

Seed size predicts community composition and carbon storage potential of tree communities in rain forest fragments in India's Western Ghats

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Summary

1. Fragmentation is ubiquitous across tropical forests and drives marked shifts in tree community composition by differentially affecting species' dispersal, establishment and survival. Such compositional shifts can potentially alter ecosystem-level properties such as above-ground carbon storage, but our understanding of the factors linking compositional shifts to carbon storage is limited.

2. We compared tree communities of contiguous and fragmented tropical rain forests in the Western Ghats (India) and assessed the ability of various plant functional traits associated with seed dispersal, establishment and survival processes to predict species' responses to fragmentation.

3. Further, we assessed relationships between functional traits that predict tree community turnover and those that govern carbon storage to examine how fragmentation effects on species' composition can alter the ability of tree communities to store carbon.

4. Seed size, as indexed by seed length, was the best predictor of species' responses, with larger-seeded species declining in fragments. Across species, seed length was positively correlated with maximum attainable height, which decreased by 10% on average at the community level in fragments. Such shifts towards smaller-seeded communities could decrease forest stature and reduce above-ground carbon stocks by 8%.

5. *Synthesis and applications.* Our study highlights a previously undescribed mechanism by which fragmentation-driven declines of large-seeded tree species can reduce above-ground carbon stocks by promoting shorter-statured forests. These results imply that strict protection alone might be insufficient and that a multipronged conservation strategy would be required to sustain carbon stocks in tropical forest fragments. Such interventions will need to combine restoration programmes for large-seeded tree species in fragments with broader-scale efforts to maintain hospitable and well-connected landscapes for their seed dispersers.

Key-words: above-ground carbon storage, effect traits, habitat fragmentation, India, response traits, seed dispersal, tree community turnover, tropical forests

Introduction

Habitat fragmentation is among the most pervasive forms of anthropogenic disturbance to natural ecosystems across the tropics (Saunders, Hobbs & Margules 1991; Haddad *et al.* 2015). Fragmentation is known to disrupt ecosystem processes and alter biological communities, but forest fragments are nevertheless important for sustaining

biodiversity and providing ecosystem services such as carbon storage in an increasingly human-dominated world (Laurance & Bierregaard 1997; Gardner *et al.* 2009; Berenguer *et al.* 2014; Magnago *et al.* 2015). Given that the above-ground vegetation of tropical forests constitutes a large carbon pool which regulates atmospheric CO₂ levels and global climate (Malhi, Baldocchi & Jarvis 1999), understanding how fragmentation-driven shifts in the composition of tree communities in turn affect their ability to store carbon is becoming increasingly important.

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It is well recognized that fragmentation can substantially alter the composition of tropical forest tree communities (Laurance *et al.* 2006b; Magnago *et al.* 2014; Santos *et al.* 2014). Fragmentation can drive tree community turnover through abiotic edge effects that alter species' survival, and by disrupting habitat connectivity, which affects seed dispersal (Hobbs & Yates 2003). Edge effects can also increase mortality of old-growth species and promote succession by pioneer species, particularly when fragments are embedded in open, fire-exposed and wind-exposed landscapes (Laurance *et al.* 2006a,b). Studies have also shown that fragmentation can favour tree species that depend less on large-bodied fauna for seed dispersal (Santos *et al.* 2008; Santo-Silva *et al.* 2013). Thus, while it is clear from the existing literature that plant functional traits related to seed dispersal, establishment and survival are important for understanding fragmentation effects, the relative importance of different traits in determining the composition of fragmented tropical forest tree communities is unclear. Moreover, while it has been well documented that fragmentation can reduce above-ground carbon stocks (Laurance *et al.* 1997; Paula, Alves-Costa & Tabarelli 2011; Berenguer *et al.* 2014; Osuri, Kumar & Sankaran 2014), our understanding of how compositional shifts caused by fragmentation translate to changes in carbon storage potential of tree communities remains incomplete (Magnago *et al.* 2015; Poorter *et al.* 2015).

The effects of fragmentation on the carbon storage potential of tree communities resulting from shifts in community composition can be addressed using a response-and-effect framework based on plant functional traits (Lavorel & Garnier 2002; Suding *et al.* 2008). The role of tree community shifts in mediating fragmentation effects on carbon stocks is governed by whether the traits that influence species' responses to fragmentation (response traits) are related to those which determine carbon storage potential (effect traits). Fragmentation may have predictable effects on above-ground carbon storage via shifts in tree community composition if there is direct overlap or correlation between response-and-effect traits, but not if the two groups of traits are unrelated (Suding *et al.* 2008). For example, when increased wind and light penetration caused by edge effects promotes the proliferation of species with low adult stature (response trait) (Laurance *et al.* 2006a; Oliveira, Santos & Tabarelli 2008), this represents a case of direct overlap because adult stature is also a key determinant of how much carbon a tree can potentially store (effect trait). In contrast, when tree community turnover is driven by processes affecting seed dispersal, resultant effects on carbon storage depend on how species' seed dispersal traits are correlated with effect traits such as adult size and wood density. However, these relationships are not well understood in most tropical forests, and few empirical studies have looked at the effects of altered seed dispersal on carbon storage potential of tree communities (but see Kurten, Wright & Carson 2015).

Here, we use a response-and-effect trait framework to investigate how fragmentation affects above-ground carbon storage through shifts in adult and regenerating tree community composition in relatively old (>40–50 years) rain forest fragments in the Western Ghats Mountains of southern India. Based on the literature, we *a priori* identified seed dispersal mode (Santos *et al.* 2008), seed size (Santos *et al.* 2008; Santo-Silva *et al.* 2013), specific leaf area (SLA), wood density (Laurance *et al.* 2006b) and maximum attainable height (Laurance *et al.* 1997; Oliveira, Santos & Tabarelli 2008) as candidate response traits, and wood density and maximum attainable height as effect traits. Higher SLA corresponds to higher leaf-nitrogen, lower longevity and higher growth rates (Wright *et al.* 2004), which have been previously shown to influence species' responses to fragmentation (Laurance *et al.* 2006b). Both wood density and height are important predictors of above-ground carbon storage (Chave *et al.* 2005), with higher values corresponding to increased carbon storage potential of individual trees for a given basal area. Specifically, we asked (i) how well do seed dispersal traits and leaf and woody traits associated with establishment and survival predict tree species' responses to fragmentation (i.e. what are the key response traits)? (ii) What are the relationships between the response traits that govern tree community responses to fragmentation and effect traits that influence carbon storage? and (iii) How do contiguous and fragmented forests differ at the community level in effect traits that govern carbon storage, and how might these compositional shifts alter above-ground carbon stocks?

Materials and methods

STUDY AREA

The study was conducted in Kodagu District, Karnataka state, in the Western Ghats Mountains of peninsular India (12.17°N, 75.80°E; Fig. 1). The study area features deep, well-drained soils of clay and loam on plateaus and moderate hill slopes ranging from 700 to 1000 m a.s.l. (Anonymous 1998). Annual precipitation ranges from *c.* 2400 mm in the east to *c.* 3800 mm in the west (Hijmans *et al.* 2005). Intact forests in the study area comprise mid-elevation wet-evergreen forests characterized by old-growth evergreen species *Mesua ferrea* L. and *Palaquium ellipticum* (Dalzell) Baill (Pascal 1986). These forests occur both as contiguous swaths (>500 km²) and as fragments (<1 to >20 ha) embedded in a matrix dominated by shade coffee plantations. While exact ages of the fragments are unknown, government records and satellite data suggest that the study area had extensive forest cover in the 1920s, which was fragmented in subsequent decades (Menon & Bawa 1997). Both contiguous and fragmented forests are protected by state laws that prohibit timber felling and regulate access and use, while fragments are additionally protected by local communities as sacred groves. See Osuri, Kumar & Sankaran (2014) for more details of the study area.

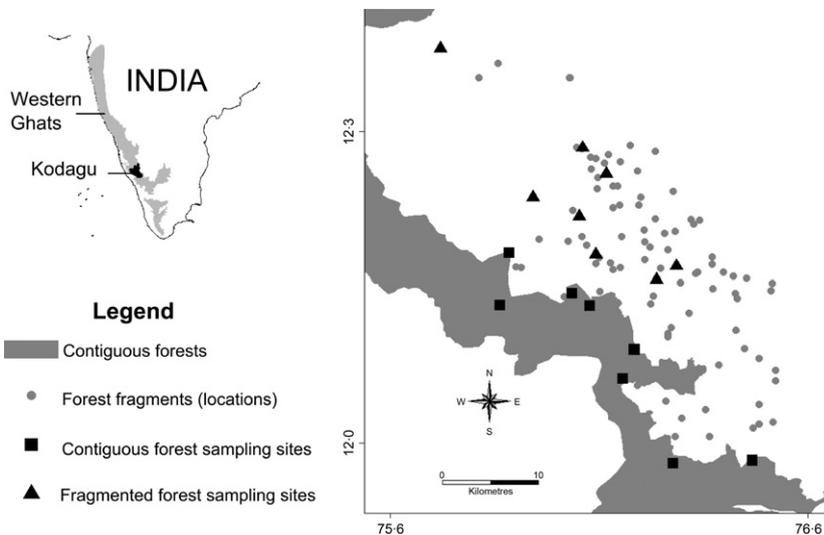


Fig. 1. Map showing the distribution of evergreen forests in the study area which comprises the southern part of Kodagu district in the Western Ghats Mountains, India. Contiguous and fragmented forest sampling sites are represented by square and triangle symbols, respectively.

TREE COMMUNITY SAMPLING

We sampled adult tree communities in eight forest fragments and eight contiguous forest sites during January–December 2011. Sampled fragments were of medium size (5–10 ha) and well protected, with little evidence of secondary anthropogenic disturbances. We did not consider smaller fragments because these were generally highly disturbed, while larger fragments were too few in number. Trees were sampled in 31 plots (0.09 ha, 30 × 30 m) within the eight contiguous forest sites (3–4 plots per site) and 19 plots within the eight fragmented forest sites (2–3 plots per site). Sites were located at a minimum distance of 2.5 km from one another. A minimum distance of 50 m was maintained between plots within sites, which restricted the number of plots in each fragment site to 2 or 3. Plots were located in areas that showed no evidence of recent disturbance in the form of selective logging, clearing of understorey, fuel wood extraction, cattle grazing and alien invasive shrub species. Tree species identity, d.b.h. (using measuring tape) and height (using a Bushnell Yardage Pro 450 laser range finder) of all trees over 3 cm d.b.h. were recorded within each plot. Species were identified by experienced field botanists using field keys and floras (Pascal & Ramesh 1997; Ramesh *et al.* 2007). Individuals not identified to genus or species level for a variety of reasons (e.g. tree not in leaf; tall canopy obscured by climbers) constituted *c.* 4% of all individuals in the data set.

Fragmented and contiguous forest sites were located in areas of similar elevation (830–997 m a.s.l.) and slopes (6–12%). These sites also spanned overlapping ranges of mean annual precipitation (2350–3820 mm in fragments; 2900–3700 mm in contiguous forests) but precipitation was lower on average in the fragmented (2760 mm) than in contiguous (3200 mm) sites. However, all sites fell well within the known distributions of the study species, which spanned a rainfall range (mean ± 1 SD) of 1245 ± 524–5340 ± 729 mm (N. Page, unpublished data).

In addition to adult tree communities, we also sampled regenerating tree communities (0–10 cm d.b.h.) at seven fragmented forest sites in forty four 5 × 5 m plots. Regenerating trees were identified and categorized into four groups: (i) 0–20 cm height, (ii) 20–50 cm, (iii) 50–100 cm and (iv) >100 cm in height but <10 cm d.b.h. Fragments sampled for tree regeneration overlapped only partly (four out of seven sites) with those sampled for adult communities, because they were sampled as part of a

separate campaign (March–December 2010). However, the fragments were of similar size and lay within the same vegetation type, climatic envelope and disturbance level as those sampled for adult communities.

PLANT FUNCTIONAL TRAITS

Plant functional trait data were collected following standard protocols (Cornelissen *et al.* 2003) within, and adjacent to, sites sampled for tree community composition. Data on SLA, wood density, seed size, maximum attainable height and seed dispersal mode were collected between November 2011 and January 2013.

For SLA, five mature, healthy, sun-exposed canopy leaves were collected per tree at the end of the wet season (October–December). Leaf areas were estimated using the Black Spot Leaf Area Calculator (Varma & Osuri 2013). Leaves were then oven-dried at 60 °C for 72 h to obtain dry weights. SLA at the level of individual trees was estimated by dividing fresh leaf areas by dry weights of the five leaves collected. SLA was estimated for 358 trees representing 79 species (1–10 replicates per species; median = 5).

For wood density, trunk wood cores were collected using an increment wood borer. Wood density was estimated by dividing dry weight by fresh volume of trunk wood cores (Chave 2005). In cases where trunk wood cores were not available (as collection of wood cores was not permitted at certain sites), trunk wood density was estimated by multiplying the wood density of debarked canopy twigs (1–2 cm diameter) by a correction factor of 1.12. Previous work based on 127 trees spanning 94 tree species in the study area has shown that trunk wood density can be reasonably well estimated from twig wood density using this correction factor (linear model $R^2 = 0.93$; see Osuri, Kumar & Sankaran (2014)). Wood density data were collected from 352 trees representing 74 species (1–10 replicates per species; median = 5). In the absence of primary data, wood density data from secondary sources (36 species) were used (Chave *et al.* 2009; Zanne *et al.* 2009). In cases where species-level wood density data were not available from either primary or secondary sources, average wood density across congeneric species within the community was used.

Seed size was quantified as the length of the primary seed axis (Vanthomme, Bellé & Forget 2010) for 1879 seeds spanning 34

species (median of 46 seeds per species). In addition to measurements at our study site, seed size data were obtained from two other mid-elevation evergreen forests in the Western Ghats (D. Mudappa, unpublished data). All seeds were collected either from ripe fruits on trees or from fruits fallen directly under parent trees, and only collected when there was no ambiguity regarding species identity. In the case of species for which primary measurements were not obtained, seed lengths were collated from published secondary sources (Matthew 1983; Saldanha & Ramesh 1984; Ramesh *et al.* 2007).

Maximum heights for each species were obtained from primary and secondary sources including: (i) height measurements in plots during this study and (ii) published secondary sources on wet-evergreen forests in the Western Ghats (Matthew 1983; Saldanha & Ramesh 1984; Ramesh *et al.* 2007). The maximum height from across these data sources was considered to be the species' maximum attainable height.

For seed dispersal mode, species were classified as either (i) animal-dispersed (primarily by birds and/or mammals) or (ii) abiotically dispersed (by wind, gravity or water) based on published genus-level and species-level observations from the Western Ghats (Ganesh & Davidar 2001; Puyravaud, Dufour & Aravajy 2003), and elsewhere (Snow 1981; Corlett 1998; Royal Botanic Gardens Kew 2014).

ANALYSIS

As both contiguous and fragmented forests spanned a gradient in mean annual precipitation, we first tested for correlations between community-weighted trait averages (weighted by species basal areas) and mean annual precipitation (Hijmans *et al.* 2005) across our contiguous and fragmented sites. Community-weighted averages of all traits considered in this study were not correlated with mean annual precipitation (Pearson's correlation $R_p < 0.27$ and $P > 0.30$ for all traits across 16 sites), and hence, we did not include mean annual precipitation as a predictor in subsequent analysis.

We examined whether differences in tree species' relative abundances between contiguous forests and fragments could be explained based on species' seed dispersal traits and/or leaf and woody traits that influence establishment and survival. For each species, we quantified its response to fragmentation as the log ratio of average relative basal area of trees (>3 cm d.b.h.) between fragmented and contiguous forests (Hedges, Gurevitch & Curtis 1999). The response ratio was calculated using average relative basal area of each species within eight fragmented and eight contiguous forest sites, respectively, with data from individual plots pooled within each site. We then related variation in this response ratio to species' traits using multiple linear regressions to identify which traits best predict species' responses to fragmentation. A candidate set of predictor models comprising 15 linear combinations of seed size, wood density, SLA and maximum height as covariates was developed, including a global model comprising all four traits (excluding interactions) as well as 14 nested models comprising 1, 2 and 3 predictor combinations of these traits. As tree communities in this study were dominated by animal-dispersed species (92% individuals, 90% species, 87% basal area), seed dispersal mode (animal vs. abiotic dispersal) was not included as a factor in the analysis. Species that were rare in both treatments ($\leq 1\%$ relative abundance) were excluded from the analysis. We evaluated the likelihood of each candidate model

using small-sample corrected AIC (AIC_c) scores and identified models within two AIC_c units of the most likely model (i.e. the model with the lowest AIC_c score) as being those with the greatest empirical support (Burnham & Anderson 2002). We assessed the relative importance of individual predictors (w) by summing the Akaike weights (a likelihood estimate derived from AIC_c scores) of all models in which that predictor was present (Burnham & Anderson 2002).

Next, we investigated the strength and prevalence of post-germination filtering mechanisms by comparing dominance patterns between seedling communities and larger sized recruits in fragments and assessed whether differences in species' dominance patterns between these regenerating classes could be explained based on species' functional traits. For this, we used data on seedlings (regeneration class 1; 0–20 cm height; see Tree community sampling) and pooled data from regeneration categories 3 and 4 (>1 m height and <10 cm d.b.h.) into a group called large recruits. We reasoned that if tree community composition of fragments is more strongly influenced by filtering before and during germination rather than post-germination, then species' dominance patterns between the seedling and large-recruit classes would be highly correlated. On the other hand, increasing levels of post-germination filtering would weaken the correlations between species' ranks of seedlings and large recruits. For both seedlings and larger recruit classes, we pooled data across all fragments and ranked species based on their abundances. We then assessed the correlation between species' ranks of seedling and large-recruit stages and examined whether differences in species' ranks could be predicted by seed size, SLA, wood density and maximum attainable height by correlating differences in species' ranks between large recruits and seedlings with these candidate traits.

Finally, to evaluate how compositional shifts associated with fragmentation could influence their carbon storage potential, we assessed relationships between species' traits that potentially influence their response to fragmentation (response traits: seed size, SLA, wood density, maximum attainable height) and those that govern their carbon storage potential (effect traits: wood density, maximum attainable height) by computing pairwise Pearson correlation coefficients between the two. Next, we assessed community-level differences in effect traits by comparing community-weighted averages of wood density and maximum attainable height between contiguous and fragmented forests. Species' wood densities and maximum attainable heights were weighted by their corresponding basal areas at each site (Slik *et al.* 2013), and comparisons were made between eight contiguous and eight fragmented forest sites using a *t*-test. Finally, we used simulations to isolate the likely effects of compositional shifts on above-ground carbon stocks, while controlling for stand-level differences in basal areas. Constant basal area stands were simulated for contiguous and fragmented forests by drawing individuals at random from their respective pools to make up a basal area of $51 \text{ m}^2 \text{ ha}^{-1}$ (the average basal area of contiguous forest stands). Carbon stored by these simulated stands was estimated using an allometric equation that assumes a constant height–diameter ratio (Chave *et al.* 2005). Simulations were run over 1000 iterations, and the resultant distributions of carbon stocks between contiguous and fragmented forests were compared.

The R statistical environment version 3.0.2 (R Development Core Team 2013) was used for all analyses and preparation of figures.

Results

Differences in species' composition between contiguous and fragmented forests were best explained by seed size and wood density, with the model comprising these two covariates emerging as the best predictor of species' responses to fragmentation (Akaike weight = 0.38, $R^2 = 0.39$; Table 1). Large-seeded and hardwood species declined in relative basal area in fragments (standardized model-averaged slope coefficients (mean \pm 1 SE) = -1.67 ± 0.5 and -1.01 ± 0.44 , respectively; see Fig. 2), as did, to a lesser extent, large-statured species (standardized model-averaged slope coefficient mean \pm 1 SE = -0.73 ± 0.58), but species' responses were unrelated to SLA (-0.37 ± 0.63). Among candidate predictors, seed size featured most consistently in the highest ranking models (Table 1) and thus had the greatest covariate weight ($w = 0.98$), followed by wood density (0.79), maximum attainable height (0.39) and SLA (0.25). Although we did not control for phylogeny in this analysis, we observed large variation within families in species' responses to fragmentation (Appendix S1, Supporting information), suggesting that our results are not driven by closely related species showing similar responses.

Among regenerating communities in fragments, abundance-based species' rank orders of large recruits were closely correlated with rank orders among seedlings ($R_p = 0.77$, $P < 0.0001$; Fig. 3). Differences in species' ranks between large recruits and seedlings were positively correlated with wood density ($R_p = 0.33$, $P < 0.05$), suggesting that even as hardwood species decline in fragments overall, species with higher wood densities were relatively better at establishing post-germination in fragments (Fig. 3). In contrast, seed size ($R_p = -0.20$,

$P > 0.15$), SLA ($R_p = 0.02$) and maximum attainable height ($R_p = -0.01$) were uncorrelated with differences in species' ranks and appeared to have little influence on post-dispersal community filtering.

Across species, seed size was positively correlated with maximum attainable height ($R_p = 0.48$, $P < 0.001$; Fig. 4). Both seed size ($R_p = -0.37$; $P < 0.01$) and maximum attainable height ($R_p = -0.27$; $P < 0.05$) were negatively correlated with SLA. Species' wood densities were correlated with neither seed size ($R_p = 0.01$, $P > 0.90$), SLA ($R_p = -0.01$, $P > 0.9$) nor maximum attainable height ($R_p = -0.09$; $P > 0.45$). See Appendix S2 for species' functional traits data.

At the community level, fragmented forest plots had 10% lower community-weighted average maximum attainable height ($t = 2.77$; $P < 0.05$) and 4% lower wood density (although not significant at $\alpha = 0.05$). Our simulations suggest that even in the absence of changes in total basal area or tree allometry, shifts in tree community composition resulting from fragmentation could reduce above-ground carbon stocks by 22 Mg ha⁻¹ on average (Fig. 5).

Discussion

Our study shows that seed size and wood density strongly predict tree species' responses to fragmentation, with large-seeded and hardwood species showing declines in a fragmented Indian rain forest. Further, our results reveal a strong positive correlation between seed size and maximum attainable height, because of which, shifts towards smaller-seeded tree communities are likely to result in declines in forest stature in fragments. Based on simulations, we predict that these shifts are likely to drive marked declines in above-ground carbon stocks over time.

Multiple lines of evidence suggest that differences in tree community composition between contiguous and fragmented forests in this study are driven by shifts in seed dispersal processes. First, our results are consistent with the seed disperser limitation hypothesis, which is that losses of large-bodied frugivores can drive declines of large-seeded animal-dispersed tree species (Santos *et al.* 2008; Markl *et al.* 2012; Santo-Silva *et al.* 2013; Kurten, Wright & Carson 2015). Bird surveys conducted during our study provide further support for this hypothesis, with large frugivores (100–600 g) such as fruit pigeons having markedly lower encounter rates in fragments (38% decrease), and attendant increases (22%) in encounter rates of small-bodied frugivores (6–86 g) such as bulbuls (Appendix S3). Other potential explanations for smaller-seeded assemblages are that abiotic conditions in fragments could favour germination (Pearson *et al.* 2002) and establishment (Foster & Janson 1985) of small-seeded species. While effects on germination were not assessed in this study, our results suggest that there is relatively weak post-germination filtering across species within fragments, with dominance patterns among young, establishing trees

Table 1. Δ AIC_c, Akaike weights and goodness-of-fit (R^2) of 15 candidate linear models comprising species' traits seed size (SS), wood density (WD), specific leaf area (SL) and maximum attainable height (MH) which were used to predict species' responses to fragmentation. Models are ranked in decreasing likelihood order (high-to-low Akaike weights)

Rank	Model	Δ AIC _c	Akaike weight	R^2
1	SS + WD	0.0	0.3783	0.386
2	SS + WD + MH	1.2	0.2098	0.395
3	SS	2.7	0.0979	0.306
4	SS + WD + SL	2.7	0.0961	0.366
5	SS + WD + SL + MH	3.0	0.0863	0.395
6	SS + MH	4.1	0.0485	0.308
7	SS + SL + MH	5.0	0.0317	0.324
8	SS + SL	5.0	0.0304	0.288
9	WD + MH	6.9	0.0118	0.248
10	WD + SL + MH	9.5	0.0033	0.227
11	MH	10.1	0.0024	0.137
12	WD	11.2	0.0014	0.109
13	SL + WD	11.9	0.0010	0.130
14	SL + MH	12.2	0.0009	0.122
15	SL	15.1	0.0002	0.002

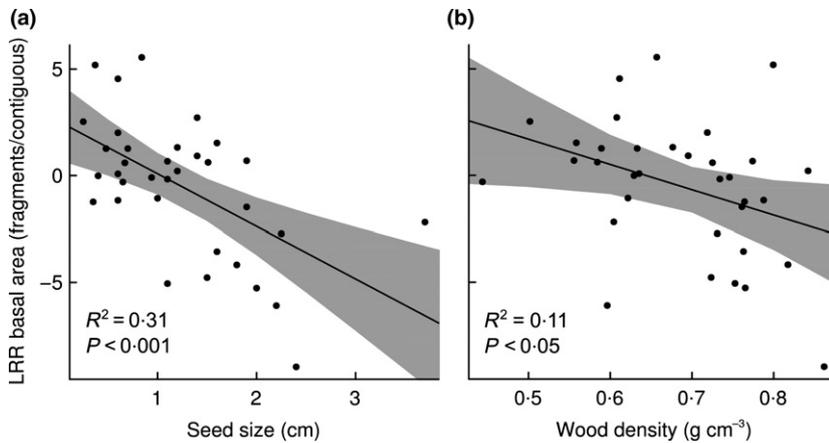


Fig. 2. Scatterplot showing that species with larger seeds (a) and higher wood density (b) decline in fragments and thus the log ratios of their relative basal areas in fragments to contiguous forests (LRR) are lower. The linear fit and associated 95% confidence intervals of single covariate linear models comprising these two predictors are also depicted, and their respective R^2 and P -values are reported.

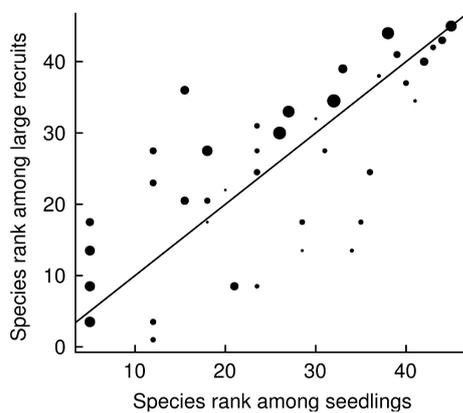


Fig. 3. Scatterplot showing abundance-based species' ranks among large recruits to be strongly and positively correlated with corresponding ranks among seedlings, with the one-to-one line depicted. Larger numbers indicate greater dominance, and larger circles depict species with higher wood densities.

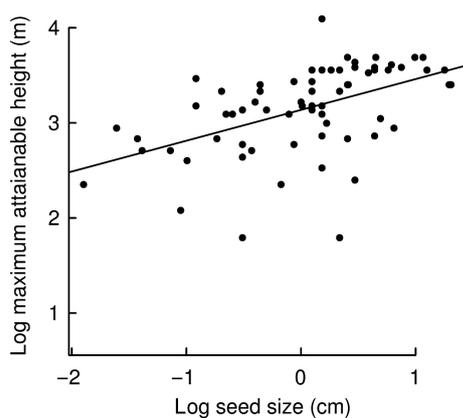


Fig. 4. Scatterplot showing positive correlation between seed size and maximum attainable height (both axes log-transformed) along with fitted linear regression line.

strongly correlated with dominance patterns among small seedlings, and unrelated to seed size.

Although hardwood species appear to have high post-germination survival in fragments, they decline in relative

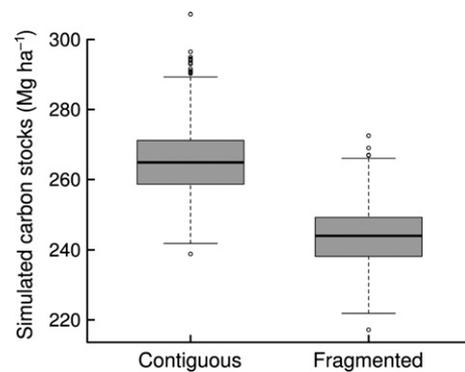


Fig. 5. Boxplots illustrating that differences in species' compositions can result in lower above-ground carbon stocks in fragments, based on simulations which controlled for the confounding effects of differences in stand basal area and tree height–diameter ratios between contiguous and fragmented forests.

abundance overall. Our results suggest that these declines are driven by processes that reduce seed dispersal and germination of hardwood species in fragments, which outweigh their advantage during post-germination stages. The positive relationship between wood density and seedling establishment success in our study is consistent with patterns observed in undisturbed tropical forests (Kraft *et al.* 2010) and is potentially explained by the prevalence of tree-covered habitats in the landscape matrix surrounding our study fragments (mainly, shade coffee plantations). These tree-covered matrix habitats potentially buffer fragments from severe edge effects (Mesquita, Delamônica & Laurance 1999; Kupfer, Malanson & Franklin 2006), which are known to promote light-loving pioneer species with low wood density in fragments embedded in more open matrix habitats (Laurance *et al.* 2006a).

Because species' seed sizes and maximum attainable heights are strongly and positively correlated, individuals of larger-seeded species tend to attain larger sizes and therefore store more carbon (Fig. 6). Compositional shifts that favour small-seeded species are therefore likely to

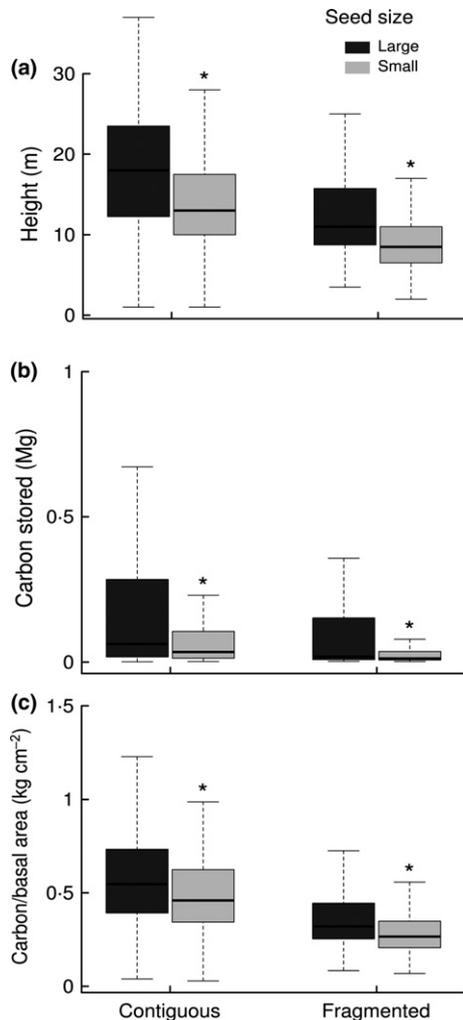


Fig. 6. Individuals of large-seeded species (length > 1.5 cm) attain taller heights (a) and store more carbon, overall (b) and per unit basal area (c) than do individuals of smaller-seeded species in both contiguous and fragmented forests (*depicts $P < 0.001$).

promote smaller-statured tree communities and drive declines of above-ground carbon stocks. Our simulations suggest that this compositional effect can reduce carbon stocks by 22 Mg ha^{-1} (8.5%), assuming no change in basal area. However, actual reductions in tree heights and carbon stocks are likely to be even greater because of intraspecific shifts in tree allometry, whereby trees in fragments are shorter for a given basal diameter than conspecifics in contiguous forests (Osuri, Kumar & Sankaran 2014). Interestingly, the correlation between seed size and maximum attainable height remains strongly positive even after covariance of these two traits with SLA is controlled for (partial $r = 0.43$, $P < 0.001$). This indicates that the relationship also exists among old-growth forest tree species, and is not solely an artefact of differences in seed size and maximum attainable height between old-growth (low SLA) and pioneer (high SLA) species. These patterns suggest that fragmentation effects mediated by defaunation and isolation, which limit the dispersal of large-

seeded species, can drive marked declines in the potential for tropical forest tree communities to store carbon. Importantly, they may do so even in fragments which are protected from abiotic drivers such as wind and desiccation that are known to drive declines of large-statured and hardwood species and cause carbon losses (Laurance *et al.* 1997).

Positive correlations between seed size and maximum attainable height are thought to exist either because larger-statured species invest in fewer, larger seeds as an evolutionary strategy (Moles *et al.* 2005; Wright *et al.* 2007), or because biomechanics limit seed sizes of smaller species (Grubb, Coomes & Metcalfe 2005). Even as the drivers remain unclear, this positive relationship observed in our study is also reported from other tropical sites (Grubb, Coomes & Metcalfe 2005; Wright *et al.* 2007) and could therefore provide a robust empirical basis to link fragmentation effects on species' compositions of tropical forest tree communities to resultant effects on their potential to store carbon. However, a wider representation of data is needed to test for the prevalence of this relationship across the tropics, including data on differences in adult stature and carbon storage potential across seed dispersal modes. While our results highlight seed size–maximum height relationships as an important factor mediating fragmentation effects on carbon storage potential of tree communities dominated by animal-dispersed species, its influence on carbon storage responses in communities with more abiotically dispersed species remains unknown.

CONCLUSIONS

A substantial proportion of above-ground carbon stocks in the tropics presently reside in human-modified forests and are vulnerable to pervasive drivers such as fragmentation, selective logging and defaunation (Brodie & Gibbs 2009; Paula, Alves-Costa & Tabarelli 2011; Poulsen, Clark & Palmer 2013; Berenguer *et al.* 2014; Osuri, Kumar & Sankaran 2014). The ability of tropical forests to store carbon and regulate future climate therefore depends on how tree communities in these disturbed ecosystems are conserved and managed (Ashton *et al.* 2012). Our results suggest that carbon losses from fragments can be partially mitigated by reversing declines of tree species that depend on large fauna for seed dispersal, which also tend to be large-statured and have high carbon storage potential. In the Western Ghats and elsewhere in the tropics, many forest fragments today are protected by law but efforts to restore species' assemblages and ecological processes in these fragments remain rare (Raman & Mudappa 2003). At the same time, human land use around these fragments continues to intensify across the tropics (Kupfer, Malanson & Franklin 2006; Gardner *et al.* 2009), driving further losses of large-bodied frugivores and dispersal limitation of large-seeded tree species (Farwig & Berens 2012; Markl *et al.* 2012; McConkey *et al.* 2012). Thus, in addition to local-scale measures to minimize anthropogenic distur-

bances within individual fragments, and species-specific restoration programmes, landscape-scale management efforts to control defaunation through protection, biodiversity-friendly matrixes and wildlife corridors are likely to help restore and sustain above-ground carbon stocks in the human-dominated tropics, besides providing important biodiversity benefits.

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Data accessibility

Species' traits data uploaded as online supporting information.

Tree community data are available from Dryad Digital Repository doi: 10.5061/dryad.7s7r1 (Osuri & Sankaran 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Plot depicting variation across species within plant families in responses to fragmentation.

Appendix S2. Functional traits of common tree species in the study area.

Appendix S3. Avian frugivores in contiguous and fragmented forests.