were performed using the R statistical and computing environment. GLMM analyses were run using the lme4 package in R (Bates *et al.* 2015).

RESULTS

We recorded 955 saplings of at least 110 tree species during the study, including 538 individuals (87 species) in continuous-forest plots and 417 individuals (65 species) across plots in forest fragments. Overall sapling densities ranged from 1–23 individuals per plot (0.0025 ha) across continuous forest plots and 2–25 individuals per plot across plots in forest fragments. Sapling species richness ranged from 1–18 species and 1–12 species per plot in continuous forests and forest fragments, respectively. At the site level, Akkamalai (continuous forest) had the highest average rarefaction species richness across 15 plots (mean ± SD = 51.1 ± 3.3), followed by Old Valparai (fragment: 42.9 ± 2.7) and Manamboli (continuous forest: 37.9 ± 2.4), while the more disturbed Injipara fragment had fewest species per 15 plots (28.6 ± 1.6).

Overall sapling densities and species richness were not consistently related to fragmentation status (Figure 2), with 95% CIs of the estimated difference between continuous forests and fragments having a range that spanned zero (in other terms, mean density estimates for continuous forests falling within the 95% CI range of sapling densities for fragments, and vice versa; Table 2). However, there were marked differences when species' successional status was considered, with saplings of old-growth species showing strong declines and early-successional species increasing in density and richness in fragments (Figure 2). Our GLMMs estimated 62% lower densities of old-growth tree species on average in fragments than in continuous forests, while densities of early-successional species showed over a twofold increase in fragments (Figure 2a, Table 2). Similar patterns were noted in sapling species richness per plot. Species richness of old-growth trees decreased by 48% in fragments, while richness of early-successional species was over twice as high in fragments compared with continuous forests (Figure 2b, Table 2).

Although continuous forests and fragments had similar sapling densities overall, there were 39% fewer immigrant recruits (i.e. belonging to species not present in the neighbourhood overstorey) in forest-fragment plots (mean = 5.1 saplings per plot, 45% of total saplings, 95% CI = 4.3–6.1 saplings per plot) than in plots in continuous forests (mean = 8.3 saplings per plot, 72%
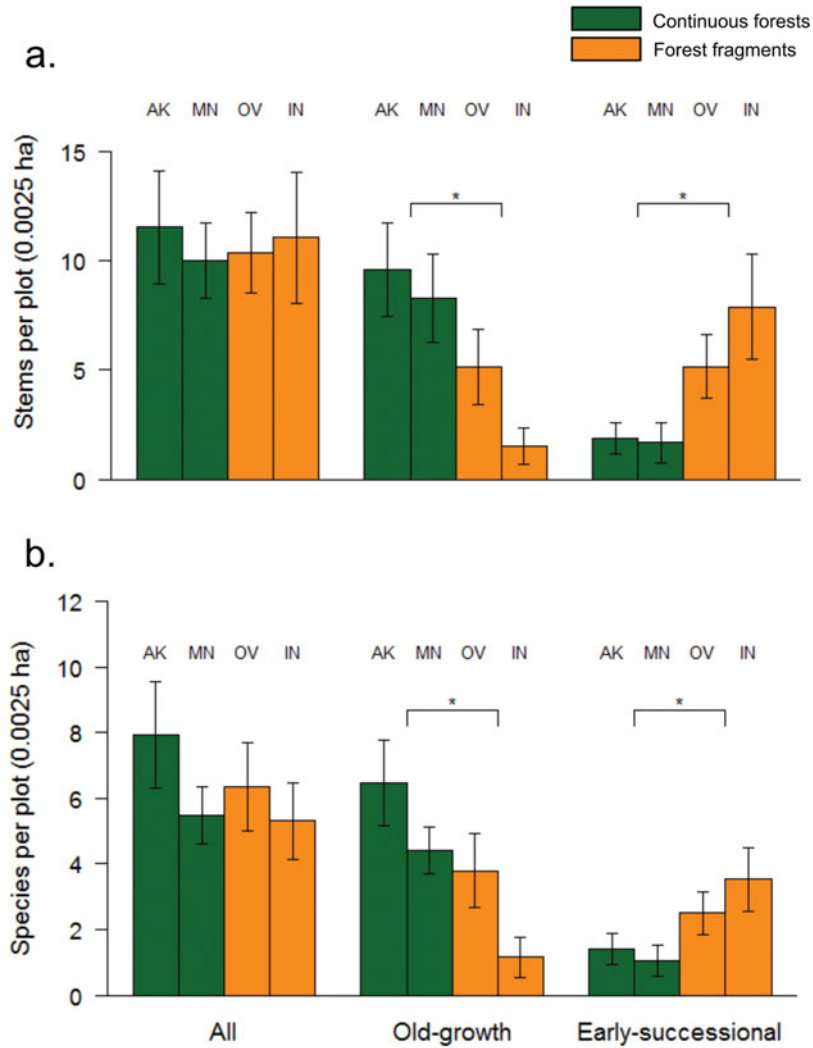
Figure 2. Regeneration plot-level stem densities (a) and species richness (b) of all species, old-growth species and early-successional species in continuous (AK and MN) and fragmented (OV and IN) rain forests in the Anamalai Hills, Western Ghats. Bars represent means and error bars represent 95% CIs. Statistically significant differences between continuous forests and fragments are indicated by *.

of total saplings, 95% CI = 7.6–9.2 saplings per plot; Table 3). Among seed-dispersal modes, sapling densities of immigrant bird-dispersed species and abiotically dispersed species were 48% and 56% lower, respectively, in fragments than continuous forests, while densities of immigrant mammal-dispersed species increased by 71% in fragments (Figure 3a; Table 3). Densities of immigrant old-growth species that are dispersed by birds, and those dispersed by both birds and mammals, were lower in fragments by 79% and 71%, respectively, and old-growth species with abiotic dispersal decreased by 71% (Figure 3b). In contrast, densities of immigrant early-successional species increased four-fold in fragments (Table 3).

Overall immigrant species richness was 24% lower in forest fragments (mean = 3.2 species per plot,

48% of total species, 95% CI = 2.4–4.1 species per plot) than in continuous forests (mean = 4.2 species per plot, 61% of total species, 95% CI = 3.5–4.9 species per plot), and richness of bird-and-mammal-dispersed species decreased by 67% (overall) and 83% (old-growth species) in fragments (Table 3). Patterns of immigrant species richness of old-growth species and of other seed-dispersal groups were qualitatively similar to corresponding immigrant density patterns, but with overlapping means and 95% CIs of richness estimates between habitats suggesting relatively weak differences in most of the cases (Table 3). As over 78% of early-successional saplings belonged to a single seed-dispersal category (bird-dispersed), with relatively few individuals (9–16 individuals) and species (3–4 species) within other dispersal mode groups, responses of different seed dispersal

Table 2. Generalized linear mixed model intercept, slope and R^2 values for tree sapling density and species richness responses to fragmentation and overstorey tree species richness in rain forests of the Anamalai Hills, Western Ghats. Intercepts represent average sapling densities and species richness per plot (0.0025 ha), and slopes represent proportional changes in these responses for unit increase in overstorey tree species richness. Values in parentheses indicate 95% CIs of the parameter estimates. Statistically significant differences between continuous forests and fragments, inferred from 95% CI ranges of parameter estimates (see text), are indicated by # (intercept) and * (slope). Marginal R^2 values representing variance explained by fixed factors of GLMMs (Nakagawa & Schielzeth 2013) are reported.

Response	Intercept		Slope		R^2
	Continuous	Fragment	Continuous	Fragment	
Density: All *	11.5	11.4	−0.03	0.03	0.03
	(10.1–13.0)	(9.4–13.8)	(−0.05—−0.01)	(−0.02–0.08)	
Richness: All *	6.9	6.7	−0.02	0.06	0.09
	(5.6–8.6)	(4.9–9.2)	(-0.05–0.01)	(0.00–0.14)	
Density: Old-growth #,*	9.5	3.6	−0.03	0.10	0.43
	(6.3–14.5)	(1.9–6.7)	(−0.06—−0.01)	(0.02–0.21)	
Richness: Old-growth #,*	5.7	2.9	−0.03	0.15	0.44
	(3.8–8.4)	(1.6–5.3)	(−0.06—−0.01)	(0.04–0.30)	
Density: Early-successional #	1.9	6.4	−0.03	0.00	0.38
	(1.4–2.6)	(4.3–9.5)	(−0.08—−0.03)	(−0.07–0.09)	
Richness: Early-successional #	1.2	3.0	0.01	0.00	0.27
	(0.9–1.6)	(2.0–4.5)	(−0.06–0.09)	(−0.09–0.12)	

Table 3. GLMM-derived average immigrant sapling densities and species richness per 0.0025 ha plot (associated 95% confidence intervals in parentheses) across successional status and seed-dispersal mode groups in continuous rain forests and fragments in the Anamalai Hills, Western Ghats. Responses showing significant differences between continuous forests and fragments, based on 95% CI ranges (see text), are indicated using # (density) and * (richness).

	Dispersal mode	Immigrant density		Immigrant richness	
		Continuous forest	Fragments	Continuous forest	Fragment
All species	Bird #	5.6	2.9	2.5	2.0
		(5.0–6.3)	(2.3–3.6)	(2.0–3.2)	(1.4–2.8)
	Mammal #	0.7	1.2	0.4	0.7
		(0.5–1.0)	(0.8–1.9)	(0.2–0.6)	(0.4–1.3)
	Bird and Mammal *	0.7	0.6	0.6	0.2
		(0.5–1.0)	(0.4–1.0)	(0.4–0.8)	(0.1–0.5)
	Abiotic #	0.9	0.4	0.5	0.2
		(0.5–1.4)	(0.1–0.7)	(0.3–0.7)	(0.1–0.5)
	Overall #,*	8.3	5.1	4.2	3.2
		(7.6–9.2)	(4.3–6.1)	(3.5–4.9)	(2.4–4.1)
Old-growth species	Bird #	4.8	1.0	1.9	0.9
		(2.2–10.3)	(0.3–3.2)	(1.0–4.0)	(0.3–2.6)
	Mammal	0.7	0.9	0.4	0.5
		(0.5–1.0)	(0.6–1.4)	(0.2–0.6)	(0.3–1.0)
	Bird and Mammal # *	0.7	0.2	0.6	0.1
		(0.5–1.0)	(0.1–0.4)	(0.4–0.8)	(0.0–0.3)
	Abiotic #	0.7	0.2	0.4	0.2
		(0.4–1.2)	(0.1–0.5)	(0.2–0.6)	(0.1–0.4)
	Overall #	6.9	2.4	3.3	1.7
		(4.5–10.8)	(1.2–4.5)	(2.1–5.1)	(0.9–3.4)
Early-successional species	Overall #	0.5	2.0	0.6	1.1
		(0.5–1.8)	(0.9–4.7)	(0.4–0.9)	(0.6–2.0)

modes within early-successional species were not assessed separately.

The responses of sapling density and species richness per plot to gradients in overstorey tree species richness varied across species groups and differed between continuous and fragmented forests. Overall sapling densities showed a weak negative relationship with overstorey species richness in continuous forests (average change in sapling density for unit increase in overstorey richness = −3%; 95% CI = −5% to −1%), but was unrelated to overstorey richness in fragments (mean = 3%; 95% CI = −2% to 8%; Table 2). Overall sapling species richness was unrelated to overstorey richness in continuous forests, but increased by 6% on average
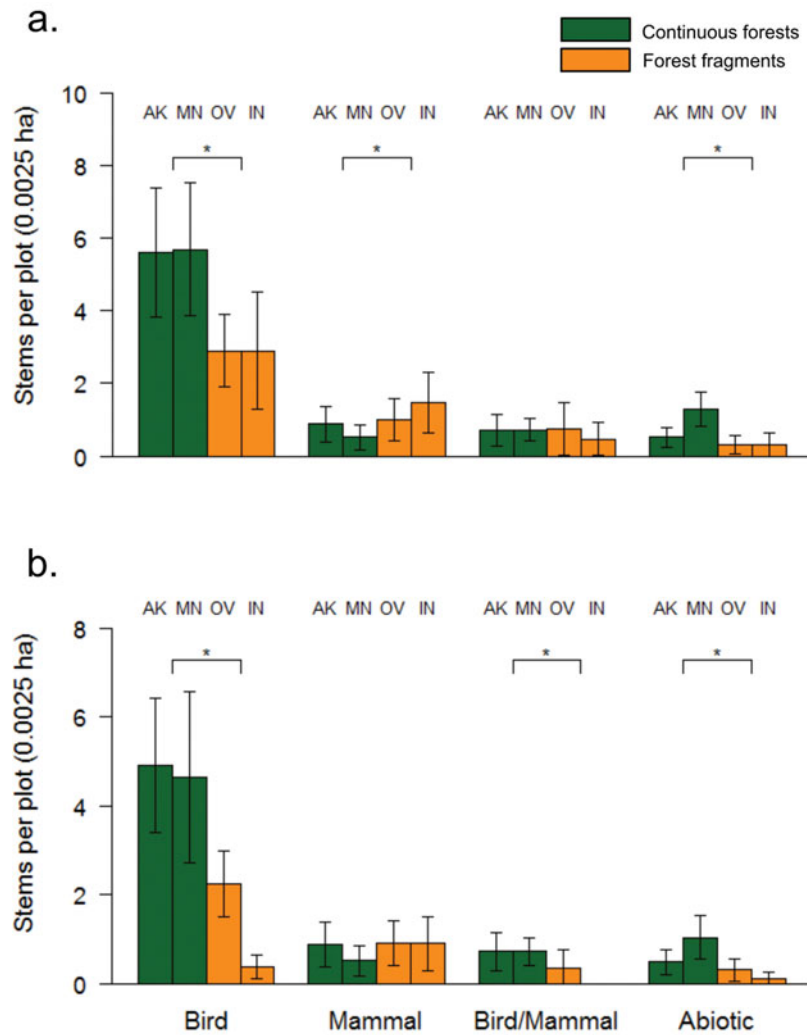
Figure 3. Densities of immigrant saplings in regeneration plots belonging to different seed dispersal modes across all species (a) and old-growth species (b). Bars represent means and error bars depict 95% CIs of the means for continuous rain-forests (AK and MN) and fragments (OV and IN) in the Anamalai Hills, Western Ghats. Statistically significant differences between continuous forests and fragments are indicated by *.

in fragments for unit increase in overstorey richness (Figure 4a; Table 2). This overall pattern was driven by responses of old-growth species saplings, which increased in density by 10% and richness by 15% for unit increase in overstorey richness in fragments, but were weakly related or unrelated to overstorey richness in continuous forests (Figure 4b; Table 2). In contrast, sapling density and richness of early-successional species were unrelated to overstorey species richness in continuous and fragmented forests (Table 2).

DISCUSSION

Our study shows that tree sapling communities in tropical rain-forest fragments in the Western Ghats have similar overall sapling densities and species

richness as nearby continuous rain forests. At the site-level, the larger and less-disturbed fragment (OV) had greater overall rarefied species richness than one of the continuous rain forest sites (MN). The lack of consistent differences in overall species richness between fragments and continuous forests distinguish our findings from previous work (Santo-Silva *et al.* 2013), and highlight the value of fragments for sustaining tree diversity in human-dominated tropical landscapes (Muthuramkumar *et al.* 2006, Turner & Corlett 1996). However, there were marked differences in sapling species composition between continuous forests and fragments in this study. Sapling densities and species richness of old-growth species were substantially lower in fragments, while early-successional species that are typically associated with open and degraded forests showed an increase. These shifts favouring regeneration
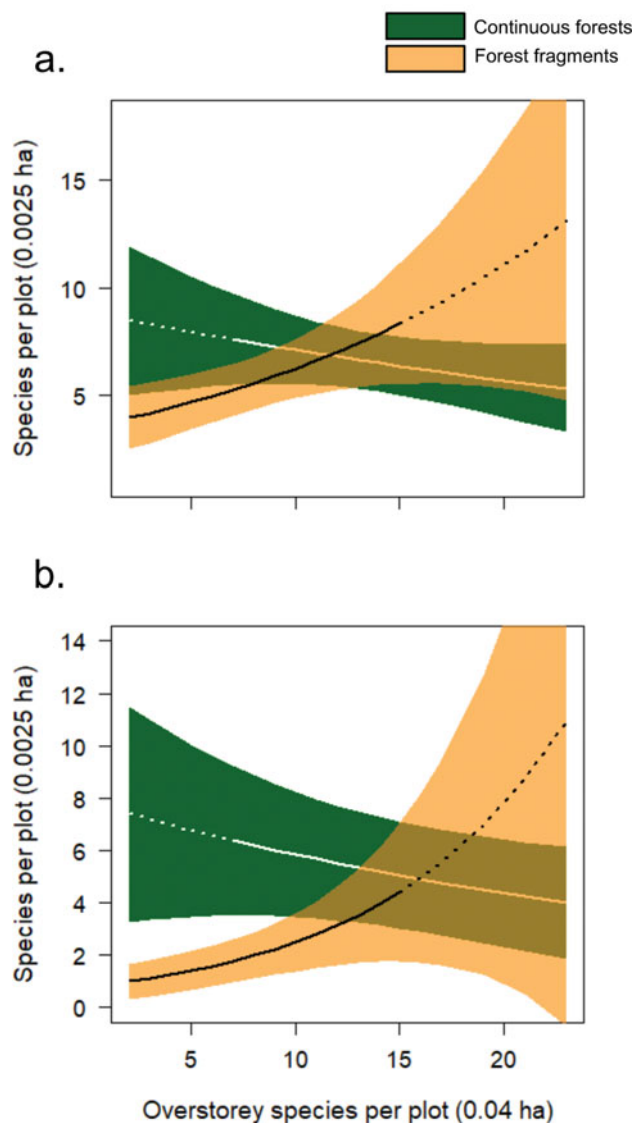
Figure 4. Fitted GLMMs of regeneration plot-level sapling species richness (a) and old-growth sapling species richness (b) in relation to overstorey tree richness and fragmentation in the Anamalai Hills, Western Ghats. Mean fitted lines in continuous and fragmented forests are marked and shaded areas represent corresponding 95% CIs. Model predictions outside the observed range of overstorey richness in each habitat are represented using broken lines.

of early-successional species over old-growth species are consistent with fragmentation effects seen elsewhere in the tropics (Laurance *et al.* 2006a, Santo-Silva *et al.* 2013, Tabarelli *et al.* 2008), and similar to effects of other forest disturbances in the Western Ghats (Anitha *et al.* 2010, Bhat *et al.* 2000, Daniels *et al.* 1995, Parthasarathy 1999).

The decreased recruitment of old-growth tree species is likely to be driven by a combination of factors affecting reproduction, seed dispersal and post-dispersal establishment in fragments (Benítez-Malvido

1998, Benítez-Malvido & Martínez-Ramos 2003). The contrasting patterns of immigrant saplings belonging to different seed-dispersal modes provide insights into shifts in regenerating communities that have most probably arisen due to varying levels of seed-dispersal limitation in fragments. Consistent with previous studies (Cramer *et al.* 2007, Melo *et al.* 2010), fragments had fewer saplings of old-growth species inferred as having arrived via seed dispersal than continuous forests. Interestingly, responses also differed among old-growth species, wherein species that depend partially or entirely on birds for seed dispersal consistently declined in fragments, while immigrant densities of mammal-dispersed species either did not differ between fragments and continuous forests, or increased in fragments. These contrasting responses correspond well with what is known about the composition of faunal communities in the study area – particularly reductions in densities of large avian frugivores such as hornbills and pigeons (Raman 2006), but not densities of large-mammal species in fragments (Sridhar *et al.* 2008).

In the case of smaller-seeded early-successional species, which are dispersed either abiotically or by smaller frugivores that are less sensitive to forest fragmentation (Raman 2006), densities in fragments are also likely to be increased by favourable edge effects – such as desiccation and increased light availability – which are known to penetrate as far as 150 m into fragments (Laurance *et al.* 2006a). Edge effects and other past disturbances such as understorey crop planting, tree felling and planting of non-native shade trees, could have exacerbated this effect in a part of one of our fragment sites (IN). Such disturbances are also known to increase regeneration of non-native trees and shrubs such as *Coffea canephora* in fragments, which could further impede regeneration and recovery of old-growth rain-forest tree species in fragments (Joshi *et al.* 2009, 2015).

Previous single-species studies have shown that reduced seed dispersal distances can restrict natural regeneration of old-growth species to areas of fragments having nearby conspecific adults (Cordeiro & Howe 2003, Cordeiro *et al.* 2009, Ismail *et al.* 2017). Our results suggest that at the community level, seed-dispersal limitation due to fragmentation can alter local relationships of sapling density and richness with overstorey tree species richness. Sapling density and richness were similar across areas of low and high overstorey richness in continuous forests, suggesting that there is potential for natural forest regeneration and recovery even in areas where overstorey disturbances or other factors have reduced adult tree species richness locally. In contrast, sapling densities and richness, particularly of old-growth tree species, were considerably lower in areas with depauperate tree overstoreys in fragments, suggesting that fragmentation decreases the potential for rain-forest tree communities to

naturally recover following overstorey disturbances and species loss.

Conclusions

With large, continuous tropical forests presently restricted to just a few regions such as the Amazon and Congo basins, fragmented forest landscapes are gaining importance for biodiversity conservation and ecosystem services across the human-dominated tropics (Gardner *et al.* 2009, Turner & Corlett 1996). However, decreased recruitment of old-growth tree species in ageing fragments of the Western Ghats (this study), and elsewhere in the tropics (Santo-Silva *et al.* 2013), underlie persistent losses of floristic integrity, biodiversity values and ecosystem services that are widely associated with tropical forest fragmentation and associated disturbances (Laurance & Cochrane 2001, Tabarelli *et al.* 2008). Furthermore, our results suggest that the potential for natural regeneration and recovery of old-growth tree communities is especially limited in fragments that have species-poor tree overstoreys. This suggests that restoration of old-growth tree species could be important for facilitating recovery of rain-forest tree communities in degraded forest fragments.

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Appendix 1. List of species encountered as saplings (1–5 cm dbh) in regeneration plots in continuous and fragmented rain forests in the Anamalai Hills, Western Ghats. Information on species abundances in the two habitats and species traits are also provided. Column codes are as follows: Successional status: O = Old-growth species; E = Early-successional species; I = Introduced species; U = Unknown; Seed-dispersal mode: B = Bird; M = Mammal; BM = Bird and mammal; G = Gravity; W = Wind; U = Unknown; Seed size: L = Large (> 3 cm); M = Medium (1–3 cm); S = Small (<1 cm). *indicates shrub species recorded in regeneration plots but not included in the present analysis. Species traits information was collated from BIOTIK (http://www.biotik.org/), Flowers of India (http://www.flowersofindia.net/), India Biodiversity Portal (http://indiabiodiversity.org/), Global wood density database (doi: http://dx.doi.org/10.5061/dryad.234/1) and Osuri *et al.* (2014).

Species	Total individuals (Relative abundance)		Successional status	Seed dispersal mode	Seed size (cm)	Wood density (g cm^{-3})	Max. adult height (m)
	Continuous	Fragment					
Acronychia pedunculata (Rutaceae)	0 (0.00)	10 (2.28)	E	BM	S	0.54	10
Actinodaphne gullavara (Lauraceae)	4 (0.67)	1 (0.23)	E	B	S	0.51	10
Actinodaphne bourdillonii (Lauraceae)	0 (0.00)	3 (0.68)	E	B	S	0.51	10
Actinodaphne tadulingamii (Lauraceae)	3 (0.50)	0 (0.00)	E	B	S	0.51	10
Aglaia elaeagnoidea (Meliaceae)	5 (0.84)	0 (0.00)	O	BM	M	0.63	10
Aglaia exstipulata (Meliaceae)	1 (0.17)	2 (0.46)	O	B	L	0.80	20
Aglaia simplicifolia (Meliaceae)	17 (2.85)	0 (0.00)	O	U	L	0.76	6
Agrostistachys borneensis (Euphorbiaceae)	1 (0.17)	0 (0.00)	O	G	S	0.82	15
Agrostistachys indica (Euphorbiaceae)	3 (0.50)	1 (0.23)	O	B	S	0.71	5
Antidesma montanum (Phyllanthaceae)	1 (0.17)	1 (0.23)	O	BM	S	0.63	10
Antidesma alexiteria (Phyllanthaceae)	1 (0.17)	0 (0.00)	O	BM	S	0.66	5
Aphanamixis polystachya (Meliaceae)	3 (0.50)	1 (0.23)	O	B	L	0.57	20
Aporosa acuminata (Phyllanthaceae)	0 (0.00)	6 (1.37)	O	B	S	0.37	5
Apollonias arnottii (Lauraceae)	2 (0.34)	2 (0.46)	O	B	S	–	6
Aporosa cardiosperma (Phyllanthaceae)	0 (0.00)	1 (0.23)	O	B	S	0.61	15
Ardisia blatteri (Primulaceae)	1 (0.17)	0 (0.00)	O	B	S	0.59	4
Ardisia pauciflora (Primulaceae)	2 (0.34)	0 (0.00)	O	B	S	0.59	6
Ardisia rhomboidea (Primulaceae)	18 (3.02)	1 (0.23)	O	B	S	0.59	5
Artocarpus heterophyllus (Moraceae)	1 (0.17)	3 (0.68)	O	M	L	0.56	20
Atalantia racemosa (Rutaceae)	5 (0.84)	0 (0.00)	E	M	S	–	4
Atalantia wightii (Rutaceae)	0 (0.00)	1 (0.23)	O	M	S	–	4
Beilschmiedia wightii (Lauraceae)	2 (0.34)	0 (0.00)	O	B	L	0.54	25
Calophyllum austroindicum (Clusiaceae)	1 (0.17)	0 (0.00)	O	M	L	0.55	35
Canarium strictum (Burseraceae)	0 (0.00)	1 (0.23)	O	B	L	0.51	30
Casearia esculenta (Salicaceae)	4 (0.67)	0 (0.00)	O	B	S	0.50	15
Casearia rubescens (Salicaceae)	2 (0.34)	2 (0.46)	O	B	S	0.57	16
Cinnamomum malabatrum (Lauraceae)	5 (0.84)	29 (6.61)	E	B	S	0.59	15
Cinnamomum sulphuratum (Lauraceae)	6 (1.01)	1 (0.23)	O	B	S	0.50	8
Clerodendrum infortunatum (Lamiaceae)	16 (2.68)	83 (18.91)	E	B	S	0.50	4
Coffea arabica (Rubiaceae) *	40 (6.71)	3 (0.68)	I	M	S	0.66	6
Coffea canephora (Rubiaceae) *	0 (0.00)	1 (0.23)	I	M	S	0.66	6
Croton laccifer (Euphorbiaceae)	1 (0.17)	0 (0.00)	O	G	S	0.55	10
Croton malabaricus (Euphorbiaceae)	6 (1.01)	0 (0.00)	E	G	S	0.55	18
Croton zeylanicus (Euphorbiaceae)	37 (6.21)	8 (1.82)	O	G	S	0.55	4
Cryptocarya wightiana (Lauraceae)	21 (3.52)	1 (0.23)	O	B	M	0.62	25

Appendix 1. Continued

Species	Total individuals (Relative abundance)		Successional status	Seed dispersal mode	Seed size (cm)	Wood density (g cm^{-3})	Max. adult height (m)
	Continuous	Fragment					
Cullenia exarillata (Malvaceae)	1 (0.17)	2 (0.46)	O	G	L	–	40
Datura sp. (Solanaceae) *	0 (0.00)	2 (0.46)	E	G	U	–	–
Debregeasia longifolia (Urticaceae)	1 (0.17)	0 (0.00)	E	B	S	–	5
Dendrocnide sinuata (Urticaceae)	24 (4.03)	3 (0.68)	E	B	S	0.21	5
Dimorphocalyx beddomei (Euphorbiaceae)	4 (0.67)	0 (0.00)	O	G	S	0.82	8
Dimocarpus longan (Sapindaceae)	8 (1.34)	29 (6.61)	O	M	S	0.75	25
Diospyros ebenum (Ebenaceae)	5 (0.84)	2 (0.46)	O	M	S	0.68	30
Diospyros bourdillonii (Ebenaceae)	1 (0.17)	0 (0.00)	O	M	M	0.68	28
Diospyros nilagirica (Ebenaceae)	1 (0.17)	0 (0.00)	O	M	S	0.68	20
Diospyros sylvatica (Ebenaceae)	9 (1.51)	2 (0.46)	O	M	S	0.70	35
Discospermum apiocarpum (Rubiaceae)	1 (0.17)	0 (0.00)	O	M	S	0.10	15
Drypetes venusta (Putranjivaceae)	3 (0.50)	0 (0.00)	O	G	L	0.82	30
Drypetes malabarica (Putranjivaceae)	7 (1.17)	2 (0.46)	O	G	S	0.69	20
Dysoxylum malabaricum (Meliaceae)	6 (1.01)	2 (0.46)	O	B	L	0.58	35
Erythrina variegata (Leguminosae)	1 (0.17)	0 (0.00)	E	G	S	0.23	12
Excoecaria oppositifolia (Euphorbiaceae)	0 (0.00)	1 (0.23)	O	G	S	0.57	5
Ficus exasperata (Moraceae)	0 (0.00)	1 (0.23)	E	BM	S	0.40	18
Ficus hispida (Moraceae)	0 (0.00)	7 (1.59)	E	M	S	0.42	10
Ficus nervosa (Moraceae)	1 (0.17)	0 (0.00)	O	BM	S	0.28	35
Garcinia gummi-gutta (Clusiaceae)	2 (0.34)	3 (0.68)	O	M	L	0.69	12
Garcinia morella (Clusiaceae)	5 (0.84)	1 (0.23)	O	M	S	0.73	12
Garcinia talbotii (Clusiaceae)	1 (0.17)	0 (0.00)	O	M	M	0.74	20
Glochidion ellipticum (Phyllanthaceae)	0 (0.00)	1 (0.23)	O	G	S	0.58	8
Glycosmis pentaphylla (Rutaceae)	2 (0.34)	0 (0.00)	E	B	S	0.44	4
Gomphandra coriacea (Stemonuraceae)	2 (0.34)	3 (0.68)	O	B	M	0.46	10
Harpullia arborea (Sapindaceae)	1 (0.17)	0 (0.00)	O	G	M	0.54	15
Heritiera papilio (Malvaceae)	8 (1.34)	0 (0.00)	O	W	M	0.70	30
Heynea trijuga (Meliaceae)	0 (0.00)	9 (2.05)	E	B	M	–	10
Isonandra lanceolata (Sapotaceae)	2 (0.34)	0 (0.00)	O	BM	S	0.93	5
Lantana camara (Verbenaceae) *	0 (0.00)	4 (0.91)	I	BM	S	–	5
Leea indica (Vitaceae)	0 (0.00)	4 (0.91)	E	U	S	0.44	5
Lepisanthes deficiens (Sapindaceae)	2 (0.34)	0 (0.00)	O	M	L	0.66	5
Litsea bourdillonii (Lauraceae)	9 (1.51)	7 (1.59)	O	B	S	0.42	18
Litsea floribunda (Lauraceae)	1 (0.17)	14 (3.19)	E	B	S	0.67	10
Litsea oleoides (Lauraceae)	44 (7.38)	3 (0.68)	O	B	M	0.42	12
Litsea sp. (Lauraceae)	2 (0.34)	0 (0.00)	O	B	S	0.42	10
Litsea sp_1 (Lauraceae)	4 (0.67)	0 (0.00)	O	B	S	0.42	10
Macaranga peltata (Euphorbiaceae)	1 (0.17)	0 (0.00)	E	BM	S	0.48	12
Maesopsis eminii (Rhamnaceae)	0 (0.00)	8 (1.82)	I	BM	L	0.34	30
Maesa indica (Primulaceae)	3 (0.50)	27 (6.15)	E	BM	S	–	4
Mallotus resinosus (Euphorbiaceae)	2 (0.34)	0 (0.00)	O	G	S	0.50	5
Mallotus tetracoccus (Euphorbiaceae)	0 (0.00)	1 (0.23)	E	B	S	0.46	12
Mastixia arborea (Cornaceae)	2 (0.34)	1 (0.23)	O	M	L	0.47	20
Meiogyne pannosa (Annonaceae)	5 (0.84)	2 (0.46)	O	B	S	–	8
Melicope lunu-ankenda (Rutaceae)	0 (0.00)	6 (1.37)	E	M	S	0.51	10

Appendix 1. Continued

Species	Total individuals (Relative abundance)		Successional status	Seed dispersal mode	Seed size (cm)	Wood density (g cm^{-3})	Max. adult height (m)
	Continuous	Fragment					
Meliosma arnottiana (Sabiaceae)	0 (0.00)	1 (0.23)	E	B	S	0.32	18
Meliosma simplicifolia (Sabiaceae)	0 (0.00)	1 (0.23)	O	B	S	0.45	15
Memecylon sisparense (Melastomataceae)	0 (0.00)	3 (0.68)	O	B	S	0.77	7
Mesua ferrea (Calophyllaceae)	9 (1.51)	2 (0.46)	O	G	L	0.86	35
Miliusa wightiana (Annonaceae)	14 (2.35)	0 (0.00)	O	B	S	0.65	8
Murraya paniculata (Rutaceae)	2 (0.34)	0 (0.00)	E	B	S	0.87	12
Myristica dactyloides (Myristicaceae)	13 (2.18)	2 (0.46)	O	B	L	0.60	20
Nageia wallichiana (Podocarpaceae)	2 (0.34)	0 (0.00)	O	U	L	0.46	30
Neolitsea zeylanica (Lauraceae)	1 (0.17)	0 (0.00)	O	B	S	0.55	16
Nothopegia racemosa (Anacardiaceae)	4 (0.67)	0 (0.00)	O	M	S	0.77	15
Ocotea lancifolia (Lauraceae)	3 (0.50)	2 (0.46)	O	B	M	0.52	8
Olea dioica (Oleaceae)	0 (0.00)	3 (0.68)	E	M	S	0.79	15
Oreocnide integrifolia (Urticaceae)	4 (0.67)	44 (10.02)	E	B	S	–	8
Paracroton pendulus (Euphorbiaceae)	8 (1.34)	0 (0.00)	O	G	S	–	30
Persea macrantha (Lauraceae)	12 (2.01)	10 (2.28)	E	B	S	0.46	30
Phoebe paniculata (Lauraceae)	2 (0.34)	4 (0.91)	O	B	S	0.52	15
Psychotria globicephala (Rubiaceae)	6 (1.01)	13 (2.96)	O	BM	S	0.45	–
Psychotria sp. (Rubiaceae)	1 (0.17)	0 (0.00)	O	BM	S	0.45	–
Rauvolfia verticillata (Apocynaceae) *	0 (0.00)	2 (0.46)	E	B	S	0.49	4
Reinwardtiodendron anamalaiense (Meliaceae)	85 (14.26)	0 (0.00)	O	B	S	0.84	20
Saprosma glomeratum (Rubiaceae) *	0 (0.00)	1 (0.23)	O	U	S	–	5
Sarcandra chloranthoides (Chloranthaceae) *	1 (0.17)	0 (0.00)	O	U	S	–	5
Scolopia crenata (Salicaceae)	3 (0.50)	0 (0.00)	O	BM	S	0.74	18
Semecarpus travancorica (Anacardiaceae)	0 (0.00)	1 (0.23)	O	M	L	0.34	35
Solanum giganteum (Solanaceae)	1 (0.17)	1 (0.23)	E	B	S	0.35	3
Spathodea campanulata (Bignoniaceae)	0 (0.00)	23 (5.24)	I	W	S	0.48	15
Symplocos macrophylla (Symplocaceae)	0 (0.00)	2 (0.46)	O	B	M	0.50	10
Syzygium caryophyllatum (Myrtaceae)	4 (0.67)	0 (0.00)	O	BM	S	0.66	6
Syzygium densiflorum (Myrtaceae)	13 (2.18)	5 (1.14)	O	BM	M	0.66	15
Syzygium gardneri (Myrtaceae)	2 (0.34)	0 (0.00)	O	BM	S	0.74	60
Syzygium hemisphericum (Myrtaceae)	2 (0.34)	2 (0.46)	O	BM	M	0.66	20
Syzygium laetum (Myrtaceae)	3 (0.50)	0 (0.00)	O	BM	M	0.76	7
Tabernaemontana gamblei (Apocynaceae)	2 (0.34)	0 (0.00)	O	BM	M	0.58	5
Thottea siliquosa (Aristolochiaceae) *	16 (2.68)	4 (0.91)	O	G	S	–	3
Unidentified_Celastraceae	1 (0.17)	1 (0.23)	U	U	U	–	–
Unidentified_Rubiaceae	1 (0.17)	0 (0.00)	U	U	U	–	–
Vepris bilocularis (Rutaceae)	1 (0.17)	0 (0.00)	O	M	S	–	16
Vernonia arborea (Compositae)	0 (0.00)	2 (0.46)	E	W	S	0.33	15