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Varying impacts of logging frequency on tree communities and carbon storage across evergreen and deciduous tropical forests in the Andaman Islands, India

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ABSTRACT

The majority of Earth's tropical forests have been selectively logged; some on repeated occasions. Selective logging is known to affect forest structure, composition and function in various ways, but how such effects vary with logging frequency and across forest types remains unclear. In the Andaman Archipelago in India, we examined adult and pole-sized trees in baseline (unlogged since 1990s), once-logged (logged between 2007 and 2014) and twice-logged (logged in early 1990s and between 2007 and 2014) evergreen and deciduous forests, and tested whether higher logging frequency was associated with lower canopy cover, tree density, tree diversity, aboveground carbon stocks and divergence in species composition, including increased relative abundances of deciduous species in these forests. While once-logged evergreen and deciduous forests were similar to their respective baselines for most attributes assessed, and twice-logged evergreen forests had 22–24% lower adult tree density and diversity, twice-logged deciduous forests had 17–50% lower canopy cover, pole density, adult species diversity and above-ground carbon stocks, and 12% higher deciduous fractions compared to the baselines. Collectively our results reveal lasting impacts of repeated selective logging, even at relative low intensity, on tree communities and carbon storage. These impacts can potentially be mitigated by reducing logging frequency and retaining unlogged patches in logged landscapes, but management must also incorporate heterogeneity in responses and recovery across different forest types. In the Andaman Islands, all forests may require more than 15–25 years between logging events, with deciduous forests potentially requiring more stringent extraction limits compared to evergreen forests.

1. Introduction

Foresters and applied ecologists have long tried to identify when, where, and how tropical forests can be selectively logged such that biodiversity and ecosystem functions are maintained (Cerullo and Edwards, 2019; Putz et al., 2012). Insights from such assessments have been consolidated into sustainable forest management practices that stipulate 40–60 year cutting cycles, with the intention of revisiting logged patches after the stipulated period for subsequent harvests (Blaser et al., 2011; Gustafsson et al., 2012; Putz et al., 2008; Wiersum, 1995; Zimmerman and Kormos, 2012). With primary forests becoming increasingly scarce and regulations restricting logging in previously unlogged protected areas, repeat logging is likely to become increasingly common and a necessity for meeting future demand for timber (Edwards et al., 2014; Malhi et al., 2014; Margono et al., 2014). However, little is known about the impacts of repeat logging on biodiversity and ecosystem functions, and how these impacts vary by forest type.

Selective logging of primary forests causes immediate structural damage and a reduction in diversity and standing biomass (Clark and Covey, 2012). Like other forms of forest disturbance, selective logging also alters abiotic factors like light, soil moisture and soil carbon, and disrupts plant interactions with dispersers, pollinators, soil microbes, herbivores and pathogens (Carneiro et al., 2011; Fredericksen and Mostacedo, 2000; Jin et al., 2019; Krishnadas et al., 2018; Markl et al., 2012; Pereira et al., 2002). Reducing damage through improved logging practices may improve rates of recovery but not necessarily mitigate

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immediate loss of biomass or diversity (Martin et al., 2015).

In the case of repeated logging, forest structure, tree diversity and ecosystem function of repeat-logged forests will not only depend on logging intensity, logging frequency and the inter-logging interval, but also on historical contingency - the density and diversity of remnant trees from the first logging event (Gourlet-Fleury et al., 2013; Johnstone et al., 2016; Martin et al., 2015; Roopsind et al., 2018). Recovery will also depend on forest type - drier secondary forests in the Neotropics show divergent recovery patterns compared to wetter secondary forests (Poorter et al., 2019, 2016). Moreover, repeat-logged forests may remain in a state of arrested succession or recover along an entirely different trajectory (Ghazoul et al., 2015; Katovai et al., 2016).

A handful of field studies that examined the impact of repeat-logging of tropical forests on birds, insects and bats in South-East Asia found no declines in diversity but shifts in species composition (Edwards et al., 2014; Struebig et al., 2013). However, tree diversity, structure and standing biomass may not be as resilient – while twice-logged areas retained ~75% of the original faunal diversity, timber stocks declined by 80% in twice-logged forests (Fisher et al., 2011a). One study found predictable declines in tree diversity and tree density from very frequent (up to 5 times) and intense logging (32% of total basal area lost to logging), but the impact of repeat logging under realistic inter-logging intervals (>10 years) and intensities is not known (Khai et al., 2016). This paucity of studies, may at least in part be because repeat-logged forests are presently not common – depleted timber stocks in once-logged forests and increasing demand for arable land incentivizes land conversion rather than retention of logged forests for biodiversity or future timber (Dauber et al., 2005; Fisher et al., 2011b; Zimmerman and Kormos, 2012).

In the tropical forests of Andaman Islands of India however, repeat logging is widely practiced. These islands have a 150 year long history of selective logging, but taking cognizance of increased forest degradation, since 2005, there has been an official ban on any future logging in previously unlogged areas, while restricted low-intensity logging is practised in previously logged areas (Sekhsaria, 2004; Singh, 2003; See methods for details). Further, an interesting feature of the Andaman forests is that they occur as a mosaic of distinctly deciduous and evergreen forest patches, thought to be underlain by edaphic differences (Parkinson, 1923), with both forest types having been subjected to the same logging regimes. These forests thus provide a rare opportunity to study the impacts of repeat logging on forest structure and function, as mediated by differences in forest type.

Although systematic studies are lacking, the forest management policies in the Andaman Islands, while considered successful from a forestry perspective, have been thought to be detrimental to forest structure and composition (Sekhsaria and Pandya, 2010). Since the 1980s, a widely-held belief has been that post-logging, evergreen forests have become more deciduous, due to an increase in the relative frequency of deciduous species (Sekhsaria and Pandya, 2010), consistent with similar reports from Amazonia where canopy deciduousness increased in response to logging (Koltunov et al., 2009). This idea is supported by some evidence from the region which suggests that deciduous hardwood species (often commercially valuable) are more likely to occur in selectively logged forests (Rajesh and Alappatt, 2016; Saha, 1992), but requires more systematic study. Patterns of regeneration of juvenile (pole-sized) trees after early-stage mortality may provide strong signals of future shifts in composition, but these trends are yet to be examined in the region. Evergreen forests are associated with higher tree, bird and butterfly diversity and higher tree basal area (Davidar et al., 2001; Padalia et al., 2004; Prasad et al., 2010; Tripathi et al., 2004), making their conversion to deciduous patches a matter of concern.

In this study, we sampled tree communities in different logging treatments across evergreen and deciduous forests in the Andaman Islands. We examined responses of canopy cover, stem density, tree diversity, deciduous fraction and above-ground carbon, to logging frequency (baseline, once-logged and twice-logged) and asked how these responses differed across evergreen and deciduous patches. We expected lower density and diversity of adult and juvenile (pole) trees, and lower above-ground carbon stocks in twice-logged compared to once-logged forests. We also expected deciduous forests to show a stronger response to logging compared to evergreen patches, both due to higher timber extraction (a greater fraction of species in deciduous patches are commercially valuable) and reduced recovery (dry season water stress likely exacerbated by an open canopy). Finally, we expected the proportion of stems belonging to deciduous species to increase with logging frequency, consistent with anecdotal evidence suggesting logging-related increase in deciduousness of evergreen forests (Sekhsaria and Pandya, 2010).

2. Methods

2.1. Study site

The study was conducted in the Andaman archipelago (hereafter, the Andamans) situated in the Indian Ocean (10.5° – 13.7°N, 92.2° – 94.3°E). The Andamans extends for c. 360 km in the North-South direction and are up to c. 40 km wide. Average annual rainfall is about 4000 mm, with a short dry season between January and April (Davidar et al., 2002). Five islands, collectively called 'Greater Andaman', comprise 68% of the archipelago's area and are nearly contiguous, separated by narrow straits <500 m wide. Situated in the Indo-Myanmar floristic region, the Andamans primarily consist of *Dipterocarpus*-dominated evergreen forest patches and *Pterocarpus*-dominated moist deciduous forest patches that are edaphically structured (Champion and Seth, 1968; Parkinson, 1923). Evergreen patches are found on alluvial soils where streams meet the ocean and on deep clayey or dark red loam soil on hilly ridges, while moist deciduous patches are found on gently undulating ground in between alluvial and hilly evergreen, characterized by clayey loam to coarse sandy loam and identified by low visible humus (Chengappa, 1934).

Forests in the Andaman Islands have a long history of human use going back at least 20,000 years (McColl et al., 2018). However, large-scale timber extraction and forest clearing began the 1800s with Britain setting up a penal colony for mainland Indian prisoners, and subsequent waves of immigration from mainland India primarily as labour for timber extraction (Bhattee, 1958). Today, most forests of the archipelago, except small out-lying islands and a c. 1600 km^2 tribal reserve for the Jarawa people, have experienced some form of logging-associated disturbance. This long history of selective logging was a forestry and commercial success, evidenced by the development of indigenous forestry practices like the Andaman Shelterwood Canopy Lifting System, a method to produce even-aged stands with sufficient regeneration, with the use of captive elephants for timber removal (Chaudhry, 1998; Chengappa, 1944).

However, much of the logging until early 2000s was not aimed at sustainability or biodiversity conservation, prompting citizen activists to successfully petition the Supreme Court of India demanding a change in logging policies (Sekhsaria, 2004; Sekhsaria and Pandya, 2010; Singh, 2003). The present Working Plan caps logging intensity at 3 trees/hectare and a harvest of up to one-third of all commercial trees above logging girth (180 cm) every 30 years (an intended total logging cycle of 90 years), not unlike reduced-impact logging practiced elsewhere of the tropics (Putz et al., 2008; Singh, 2003). Additionally, both logged and unlogged forests have experienced substantial herbivory by invasive mammals – Spotted Deer (*Axis axis*), Indian Muntjac (*Muntiacus muntjak*) and free-ranging domestic Asian Elephants (*Elephas maximus*) – for at least half a century, but this has subsequently declined since the 1970s on most large islands (Ali and Pelkey, 2013; Mohanty et al., 2016).

2.2. Logging treatments

We used GPS-based maps from post-2005 Working Plans and hand-drawn maps from pre-2005 Working Plans created by the Department of Environment, Forests and Climate Change, Andaman and Nicobar Administration to delineate logging treatments (Singh, 2003). Records from before 1960s were difficult to obtain and if present, were difficult to ground-truth with precision. We therefore regarded all forests with no history of logging prior to 1960s as an undisturbed baseline. We subsequently grouped worked forests into three categories – recent once-logged forests that were logged between 2007 and 2014 (henceforth L1), recent twice-logged forests that were logged between 2007 and 2014 but also in early 1990s (henceforth L2), and baseline forests that have not been logged since *at least* early 1990s - most of these patches have no record of logging since the 1960s (henceforth B).

We conducted this study between December 2017 and May 2018 in Baratang and Middle Andaman Forest Divisions of central Andaman Islands, India (Fig. 1A-C). The Bajalungta region of Middle Andaman (L1) and Nilambur region of Baratang (L2) were logged under Felling Series-1 between 2007 and 2014. The Nilambur (L2) region was also logged in the early 1990s. While the Gandhighat region, Flat Bay and nearby islands have no record of logging at least since the 1960s and until the time of study, areas around Adajig have not been logged since the early 1990s (B) (Fig. 1C). Each of these three logging treatments (L1, L2 and B) straddled evergreen and deciduous patches that were easily identified in the field, especially in the dry season when canopy trees in deciduous patches were mostly leafless (Fig. 1-E).

Spatial clustering of plots within treatment is largely unavoidable given that logging is managed on the basis of spatial blocks or coupes. One strategy we adopted to minimize the confounding effects of fine scale autocorrelation of environmental characteristics was to maintain a minimum distance of 300 m between plots (Fuller and Enquist, 2012). We also verified that environmental characteristics such as mean annual precipitation, mean annual temperature, elevation and slope were very similar across treatments (Chamberlain et al., 2020; Fick and Hijmans, 2017) (Table 1). Moreover, while previous work has shown that evergreen and deciduous forests in the region have distinct soil properties, logging treatments within forest types are unlikely to differ markedly in soil properties (Chengappa, 1934; Parkinson, 1923). Finally, while plots were largely placed away from edges (median distance from edge: 1.25 km), seven plots in logged evergreen forests lay <300 m edges due to small patch sizes. However, because the matrix abutting these patches was paddy fields and not settlements, and given the low prevalence of biomass extraction and livestock grazing in these forests (AS pers. obs.), we do not expect anthropogenic disturbance to vary across treatments.

2.3. Plot design and data collection

Selective logging is inherently patchy with the most discernible impacts around felled trees (de Carvalho et al., 2017). In order to capture this effect, we aligned each plot along the direction of treefall, beginning with a logging stump (Fig. 1D). If an old logging stump could not be found in baseline forests, we aligned the plot in an arbitrary direction beginning with a commercially-valuable tree above logging girth at its origin. The cutting step on each stump and discarded tops-and-boughs helped identify the direction of treefall. Each plot consisted of two nested plots: pole-sized juvenile and understory trees (henceforth pole trees, 10 cm $\leq$ girth < 30 cm) were recorded in a 10x10m plot closest to the stump and adult trees (girth $\geq$ 30 cm) were recorded in an overlapping 50x10m rectangular plot whose long axis was aligned along the direction of tree fall (Fig. 1D). We identified each qualifying stem to the highest taxonomic level possible and recorded its girth at breast height (~1.3 m above ground, henceforth girth). Tree height was recorded with a laser rangefinder. To estimate canopy cover, we walked the length of the rectangular plot (50 m) along its centre, and visually estimated presence (1) or absence (0) of overstory canopy (above ~ 20 m) and understory canopy (below ~ 15 m) at every meter. Canopy cover was then expressed as the proportion of points where presence was recorded.

2.4. Data processing and analysis

Trees were identified using expert help, floristic keys and comparisons with herbarium specimens at the Botanical Survey of India, Port Blair (Alappatt, 2018; Parkinson, 1923, N. Page pers. comm., J. Alappatt pers. comm.). Unidentified species were classified as unique morphospecies or using unique local names, as much as possible. Forest type was visually identified in the field – in order to reduce subjectivity, we performed a k-means cluster analysis with two a-priori clusters on the Hellinger-transformed Bray-Curtis distance measure of composition of adult trees (Hartigan and Wong, 1979; Oksanen et al., 2007). This procedure revealed that four plots were likely misclassified (within-cluster SS / total SS = 14.7%) in the field; these plots were discarded and 72 correctly classified plots were used for subsequent analysis (Fig. S2, Supplementary Material).

We calculated stem density as the number of trees per plot using all recorded trees above the girth cut-off regardless of species identity. Canopy cover percentage was separately calculated for the understory (<15 m) and overstory (>20 m), by adding the number of canopy presences (1) as a fraction of total observations. To calculate above-ground carbon (AGC), we first calculated above-ground biomass for each adult tree using the pan-tropical allometric equation that uses height (H) and diameter (D; girth/π measurements in the field), above-ground biomass = $0.0673\times(\rho D^2H)^{0.976}$ and is robust to differences in forest type (Chave et al., 2014). We obtained wood density (ρ) values from the Global Wood Density Database (Zanne et al., 2009). Species-average values were used for 47.7% of the stems, Genus-averaged values were used for 43.3% of the stems and plot-averaged values were used for the remaining 9% of stems (Zanne et al., 2009). These values were multiplied by the carbon fraction (0.5), pooled to obtain total above-ground carbon per plot and scaled to per-hectare estimates (Chave et al., 2005). To calculate tree species diversity, species richness was calculated using all stems identified at the genus level or lower, as well as unknown morphospecies. If a plot contained some stems identified to the Genus level (e.g. *Garcinia* sp.) and other stems in the same Genus at a species level (e.g. *Garcinia andamanica*), Genus-identified stems were excluded from the species richness calculation to minimize potential double-counting. We used exponentiated Shannon diversity as a measure of tree diversity, as it accounted for number of species and their relative abundance, and is directly interpreted as effective species richness (Jost, 2007). Each morphospecies in the plot was assigned a dry-season phenology status of "deciduous" if it lost a majority of its leaves during the dry season for a month or more – all other trees were categorized as "evergreen". Species-specific information in the Andaman Islands is scant – we therefore used information from Floras in the Indo-Burma region, expert knowledge and field-observations to identify a phenology status (Alappatt, 2018; Parkinson, 1923; J. Alappatt pers. comm.). Morphospecies whose phenology status is unknown, higher taxonomic levels that include both deciduous and evergreen species, species with a brief deciduous period (e.g. *Parishia insignis*, less than two weeks while fruiting) and brevi-deciduous species (e.g. *Dipterocarpus incanus*) were all categorized as evergreen – our results therefore represent a lower-limit of deciduous fraction. We used the proportion of stems belonging to deciduous morphospecies as the deciduous fraction response variable. To calculate differences in species composition, we used the adult tree dataset to first compute pairwise Bray-Curtis distances using Hellinger-transformed plot-abundance data (Oksanen et al., 2007) and visualized these distances in 2-D space by running a Non-metric Multi-Dimensional Scaling (NMDS) procedure on these distances and plotted the first two axes (Minchin, 1987).

We modelled each response variable against logging treatment (as a three-level factor) using generalized linear models or beta regression models (Response ~ logging treatment, separately for each forest type).

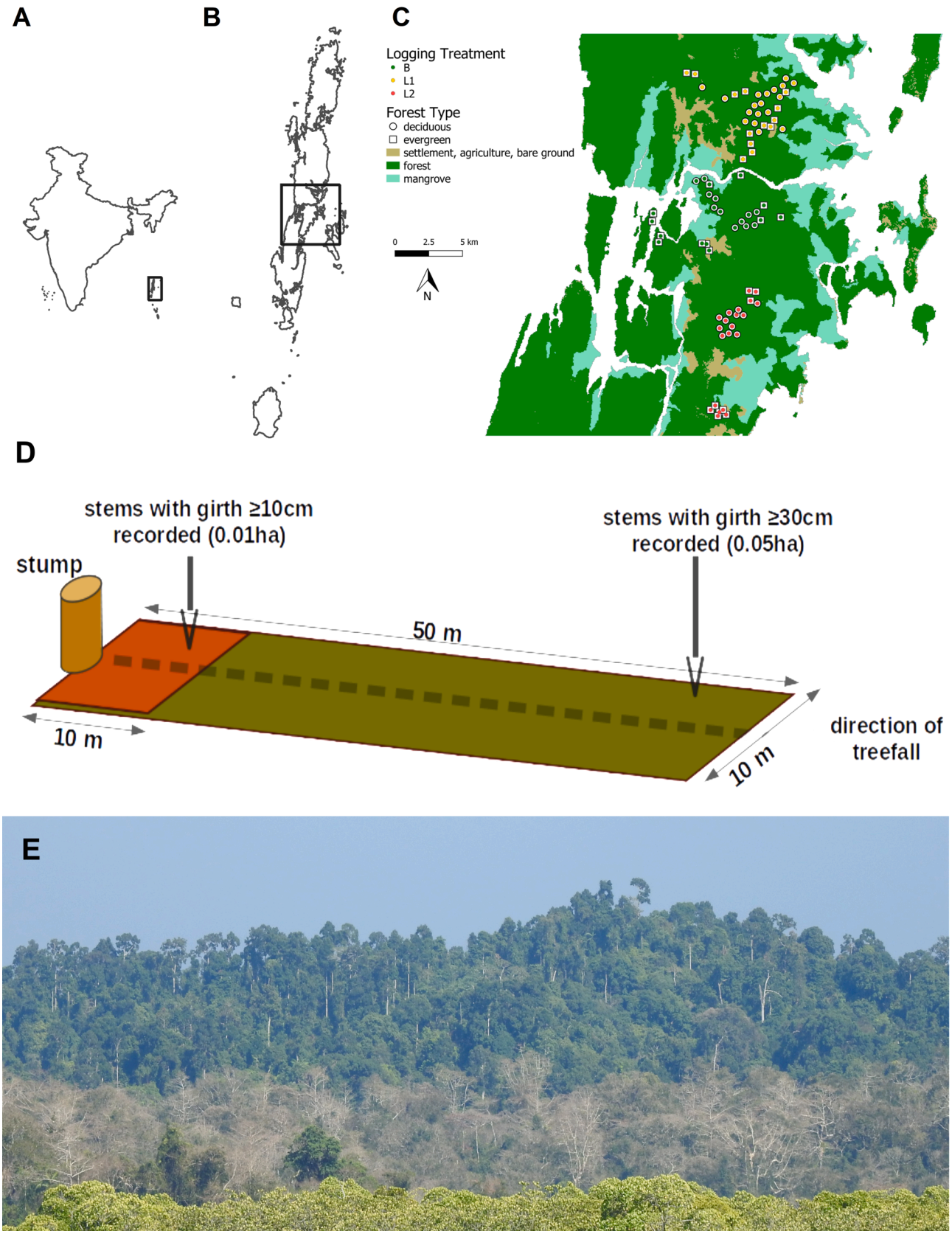

Fig. 1. The study was conducted in the Andaman Islands, India (A, B). We placed plots in the central archipelago, on near-contiguous islands in Middle Andaman and Baratang forest division (C: map prepared using National Remote Sensing Centre's (NRSC) Bhuvan Land-use land-cover data, 2015). Each plot (D) consisted of two nested plots that began at a logging stump and was aligned in the direction of treefall. Within each sub-plot, stems above plot-specific girth cut-offs were identified and measured. The field season overlapped with the dry season, when canopy trees in deciduous forests lost most of their leaves (E – central band) while canopy trees in evergreen forests retained all leaves (E – top band; bottom band: mangrove forest near the sea).

Table 1
Plot characteristics: Number of plots, median (min–max) values of environmental variables (temperature, precipitation, elevation and slope) and distance to the nearest forest edge for each logging treatment in each forest type. Two plots* each in L1- and L2-evergreen were misclassified in the field and therefore discarded (see Methods).

Logging treatment	Forest type	Number of plots	Mean annual temperature (C)	Mean annual precipitation (mm/year)	Elevation (m, above sea level)	Slope ()	Distance to the nearest forest edge (m)
B	Deciduous	12	26.6 (26.5–26.8)	2944 (2905–2999)	45 (26–94)	7.8 (1.7–11.3)	1886 (905–2326)
B	Evergreen	12	26.7 (26.5–26.9)	2906 (2838–2999)	32 (0–114)	8.1 (1.8–21.3)	1434 (0–3453)
L1	Deciduous	18	26.6 (26.5–26.8)	2991 (2953–3016)	66.5 (28–83)	5.3 (1.7–10.5)	1118 (388–2333)
L1	Evergreen	13*	26.7 (26.6–26.7)	2975 (2920–3014)	43 (31–116)	6.2 (2.6–13.1)	864 (19–2121)
L2	Deciduous	12	26.6 (26.4–26.7)	2917 (2897–2939)	68 (33–97)	4.5 (0.6–12.5)	1657 (379–2255)
L2	Evergreen	9*	26.6 (26.5–26.7)	2894 (2857–2914)	63 (36–123)	6.8 (4.2–12.4)	481 (0–1246)

Table 2
Model outputs for canopy cover, stem density, tree diversity and above-ground carbon modelled against logging treatment, separately for each forest type. Statistically significant predictors ($p \leq 0.05$) are in bold.

		Deciduous patches			Evergreen patches		
Response variable	Predictor	Beta-coefficient (SE)	p-value	% change from B	Beta-coefficient (SE)	p-value	% change from B
Stem density (pole trees) Poisson-link	Intercept (B)	2.74 (0.07)			1.90 (0.11)		
Deciduous: F = 5.92, df = 39	L1	−0.08 (0.1)	0.42	−7.5	0.19 (0.15)	0.21	+21.4
Evergreen: F = 1.68, df = 27	L2	**−0.26 (0.11)**	**0.02**	**–23.1**	0.15 (0.18)	0.41	+15.7
Stem density (adult trees)	Intercept (B)	3.15 (0.06)			3.31 (0.06)		
Poisson-link	L1	**0.214 (0.07)**	**0.00**	**+23.9**	0.03 (0.08)	0.70	+3.1
Deciduous: F = 10.29, df = 39	L2	0.042 (0.08)	0.62	+4.3	**−0.25 (0.1)**	**0.01**	**−21.8**
Evergreen: F = 8.90, df = 27							
Canopy cover (understory)	Intercept (B)	0.84 (−0.17)			1.11 (−0.19)		
Beta-regression (Logit link)	L1	**− 0.76 (−0.21)**	**0.00**	**−17.8**	**−0.85 (−0.25)**	**0.00**	**−18.8**
Deciduous: df = 38	L2	**−0.86 (−0.23)**	**0.00**	**−20.5**	**−0.99 (−0.29)**	**0.00**	**–22.2**
Evergreen: df = 26							
Canopy cover (overstory)	Intercept (B)	0.12 (−0.21)			0.96 (−0.3)		
Beta-regression (Logit link)	L1	−0 (−0.27)	0.99	−0.1	−0.39 (−0.42)	0.36	−8.3
Deciduous: df = 38	L2	−0.70 (−0.3)	**0.01**	**−17.1**	−0.82 (−0.48)	0.09	−18.8
Evergreen: df = 26							
Above-ground carbon (log_{10})	Intercept (B)	2.02 (0.06)			2.20 (0.09)		
Gaussian link	L1	0.051 (0.08)	0.53	+12.5	−0.03 (0.13)	0.80	−7.3
Deciduous: F = 0.88, df = 39	L2	**−0.29 (0.09)**	**0.00**	**−49.5**	−0.06 (0.15)	0.69	−12.7
Evergreen: F = 0.02, df = 27							
Tree diversity (pole trees)	Intercept (B)	1.47 (0.14)			1.39 (0.14)		
Poisson-link	L1	**0.50 (0.16)**	**0.00**	**+65.4**	0.29 (0.19)	0.13	+34.0
Deciduous: F = 10.05, df = 39	L2	0.30 (0.18)	0.10	+34.6	0.16 (0.23)	0.47	+17.8
Evergreen: F = 2.30, df = 27							
Tree diversity (adult trees)	Intercept (B)	2.54 (0.08)			2.52 (0.08)		
Poisson-link	L1	−0.111 (0.11)	0.30	−10.5	0.05 (0.12)	0.70	+4.7
Deciduous: F = 5.50, df = 39	L2	**−0.29 (0.12)**	**0.02**	**−25.0**	−0.28 (0.15)	0.06	−24.0
Evergreen: F = 5.22, df = 27							
Deciduous fraction (pole trees)	Intercept (B)	−1.05 (0.34)			−2.52 (0.39)		
Beta-regression (Logit link)	L1	−0.35 (0.42)	0.41	−6.1	0.34 (0.43)	0.42	+2.7
Deciduous: df = 38	L2	0.75 (0.47)	0.11	+16.7	0.17 (0.49)	0.73	+1.3
Evergreen: df = 26							
Deciduous fraction (adult trees)	Intercept (B)	−0.93 (0.22)			−1.59 (0.22)		
Beta-regression (Logit link)	L1	**0.77 (0.27)**	**0.00**	**+17.7**	0.51 (0.30)	0.09	+8.3
Deciduous: df = 38	L2	0.54 (0.30)	0.07	+12.1	−0.01 (0.36)	0.97	−0.2
Evergreen: df = 26							

We used a beta regression with logistic link to model understory canopy, overstory canopy and deciduous fraction, identity link with log-transformed response to model above-ground carbon, and Poisson link to model stem density and tree diversity (effective species richness rounded to the nearest whole number). In each case, we modelled evergreen and deciduous plots separately, and pole-sized and adult trees separately for stem density, deciduous fraction and tree diversity. In each model, we compared once-logged and twice-logged responses against baseline for statistically discernible differences. We used a permutational ANOVA procedure on points in the 2-axes NDMS plane to obtain statistical significance across logging treatments or forest type. All analysis was done using R Statistical Software (R Core Team, 2013), specifically using the *vegan* package to calculate diversity and composition change, *betareg* package for beta regressions and the *tidyverse* package for data manipulation and visualization (Cribari-Neto and Zeileis, 2010; Oksanen et al., 2007; Wickham, 2017).

3. Results

We recorded a total of 3851 woody stems that included 182 morphologically distinct species (henceforth 'species'). This included 118 species in deciduous patches and 151 species in evergreen patches,

with 81 of these species recorded in both forest types (see Table S1 for a list of dominant species and their relative abundances). We identified 82.9% of trees to the species level and 16.7% to the genus level, of which one-third of the stems (5.6%) belonged to one of three *Dipterocarpus* species - *D. alatus*, *D. grandiflorus* and *D. gracilis*. Lianas and palms (4.32% and 4.65% of recorded stems respectively) were excluded from this analysis.

3.1. Forest structure

For both evergreen and deciduous forest patches, pole-tree (girth < 30 cm) density of once-logged forests was comparable to baseline forests (deciduous: $p = 0.42$; evergreen: $p = 0.21$). While twice-logged evergreen patches had comparable pole-tree density to baseline ($p = 0.41$), pole-tree density was 23% lower in twice-logged deciduous patches ($p = 0.02$); (Fig. 2-a). Adult-tree density (girth ≥ 30 cm) also varied by forest type. In deciduous patches, adult-tree density in once-logged forests was higher than baseline ($p < 0.01$) but twice-logged forests had values comparable to baseline ($p = 0.62$). In evergreen patches, adult-tree density of once-logged forests were comparable to baseline ($p = 0.70$) but 22% lower in twice-logged forests ($p = 0.01$) (Fig. 2-b).

Compared to baseline forests, understory canopy was 18–22% lower in both once-logged and twice-logged forests irrespective of forest type ($p < 0.01$) (Fig. 2-c). Overstory canopy was not lower in once-logged forests for either forest type (deciduous: $p = 0.99$; evergreen: $p = 0.36$). However, overstory canopy declined by 17% in twice-logged deciduous forests ($p = 0.01$) and declined marginally by 19% in twice-logged evergreen forests ($p = 0.09$) compared to baseline (Fig. 2-d). Above-ground carbon stocks in evergreen patches were comparable among baseline, once-logged and twice-logged forests ($p = 0.69$; $p = 0.80$). In deciduous patches, twice-logged forests had 50% lower above-ground carbon stocks than baselines ($p < 0.01$), while carbon stocks of once-logged and baseline forests did not differ consistently ($p = 0.53$) (Fig. 2-e).

3.2. Tree diversity, deciduous fraction and composition

In deciduous patches, pole-tree diversity was 65% greater ($p < 0.01$) in once-logged forests and 35% greater ($p = 0.10$, marginal) in twice-logged forests. In evergreen patches, pole-tree diversity did not change in logged forests ($p = 0.13$ and $p = 0.47$) despite a trend in mean response that was qualitatively similar to pole-tree diversity in deciduous patches (Fig. 3-a). Adult-tree diversity of once-logged forests was comparable to baseline forests (deciduous: $p = 0.30$; evergreen: $p = 0.70$), but declined in twice-logged forests by 25% ($p = 0.02$) in deciduous and by 24% ($p = 0.06$) in evergreen patches (Fig. 3-b).

Among pole-sized trees, the fraction of deciduous stems in logged (once-logged and twice-logged) forests was comparable to baseline forests (deciduous: $p = 0.41,0.11$; evergreen: $p = 0.42,0.73$) (Fig. 3-c). However, among adult trees, the fraction of stems belonging to

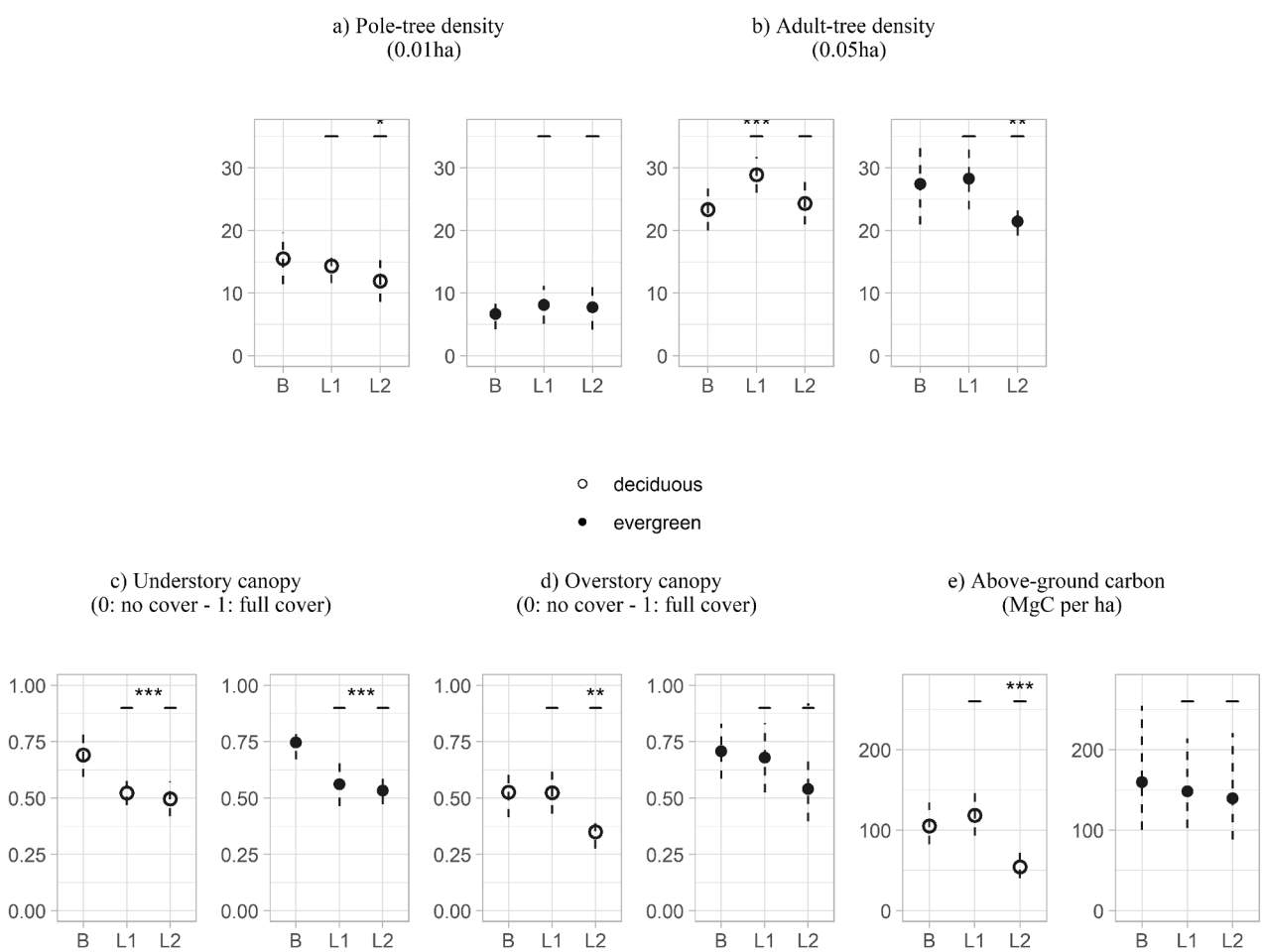

Fig. 2. Forest structure: (a) pole-tree density (trees/0.01 ha), (b) adult-tree density (trees/0.05 ha), (c) understory canopy (0–100%), (d) overstory canopy (0–100%) and (e) above-ground carbon (Mg/ha). In each sub-plot, once-logged (L1) and twice-logged (L2) forests are compared against baseline (B) forests. Hollow (deciduous) or filled (evergreen) circles indicate mean response; vertical lines indicate 95% confidence intervals and stars ($p \leq 0.5$) or a dot ($0.05 < p \leq 0.1$) above L1 and/or L2 indicate the statistically significance of their corresponding beta-coefficients being different from the intercept B (Table 2).

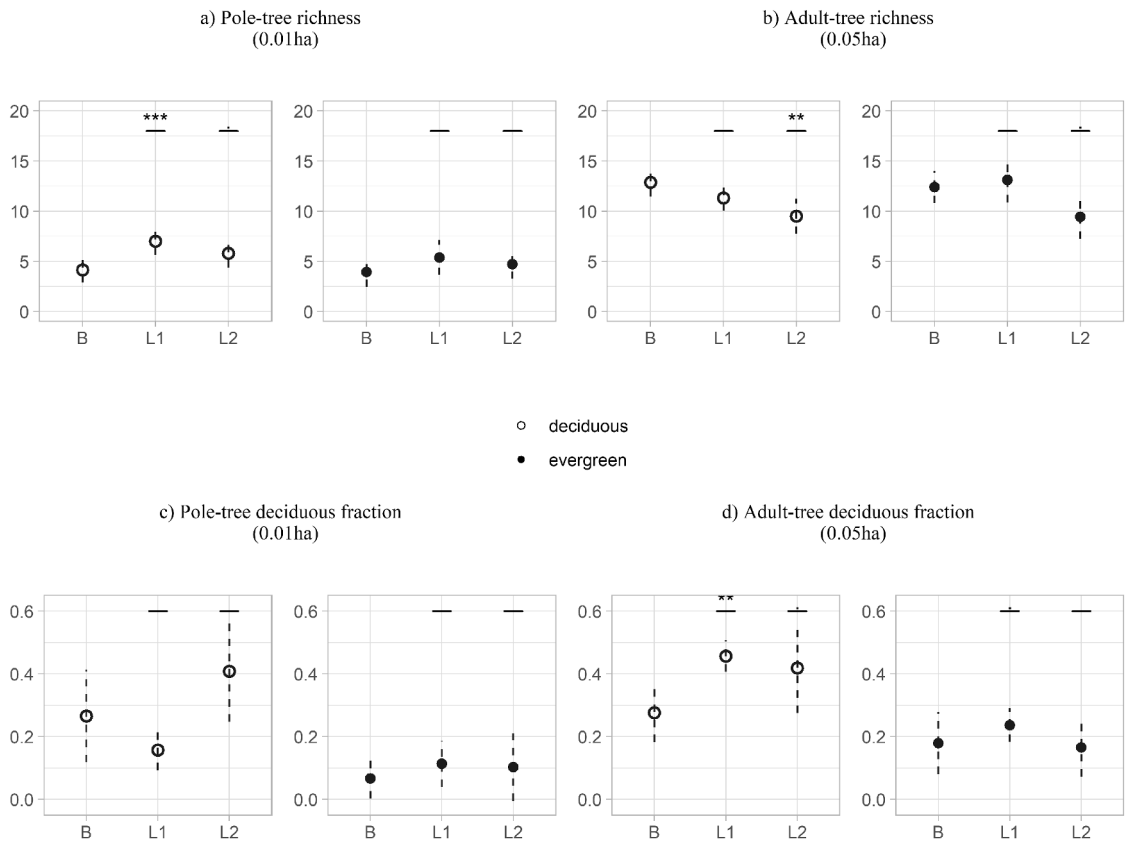

Fig. 3. Diversity: (a) Pole-tree species richness in 0.01 ha, (b) Adult-tree species richness in 0.05 ha, (c) Pole-tree deciduous fraction (proportion, 0–1) in 0.01 ha and (d) Adult-tree deciduous fraction (proportion, 0–1) in 0.05 ha. Symbols, text and graphics are the same as Fig. 2.

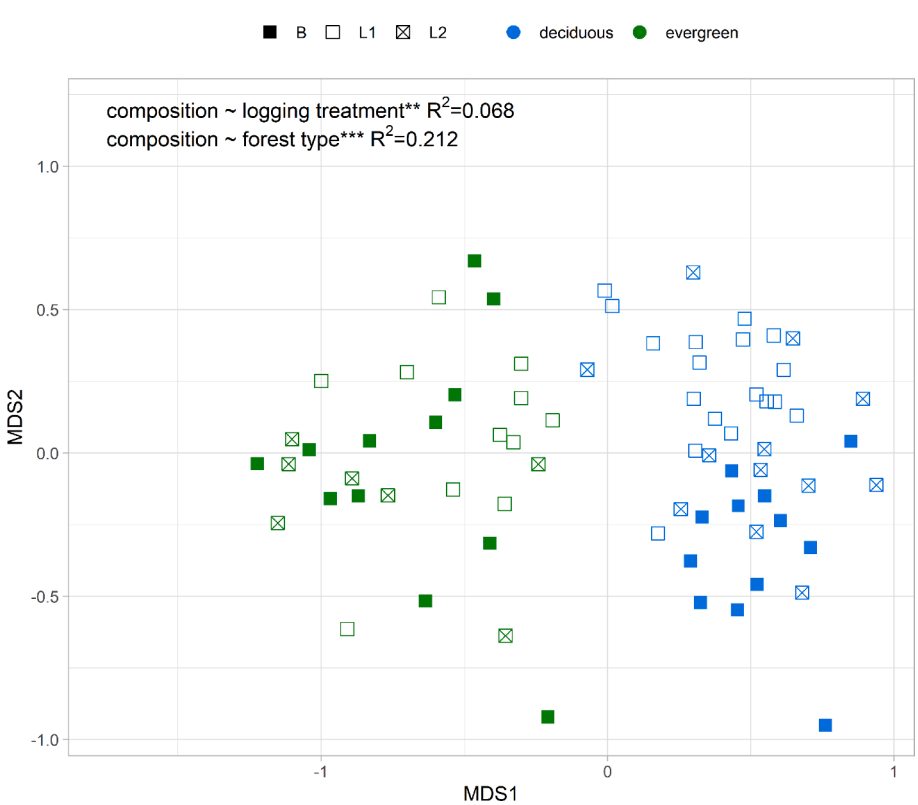

Fig. 4. Impact of repeat logging on adult tree species composition: this Non-metric Multidimensional scaling (NMDS) figure shows plots as points in transformed 2-D space, where plots close to each other are more similar in species composition than plots further apart. Plots coloured blue and green were located in deciduous and evergreen patches respectively. Solid squares are baseline forests (B), hollow squares are once-logged forests (L1) and crossed-square symbols are twice-logged forests (L2); a Permutational Analysis of Variance (PERMANOVA) provides pseudo-F statistic and p-values, as well as a coefficient of determination R^2 (Table A2). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

deciduous species increased by 18% in once-logged deciduous forests ($p < 0.01$) and marginally by 12% ($p = 0.07$) in twice-logged deciduous forests. A marginal increase of 8.3% ($p = 0.09$) in deciduous stems among adult trees was observed in once-logged evergreen but not twice-logged evergreen forests ($p = 0.97$) (Fig. 3-d).

Species composition of adult trees in baseline, once-logged and twice-logged forests although significantly different, explained only 7% of the variance (stress < 0.2, pseudo-F = 2.54, $p < 0.01$, $R^2 = 0.068$), and communities largely overlapped in species composition across logging treatments in both forest types (Fig. 4, Table S2). However, forest type explained thrice as much variance as logging treatment, and differences in species composition between the two forest types was stark (pseudo-F = 18.79, $p < 0.01$, $R^2 = 0.212$, Fig. 4, Table S2).

4. Discussion

Our results reveal that, under the selective logging regimes followed in the Andaman Islands, once-logged forests were largely comparable to baseline forests in both evergreen and deciduous forest types. However, a second logging event resulted in reduced canopy cover, tree density and diversity and aboveground carbon, particularly in deciduous patches. Moreover, we consistently detected a small but significant increase in the representation of deciduous species in the adult tree communities of all logged forests, except twice-logged evergreen forests.

Immediately following selective logging, the forest floor is characterized by high light availability from structural damage and low soil moisture, resulting in compensatory sapling recruitment of ruderal and pioneer species (Chazdon, 2003; Hector et al., 2011; Leverkus et al., 2015). The immediate impact of a falling tree along tree fall lines is on understory and mid-story trees, but not canopy trees, due to naturally infrequent large trees and reduced-impact logging practices (Chazdon, 2003; Lutz et al., 2018), such as those in the Andaman Islands (Singh, 2003). At the same time, in the first decade post-logging, a surfeit of saplings grow in gaps, some which of recruit into pole-sized individuals at densities matching or even exceeding pre-logging levels (Hector et al., 2011). Our findings are largely consistent with these expectations – compared to baselines, once-logged forests had lower understory canopy cover, comparable or higher pole-tree density and diversity, and comparable above-ground carbon, regardless of forest type. We sampled all trees no more than 11 years after the most recent logging event, such that adult trees were likely to be post-logging remnants while pole-trees, sampled at site of maximum structural damage closest to the stump, were likely to be post-logging recruits (Gourlet-Fleury et al., 2013; Hall, 2008; Roopsind et al., 2017).

Unless the time between logging events is sufficiently long, a second logging event in an already logged forest exacerbates structural damage and slows regeneration (Ghazoul, 2016). The interval between logging events in our study – 10 –25 years – may not have been sufficient to limit these negative impacts (Khai et al., 2016). Consequently, in twice-logged forests, we observed greater structural damage (lower adult-tree density and diversity compared to baseline), reduced compensatory growth (lower pole-tree density and diversity compared to once-logged forests) and consequent losses in above-ground carbon and overstory canopy cover. However, this pattern was statistically discernible only in deciduous forests. In evergreen forests, although adult tree density (and diversity) reduced marginally, repeat logging did not appear to affect regrowth potential (pole-trees) and overall canopy tree density (above-ground carbon and overstory canopy).

In the Andaman Islands, evergreen and deciduous forest patches co-occur at small scales and thereby share the same rainfall regime, but differ in underlying soil type (Chengappa, 1934; Parkinson, 1923). Differences in soil water-holding capacity, among others, contribute to more water-limited soils in deciduous forests (Parkinson, 1923; Poorter et al., 2019). This may explain the stronger response of deciduous forests to repeat logging, especially with a short inter-logging interval as in this study. On the other hand, evergreen forests, may experience less soil-related water stress, even when repeat logged. Additionally, as shown elsewhere, the faster growth rates of evergreen forest species, rapid closure of canopy gaps and low canopy deciduousness may enable these forests to be resilient following disturbances (Lebrija-Trejos et al., 2010). In the Asian tropics, evergreen mixed dipterocarp forests with fast-growing species have naturally high tree density and diversity, such that even repeat-logged forests may retain a high fraction of pre-logging structure and diversity as remnant trees, enhancing resilience (Freitas and Pinard, 2008; Ghazoul, 2016). Finally, in this study, such differences between forest types may have been exacerbated by higher historic logging intensity in deciduous forests, which have a higher fraction of commercially valued species and occur on more even terrain than the evergreen forests (Chengappa, 1934; Parkinson, 1923).

Grey literature from this region has proposed that logging gaps increase solar irradiation and dry out the soil, placing evergreen species at a disadvantage, thereby shifting the plant community towards more drought-tolerant deciduous species over time (Nair and Nair, 1983, in Sekhsaria and Pandya, 2010, pg. 45). Our data suggest that these claims are at least partially true among adult trees, suggesting that even low-intensity logging regimes may sometimes change light and water conditions enough that the recruitment of evergreen species is further limited. Our data also suggest that the increase of deciduous species may be a transient phenomenon in evergreen forests, where rapidly closing canopy gaps may soon exclude these light-adapted species. However, in deciduous forests, where evergreen species are already outside their optimal environments, the opening of canopy gaps post-logging may further exclude evergreen species and result in a more persistent increase in deciduous species (Koltunov et al., 2009; Poorter et al., 2019). Our study indicates that despite little overall change in composition over short time scales (Fig. 4), there is a small but significant shift in composition towards increasing deciduousness (Fig. 3-c, d). By gathering species-specific information on successional status and growth rates, and tracking variously logged forests over longer time scales, the causes and persistence of logging-driven increases in deciduousness in these forests may be better understood.

An interval of 10–25 years between logging events is not sufficient for forests in the Andaman Islands, especially deciduous forests, to recover from the first logging cycle. Future forest management in the Andaman Islands can mitigate these negative effects by reordering the sequence of extraction to maximize time for recovery, reducing extraction quotas in deciduous forests and minimizing logging-associated damage.

5. Conclusion

Selective logging is considered to be among the least destructive types of tropical forest disturbance (Gibson et al., 2011). It is also known that the detrimental effect of selective logging could be further reduced by maintaining low logging intensities (<3 trees/ha) and incorporating improved logging practices like reduced-impact logging (Clark and Covey, 2012; Gibson et al., 2011; Martin et al., 2015; this study). However, repeat-logging, at least under relatively short logging intervals of 10–25 years, has marked negative impacts on tree diversity, forest structure, carbon stocks and timber value, with greater impacts in deciduous than evergreen forests (Fisher et al., 2011b; Khai et al., 2016). Our findings thus reveal the critical importance of including underlying differences among forest types while stipulating harvest intensity and subsequent regeneration policy (see also Poorter et al., 2019). Our findings also suggest that given expected future increases in repeat logging world over, maintaining unlogged patches within logging concessions are likely to gain importance for sustaining biodiversity and other ecosystem functions in tropical logging landscapes (Putz et al., 2019; Runting et al., 2019).

Credit authorship contribution statement

Akshay Surendra: Conceptualization, Writing - original draft. **Anand M. Osuri:** Conceptualization, Writing - review & editing. **Jayashree Ratnam:** Conceptualization, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118791.

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