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Impacts of selective logging on diversity, species composition and biomass of residual lowland dipterocarp forest in central Western Ghats, India

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Abstract: Studies on the residual impact of logging on the diversity and composition of tropical forests are scarce in India. We examined the impact of selective logging on tree species richness, composition and structure prevalent after 27 years. Trees ≥ 30 cm girth at breast height were inventoried in four 1 ha plots in selectively logged patches and two 1 ha plots in an adjacent unlogged patch of lowland dipterocarp forest continuum, Uppangala, central Western Ghats, India. We enumerated 2343 trees (598 trees ha^{-1}) belonging to 116 species (63 species ha^{-1}) and 1345 trees (672 trees ha^{-1}) belonging to 68 species (55 species ha^{-1}) in logged and unlogged plots, respectively. The species richness in logged plots as compared to unlogged plots varied with spatial scale of sampling: at 1 ha scale two logged plots had higher species richness whereas it was high in only one plot at 400 m^2 scale. Logged plots had low floristic similarity between them and also with the unlogged plots. Mantel and partial Mantel tests proved that logging was the main driver for the species composition rather than the elevation and spatial distance. Higher abundance of species belonging to canopy, intermediate and light wood categories and lower density of emergent, understory and medium wood types were recorded in the logged plots. As compared to unlogged plots, logged plots had 20–59% less above ground biomass (AGB) due to paucity of larger trees, especially in the emergent and medium wood types but higher AGB in canopy and hardwood categories. Our study shows the residual impact of logging even after 27 years and suggests that the recovery process may depend on the resurgence of emergent and medium wood categories.

Key words: Above ground biomass, residual impact of logging, structural ensembles, trees, tropical forest, wood density categories.

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Introduction

Tropical forests cover only 6% of the Earth's surface and harbour half of all known species. They are quite often subjected to anthropogenic perturbations. Logging is one of the major activities causing habitat degradation and loss of species. Recent estimates indicate that secondary and degraded tropical forests occupy a larger area than undisturbed primary forests (FAO 2010). In fact, most of our knowledge on tropical forests is obtained from studies carried out in undisturbed forests and investigations on the long-term effects of silviculture on forest dynamics and ecology

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remain scarce (Sist *et al*. 2015). Understanding the structure, diversity and ecosystem processes of disturbed forests is increasingly important as such forests play a key role in the trade-off between provision of goods, maintenance of carbon stocks, biodiversity and other services (Berry *et al*. 2010; Chazdon *et al*. 2009; Clark & Covey 2012; Edwards *et al*. 2011; Gardner *et al*. 2009; Kauffman *et al*. 2009; Picard *et al*. 2012; Putz *et al*. 2012; Sist *et al*. 2015; Sodhi *et al*. 2009; Yamada *et al*. 2013; Yosi *et al*. 2011). There was also a considerable uncertainty about those values due to lack of knowledge regarding the impact of logging and the rate of recovery of forests (Yosi *et al*. 2011). Recently, a network of permanent sample plots in logged forests, the Tropical managed Forests Observatory (TmFO), was initiated with the objective of gathering long-term data on the resilience of logged tropical forests at regional and global scales (Sist *et al*. 2015).

The lowland dipterocarp forests in Western Ghats, one of the eight "hotspot" of biological diversity in the world (Myers *et al*. 2000), were subjected to large-scale logging operation until its ban in 1988. Explorations of selectively logged forests in the region to assess the residual impact are limited (Bhat *et al*. 2011; Parthasarathy 1999). Studies focussing on impacts of disturbance require sampling at a scale large enough to include spatial variation in environmental conditions and species composition resulting from disturbance (Berry *et al*. 2008). Most of the available literature on the impact of disturbance in the Western Ghats either adopted small sampling units (Chandrashekara & Sreejith 2006; Nagaraja *et al*. 2005; Pélissier *et al*. 1998) or focussed on selected species (Ganesan & Davidar 2003). Short term monitoring (1986–1993) of selectively logged (sample of 0.84 ha) and adjacent unlogged forest patches (sample of 3.12 ha) of Uppangala forest revealed that no significant difference in forest structure, composition and dynamics between logged and adjacent unlogged forest patches (Pélissier *et al.* 1998). This study also suggested that the logged patches gradually recover and resemble unlogged forest within 20 years. On the contrary, recovery of selectively logged forests in the tropical regions require longer time than the estimated cutting cycles shorter than 50 years (Chua *et al.* 2013; Huth & Ditzer 2001; Yamada *et al.* 2013).

Recently, carbon storage and the potential revenues that could be accrued from Reducing Emissions from Deforestation and Forest Degradation (REDD+) mechanisms have drawn attention of ecologists to identify an appropriate allometric models for biomass estimation (eg. Brown 1997; Chave *et al.* 2005, 2014; Clark & Kelner 2012; Ploton *et al.* 2012). Amongst these, the pantropical allometric models for moist forests (Chave *et al.* 2005) are the most commonly employed for aboveground biomass estimation (Clark 2007; Rutishauser *et al.* 2013). This model integrates tree heights, tree diameter and wood specific density for AGB calculation. Currently, the model has been proposed for inclusion in the IPCC Emission Factor Database and by the REDD protocol (Chave *et al.* 2014). To the best of our knowledge, estimation of AGB in the Indian evergreen forest by adopting Chave *et al.* (2005) allometric model is none (Bhat *et al.* 2011; Devagiri *et al.* 2013; Murali *et al.* 2005; Ploton *et al.* 2012; Rai & Proctor 1986; Rajkumar & Parthasarathy 2008). However, Ploton *et al.* (2012) estimated AGB for the Uppangala forest at 1 ha scale using the destructive samples of trees with stem diameter ranged 8.3 to 60.9 cm of Rai (1981). This model has several drawbacks; notably the stem diameter range used in the calculation is far smaller than the trees enumerated in the study area. Besides, the other important components such as wood specific density and tree height were not included in the calculation. Inclusion of those two parameters significantly improves the accuracy of the AGB estimate (Chave *et al.* 2005; Feldpausch *et al.* 2012; Rutishauser *et al.* 2013).

Logging impact studies on a relatively large spatial scale and long term in this region is scarce; hence the present study was conducted to appraise the tree community in the logged forests 27 years after post logging operation in the lowland dipterocarp forest. The specific objectives were 1) to determine diversity and species composition with reference to structural, functional and ecological attributes of species of logged and adjacent unlogged patches; 2) to estimate the aboveground biomass of both logged and unlogged patches adopting the Chave *et al.* (2005) model; and 3) to determine how far the logged forest resembles the undisturbed patch in terms of diversity, density, basal area and aboveground biomass.

Materials and methods

Study area

The study area is situated between the south Malanad (Karnataka plateau) and the coastal

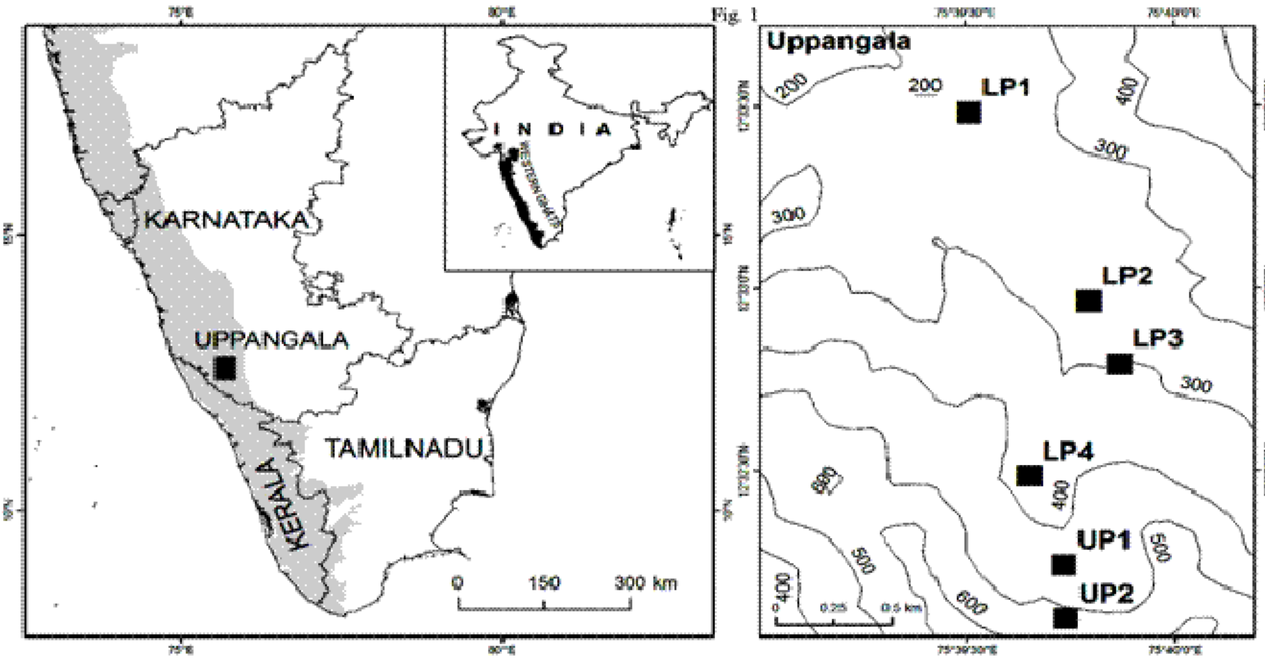

Fig. 1. Location of Uppangala study site in the central Western Ghats, Karnataka, India. Location of logged (LP) and unlogged (UP) sample plots in Uppangala.

plains of Mangalore region (South Kanara) near Uppangala in the central Western Ghats, Karnataka, India (12°32′N latitude and 75°39′E longitude; Fig. 1). The study area is composed of gneisses form of archean rocks and dystric combisol type of soil (Ferry 1994). Mean annual precipitation in the region is 5119 mm (range 3908 to 5989 mm yr^{-1}, data collected in Uppangala, from 1994 to 2011). Pascal (1988) classified the study area as *Dipterocarpus indicus-Kingiodendron pinnatum-Humboldtia brunonis* type of tropical wet evergreen forest, which corresponds to the West coast tropical evergreen forest type of Champion & Seth (1968). The most common emergent and upper canopy species are *Dipterocarpus indicus* and *Vateria indica*, both members of Dipterocarpaceae, followed by *Calophyllum polyanthum*, *Kingiodendron pinnatum*, *Mesua ferrea*, *Palaquium ellipticum* and *Syzygium gardneri*. The intermediate stratum is dominated by *Drypetes elata*, *Garcinia talboti*, *Knema attuenata* and *Myristica dactyloides*. *Humboldtia brunonis*, *Reinwardtiodendron anamallayanum* and *Archidendron monoadelphum* are the most common species in the understory. The study area was subjected to selective logging between 1974 and 1983 (Loffeier 1988). During the logging operation, the forest was divided into compartments of 28 ha each, 237 to 359 large trees (stems ≥ 180 cm) of medium wood (> 0.5 but ≤ 0.72 g cm^{-3}) dipterocarp species viz., *Dipterocarpus indicus* and *Vateria indica* were logged per compartment. An average of 8 to 13 dipterocarp trees ha^{-1} were logged manually and hauled using elephants locally, a method that causes much less damage than mechanized skidding. A few patches of forest remain unlogged.

Tree inventories

The fieldwork was carried out between November 2010 and April 2011. Trees ≥ 30 cm girth at breast height (gbh) were inventoried in six 1-ha plots (100 m x 100 m). Of these, four plots LP1, LP2, LP3 and LP4 were established in the logged area along the altitudinal gradient at elevations of 200–220 m, 250–270 m, 300–340 m and 380–420 m, respectively. The other two plots UP1 and UP2 are located in one of the unlogged compartments at altitudes of 450–490 m and 530–570 m, respectively. The plot UP2 was installed in 1990 as part of the Uppangala permanent sampling plot, wherein trees ≥ 30 cm gbh were identified, fitted with dendrometer belts for girth measurement and recorded periodically, and their specimens were lodged in the herbarium of French Institute of Pondicherry (HIFP). Five 1 ha plots (LP1, LP2, LP3, LP4 and UP1) were installed during 2010–2011, wherein stems ≥ 30 cm gbh were permanently tagged with sequentially numbered aluminium tags, their girths measured at 1.3 m or above the buttresses and identified at species level. The plot UP2 was inventoried in March–April 2011. Voucher specimens were collected from all trees, processed and deposited in HIFP. Species were identified using vegetative key (Pascal & Ramesh 1987), interactive identification system (Ramesh *et al*. 2010) and the flora of Coorg district (Murthy & Yoganarasimhan 1990), and their identities were confirmed at HIFP. Height of 1035 trees (744 in logged plots and 291 in unlogged plots with at least one tree per species in girth class interval of 30 cm) was measured using Vertex laser rangefinder (VL402, Haglof). Heights of other trees were estimated from their girth using height-girth linear regression equations obtained from the sampled trees separately for logged and unlogged forest types. Wood specific density (WSD) value of each taxon was obtained from various literatures (Agarwal 1970; Bhat 1985; 1994; Chowdhury & Ghosh 1958, 1963; Gamble 1922; Purkayastha 1982, 1985, 1999; Rai & Proctor 1986; Zanne *et al*. 2009).

Data analysis

Tree species richness, density and diversity indices (Shannon and Simpson) were determined for each plot. Live above ground biomass (AGB) of individual trees were determined using the regression equation of tropical moist forest stands: AGB = $\exp(-2.977 + \ln(\rho D^2 H))$ where D is the diameter at breast height in cm, H is total height in m and ρ is wood density in g cm^{-3} (Chave *et al.* 2005). One-way ANOVA and Tukey's HSD post-hoc tests were used to check for any significant difference between the six 1 ha plots in mean species richness, tree density, basal area and AGB of trees ≥ 30 cm gbh (all trees), ≤ 60 cm gbh (small trees), > 60 and ≤ 180 cm gbh (medium) and > 180 cm gbh (large) per 400 m^2 samples. Sorenson index of floristic similarity between plots was calculated using "fossil" package (Vavrak 2011). Detrended correspondence analysis (DCA) was employed to determine the variation in species composition in 400 m^2 sampling areas of all the plots using species presence-absence data matrix as per Lieberman *et al*. (1996). All the twenty five subplots in each 1 ha plot were used as samples for DCA. Axes generated by this technique rank subplots on the basis of their species composition and species according to the subplots in which they occur. The first axis scores of each subplot were ordinated against the corresponding plot's altitude. Mantel tests was conducted to examine the influence of predictor variables viz., spatial distance (x-y coordinates of individual 400 m^2 sample area of each plot), elevation and treatment (logged and unlogged) on species composition and diversity using "vegan" package (Oksanen *et al.* 2008) as per Chua *et al.* (2013). This test was performed separately for all trees, small, medium and large trees using a sample area of 400 m^2. Euclidean distance matrices were obtained for all predictors and species diversity individually, and for floristic composition Bray-Curtis dissimilarity index was used. For the treatment matrices, we assigned a value of "1" for all subplot pairs when the treatment was different and "0" in the case of same treatment. Partial Mantel tests were conducted to appraise the partial effect of each predictor variable on the dependent variable (Manly 1986). All the analyses were performed using program R 2.15.0 (R Development Core Team 2012). The variation in species composition between logged and unlogged plots was determined in terms of structural ensembles (emergent, canopy, lower canopy/intermediate stratum and understory as per Pascal 1988), functional groups (wood density: light, medium and heavy wood as per Melo *et al*. 1990; Nogueira *et al*. 2005) and ecological behavior (secondary/ deciduous species "SDS" and primary species categories). The primary species were further classified into primary non-dipterocarps (PND), medium wood dipterocarps (MWD) and heavy wood dipterocarps (HWD). Population structure of the species categories SDS, PND, MWD and HWD trees were determined.

Results

Species richness and diversity

A total of 3738 trees (≥ 30 cm gbh) representing 126 species belonging to 41 families was enumerated in six 1-ha plots in the tropical evergreen forest at Uppangala, central Western Ghats (Table 1). The species richness of plots varied between treatments: logged plots harboured 56 species (in LP4) to 72 species (LP2) with an average of 63.3 species ha^{-1}, while unlogged plots contained 53 species (UP1) and 57 species (UP2) with an average of 55 species ha^{-1}. One-way ANOVA for the mean species richness of stems ≥ 30 cm gbh at 400 m^2 sampling area showed significant differences across the six plots (Table 2). The post-hoc multiple comparison tests at 400 m^2 between the plots showed that the second most speciose plot LP3 differed significantly with all the

Table 1. Summary details of species richness, diversity indices, stand density, basal area and above-ground biomass (AGB) for trees ≥ 30 cm gbh at 1 ha scale of four logged (LP1, LP2, LP3 and LP4) and two unlogged (UP1 and UP2) plots in Uppangala, central Western Ghats, India.

Variables	Logged forest plot (LP)				Unlogged forest plot (UP)		Total (mean)
	LP1	LP2	LP3	LP4	UP1	UP2	
Altitudinal range (m)	200–220	250–270	300–340	380–420	450–490	530–570	
Species richness	59	72	66	56	53	57	126 (60.5)
Family richness	32	28	25	23	24	25	41 (26.2)
Shannon index	3.21	3.35	3.54	3.18	2.88	2.89	3.70
Simpson index	0.07	0.06	0.04	0.07	0.10	0.10	0.05
Stem density	572	513	636	672	665	680	3738 (623)
Basal area (m^2 ha^{-1})	28.15	39.30	41.37	48.23	51.19	51.00	259.24 (43.21)
AGB (Mg ha^{-1})	268.05	396.71	454.84	491.44	611.59	649.82	2872.45 (478.74)

Table 2. Mean species richness, density, basal area and AGB at 400 m^2 samples for all trees (stems ≥ 30 cm gbh) and tree size categories of small (≤ 60 cm gbh), medium (> 60 and ≤ 180 cm gbh) and large (> 180 cm gbh) trees with F value (one-way analysis of variance) of six 1 ha plots in Uppangala, central Western Ghats, India.

Tree size	Logged plots				Unlogged plots		
	LP1	LP2	LP3	LP4	UP1	UP2	F-value
Species richness							
All trees	12.6	11.96	15.24	14.24	12.36	12.4	4.57***
Small trees	9	6.92	9.36	8.72	8	8.72	2.76*
Medium trees	5.76	5.8	7.52	7.04	6.04	5.8	2.33*
Large trees	0.64	1.24	1.2	1.56	1.32	1.44	2.7*
Tree density							
All trees	22.88	20.52	25.44	26.88	26.6	27.2	4.77***
Small trees	14.6	11	13.28	15.76	15.8	16.28	4.89***
Medium trees	7.56	8.12	10.84	9.32	9	9.08	2.75*
Large trees	0.72	1.4	1.32	1.8	1.8	1.84	3.09**
Basal area (m^2)							
All trees	1.13	1.57	1.65	1.93	2.05	2.04	4.65***
Small trees	0.21	0.17	0.2	0.22	0.21	0.22	2.33*
Medium trees	0.61	0.64	0.84	0.74	0.75	0.74	1.88
Large trees	0.31	0.76	0.62	0.97	1.09	1.08	3.93**
AGB (Mg)							
All trees	10.72	15.87	18.19	19.66	24.46	25.99	5.34***
Small trees	1.1	0.75	0.96	1.05	1.12	1.24	5.04***
Medium trees	5.56	5.01	7.27	6.31	7.53	7.51	2.86*
Large trees	4.06	10.1	9.96	12.29	15.81	17.24	4.21**

*** $P < 0\text{-}001$; ** $P < 0.01$; * $P < 0.05$.

plots ($P < 0.05$) except LP4 . Mean species richness of small (stems < 60 cm gbh), medium (stems > 60 and ≤ 180 cm gbh) and large trees (stems > 180 cm gbh) at 400 m^2 samples did not vary significantly between plots (Table 2). The unlogged plots had similar values of Shannon index, which were lower than those of logged forest plots (Table 1). In contrast, the Simpson index of unlogged plots was higher than those of the logged plots.

Tree density, basal area and live above ground biomass (AGB)

Tree density ha^{-1} was higher in unlogged plots when compared to the logged plots, except for LP4, which had almost similar density of trees with unlogged plots (Table 1). One-way ANOVA and post-hoc multiple comparison tests at 400 m^2 revealed that the mean density of medium and large trees did not differ significantly between plots ($P > 0.01$; Table 2). In the cases of all trees and small trees the plot LP2 was significantly different to UP1, UP2 and LP4 ($P < 0.05$) but not to the other two logged plots LP1 and LP3.

A total of 259.2 m^2 stand basal area for trees ≥ 30 cm gbh with a mean of 43.2 m^2 ha^{-1} was recorded in the study (Table 1). Both the unlogged plots had similar basal area of about 51 m^2 ha^{-1}, which was higher than the logged plots. Mean basal area at 400 m^2 samples did not differ significantly between plots for small and medium trees, whereas it differed significantly for all trees (≥ 30 cm gbh) and large trees (Table 2). The plot LP1 had significantly lower mean basal area when compared to UP1, UP2 and LP4 ($P < 0.05$ for both all and large trees).

The height-girth relationship varied among the forest types (logged forest: height = 0.1083 × girth + 8.460, R^2 = 70.9%; unlogged forest: height = 0.1144 × girth + 10.177, R^2 = 71.9%). The live AGB of the plots ranged from 268.05 Mg ha^{-1} (LP1) to 491.44 Mg ha^{-1} (LP4) in the logged plots, and 611.59 Mg ha^{-1} (UP1) to 649.82 Mg ha^{-1} (UP2) in the unlogged plots (Table 1). The mean AGB at 400 m^2 samples differed significantly among the plots for all trees, small and large sized categories (Table 2) but not for medium sized trees. The post-hoc multiple comparison tests revealed that both the unlogged plots differed significantly with LP2 (in the case of small trees; $P < 0.05$) and LP1 (in the cases of large and all trees; $P < 0.05$) but did not differ significantly with the other two logged plots LP3 and LP4.

Species composition, density and predictor factors

Floristic similarity at 1 ha scale based on Sorenson's index between plots varied widely from 0.41 to 0.76 (Table 3). The unlogged plots had the highest similarity. The logged plot LP1 had low floristic similarity with all the other plots (index value ranged from 0.41 to 0.43 with the unlogged plots and 0.45 to 0.56 with the logged plots). The other three logged plots had a slightly higher index value between them (0.64 to 0.72). Floristic affinity between all pairs of 400 m^2 subplots was obtained based on species composition utilizing detrended correspondence analysis. The axis 1 score of each sample is ordinated with the plot's altitude (Fig. 2) and the ranking of species is summarized in Supplementary Table S1. The higher axis 1 scores were from the lower altitude plot LP1. The floristic affinity was higher for the plots situated adjacent to each other in the elevational gradients; the overlap was greater between higher altitude plots (LP4, UP1 and UP2).

The ranking of species displayed species distribution and dominance across the plots. Of the total of 126 species encountered, 58 species were common to the logged and unlogged forest types and contributed 72.3% and 96.1% of their respective stand density. Of the 19 species occurring in all the six 1-ha plots, *Vateria indica*, *Myristica dactyloides* and *Knema attuenata* are notable for their contribution to the stand density (33.7% and 20.3% of the unlogged and logged forests, respectively). Species specific to the forest types were found in low density. A total of 58 species (27.3% of stand density) occur only in logged forest plots and 26 of them belong to secondary/deciduous category. Most common among these were *Archidendron monoadelphum*, *Aporosa lindleyana* and *Terminalia paniculata* and they collectively contributed 9% of the total density of logged plots. Of the 10 species found exclusively in the unlogged forest, only 2 viz., *Dimorphocalyx lawianus* (with 1.9% of stand density) and *Rinorea bengalensis* (1.4%) were represented by more than 10 individuals each. *Vateria indica* and *Humboldtia brunonis* were the two most abundant species in the unlogged plots with collective densities of 253 and 260 individuals in UP1 and UP2, respectively (Supplementary Table S1). The dominant species in each logged plot varied: *Hopea parviflora* and *Aporosa lindleyana* in LP1 (163 trees); *Vateria indica* and *Archiden-dron monoadelphum* in LP2 (143 trees); *Vateria indica* and *Myristica dactyloides* in LP3 (117 trees); *Vateria indica* and *Humboldtia brunonis* in LP4 (201 trees).

The Mantel test revealed that all the three predictor variables viz., spatial distance, elevation and treatment (logged and unlogged) of 400 m^2 sample area were strongly correlated with floristic composition ($P < 0.01$; Table 4). The partial Mantel test also showed that treatment was most strongly

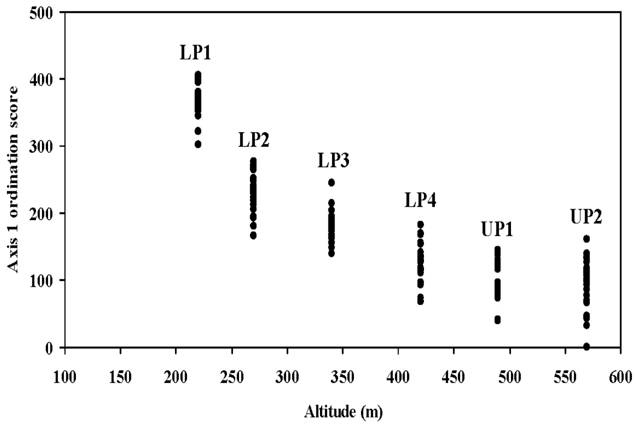

Fig. 2. Detrended correspondence analysis ordination scores of 400 m^2 samples (based on species composition) plotted in relation to plot's altitude for the logged and unlogged forest.

correlated with floristic composition and explained the greater amount of variation than the others. This correlation decreased with increasing tree sizes (r = 0.730, 0.655, 0.565, 0.138 after accounting for spatial distances, for all, small, medium and large trees, respectively with $P <$ 0.001 for all cases; Table 4). Elevation was the second most important predictor of the floristic composition, after controlling the distance, whereas the effect of distance was not significant after accounting for treatment in all cases except for large trees that had significant but weak correlation ($r = 0.065$, $P < 0.01$).

Structural and functional group's composition

The logged plots had a slightly higher number of species in canopy, intermediate and understory strata but the same number of species in emergent stratum when compared to the unlogged plots (Fig. 3a). In terms of tree density, the two unlogged plots exhibited a more or less matching number of trees with respect to structural ensembles (Fig. 3b). All the logged plots harboured fewer trees in the emergent and understory categories but slightly higher number of trees in canopy stratum when compared to the unlogged plots. The logged plot LP3 contained markedly higher number of trees in the intermediate stratum when compared to all the other plots. Compared to the unlogged plots, all the logged plots had higher AGB in the canopy category but low AGB in emergent, intermediate and understory categories (Fig. 3c; Table 1). The plot LP1 contained extremely low AGB in the emergent category, 18.51 Mg ha^{-1},

Table 3. Sorensen's similarity index of floristic composition between six 1 ha plots for trees ≥ 30 cm gbh.

	LP2	LP3	LP4	UP1	UP2
LP1	0.56	0.53	0.45	0.43	0.41
LP2		0.71	0.66	0.61	0.53
LP3			0.64	0.66	0.67
LP4				0.72	0.64
UP1					0.76

when compared to the other logged plots (ranging from 195.92 in LP3 to 250.03 Mg ha^{-1} in LP4) and the unlogged plots (419.08 and 474.97 Mg ha^{-1} respectively for UP1 and UP2), and the plot ranked least in terms of total AGB among the plots. Despite this, the plot LP1 contained higher AGB in canopy (20% to 50%) and understory species (40% to 60%) as compared to all other plots.

The logged plots had a slightly higher number of species in medium and light wood categories as compared to the unlogged plots but almost the same number of species in heavy wood type (except the plot LP2 that had 3 to 5 species more; Fig. 4a). In terms of tree density, LP1 harboured exceptionally high number of heavy wood trees (35.5% of the stand density as against the <16% in the case of the other plots; Fig. 4b). The proportion of medium wood trees in the logged forest plots was 9% to 49% lower when compared to the unlogged forest plots. On the contrary, light wood trees were ca. 15% to 73% more in the logged plots than the unlogged plots. As for AGB, the medium wood category contributes the major portion in all the plots (Fig. 4c), ranging from 38–67% in the logged plots and from 75%–83% in the unlogged plots. The AGB of heavy wood species was 1.2 to 2.8 times higher in the logged plots when compared to unlogged plots. The AGB of light wood species varied widely: 13.65 Mg ha^{-1} to 100.47 Mg ha^{-1} within the logged plots and 34.08 Mg ha^{-1} to 82.57 Mg ha^{-1} in the unlogged plots.

Population structure

The population structure of each plot based on girth class distribution of individuals displayed a reverse J-shaped curve, which indicates the healthy population of the forest stand (Fig. 5). Among the species categories, primary non-dipterocarps contributed a major portion (40%–83%) of tree density in almost all girth classes. Number of

Table 4. Summary of simple and partial Mantel correlation coefficient between floristic dissimilarity (Bray-Curtis index) and predictor variables viz., spatial distance, elevation and treatment (logged and unlogged plots) for all trees (stems ≥ 30 cm gbh) and tree size categories of small (≤ 60 cm gbh), medium (> 60 and ≤ 180 cm gbh) and large (> 180 cm gbh) trees of six 1 ha plots.

Tree size category	Predictor variable	Simple Mantel correlation	Partial Mantel correlation		
		Floristic dissimilarity	F|spatial distance	F|elevation	F|treatment
All trees	Spatial distance	0.73***	-	0.06*	–0.15
	Elevation	0.49***	0.62***	-	–0.28
	Treatment	0.11**	0.73***	0.54***	-
Small trees	Spatial distance	0.65***	-	0.12***	–0.14
	Elevation	0.48***	0.51***	-	–0.30
	Treatment	0.08**	0.66***	0.54***	-
Medium trees	Spatial distance	0.55***	-	-0.11	–0.15
	Elevation	0.28***	0.51***	-	–0.17
	Treatment	0.04**	0.57***	0.32***	-
Large trees	Spatial distance	0.15***	-	0.18***	0.07**
	Elevation	0.20***	0.11***	-	–0.05
	Treatment	0.08**	0.14***	0.19***	-

***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

stems of primary non-dipterocarps in the girth class 30–60 cm was lower (27%–56%) in three logged plots (LP1, LP2 and LP3). Notably, these three plots had a healthy population of secondary/deciduous species. Exceptionally, the plot LP1 harboured a considerable population of heavy wood dipterocarps (with 122 trees). Both the unlogged plots had almost a similar trend and healthy population structure of medium wood dipterocarps. In all the logged plots, medium wood dipterocarps trees in each girth class were lower than in the unlogged plots.

Discussion

Diversity and species composition

The studies on the impact of selective logging on tropical forests that are available today show that the species richness may increase (Berry *et al.* 2010; Cannon *et al.* 1998; Plumptre 1996), decrease (Brearley *et al.* 2004; Clark and Covey 2012; Gutiérrez-Granados *et al.* 2011; Okuda *et al.* 2003; Makana and Thomas 2006) or remain unchanged (Bischoff *et al.* 2005; Foody & Cutler 2003; Hall *et al.* 2003; Medjibe *et al.* 2011; Slik *et al.* 2002; Verburg & van Eijk-Bos 2003) in response to disturbance. The response depends on the status of the forest prior to logging (Tilman 1999) and on the distribution of disturbed sites across a landscape (Bongers *et al.* 2009; Cadotte 2007; Sheil & Burslam 2003). Higher diversity is predicted when recurrent local disturbances are frequent enough to prevent competitive exclusion of species over an entire area but not so frequent as to eliminate most species (Connell 1978; Hubbell *et al.* 1999; Whittaker *et al.* 2001).

In the present study, species richness at 1 ha scale for trees ≥ 30 cm gbh ca. three decades after logging exhibited two different responses: two plots had an almost equal number of species (LP1 and LP4) as adjacent unlogged plots and the other two plots had a slightly higher number of species (LP2 and LP3). The proximity of the plot LP1 to human settlement may be the reason for higher and frequent disturbances associated with human activities in the past that led to more degradation as evidenced by the presence of higher number of secondary/deciduous (17) species among the four logged plots. The plot LP4 had a higher population of *Dipterocarpus indicus* and *Vateria indica* than the other logged plots and occupation of logging-created habitat by these species might have reduced the available niche for the establishment of other species. In addition, the plot LP4 had ca. 0.14 ha of swamps, which favours *Gymnacranthera farquhariana* of Myristicaceae rather than other species. The higher species richness in LP2 and LP3 is due to the presence of secondary tree species, marginally more species belonging to structural ensembles of canopy, intermediate and

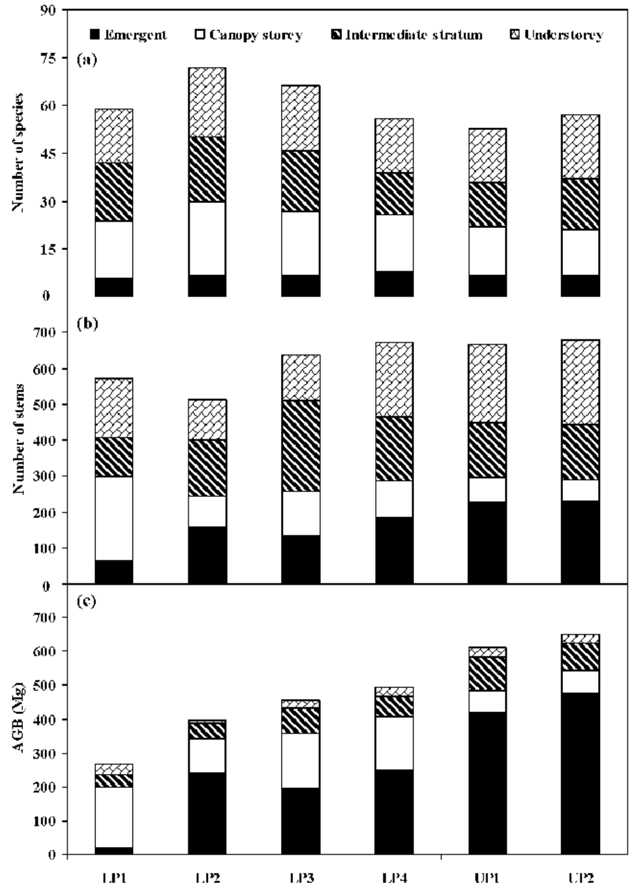

Fig. 3. Stratum-wise (emergents, canopy, lower canopy/intermediate stratum and understory) distribution of species, density and AGB of four logged (LP1, LP2, LP3 and LP4) and two unlogged (UP1 and UP2) plots.

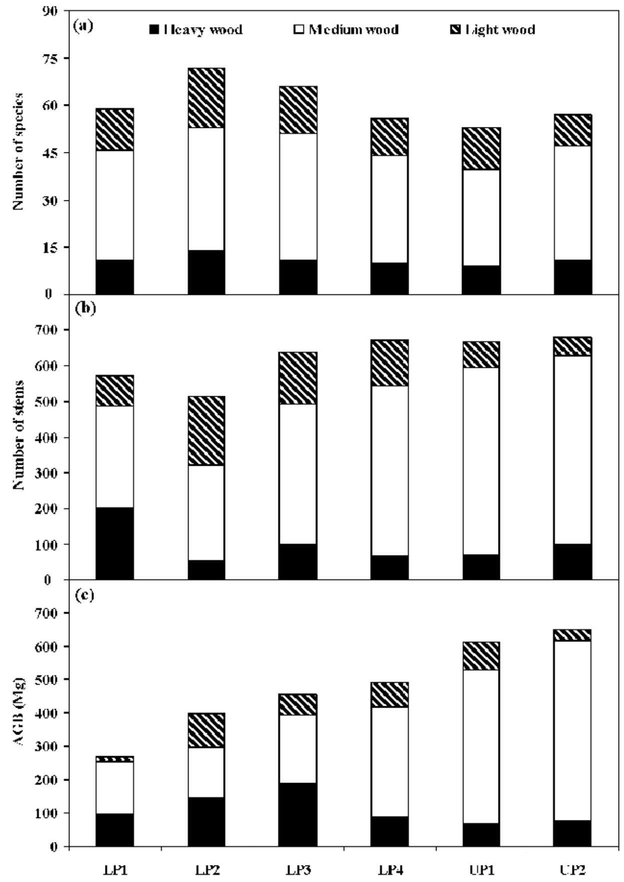

Fig. 4. Wood density category-wise [light (≤ 0.5 g cm^{-3}), medium (> 0.5 ≤ 0.72 g cm^{-3}) and heavy wood (> 0.72 g cm^{-3})] distribution of species, density and AGB of four logged (LP1, LP2, LP3 and LP4) and two unlogged (UP1 and UP2) plots.

understory strata (Fig. 3a) and in medium and light wood categories (Fig. 4a). In this study, the comparatively low floristic similarity between plots of logged and unlogged types as well as between the logged plots confirms the occurrence of higher number of unique species among the logged plots (16 to 33 species per plot among the logged plots versus 3 to 9 species in the respective unlogged plots; Table 3). Further, most of the unique species (26 species) found in the logged plots are of secondary/deciduous category, which also indirectly supports the logging had altered the community composition. Comparatively, the logged plots had a slightly more number of species, especially unique species with fewer individuals, which resulted in higher Shannon index values and lower Simpson index values when compared to the unlogged plots. While the unlogged plots displayed a species oligarchy (for instance, 90% of the respective plots' density was shared by just 19 species in unlogged plots whereas by 25 to 33 species in logged plots). However, the species richness encountered at 1 ha scale in the study falls well within the range of species richness reported for the old-growth evergreen forests in the Western Ghats: 47 species ha^{-1} at Agumbe, central Western Ghats (Srinivas & Parthasarathy 2000) to 85 species ha^{-1} at Kalakad, southern Western Ghats (Parthasarathy 1999).

At smaller scales of 400 m^2, there was not much difference in species richness of trees ≥ 30 cm gbh, small, medium and large sized trees between logged and unlogged plots (except for the group all trees in the case of LP3; Table 2). However the existence of difference in species richness at larger scale in two logged plots and the results of others (Berry *et al.* 2008; Cadotte 2007; Imai *et al.* 2012) suggest that the species richness

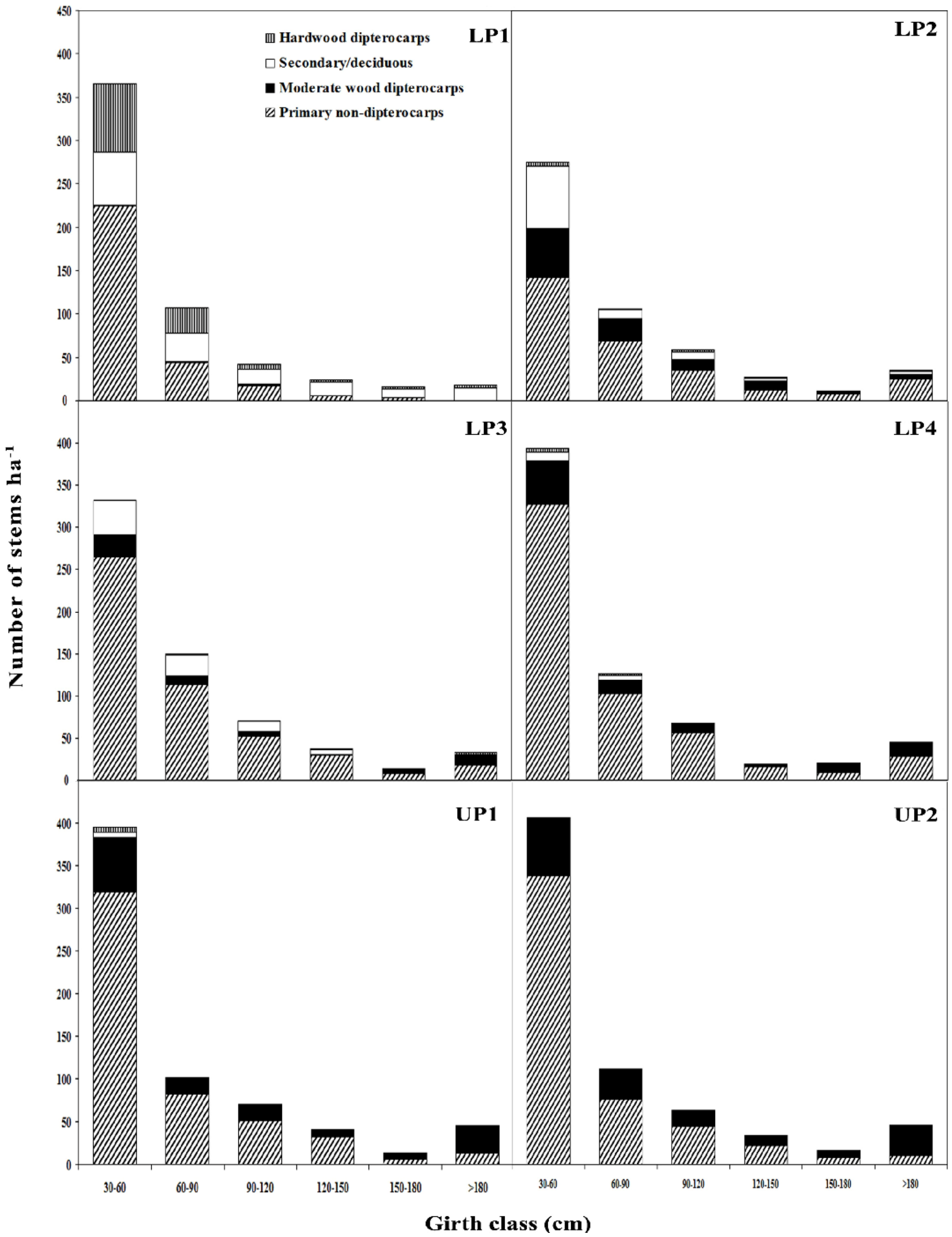

Fig. 5. Population structure of trees (with proportion of primary non-dipterocarps-PND, medium wood dipterocarps-MWD, heavy wood dipterocarps-HWD and secondary/deciduous species-SDS) in the four logged and two unlogged plots.

response to logging vary with sample size. At finer scales, the difference is minimal since the sample area covers smaller areas of dense unharvested forest stand and open gaps with a less heterogeneous vegetation structure. In contrast, at larger scale, the responses differed due to the inclusion of mosaics of patches affected by different intensities of disturbance (volume of timber extraction, severity of damage, including roads, trails, etc.) with more heterogeneity in vegetation structure and patchiness in tree species composition (encompassing different environmental conditions, which encourage different species from the local species pool). Variation in species composition at

400 m^2 samples was small within each 1 ha plot as compared to differences across the plots, which suggests spatial decay in the species similarity (Fig. 2). Higher axis scores for the logged plots in general, when compared to unlogged plots, reflect the expected change in spatial pattern of species composition in logged plots. Among the logged plots, LP1 had noticeably different floristic composition when compared to the other logged and unlogged plots. Samples of the other 5 plots showed a certain degree of overlapping in the scores, which was higher between neighbouring plots. Mantel and partial Mantel tests clearly demonstrated that, among the predictor variables, treatment (logging) was the main driver of species assemblages, followed by elevation and spatial distance in order (Table 3).

Tree density, basal area and AGB

The effect of selective logging on stem density, stand basal area and AGB in 1 ha and 400 m^2 samples was evident even 27 years later. Exceptionally, the plot LP4 almost matched the unlogged plots in stem density and basal area of all, small, medium and large sized trees (Table 1 and Table 2) but the AGB was lower by ca. 15% and 20%–34% in the case of medium and large sized trees, respectively. It suggests that recovery in terms of AGB will take significantly longer period. Therefore, our findings suggest that accounting biomass in addition to density and basal area as one among the component in the assessment of logged forest recovery. In the other three logged plots stem density, basal area and AGB per hectare were lower than in the unlogged plots by 4.4%–24.6%, 18.9%–45% and 25.6%–58.8%, respectively. This is consistent with the result of other studies in regenerating forests in Borneo (1 and 8 years after logging; Cannon *et al.* 1998), in Pasoh, Malaysia (39 years after logging; Okuda *et al.* 2003) and in Africa (18 years after logging; Hall *et al.* 2003). The low tree density in logged plots of the present study could be attributed to the poor representation of primary non-dipterocarps species (19% to 58% of trees ha^{-1}) and medium wood dipterocarps species (11% to 98% of trees ha^{-1}) especially in the 30–60 cm gbh class (Fig. 5). The logging has significantly reduced the regeneration of primary species. This is in conformity with the results of other studies: selective logging reduces the number of shade tolerant species and stimulates light-demanding species (Okuda *et al.* 2003; Pelisier *et al.* 1998; Silva *et al.* 1995; Villela *et al.* 2006). LP2 recovered to a lesser extent than the other logged plots: trees in 30-60 cm gbh class constituted ca. 27% of the stand density in LP2 as compared to ca. 39% to 49% in the other plots (Fig. 5). Comparatively high population of canopy and intermediate strata species and low population of the emergent and understory strata species in the logged plots suggests that logging promotes the former categories and deters the latter (Fig. 3b). Further, logging favours the growth of light wood species population and deters medium wood trees (Fig. 4b). The population recovery of targeted species, medium wood dipterocarps in the logged forests indicates that those species in various degrees of recovery in each plot: higher recovery in LP2 and LP4, moderate in LP3 and poor in LP1 (Fig. 5).

Lower stand basal area (6% to 45%) and AGB (20% to 59%) of logged plots with reference to the unlogged plots could be due to the paucity of larger trees (Fig. 5). LP1 ranked lowest among all the plots in terms of stand basal area and AGB due to the poor representation of the dominant species of the vegetation, only two trees each of *Dipterocarpus indicus* and *Vateria indica*. The plot LP3 is distinct with altered forest structure; the density, basal area and AGB of medium sized trees of *Myristica dactyloides*, *Archidendron monadelphum*, *Garcinia talbotii*, *Knema attenuata*, *Croton malabaricus* and *Macaranga peltata*, which belong to middle storey species, are higher when compared to all the other plots (Table 2). However, stem density and basal area found for the six 1 ha plots in the study (Table 1) are well within the range reported for the other evergreen forests of the Western Ghats: stand density of 273 trees ha^{-1} in Varagalaiar (Ayyappan & Parthasarathy 2001) to 965 trees ha^{-1} in Kalakad (Parthasarathy 2001); the basal area ranged from 25 to 94.6 m^2 ha^{-1}, respectively for Varagalaiar and Kalakad (Ayyappan & Parthasarathy 2001; Parthasarathy 1999).

Only a few AGB estimates for the Indian forests are available, but girth/diameter threshold and estimation methods considered in those studies varied, which renders comparison difficult. Yet, a compilation of published values reveals a lowest range of 210.09 Mg ha^{-1} to 293.97 Mg ha^{-1} for trees $\geq$ 10 cm gbh in three, 1 ha plots of evergreen forests at Uttara Kannada (Bhat *et al.* 2011), a moderate range of 332 Mg ha^{-1} to 353 Mg ha^{-1} for trees $\geq$ 30 cm gbh in the evergreen forests at Andamans (Rajkumar & Parthasarathy 2008) and a higher range of 420 Mg ha^{-1} to 649 Mg ha^{-1}

for trees ≥ 15 cm gbh from destructive samples in the evergreen forests at Agumbe, Bannadpare, Kagneri and South Bhadra (Rai & Proctor 1986). Remote sensing and GIS based approach yielded an AGB value of 287.05 Mg ha^{-1} for trees ≥ 10 cm dbh in the evergreen forest at Kodagu, a site close to the present study (Devagiri *et al*. 2013). Ploton *et al.* (2012) estimated a slightly higher AGB for LP1, LP2, LP3 and LP4 (347.3, 446.1, 519.2 and 588.1 Mg ha^{-1} respectively) and lower AGB for the unlogged plot UP2 (631.6 Mg ha^{-1}) when compared to the present study (Table 1). This variation could be due to the lack of larger trees in the Rai's data set (1981), which includes stems ≥ 8.3 to 60.9 cm diameter. Large trees (diameter greater than 70 cm) contributes the bulk of AGB (Slik *et al.* 2013). Moreover, our estimates include wood specific gravity and tree height, which significantly improves the accuracy of AGB prediction (Chave *et al.* 2005; Feldpausch *et al.* 2012; Rutishauser *et al.* 2013). The AGB ha^{-1} of unlogged plots of the present study (611.59 and 649.82 Mg ha^{-1} for trees ≥ 30 cm gbh respectively, for UP1 and UP2) is high compared to the available data on Indian forests and the other tropical forests across the continents: a mean of 287.8 ± 105.0 Mg ha^{-1} for South America, 393 ± 109.3 Mg ha^{-1} in Asia and 418 ± 91.8 Mg ha^{-1} in Africa for trees ≥ 10 cm dbh (Slik *et al*. 2013).

The proximity of the logged patches to unlogged areas in the landscape matrix is advantageous for rapid recovery, particularly species composition. However, the study area showed the residual impact of logging on diversity, density, basal area, composition (species assemblages, structural ensembles, wood density categories) and population structure even around three decades after the logging. In conclusion, our findings in agreement with the other recent studies (Chua *et al.* 2013; Yamada *et al.* 2013) that the recovery of selectively logged forests require a longer time than the predicted. The process of recovery of logged areas in the study area, at least of the structural elements, may depend on the recovery of species belonging to the emergent and moderate wood categories. The floristic result of this study provides the importance of logged forests as reservoirs of biodiversity in the tropical landscapes. Further monitoring of these permanent plots will provide data on forest recovery and factors affecting the processes. Such data will be useful for conservation and management of forests in the region.

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Supporting Information

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

Table S1. List of all tree species (with their family and arranged according to their axis 1 ordination scores) in the six 1 ha permanent plots at central Western Ghats.