Altered stand structure and tree allometry reduce carbon storage in evergreen forest fragments in India's Western Ghats

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Abstract

Tropical forests are among the largest terrestrial reservoirs of carbon, and play an important role in regulating global climate. However, as a result of historic and ongoing deforestation, carbon storage in this biome is increasingly dependent on forests that are fragmented and used by humans, with considerable uncertainty about how such disturbance alters carbon storage potential and cycling. Here, we evaluate differences in above-ground carbon stocks between fragmented and contiguous evergreen forests in the central Western Ghats, India. We also assess differences in the structure, tree allometry and functional composition of forest stands between contiguous and fragmented forests, and explore how these differences influence carbon storage in fragmented forests. Relatively large, well-protected forest fragments currently store 40% less carbon per hectare above ground than contiguous forests. These differences in carbon are related to i) lower tree density and basal area in fragments, ii) lower average stand height in fragments, and iii) compositional shifts favouring species with lower wood densities. Reduced stand height in fragments was associated with intra-specific variation in tree allomety, with trees in fragments being relatively shorter at any given diameter than conspecifics in contiguous forests. Further, the relatively skewed distribution of carbon storage within a few large trees in current-day fragments is added cause for concern: carbon stocks in fragments are likely to decline further in the future, following the eventual death of large trees. Active management and restoration to mitigate ecologically driven changes in habitat structure and species composition might be as important as improved management of resource use and protection from exploitation in order to sustain carbon storage ecosystem services provided by these tropical forest fragments.

Keywords

1.0 Introduction

Carbon storage by tropical forest vegetation, currently estimated at nearly 250 Gt, strongly influences the global carbon cycle and plays a crucial role in regulating the concentrations of greenhouse gases in the atmosphere (Lewis et al. 2009; Malhi and Grace 2000; Pan et al. 2011; Saatchi et al. 2011). However, deforestation and fragmentation continue to be widespread in the tropics, with resultant carbon emissions and loss of sequestration potential a cause for global concern (Achard et al. 2002; Harris et al. 2012). While deforestation clearly has negative impacts on carbon storage, there is considerable uncertainty surrounding ecosystem and carbon dynamics within tropical forests that are fragmented or otherwise disturbed.

While, in the absence of disturbance, intact tropical forests likely act as carbon sinks (Lewis 2006; Phillips et al. 2009), fragmented forests may be vulnerable to carbon losses and accelerated carbon cycling (Nascimento and Laurance 2004). These losses may be brought about by changes in habitat structure and tree species composition (Laurance et al. 2006a). In central and southern America, major biomass losses occur in the immediate aftermath of fragmentation, resulting from the death of large, old-growth trees, especially close to fragment edges that are exposed to wind and fire (Laurance et al. 2000; Laurance et al. 1997; Laurance et al. 2006a). As fragments age, aboveground biomass can decline further due to the proliferation of relatively softer-wooded, shorter-statured pioneer species (Laurance et al. 2006b). Wind and other abiotic stresses can also change tree allometry, with trees in fragments being shorter for a given basal diameter (Dantas de Paula et al. 2011; Oliveira et al. 2008). Through these multiple processes, some with immediate effect and others acting more slowly over the timescales of species turnover and forest succession, carbon stocks and sequestration potential in fragmented forests may be depleted over time.

While forest fragmentation is ubiquitous across the tropics, scientific insights into fragmentation impacts on carbon dynamics are largely derived from work in central and southern America. Whether taxonomically different tree communities elsewhere in the tropics show functionally similar responses to fragmentation is unknown. In south Asia, and the Western Ghats in peninsular India in particular, a large proportion of the remaining forest cover is fragmented and otherwise affected by humans (Bawa et al. 2007; Menon and Bawa 1997). A substantial extent of these forests, particularly in the wet evergreen zone, fall outside the current network of strictly protected areas, with many biologically rich and unique forests persisting as isolated fragments with varying levels of protection in agro-forestry landscapes (Anand et al. 2010; Bhagwat et al. 2005b; Das et al. 2006). With payments for forest carbon emerging as an important strategy to facilitate biodiversity conservation in the densely-populated tropics (Schroth et al. 2011), understanding the impacts of fragmentation on aspects of forest carbon storage in these landscapes becomes essential both for the conservation of biodiversity and for the sustained provisioning of ecosystem services. Here, we estimate the carbon storage ecosystem services provided by tree communities in fragmented evergreen forests in the Western Ghats, in comparison with contiguous forests. We evaluate differences in the structural properties of tree stands (stand density, basal area, stand height and carbon storage) and functional traits of tree species (wood density) in response to fragmentation across a gradient of mean annual precipitation. We compare tree height to diameter (tree H:D) relationships between contiguous and fragmented forests in terms of variation within and across species and size-classes. Finally, we evaluate differences in the distribution of carbon storage across trees of different sizes within contiguous and fragmented forests and draw insights into the stability and future potential for carbon storage in fragmented forests based on the skewedness of these distributions.

2.0 Materials and Methods

2.1 Study site

The study was conducted in south-western Kodagu district, Karnataka state, in the Western Ghats of peninsular India (12.17° N, 75.8° E; Figure 1). The study area experiences a gradient of annual precipitation from 2300mm in the E to around 3800mm in the W (Hijmans et al. 2005; Kumar et al. 2012). Elevation ranges from 700 to 1000 m above sea level. Ultisol soil formations in the study area are characterized by deep, well-drained clays on plateaus and moderate slopes (Anonymous 1998; USDA Soil Survey Staff 1999). Intact, mid-elevation forests in the study area are characterized by old-growth evergreen species *Mesua ferrea* and *Palaquium ellipticum* (Pascal 1982, 1986).

Over the ~6000 years of human settlement, the landscape has witnessed multiple advances and retreats of forest cover, with present day forests likely to be a mix of primary forests and old (~400 years) regrowth (Bhagwat et al. 2012, In press). At present, the western and southern parts of the study area along the eastern slopes of the Western Ghats contain large areas of evergreen forest (hereafter, contiguous forests) which are protected by the State (Bramhagiri Wildlife Sanctuary, and adjacent Reserved Forests), and form part of a large block of evergreen forests spanning over 2000 sq.km. Immediately adjacent to this forest block, the human-dominated landscape is dotted with evergreen forest remnants (hereafter, fragmented forests), many of which are protected as sacred groves (Bhagwat et al. 2005b; Kalam 1996). Official records list over 1000 sacred groves in the district, ranging from less than a hectare to tens, and rarely, hundreds of hectares in area (Bhagwat et al. 2005b; Kalam 1996). The protected areas and reserved forests which contain the contiguous forests are presently under the administrative control of the Karnataka Forest Department, while sacred forest fragments are jointly managed by the Karnataka Forest Department and local village

temple committees. Selective logging, which was practiced across all forests in the area during the 1900s, has been banned by Indian law in these forests since the 1980s.

Forest cover maps derived from Survey of India topographic maps indicate that forests, which were widespread and contiguous across the region during the 1920s, were highly reduced and fragmented by the 1990s, except those within State protected areas (Menon and Bawa 1997). Analyses of landuse change using satellite images indicate that while forests were widespread in the study area in the 1970s, there were high rates of forest conversion to shade coffee, agriculture and other human land use during the 1977-1997 period (Garcia et al. 2009). It is therefore likely that fragmentation effects were present through the 20th century but intensified after the 1970s.

2.2 Site selection

In order to locate potential study sites, we referred to lists of sacred groves provided by the Karnataka Forest Department, published studies from the landscape that compared biodiversity patterns between contiguous and fragmented forests (Bhagwat et al. 2005a; Page et al. 2010) and pilot surveys within ~100 fragmented and contiguous forest patches. As we were primarily interested in studying changes in carbon storage brought about by ecological factors related to fragmentation, and not by forest age and secondary anthropogenic influences, we selected closed-canopy forest sites with no recent logging, fuel-wood extraction, cattle grazing, alien invasive species, or other direct and indirect signs of human use and disturbance. Based on these criteria, we excluded small fragments (<2ha) because they tended to be more disturbed than larger fragments. We also excluded very large fragments (>15ha) because they were too few in number, and focused our sampling on fragments that were of intermediate sizes (5-10ha).

Site selection decisions also considered the E-W annual precipitation gradient and the spatial configuration of the landscape, and an attempt was made to maximize the overlap between contiguous and fragmented forests in their range of mean annual precipitation values.

Thirteen relatively undisturbed fragmented forest sites of similar area (5-10ha) were selected for sampling, along with nine sites from contiguous forests (Figure 1). Selected sites in contiguous forests spanned a mean annual precipitation range of 2890-3725mm (mean=3220mm) while selected fragment sites spanned 2340-3820mm (mean=2706mm).

2.3 Vegetation sampling

Data on the structure and species composition of tree stands in contiguous and fragmented forests were obtained from three sources: (1) data collected from 49 square 0.09ha (30mX30m) plots during January-December 2011 from 8 contiguous and eight fragmented forest sites, (2) data collected from 12 square 0.0625ha (25mX25m) vegetation plots collected during March-October 2010 from four fragmented forest sites and (3) data published by Page et al. (2010) on nine square 0.0625ha vegetation plots from one contiguous and one fragmented forest site. In all, there were 35 plots sampled across nine contiguous forest sites and 35 plots sampled across 13 fragmented forest sites. All plots were placed at least 50m from one another and from the nearest forest edge, and avoided areas with constructions (e.g. temple), canopy gaps and any signs of recent disturbance. Based on the availability of locations within sites which met these requirements, 2-5 plots (median=3) were established per site. Although plots from the three sources differed in size, the effects of which are subsequently explored, they were otherwise selected and sampled in identical manner, and therefore included to increase sample sizes for more robust analyses and inferences. In every plot, all stems ≥10 cm diameter at 1.3m height from the ground (diameter at breast height: DBH) were identified, and DBH (using a measuring tape) and height to the top of the canopy (using a laser rangefinder) recorded. Diameter measurements

for trees with buttresses were taken 50cm above the buttress, and in cases of trees with

multiple branches/stems at 1.3m height, the diameters of each branch/stem ≥10 cm diameter

were recorded (Condit 1998). The DBH of these multi-stemmed individuals was estimated as

the square root of the summed squares of individual branch/stem diameters

(USDA Forest Service Staff 2007). Species identification was carried out by experienced

field botanists, and with the aid of field keys and floras (Pascal and Ramesh 1997; Ramesh et

al. 2007). A few individuals (3%), which could not be identified to genus or species levels for

a variety of reasons (e.g. tree not in leaf; tall canopy obscured by climbers) were retained in

the dataset as unidentified individuals.

2.4 Estimation of species traits and carbon storage

2.4.1 Wood density

Primary data on species wood densities were collected for 74 species, which together

comprised 86% of the individuals in the dataset that were identified to the species level.

Wood density was sampled proportional to species abundance, and ranged from two to 16

samples per species (median=5). Wood density was estimated by a combination of direct

estimation of trunk wood density with wood cores (5.15mm diameter cores collected using a

Suunto increment borer) and indirect estimation of trunk wood density through relationships

with canopy twig (1cm diameter twigs collected from fresh branches cut from the canopy and

debarked) wood density. This combination of techniques was used because collection of

trunk wood cores was not permitted within a few sites. A canopy twig and, where permitted,

a trunk wood core were collected from all trees sampled. Collected samples were transported

in an ice box to a field station where they were placed in water for one hour to rehydrate.

Fresh wood volume was estimated by water displacement, following which samples were

oven-dried at 65°C for 72 hours and weighed. Wood density was estimated as oven-dried

weight divided by fresh volume (Chave 2005).

Using data from trees for which both trunk wood core and canopy twig estimates of wood density were collected (127 trees across 94 species) a linear relationship (R-sq=93%, p<0.001) was established between twig and core wood density, wherein

$$\text{Wood density}_{core} = 1.12\ (\text{Wood density}_{twig}) \tag{1}$$

Using equation (1), twig wood densities were corrected to trunk wood core density estimates.

For species for which wood samples were not collected, wood densities were extracted from secondary sources (Rajput et al. 1991; Zanne et al. 2009). Comparison of wood density data across species for which both primary data on wood core and twig density and data from secondary sources were available suggested a strong correspondence (Pearson's correlation=0.79, p <0.001) between the primary and secondary data sources.

For trees that were identified only to the genus level, and for species for which wood density data were not available from primary and secondary sources, genus-level estimates of wood density were assigned based on primary and secondary data on congeners (Baker et al. 2004). Additionally, in the absence of genus-level data, family-level data were used. A wood density value of 0.62g/cm^3 – the average value across all sampled species – was assigned to all stems that were not identified to species or genus level, or for which genus- or family-level data were not available (6.7% of all individuals and 9% of all species).

2.4.2 Estimation of carbon storage

Carbon stored by individual trees was estimated using a general allometric equation for tropical forest trees (Chave et al. 2005):

$$B = \exp(-2.997 + \ln(\text{WD X (DBH)}^2 \text{ X H})) \tag{2}$$

$$C = 0.5 \text{ X B} \tag{3}$$

where B=biomass (kg), C=carbon storage (kg), WD=species wood density (g/cm^3), DBH=diameter at breast height (cm) and H=tree height (m). Carbon stored per plot was calculated by summing up the carbon stored by all the trees within each sampled plot, and expressed on a per-hectare basis. Due to the unavailability of general biomass equations for palms, equations (2) and (3) were used to estimate carbon content for *Caryota urens* (Arecaceae), the one species of palm in the dataset (Baker et al. 2004; Clark and Clark 2000).

2.5 Analysis

In order to determine if plot sizes (0.0625ha and 0.09ha) influenced the estimates of stand density, basal area and carbon stocks, we used paired t-tests to compare estimates from seven sites from which both 0.09ha and 0.0625ha plot data were available. Results indicate no differences between 0.09 ha and 0.0625ha plots in estimates of stand density per hectare (+7.4% in 0.09ha plots, p=0.2), basal area per hectare (+1.8% in 0.09ha, p=0.7), and carbon stocks per hectare (+7.0% in 0.09ha, p=0.4). Data from all plots were therefore pooled for all subsequent analyses.

2.5.1 Assessing fragmentation and precipitation effects on aboveground carbon, stand structure and wood density

Data on carbon stocks per hectare, stand density per hectare, average tree height and community-weighted wood density were averaged across plots within sites to obtain site-level estimates. We used multiple linear regressions and model selection to determine the effects of fragmentation and mean annual precipitation (MAP) on (i) aboveground carbon stocks per hectare, (ii) tree density per hectare, (iii) basal area per hectare, (iv) community-weighted tree height and (v) community-weighted species wood density. Candidate explanatory models considered for each response included (1) MAP, (2) whether the site was a fragmented or contiguous forest (*treat*), (3) *MAP + treat*, with no interaction term and (4) *MAP + treat* with a *MAP:treat* interaction term. The likelihoods of different candidate models

were assessed through comparisons of model small sample-corrected Akaike Information Criterion (AIC_c) estimates, with lower AIC_c values indicating more likely models (Burnham and Anderson 2004). Model Akaike weights, which weigh each model in proportional to its likelihood, were calculated from model AIC_c scores and used to derive model-averaged parameter estimates (Burnham and Anderson 2004). These model-averaged parameters were then used to predict the values of carbon storage, tree density, basal area, average tree height and average wood density in contiguous and fragmented forests at MAP values of 3220mm and 2706mm, which represent the average MAP values for contiguous and fragmented forests, respectively. The predicted responses in contiguous and fragmented forest sites at 3220mm MAP were then compared to assess treatment-level differences in stand structural and functional properties at a given MAP.

2.5.2 Evaluating tree H:D relationships

We evaluated the effects of fragmentation and MAP on variation in the ratio of tree height (m) to tree DBH (cm) (log H/log DBH; hereafter logH:D) across sites. Candidate linear models (1) to (4) described in 2.5.1 were used to predict the response of logH:D, averaged across individuals and species within sites, and AIC_c scores, Akaike weights and model-averaged parameter estimates were used to predict logH:D values for contiguous and fragmented forests at average MAP values of 3220mm and 2706mm. Not only did we expect that trees in contiguous forests would be taller at a given DBH than trees in fragmented forests, but also that larger trees in the two habitats would exhibit more similar H:D allometry than smaller ones, because many of these large trees are likely to have grown during the pre- and early-fragmentation period. We therefore tested whether the intercepts and slopes of the linear relationship between log-transformed tree height (log (ht)) and log-transformed DBH (log (DBH)) (Feldpausch et al. 2011) differed between contiguous and fragmented forests. Data were pooled across all individuals within contiguous and fragmented forests for this

analysis. Linear mixed effects models with species as the random grouping term and log (DBH) as the random slope term were used for this analysis, in order to restrict species-level differences in maximum attainable tree size and growth trajectory to the random part of the model.

Finally, we examined two potential sources of variation in logH:D across contiguous and fragmented forests: (1) intra-specific variation in logH:D resulting from differences within tree species across the two habitats and (2) inter-specific variation and community turnover in favor of species having inherently different H:D allometry. This was done using two separate analyses. First, for all species which occurred in both contiguous and fragmented forests, the average logH:D across individuals within the two habitats was calculated. We then tested whether species-averaged logH:D values differed between contiguous and fragmented forests using a paired comparison with species as replicates. To ensure that rare species did not have a disproportionately large influence on the estimated effect, the contribution of individual species responses to linear model fit were weighed proportional to the sum of their abundance across contiguous and fragmented forests. Second, we tested whether species that were relatively more abundant in fragments were inherently different in H:D allometry than species relatively more abundant in contiguous forests. For this analysis, we identified whether species were 'winners' in contiguous or fragmented forests, based on which of the two habitats they were relatively more abundant in. We then compared species-averaged logH:D values of contiguous forest winners and fragmented forest winners using a linear model, with species contributions to model fit weighed by their abundance. As we were solely interested in inherent differences in H:D allometry at the species level in this case, this analysis needed to control for habitat treatment effects on logH:D. We therefore carried out two separate comparisons: one for contiguous and fragmented forest winners within contiguous forests, and another within fragmented forests.

2.5.3 Assessing the skewedness of carbon storage distribution

We assessed differences between contiguous and fragmented forests in the partitioning of carbon storage among trees of different sizes by testing whether the relative contributions of individual trees to plot-level carbon storage at any given DBH varied between the two habitats. While slopes of this relationship are bound to be positive – as larger trees store more carbon than smaller ones – we specifically examined the nature and extent of differences in these slopes between contiguous and fragmented forests. We modeled the relative contribution to carbon storage as a function of tree DBH using Beta regression (Ferrari and Cribari-Neto 2004), as the response variable is continuous in the 0-1 interval. Models were fitted using a logit link and differences in the slope parameter between contiguous and fragmented forests were evaluated.

The open-source statistical computing software R 2.15.1 (R Core Team 2012) was used for all data analyses and preparation of figures.

3. 0 Results

A total of 2438 individual trees were sampled, comprising 1483 trees of at least 145 species in contiguous forests and 955 trees of at least 113 species in fragmented forests, from across total sampled areas of 3.01 ha and 2.89 ha, respectively. Stand densities were higher in contiguous forests but both contiguous and fragmented forests were similar in terms of the proportions of individuals across DBH classes (Figure 2). While *Palaquium ellipticum* (Sapotaceae), *Humboldtia brunonis* (Fabaceae-Caesalpinioideae), *Myristica dactyloides* (Myristicaceae), *Mesua ferrea* (Clusiaceae) and other old-growth evergreen species dominated contiguous forest stands, fragmented forests were characterized by *Xanthophyllum arnottianum* (Xanthophyllaceae), *Cinnamomum malabatrum* (Lauraceae), *Antidesma montanum* (Euphorbiaceae), *Mallotus tetracoccus* (Euphorbiaceae) and other native species typical of more disturbed ecosystems. *Dimocarpus longan* (Sapindaceae), *Olea diaoca*

(Oleaceae) and *Nothopegia beddomei* (Anacardiaceae) were abundant in both contiguous

forests and fragmented forests (Appendix A).

3.1 Lower carbon storage in fragmented forests

Forest stands in fragmented forests were, on average, 25% shorter, had 22% lower basal area

per hectare, 6% lower community-weighted wood density and stored 36% less carbon per

hectare (Table 1). With the exception of tree density, these differences were best-explained

by fragmentation (*treat*) alone, or a combination of fragmentation and precipitation

(*treat*+*MAP*) (Table 1, Appendix B). For all these responses, *MAP* on its own did not emerge

as a strong predictor, with models comprising *MAP* alone having relatively low Akaike

weight scores (0.01-0.06) and correspondingly lower model likelihood. Overall,

fragmentation effects were evident, even after controlling for the gradient in *MAP*. The one

exception to this pattern was response of tree density: although tree density was on average

27% higher in contiguous forests than in fragmented forests, this variation was best explained

by differences in mean annual precipitation between contiguous and fragmented forests

(Table 1).

3.2 Altered tree height-diameter relationships in fragmented forests

Trees in fragments were, on average, shorter for a given diameter than trees in contiguous

forests. These differences were primarily related to fragmentation, although logH:D was also

positively influenced by *MAP* (Table 1).

Differences in logH:D relationships were evident across the entire range of DBH values and

were greatest among smaller trees. Intercepts of the log (ht)~log (DBH) liner mixed model

were significantly lower in fragmented forests (mean±1SE in contiguous: 1.26±0.04;

fragmented: 0.77±0.06, p<0.001). Additionally, the relationship exhibited significantly higher

model slopes in fragments (mean±1SE in contiguous=0.46±0.01; fragmented=0.52±0.02;

p<0.01; Figure 3), causing the lines to converge and indicating that at higher DBH values, trees in contiguous and fragmented forests had more similar H:D allometry (Figure 3).

The reduction of logH:D in fragments was related to intra-specific variation – within-species, trees in fragmented forests had significantly lower logH:D than those in contiguous forests (-0.07±0.01, p<0.001). At the same time, we found no differences in species allometry between contiguous forest and fragmented forest winners, either in contiguous forests (mean±1SE of contiguous winners: 0.88±0.01; fragmented winners: 0.88±0.01, p=0.7) and fragmented forests (contiguous winners: 0.89±0.03; fragmented winners: 0.78±0.03, p=0.5).

3.3 Greater skewedness of carbon storage in fragmented forests

While the intercepts of the beta regression model relating the relative contribution to plot-level carbon storage of individual trees to their DBH did not differ between contiguous and fragmented forests, the slope of the relationship took on higher values in fragmented forests (mean±1SE in contiguous=0. 04±0.0006; fragmented=0.05±0.0008). These results suggest that larger trees in fragmented forests accounted for a greater proportion of overall carbon storage by the plot (Figure 4). The distribution of carbon storage within the tree community in fragmented forests is therefore more skewed and dependent to a greater extent on larger, older trees, than in contiguous forests.

4.0 Discussion

Carbon stored per unit area in relatively large (5-10ha), well-protected forest fragments was nearly 40% lower than carbon storage in contiguous forests at our study site in the central Western Ghats. Although fragments occurred in areas receiving, on average, 15% less MAP, differences between contiguous and fragmented forests in carbon storage and associated stand structural characteristics and functional attributes were clearly evident over and above any differences caused by MAP.

Trees in fragments were considerably shorter for any given diameter than those in contiguous forests, with large, negative consequences for stand height and carbon storage potential. Reduced H:D ratios were an outcome of within-species differences in tree allometry, with trees in fragments having lower H:D than conspecifics in contiguous forests. Although reduced tree H:D in fragments has been previously reported (Dantas de Paula et al. 2011; Oliveira et al. 2008), the processes driving these changes in tree allometry are not clear. Tree height and H:D relationships are among the plant characteristics most closely linked to structural stability (Van Gelder et al. 2006), with resource investment in height considered a risk, particularly in exposed environments. Elevated wind stress in fragmented forests is widely reported (Laurance et al. 1997; Saunders et al. 1991), and has been proposed as a likely factor constraining tree H:D in fragmented forests (Oliveira et al. 2008). In addition, the relaxing of competition for light as a result of lower stem density, more open canopies, and increased lateral light penetration from habitat edges might further reduce tree H:D in fragments. Both observational (Feldpausch et al. 2011) and experimental (Holbrook and Putz 1989) data indicate the strong positive influence of stand density and shade on tree H:D. While wind damage was not assessed in this study, the sheltering of a number of the fragments from strong winds by a matrix of shade coffee plantations and by dense fragment edges suggests that higher light availability due to reduced tree density within fragments may be the key driver of reduced tree H:D. The sensitivity of tree H:D to the abiotic environment reinforces the need to include tree height in carbon stock estimation (Feldpausch et al. 2011), particularly for assessments in disturbed forests.

Because tree H:D relationships are known to vary with age and in response to environmental conditions (Sumida et al. 2013), long-term monitoring would be required to evaluate the extent to which differences in H:D between contiguous and fragmented forests persist over time. At present, differences in tree H:D were more prevalent among smaller size classes,

while larger trees – some of which grew during the pre-fragmentation period – were more similar in their allometry. The severity of declines in carbon storage resulting from reductions in stand height would depend, to a large extent, on whether younger stands in forest fragments retain their present H:D relationships, or take on H:D values more similar to contiguous forests as stands mature.

In contrast to central and southern American fragments where high tree mortality and the absence of large trees is widely reported (Laurance et al. 2000; Nascimento and Laurance 2004; Oliveira et al. 2008), large trees in our study site are nearly as abundant in fragments as they are in contiguous forests. The survival of large trees in fragments at our study site is possibly aided by a tree-covered matrix of shaded plantation crops, which not only provide a structurally tall and complex buffer to fragment edges, but also a matrix that is mostly free of fire. While these relic large trees buffer carbon losses in fragments in the present day, the resultant concentration of carbon within a smaller number of individuals and species is likely to have undesirable long-term consequences on carbon storage. Large trees over 85cm DBH stored $33 \pm 5\%$ of the total carbon in fragments, but only $15 \pm 4\%$ in contiguous forests at our study site. These skewed distributions are suggestive of reduced stability (Balvanera et al. 2005) of carbon storage in fragmented forests – while carbon storage is likely to be very sensitive to the loss of a few individuals or species in the short term, over longer periods, the eventual loss of ageing trees might be inadequately compensated for by younger individuals.

4.1 Management implications

In addition to storing carbon and providing ecosystem services such as crop pollination (Krishnan et al. 2012), forest remnants embedded in human-modified landscapes play an important role in biodiversity conservation in the Western Ghats. Not only do these fragments harbor significant populations of threatened and endemic forest species, but they also enhance ecological connectivity at landscape scales (Anand et al. 2010). However, these

fragments appear to be an ecosystem in transition, with marked shifts in habitat structure and composition towards shorter-statured, softwood communities which store 40% less carbon than their contiguous counterparts, with future carbon losses imminent. To mitigate carbon losses and likely associated biodiversity declines, improved protection of fragments to reduce tree removal will need to be augmented with sustained efforts to restore habitat structure and tree species composition. Correspondingly, efforts to retain biologically rich and structurally complex matrixes to aid biodiversity conservation within fragments (Bhagwat et al. 2005a) are likely to be equally crucial for carbon storage, by buffering fragments from novel abiotic environments. These conservation goals would necessarily have to be pursued through partnerships with local residents and land owners, and operated through market-based incentives for conservation (Raman and Mudappa 2003), given the strong market forces (Ambinakudige and Choi 2009) and shifting cultural practices (Ormsby and Bhagwat 2010) that are reducing tree cover in general, and forest cover in particular, in the study area. While improved protection through incentive mechanisms might serve to stem the loss of these remnant forests, restoration of these forests towards the harder-wooded and taller-statured communities that characterize less disturbed, contiguous forests in the region is likely to achieve the dual goals of improved carbon storage and biodiversity conservation.

5.0 Acknowledgements

6.0 References

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Tables

Table 1: Akaike weights values and model-averaged predictions of mean estimates and slopes of aboveground carbon and other forest stand properties in contiguous and fragmented forests across a gradient in mean annual precipitation. Candidate predictive models comprised fragmentation (*treat*), mean annual precipitation (*MAP*), fragmentation and mean annual precipitation (*treat+MAP*) and fragmentation and mean annual precipitation, including an interaction between fragmentation and precipitation (*treat*MAP*).

Response	Explanatory model	Akaike weight	Predictions based on model-averaged parameter estimates		
			Contiguous forest [MAP=3220mm] (mean±1SE)	Fragmented forest [MAP=2706mm] (mean±1SE)	Fragmented forest [MAP=3220mm] (mean±1SE)
Carbon storage (t/ha)	*treat*	0.77	186.4±14.0	118.9±11.6	117.7±14.2
	treat+MAP	0.19			
	treat*MAP	0.04			
	MAP	0.01			
Tree density (trees/ha)	*MAP*	0.72	477.2±21.5	361.1±18.6	467.8±31.0
	treat+MAP	0.24			
	treat*MAP	0.04			
	treat	0.00			
Basal area (m^2/ha)	*treat*	0.77	40.04± 2.11	31.05± 1.74	31.045± 2.14
	treat+MAP	0.17			
	treat*MAP	0.03			
	MAP	0.02			
Community-weighted wood density (g/cm^3)	*treat*	0.73	0.66±0.01	0.62±0.01	0.62±0.01
	treat+MAP	0.17			
	MAP	0.06			
	treat*MAP	0.03			
Average stand height	*treat*	0.77	16.1±0.7	12.1±0.6	12.2±0.7
	treat+MAP	0.19			
	treat*MAP	0.04			

(m)	*MAP*	0.01			
Average	*treat+MAP*	0.47	0. 87±0.02	0.77±0.01	0.79±0.02
tree	*treat*	0.42			
log(H):	*treat*MAP*	0.09			
log(DBH)	*MAP*	0.02			

Figures

Figure 1
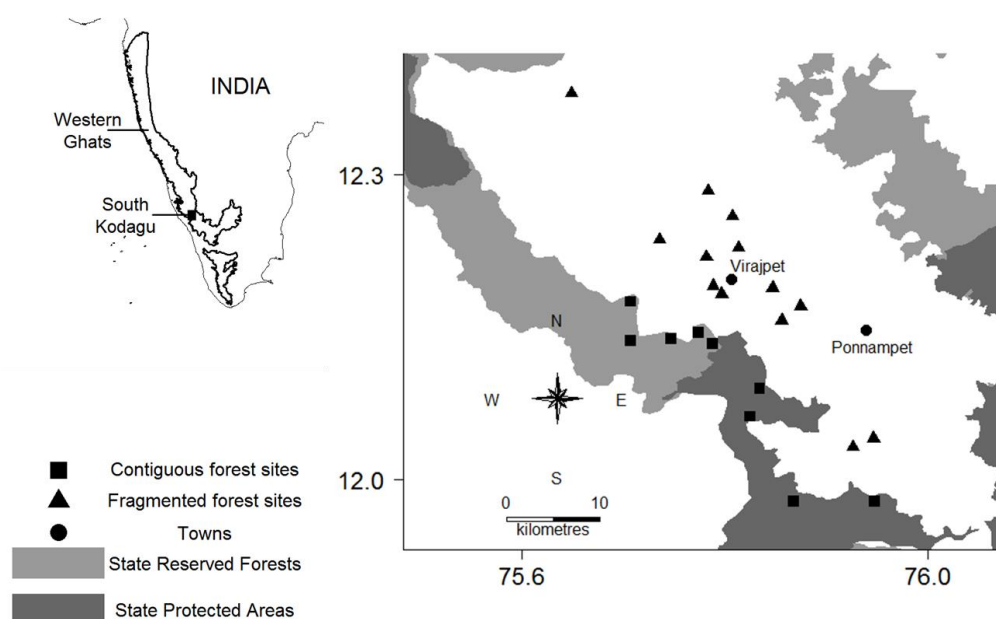
Figure 1 – Study area map: Location of study site (black rectangle) in the Western Ghats of peninsular India (inset), and map of study area showing study sites in south-western Kodagu. Forest cover data sourced from Muthu Sankar (2011) Map of the major forest types of the northern Western Ghats (Mercara-Mysore), through India Biodiversity Portal http://indiabiodiversity.org/.
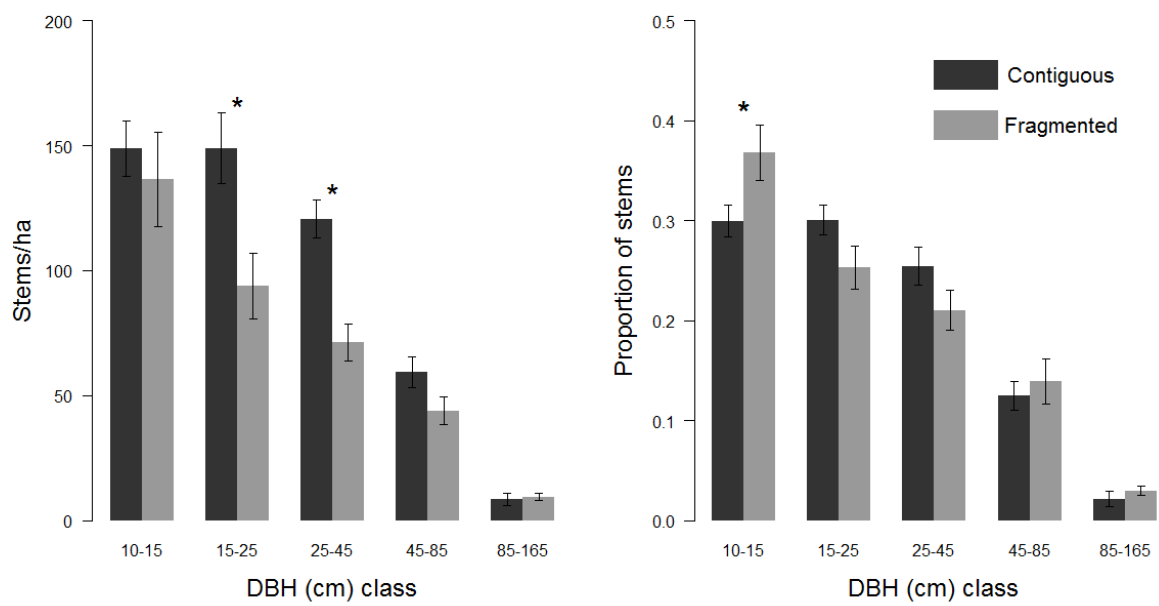
Figure 2

Figure 2 – Comparison of stand size structure between contiguous and fragmented forests:
Comparison of average stem density (left) and average proportion of total stems (right) of
tree diameter classes between contiguous and fragmented forest sites. Bars and error bars
represent mean±1SE. Significant differences at p<0.05 are indicated by *.
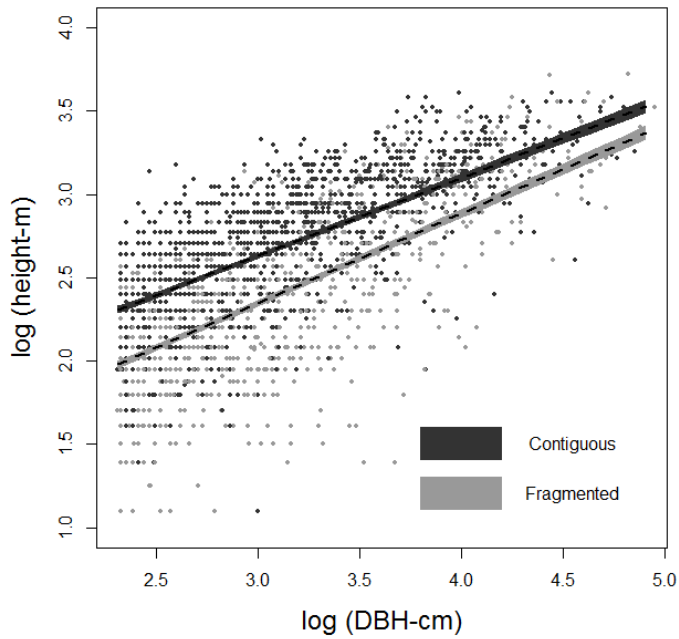
Figure 3 – Comparison of tree allometry between contiguous and fragmented forests: Plot of tree height v/s DBH on log-log axes of trees in contiguous (dark grey) and fragmented (light grey) forests. Fitted lines from linear mixed effects models (bands represent mean fit±1SE), which indicate significantly different intercepts and slopes between contiguous and fragmented forests.
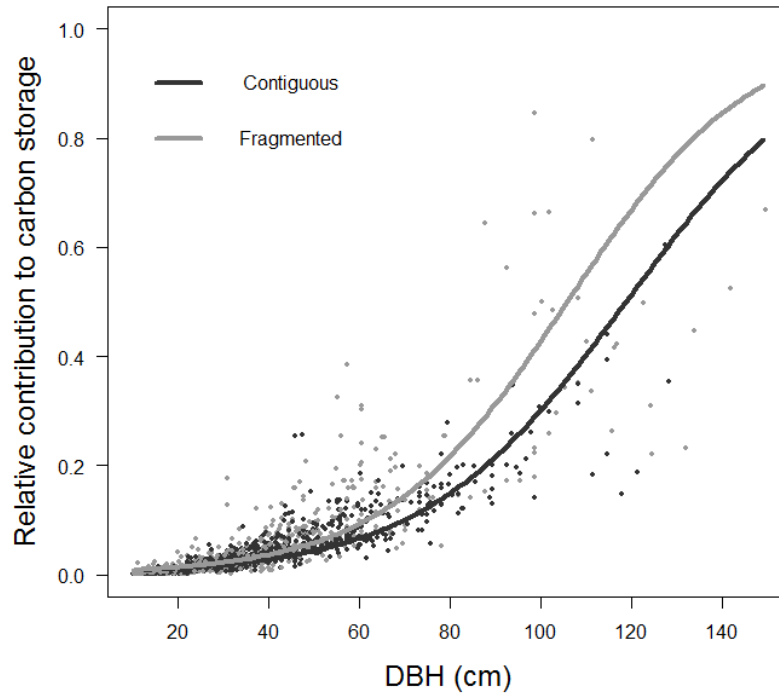
Figure 4: Distribution of carbon storage across trees within plots: Plot of relative contribution to plot-level carbon storage v/s DBH of trees in contiguous (dark gray) and fragmented (light gray) forests. Fitted curves represent fitted beta regression models for contiguous and fragmented forests.

Appendix A

Checklist of species recorded, species codes used in the study, species densities and species wood densities. Data from secondary sources (Rajput *et al.* (1991) and Zaane *et al.* (2009)) are marked as*. Species for which wood density data were not available from primary or secondary sources are labeled 'NA'.

| Sl. No. | Family | Species | Stems per hectare | | | | Wood density (g/cm^3) |
| | | | Contiguous forests | | Fragmented forests | | |
			Mean	1 SE	Mean	1 SE	
1	Anacardiaceae	*Holigarna arnottiana*	2.15	1.12	1.73	0.98	0.48
2	Anacardiaceae	*Holigarna ferruginea*	7.3	2.36	0	0	NA
3	Anacardiaceae	*Holigarna grahamii*	2.82	1.28	8.81	2.74	0.52
4	Anacardiaceae	*Mangifera indica*	1.27	0.61	2.04	0.9	0.63
5	Anacardiaceae	*Nothopegia beddomei*	12.7	3.95	14.54	5.19	0.77
6	Anacardiaceae	*Nothopegia racemosa*	0.46	0.46	4.11	2.21	NA
7	Anacardiaceae	*Spondias pinnata*	1.59	1.59	0.46	0.46	0.29*
8	Annonaceae	*Goniothalamus cardiopetalus*	0	0	0.32	0.32	0.61

9	Annonaceae	*Meiogyne pannosa*	7.62	3.43	0	0	NA
10	Annonaceae	*Meiogyne ramarowii*	0.63	0.44	0	0	NA
11	Annonaceae	*Polyalthia coffeoides*	6.98	3.87	0	0	0.62
12	Annonaceae	*Polyalthia fragrans*	1.27	1.27	0	0	0.48*
13	Apocynaceae	*Alstonia scholaris*	1.41	0.68	0.63	0.44	0.38*
14	Apocynaceae	*Tabernaemontana heyneana*	0.63	0.63	2.5	0.99	0.54
15	Araliaceae	*Schefflera micrantha*	1.37	1.01	0	0	NA
16	Arecaceae	*Caryota urens*	0.32	0.32	11.56	2.6	0.31*
17	Asteraceae	*Vernonia arborea*	0	0	6.1	2.54	0.33*
18	Bignoniaceae	*Pajanelia longifolia*	0.77	0.55	0.32	0.32	0.28*
19	Bignoniaceae	*Stereospermum colais*	0.32	0.32	0	0	NA
20	Bombacaceae	*Bombax ceiba*	0.95	0.95	0.32	0.32	0.32*
21	Burseraceae	*Canarium strictum*	4.51	1.64	5.14	1.36	0.5
22	Caprifoliaceae	*Viburnum punctatum*	0	0	0.46	0.46	NA
23	Celastraceae	*Cassine glauca*	0.32	0.32	0	0	NA
24	Celastraceae	*Euonymus indicus*	1.73	1.08	5.85	1.8	0.72

25	Celastraceae	*Microtropis Sp.*	0.95	0.53	0	0	NA
26	Celastraceae	*Microtropis wallichiana*	0.32	0.32	0	0	NA
27	Clusiaceae	*Calophyllum apetalum*	0.63	0.44	0.32	0.32	NA
28	Clusiaceae	*Calophyllum austroindicum*	0.32	0.32	0	0	NA
29	Clusiaceae	*Calophyllum polyanthum*	3.45	1.16	0	0	NA
30	Clusiaceae	*Garcinia gummi-gutta*	3.14	1.23	1.9	1.07	0.69
31	Clusiaceae	*Garcinia morella*	3.91	1.77	0	0	0.73
32	Clusiaceae	*Garcinia talbotii*	0.95	0.7	0	0	0.86
33	Clusiaceae	*Mesua ferrea*	14.84	4.11	0	0	0.83
34	Combretaceae	*Terminalia bellirica*	0	0	0.32	0.32	0.69*
35	Cornaceae	*Mastixia arborea*	4.13	1.3	2.54	1.21	NA
36	Dilleniaceae	*Dillenia bractiata*	12.09	3.33	0	0	0.57
37	Dipterocarpaceae	*Dipterocarpus indicus*	2.86	2	0	0	0.62*
38	Ebenaceae	*Diospyros candolleana*	0.32	0.32	0	0	NA
39	Ebenaceae	*Diospyros paniculata*	0.63	0.44	0	0	NA
40	Ebenaceae	*Diospyros Sp.*	0.95	0.53	0.91	0.91	NA

41	Ebenaceae	*Diospyros sylvatica*	1.27	0.61	1.73	0.74	0.7
42	Elaeocarpaceae	*Elaeocarpus serratus*	4.27	1.9	1.59	0.67	0.57
43	Elaeocarpaceae	*Elaeocarpus Sp.*	0.95	0.95	0	0	NA
44	Elaeocarpaceae	*Elaeocarpus tuberculatus*	1.59	0.81	0.77	0.55	0.56
45	Euphorbiaceae	*Agrostistachys borneansis*	0.32	0.32	0	0	NA
46	Euphorbiaceae	*Antidesma montanum*	3.81	1.36	12.15	3.16	0.68
47	Euphorbiaceae	*Aporosa lindleyana*	0	0	3.49	2.87	0.61
48	Euphorbiaceae	*Baccaurea courtalensis*	0.32	0.32	0	0	NA
49	Euphorbiaceae	*Bischofia javanica*	2.36	1.23	0.32	0.32	0.59*
50	Euphorbiaceae	*Cleidion spiciflorum*	1.59	0.81	1.37	1.37	NA
51	Euphorbiaceae	*Cleistanthus travancorensis*	0.63	0.63	0	0	NA
52	Euphorbiaceae	*Drypetes elata*	3.81	1.7	0	0	0.82
53	Euphorbiaceae	*Drypetes malabarica*	0.32	0.32	0	0	NA
54	Euphorbiaceae	*Drypetes oblongifolia*	0	0	0.95	0.7	NA
55	Euphorbiaceae	*Epiprinus mallotiformis*	5.71	3.17	0	0	NA
56	Euphorbiaceae	*Excoecaria oppositifolia*	0.95	0.7	2.86	1.39	NA

57	Euphorbiaceae	*Glochidion ellipticum*	1.73	0.87	5.5	2.01	0.58
58	Euphorbiaceae	*Macaranga peltata*	5.64	1.87	3.24	1.46	0.48
59	Euphorbiaceae	*Mallotus philippensis*	5.82	1.67	4.33	1.38	0.66
60	Euphorbiaceae	*Mallotus rhamnifolius*	1.59	1.03	0	0	NA
61	Euphorbiaceae	*Mallotus tetracoccus*	0	0	7.07	3.69	0.46
62	Euphorbiaceae	*Margaritaria indica*	0.63	0.44	1.09	0.77	NA
63	Euphorbiaceae	*Paracroton pendulus*	10.57	4.11	0	0	NA
64	Euphorbiaceae	*Paracroton Sp.*	4.13	1.99	0	0	NA
65	Euphorbiaceae	*Trewia nudiflora*	0.63	0.44	0	0	NA
66	Fabaceae	*Dalbergia latifolia*	0.95	0.7	0	0	0.72*
67	Fabaceae	*Pongamia pinnata*	0	0	0.32	0.32	0.6*
68	Fabaceae-Caesalpinioideae	*Acrocarpus fraxinifolius*	0.32	0.32	0	0	0.59*
69	Fabaceae-Caesalpinioideae	*Humboldtia brunonis*	26.44	8.62	0	0	0.72
70	Flacourtiaceae	*Casearia ovata*	0.32	0.32	0.32	0.32	NA

71	Flacourtiaceae	*Casearia rubescens*	1.59	0.81	0	0	NA
72	Flacourtiaceae	*Casearia wynadensis*	0.32	0.32	0	0	NA
73	Flacourtiaceae	*Flacourtia montana*	0.63	0.44	3.63	1.38	0.73
74	Flacourtiaceae	*Homalium zeylanicum*	0.32	0.32	0	0	NA
75	Flacourtiaceae	*Hydnocarpus pentandra*	0	0	4.61	2	0.55
76	Icacinaceae	*Apodytes dimidiata*	0.63	0.44	1.37	1.01	0.71
77	Icacinaceae	*Nothapodytes nimmoniana*	1.9	1.61	0	0	NA
78	Lauraceae	*Actinodaphne malabarica*	4.76	1.23	2.36	1.14	0.56
79	Lauraceae	*Actinodaphne Sp.*	0.32	0.32	0	0	NA
80	Lauraceae	*Alseodaphne semecarpifolia*	0.32	0.32	0	0	NA
81	Lauraceae	*Beilschmiedia dalzellii*	0.32	0.32	0	0	NA
82	Lauraceae	*Cinnamomum malabatrum*	4.13	1.21	17.47	3.41	0.59
83	Lauraceae	*Cinnamomum Sp.*	0.32	0.32	0	0	NA
84	Lauraceae	*Cryptocarya wightiana*	5.71	2.29	0.63	0.44	0.62
85	Lauraceae	*Cryptocarya Sp.*	0	0	1.37	0.77	NA
86	Lauraceae	*Litsea floribunda*	2.36	0.94	3	1.75	0.67

87	Lauraceae	*Litsea glabrata*	0.32	0.32	0	0	NA
88	Lauraceae	*Litsea laevigata*	2.04	0.78	0	0	0.59
89	Lauraceae	*Litsea mysorensis*	0.95	0.53	0	0	NA
90	Lauraceae	*Litsea oleoides*	0.32	0.32	0	0	NA
91	Lauraceae	*Litsea Sp.*	2.01	1.08	0	0	NA
92	Lauraceae	*Litsea stocksii*	0.46	0.46	0	0	NA
93	Lauraceae	*Neolitsea Sp.*	0.32	0.32	0	0	NA
94	Lauraceae	*Neolitsea zeylanica*	0.95	0.7	0	0	NA
95	Lauraceae	*Persea macrantha*	6.06	2.09	3.14	1.3	0.47
96	Lecythidaceae	*Careya arborea*	0.32	0.32	0	0	0.71*
97	Leeaceae	*Leea indica*	2.36	1.23	0.32	0.32	0.43
98	Lythraceae	*Lagerstroemia microcarpa*	4.13	2.09	0.46	0.46	0.61
99	Magnoliaceae	*Michelia champaca*	0	0	3.83	1.97	0.54
100	Malvaceae	*Grewia microcarpa*	0	0	1.9	0.85	0.55
101	Melastomataceae	*Memecylon gracile*	0.32	0.32	0	0	NA
102	Melastomataceae	*Memecylon randeriana*	0.32	0.32	0	0	NA

103	Melastomataceae	*Memecylon talbotianum*	0.95	0.53	0	0	NA
104	Melastomataceae	*Memecylon wightii*	0.32	0.32	2.86	1.15	0.8
105	Meliaceae	*Aglaia elaeagnoidea*	3.95	1.39	4.33	1.59	0.68
106	Meliaceae	*Aglaia simplicifolia*	4.13	1.65	0	0	0.76
107	Meliaceae	*Aglaia Sp.*	1.59	1.03	4.13	1.83	NA
108	Meliaceae	*Aphanamixis polystachya*	1.27	0.76	3.17	2.56	0.57
109	Meliaceae	*Dysoxylum malabaricum*	0	0	1.55	0.75	0.58*
110	Meliaceae	*Reinwardtiodendron anamalaiense*	12.06	4.03	5.71	3.42	0.84
111	Meliaceae	*Toona ciliata*	2.82	1.01	2.01	1.17	0.38*
112	Meliaceae	*Trichilia connaroides*	0	0	0.32	0.32	NA
113	Meliaceae	*Walsura trifolia*	0.32	0.32	0	0	NA
114	Moraceae	*Artocarpus hirsutus*	0.32	0.32	8.84	1.73	0.48
115	Moraceae	*Artocarpus heterophyllus*	1.73	0.87	8.88	2.09	0.59
116	Moraceae	*Ficus beddomei*	0.63	0.44	0	0	NA
117	Moraceae	*Ficus callosa*	0.46	0.46	0.32	0.32	0.29*

118	Moraceae	*Ficus hispida*	0.95	0.53	3.59	1.75	0.47
119	Moraceae	*Ficus nervosa*	2.82	1.29	0.46	0.46	NA
120	Moraceae	*Ficus Sp.*	1.27	0.88	0.46	0.46	NA
121	Myristicaceae	*Knema attenuata*	7.86	2.37	11.66	3.09	0.58
122	Myristicaceae	*Myristica dactyloides*	20.9	4.55	0.95	0.7	0.6
123	Myrtaceae	*Syzygium caryophyllatum*	0	0	0.32	0.32	NA
124	Myrtaceae	*Syzygium cumini*	0.32	0.32	0.32	0.32	0.69
125	Myrtaceae	*Syzygium densiflorum*	1.9	1.07	0.32	0.32	NA
126	Myrtaceae	*Syzygium gardneri*	5.08	1.6	0.46	0.46	0.72
127	Myrtaceae	*Syzygium laetum*	5.71	1.9	1.27	1.27	0.76
128	Myrtaceae	*Syzygium munronii*	0.63	0.44	0	0	0.77
129	Myrtaceae	*Syzygium Sp.*	4.41	1.76	0.95	0.7	NA
130	Myrtaceae	*Syzygium tamilnadensis*	0.32	0.32	0	0	NA
131	Olacaceae	*Strombosia ceylanica*	0.32	0.32	0	0	NA
132	Oleaceae	*Chionanthus courtallensis*	1.9	0.85	1.59	1.03	0.75
133	Oleaceae	*Chionanthus mala-elengi*	4.44	2.66	4.19	1.34	0.73

134	Oleaceae	*Olea dioica*	12.98	4.44	6.37	2.65	0.79
135	Rosaceae	*Prunus ceylanica*	0.32	0.32	0	0	NA
136	Rubiaceae	*Canthium dicoccum*	0	0	0.63	0.63	0.71*
137	Rubiaceae	*Coffea robusta*	0	0	4.44	3.82	0.63
138	Rubiaceae	*Ixora nigricans*	0.32	0.32	0	0	0.76
139	Rubiaceae	*Meyna laxifflora*	0.63	0.63	0	0	NA
140	Rubiaceae	*Randia Sp.*	0.32	0.32	0	0	NA
141	Rutaceae	*Acronychia pedunculata*	1.73	0.74	3.81	3.5	0.63
142	Rutaceae	*Melicope lunu-ankenda*	1.59	1.13	3.17	1.55	0.47
143	Rutaceae	*Vepris bilocularis*	0	0	1.73	0.87	NA
144	Sabiaceae	*Meliosma pinnata*	1.27	0.76	0	0	NA
145	Santalaceae	*Scleropyrum pentandrum*	0	0	0.46	0.46	NA
146	Sapindaceae	*Dimocarpus longan*	52.17	6.41	31.87	5.19	0.79
147	Sapindaceae	*Lepisanthus Sp.*	1.27	1	0	0	NA
148	Sapindaceae	*Lepisanthes tetraphylla*	0.63	0.63	0	0	0.81*
149	Sapindaceae	*Otonephelium stipulaceum*	17.87	3.55	0	0	0.75

150	Sapotaceae	*Chrysophyllum roxburghii*	2.22	1.19	0.95	0.53	0.58
151	Sapotaceae	*Isonandra lanceolata*	0.32	0.32	0	0	NA
152	Sapotaceae	*Isonandra Sp.*	0.32	0.32	0	0	NA
153	Sapotaceae	*Madhuca neriifolia*	0	0	0.32	0.32	NA
154	Sapotaceae	*Mimusops elengi*	0	0	3.14	0.93	0.63
155	Sapotaceae	*Palaquium ellipticum*	36.61	6.29	0.32	0.32	0.66
156	Staphyleaceae	*Turpinia malabarica*	0.32	0.32	0	0	NA
157	Sterculiaceae	*Sterculia guttata*	2.18	0.96	0.32	0.32	NA
158	Symplocaceae	*Symplocos coorgensis*	0	0	0.32	0.32	0.52*
159	Symplocaceae	*Symplocos macrophylla*	0.32	0.32	0	0	NA
160	Symplocaceae	*Symplocos racemosa*	0.32	0.32	3.91	2.03	0.44
161	Symplocaceae	*Symplocos Sp.*	0.95	0.53	0	0	NA
162	Ulmaceae	*Aphananthe cuspidata*	0	0	1.87	1.03	0.66
163	Ulmaceae	*Celtis philippensis*	1.9	0.96	1.59	0.81	0.78
164	Ulmaceae	*Celtis tetrandra*	0	0	0.46	0.46	0.55
165	Urticaceae	*Dendrocnide sinuata*	0.32	0.32	0	0	NA

166	Urticaceae	*Villebrunea integrifolia*	1.59	1.13	0	0	NA
167	Verbenaceae	*Callicarpa tomentosa*	1.87	1.03	1.41	1.04	0.43
168	Verbenaceae	*Clerodendrum Sp.*	0	0	0.91	0.64	NA
169	Verbenaceae	*Clerodendrum viscosum*	0.63	0.63	2.18	0.96	0.5
170	Verbenaceae	*Vitex altissima*	0	0	1.09	0.62	NA
171	Xanthophyllaceae	*Xanthophyllum arnottianum*	12.17	5.18	21.26	4.94	0.67

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Appendix B

Parameters, likelihood, and fit of candidate explanatory models of response of carbon storage and associated structural and functional properties of forest stands in contiguous and fragmented forests.

Response	Model	Contiguous forests		Fragmented forests		Akaike weight	R.sq
		Intercept	Slope	Intercept	Slope		
Carbon storage (t/ha)	MAP	22.2±78.1	4.0E-2±3E-2	22.2±78.1	4.0E-2±3E-2	0.01	0.07
	treat	186.6±13.7	0±0	118.8±17.9	0±0	0.77	0.39
	MAP+treat	226.6±90.8	-1.0E-2±3E-2	152.5±23.2	-1.0E-2±3E-2	0.19	0.36
	MAP*treat	254.4±213.2	-2.0E-2±7E-2	147.1±230.2	-1.0E-2±7E-2	0.04	0.33
Tree density (trees/ha)	MAP	-218.1±111.0	0.21±0.04	-218.1±111.0	0.21±0.04	0.72	0.60
	treat	486.1±32.0	0±0	355.0±41.5	0±0	0.00	0.30
	MAP+treat	-125.6±157.3	0.19±0.05	-159.2±40.2	0.19±0.05	0.24	0.59
	MAP*treat	-44.9±368.8	0.16±0.11	-174.9±398.2	0.2±0.1	0.04	0.57
Basal area (m^2/ha)	MAP	16.3±11.1	6E-3±4E-3	16.3±11.1	6E-3±4E-3	0.02	0.08
	treat	40.1±2.0	0±0	31.0±2.7	0±0	0.77	0.34

	MAP+treat	42.4±13.6	-7E-4±4E-3	32.9±3.5	-7E-4±4E-3	0.17	0.31
	MAP*treat	49.8±31.8	-3E-3±1E-2	31.5±34.3	-2E-4±1E-2	0.03	0.27
Community-weighted wood density (g/cm^3)	MAP	5E-1±6E-2	4E-5±2E-5	5E-1±6E-2	4E-5±2E-5	0.06	0.13
	treat	6.6E-1±1E-2	0±0	6.1E-1±1E-2	0±0	0.73	0.31
	MAP+treat	6.4E-1±7E-2	8E-6±2E-5	5.9E-1±2E-2	8E-6±2E-5	0.17	0.28
	MAP*treat	5.9E-1±2E-1	2E-5±5E-5	6.1E-1±2E-1	5E-6±6E-5	0.03	0.24
Average stand height (m)	MAP	4.0±3.8	3.0E-3±1E-3	4.0±3.8	3.0E-3±1E-3	0.01	0.21
	treat	16.1±0.7	0±0	12.1±0.9	0±0	0.77	0.49
	MAP+treat	14.1±4.4	6.0E-4±1E-3	10.4±1.1	6.0E-4±1E-3	0.19	0.47
	MAP*treat	13.2±10.3	9.0E-4±3E-3	10.6±11.1	5.0E-4±4E-3	0.04	0.44
Average tree log(H): log(DBH) (m)	MAP	5.0E-1±7E-3	1.0E-4±3E-5	5.0E-1±7E-3	1.0E-4±3E-5	0.02	0.40
	treat	9.0E-1±1E-2	0±0	8.0E-1±2E-2	0±0	0.42	0.55
	MAP+treat	7.0E-1±9E-2	5.0E-5±3E-5	6.0E-1±2E-2	5.0E-5±3E-5	0.47	0.60
	MAP*treat	7.0E-1±2E-1	4.0E-5±7E-5	6.0E-1±2E-1	5.0E-5±7E-5	0.09	0.57