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Factors influencing tree diversity and compositional change across logged forests in the Solomon Islands

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ABSTRACT

Tropical forests in the Solomon Islands have been heavily logged in the last century. However, little is known about forest recovery dynamics across this region. Extrapolating findings from logged forests in tropical mainlands or large continental landbridge islands to isolated archipelagos such as the Solomons is inappropriate because succession and diversification patterns and processes differ between the former and latter. We compared the taxonomic diversity and composition of trees between unlogged forest and sites that were logged 10, 30 and 50 years previously to provide an indication of the potential dynamics of these forests following timber harvesting. The distance to logging roads and to unlogged forest influenced post-logging recovery, emphasising the importance of edge effects in previously logged forests. At least in the first 50 years after logging, tree-community composition did not appear to converge toward that in unlogged forests over time. Although species assemblages in logged forests generally tend to shift from light demanding-pioneers to old-growth species over time, a long-lived pioneer *Camposperma brevipetiolata* dominated the forest even 50 years after logging. We suggest that recovery of the tree community in logged forests has been hindered by the persistence of *C. brevipetiolata*, and suggest that it could be thinned via careful silviculture techniques to enhance growth of mature-phase forest species. Removal of such persistent, long-lived pioneer trees could potentially help to accelerate recovery of heavily logged forests.

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1. Introduction

Industrial logging is a major driver of the decline of old-growth forests in the tropics (Putz et al., 2012; Edwards et al., 2014; Katovai et al., 2015a). Nonetheless, logging is often the economic lifeline for many developing tropical countries, generating substantial revenue through wood exports (Katovai et al., 2012; Shearman et al., 2012; Zimmerman and Kormos, 2012). Some countries have exhausted timber stocks as a result of unsustainable harvesting (see Shearman et al., 2012 for examples). However there has been an increase in logging activities in many parts of the tropics over the recent past (FAO, 2015). For example, the Eastern Melanesian islands in the northwest Pacific have recently become a logging hotspot as a result of timber depletion in neighbouring Southeast Asia (Shearman et al., 2012; Katovai et al.,

2015a). Logging operations in Eastern Melanesia have increased dramatically over the past several years, and have contributed significantly to economies in the region (Katovai et al., 2015a).

In the Solomon Islands, logging exports have generated over half of the country's annual export revenue for the past two decades (Solomon Islands National Forest Resources Assessment (SINFRA), 2011; Shearman et al., 2012; Katovai et al., 2015a). However, unregulated harvesting, exacerbated by poorly conceptualised and implemented state policies, corruption, and illegal harvesting has driven accessible timber stocks to near depletion (Kabutaulaka, 2000; Shearman et al., 2012; Katovai et al., 2015a). A collapse of the timber industry would have serious consequences for the country's economy. Furthermore, increased logging can possibly trigger a widespread loss of biodiversity and ecological functions via the disruption of species interactions (Zimmerman and Kormos, 2012).

The effects of industrial logging on tropical forest biodiversity in the mainland tropics and continental landbridge islands such as those of Southeast Asia are well documented (see review in

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Wilcove et al., 2013). These studies propose that logged forests retain much of their pre-logged biodiversity, even when intensively logged (Edwards and Laurance, 2013). This might not hold true for tropical oceanic islands, because the regional and nearby species pools that influence their local diversity differ from those in mainland regions (Gillespie et al., 2008).

Tropical oceanic islands are currently 'hot-spots' for industrial logging, but their responses to logging are relatively poorly studied to date (Katovai et al., 2012, 2015a, 2015b). The Solomon Islands, for example, currently has large tracts of forests that have been logged over the last several decades, yet little is known about biodiversity within them (Bennett, 1995, 2000; SINFRA, 2011; Katovai et al., 2012) or their temporal and spatial patterns of post-logging recovery. Such forests are highly vulnerable to further degradation by re-entry logging and subsequent land-use activities.

In an effort to inform forest-management policies, we examined tree species communities across an array of logged forests on Kolombangara Island in the Solomon Islands. We assessed the factors influencing recovery of tree diversity and species composition in previously logged forests, with a particularly focus on determining whether a half century was sufficient to allow forests to recover to pre-logging conditions.

2. Materials and methods

2.1. Study area

Forests in the Solomon Islands are rich in biodiversity and contain exceptionally high endemism (Whitmore, 1969; Olson and Dinerstein, 1998; Gillespie et al., 2008; Walter and Hamilton, 2014). For example, over half of all palm, orchid and climbing pandanus (*Freycinetia* spp.) species are endemic to the region, with some endemic to a single island or forest type (Hancock and Henderson, 1988). Such high insular biodiversity is thought to have originated via very rare dispersal events from mainland tropical locations (Gillespie et al., 2008; Keppel et al., 2009). A decline of species diversity and ecological complexity of forests as one moves eastward across Melanesia, further away from New Guinea and Southeast Asia, supports this model (Gillespie et al., 2008; Keppel et al., 2010). For instance, a 30-year census of tree dynamics in naturally disturbed forests on Kolombangara, Solomon Islands revealed a simple pattern of species replacement involving the re-establishment of particular species at various stages of succession (Burslem and Whitmore, 1999). In contrast, forests on the tropical mainland and large continental landbridge islands undergo more complex successional patterns involving a larger array of successional species, resulting in naturally disturbed forests becoming floristically divergent with time (Keppel et al., 2010).

This study was conducted on Kolombangara Island (157°E and 5°S) in the New Georgia group of the Solomon Islands. The geomorphology and floristics of large islands in New Georgia are very similar to one another and also broadly comparable to other large islands across the region (Whitmore, 1967; Hancock and Henderson, 1988). Kolombangara is an extinct Pleistocene volcano that is ~32 km in diameter and circular in shape (Fig. 1). Topography increases from the relatively flat coastal plains to the base of the central volcanic cone at ~700 m elevation and progressively steepens to the crater rim at ~1700 m elevation. The central crater, at ~600 m elevation, is ~6.5 km in diameter and topographically uneven. Rainfall is relatively uniform across the island, exceeding 3000 mm/yr, with bi-annual wet seasons from November to March and July to August (Aldrick, 1993; Katovai et al., 2012).

Kolombangara was once covered with dense wet-tropical forests, but with fewer families, genera and species compared to

the neighbouring Islands of New Guinea (Whitmore, 1969; Hancock and Henderson, 1988). However, much of Kolombangara's lowland forests have been cleared or degraded since the early 1900s (Katovai et al., 2012). For example, since 1964, heavy logging has degraded >90% of accessible lowland forests from the coastline to 400 m elevation (Bennett, 2000; Katovai et al., 2012). Logging has been more limited from 400 to 700 m elevation because of unstable soils and steep slopes.

Initial logging on Kolombangara was exclusively implemented by a single U.K. company, Lever Brothers (Katovai et al., 2012, 2015a). For this reason, harvesting strategies and extraction patterns were highly systematic and consistent among sites (Bennett, 2000). Operations began on the southeast of the island and progressed anticlockwise (Bennett, 2000). Some patches of traditionally owned land in the southwest were logged later, beginning in the 1980s, by various other foreign companies. Nonetheless, these later logging practises were relatively similar to those used by the Lever Brothers.

In the past three decades, much of Kolombangara's logged forests in the SE, NE and NW quadrants of the island have been converted into commercial wood plantations (Bennett, 2000). However, patches of both logged and unlogged forests remain scattered across these quadrants (Fig. 1). The absence of commercial plantations in the SW quadrant has allowed natural regeneration in large areas. Unlogged patches of lowland forests on the island are typically restricted to traditionally owned and church-leased lands (Whitmore, 1989; Katovai et al., 2012). However, most of these forests have already been included in logging-concession areas and are open to logging over the next few years.

2.2. Study design

From January to November 2013, we sampled 144 0.1-ha (50 m × 20 m) vegetation plots in six logged and six unlogged coupes spanning an elevation gradient from 20 to 422 m. During this process we used oral traditional information and published information to avoid establishing plots in old human settlements (e.g. Burslem et al., 2000; Bayliss-Smith et al., 2003), to exclude effects of past land use in our study.

We sampled a post-logging chronosequence, with two coupes each sampled from areas that had been logged 10, 30, and 50 years previously. Unlogged (control) coupes were largely intertwined with logged coupes to ensure they were matched topographically and elevationally (Fig. 1). In each coupe, 12 plots were established using stratified random sampling to determine plot locations, with plots stratified on the distance to the nearest logging road (e.g. Laurance et al., 2001). Distances to the nearest logging road and to unlogged forest were determined using GPS (Garmin 76cx GPS; Garmin International, Inc., Kansas City, USA).

Basal area of cut stumps was used as a proxy for harvest intensity in logged forests. We first measured the diameter and height of all cut stumps in a 50 m × 70 m quadrat centred on the plot. For each partially decomposed stump, we estimated stump diameter by visually reconstructing the cut-level circumference using available information on the buttressing and bole profile from stump base to cut level. A stem profile model developed for tropical forests was then used to generate DBH estimates for stumps that were either cut below or above the conventional DBH [~1.3 m] (see protocol details in Ito et al., 2010). Finally we estimated the basal area of harvested trees using these values for each quadrat.

In each plot, we measured elevation and soil nitrogen (N) as these variables may strongly affect floristic communities (e.g. Hardwick et al., 2004; Sundqvist et al., 2013; Asase et al., 2014). Elevation was determined using GPS. To determine N in each plot, we extracted soil samples to 30 cm depth from four randomly selected points using a cylindrical soil extractor. Samples from

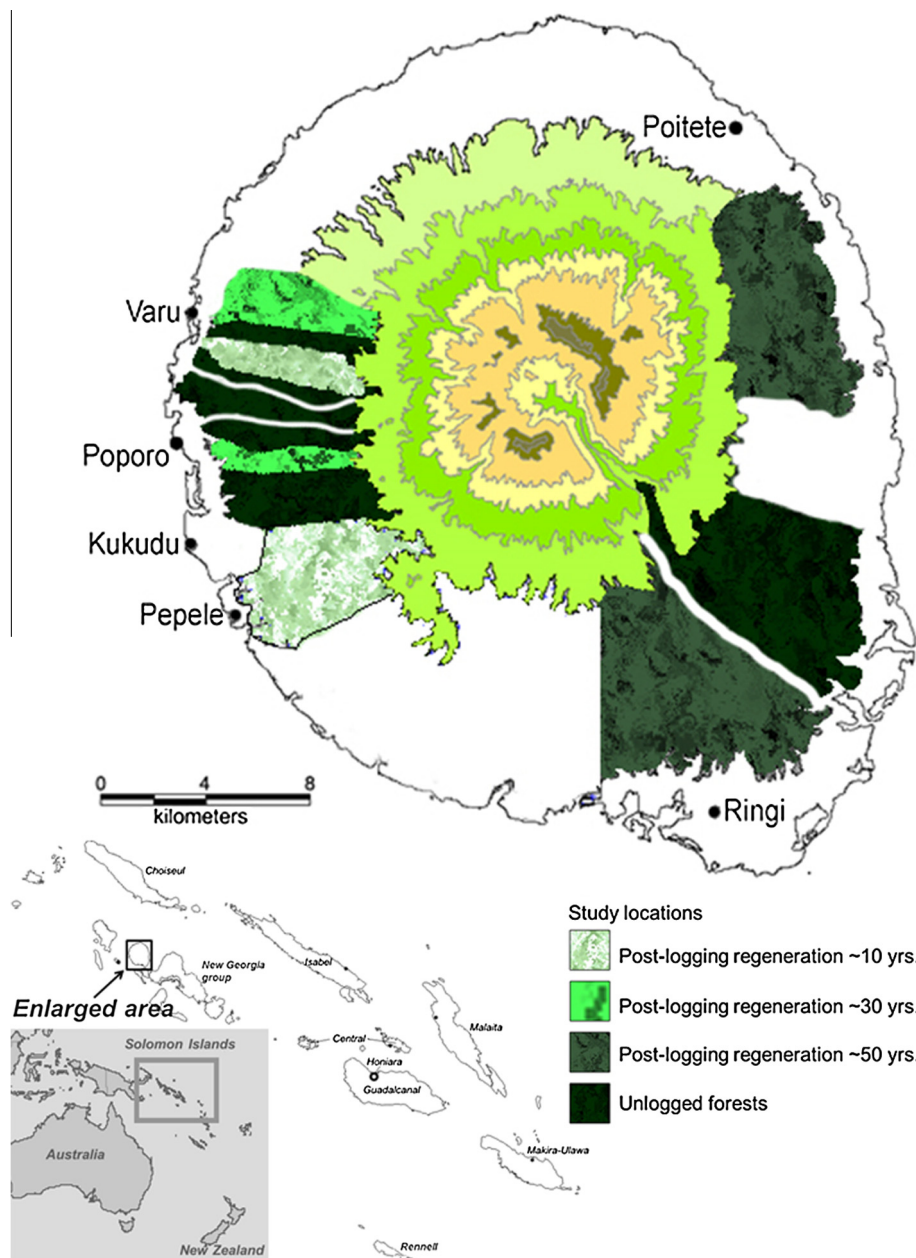


Fig. 1. Kolombangara is part of the New Georgia group of islands in the Solomon archipelago located in the northwest Pacific. Logged forest sites were demarcated according to regeneration times of 10, 30 and 50 years. Two forest coupes were selected for each timeframe. Unlogged forests were demarcated.

individual plots were air-dried, thoroughly mixed and sieved through a 2 mm mesh (e.g. Asase et al., 2014). N weight percentage (%N) was determined using a Costech Elemental Analyzer (Costech Analytical Technologies, Inc., CA, USA) and Continuous-Flow Isotope Ratio Mass Spectrometry (Bay et al., 2015).

Tree diversity surveys were conducted in 48 plots across the study area. Four plots were randomly selected per coupe, thereby covering ~33% of the sampled sites. A recent study on the Kolombangara showed the robustness of such a sample size in capturing attributes of floristic diversity across the island (Katovai et al., 2012).

2.3. Data collection

We identified and uniquely tagged all trees ≥ 10 cm DBH. Proxies used for tree diversity were species richness and Shannon–Weiner diversity index (H'), with the latter taking into

account both species richness and evenness – a measure of the relative abundance of all tagged tree species per plot (Spellerberg and Fedor, 2003). Species richness was determined by enumerating the number of morphospecies identifiable from distinctive traits in the field (e.g., Valencia et al., 2004). Species evenness was determined by measuring the relative abundance of each species per plot.

To determine species identity, we collected voucher specimens including leaves, flowers and fruits (where possible) from each tagged tree that could not be identified in the field. Voucher specimens were returned to the National Herbarium in Honiara where M. Sirikolo, an expert on the Solomon Islands flora, and E. Katovai did further taxonomical sorting. Online herbarium databases (<http://www.pngplants.org>; <http://www.rbge.org.uk/home-original>) and published floras (e.g. Whitmore, 1967, 1969; Peekel, 1984; Hancock and Henderson, 1988) were also used to aid the identification of morphospecies.

2.4. Statistical analyses

2.4.1. Spatial autocorrelation

In landscape level studies such as this, there is a potential that spatial autocorrelation will influence outcomes. Spatial eigenvector mapping (SEVM) generated through Principle Coordinates Neighbour Matrices (PCNM) was used to assess, and if necessary, account for spatial autocorrelation (Dray et al., 2006; Costion et al., 2015). GPS coordinates for all plots were formatted in decimal latitude and longitude before importation into SAM – Spatial Analyses in Macroecology (Rangel et al., 2010). A truncation distance of 13.18 km (calculated in SAM) was then used to create spatial filters. When each tree diversity and composition proxy was selected to guide filters selection, a single eigenvector filter was generated. However, in both cases the filter was neither statistically significant ($P > 0.05$) nor had sufficient explanatory power ($R^2 < 0.2$) to warrant inclusion as a candidate predictor for tree diversity models (Huang et al., 2011).

2.4.2. Recovery of tree diversity in logged forests

We used linear mixed-effect models (LMMs) to investigate the response of tree species richness and H' diversity to a series of potential predictor variables. These predictors were ordination axes generated by simplifying a much larger set of potential predictors using nonmetric multidimensional scaling (NMS) on PC-ORD (McCune and Mefford, 2011). Because plots within each coupe were not independent of each other, we included coupe as a random effect in all models. We checked for collinearity between selected predictor variables by (a) plotting pairs of variables for visual examination, (b) calculating correlation coefficients for each pair of predictor variables, and (c) examining variance-inflation factors using the package *usdm* in the program R (Naimi, 2013; R Core Team, 2014). When two variables were strongly correlated, we selected the most compelling predictor to model species richness and diversity based on biological reasoning.

Prior to modelling, H' diversity was log-transformed to minimise heteroscedasticity. We then built global models for species richness and for H' diversity, which were each modelled as functions of (a) time since logging, (b) site elevation, (c) harvest intensity (basal area harvested), (d) soil N, (e) distance to nearest logging road, and (f) distance to nearest unlogged forest (a potential source for old-growth propagules). We predicted our variables to influence species richness and diversity in the following ways: time since logging, soil N and distance to road would positively impact species richness and diversity, with increasing elevation, harvest intensity, and distance to unlogged forest having opposite effects. We also tested for interactions between any selected predictors and our random variable (logging coupe) (Asase et al., 2014).

Interactions between time since logging and all predictor variables were also included in the models. We then used the *dredge* function in the R package MuMIn to create a candidate model set with all possible simpler subsets of each global model (Barton, 2013). Models for inference were selected based Akaike's Information Criterion (AICc), corrected for sample size, which trades off model fit and model complexity (Burnham and Anderson, 2004; Mazerolle, 2015) and identifies the "best simplest model(s)". This included all models with delta AICc < 7. The parameters from these models were then averaged based on model weights (Burnham and Anderson, 2004). Inferences from averaged parameter estimates were drawn based on effect sizes and whether their 95% confidence interval (CI) overlapped zero. Finally, we used the *predictSE* function in the R package MuMIn (Barton, 2013) to generate predicted values from the averaged models for visualising results. All analyses were generated using R (R Core Team, 2014).

2.4.3. Tree richness and diversity across recovery time

We performed a one-way ANOVA to examine how means of species richness and H' differed among time-classes for logged and unlogged forests, followed by Tukey's post hoc tests. Error-bar graphs were generated to visualise any differences in tree richness and H' diversity across time. This analysis was done in Statistix 8 (Tallahassee FL 32317, USA).

2.4.4. Tree species composition across recovery time

To determine how tree community composition varied across forest age-classes, we performed an Analysis of Similarity (ANOSIM) based on Bray–Curtis similarity matrices of occurrence and abundance using *primer-E* (Clarke and Gorley, 2006). Prior to these analyses, rare species (<10 stems) were removed, as these can potentially distort the ordination (Legendre and Gallagher, 2001; Laurance et al., 2008). $\log(x + 1)$ transformations were used to give somewhat greater weight to abundant species (Clarke et al., 2006). Non-metric dimensional scaling (MDS) was then used to identify major gradients in tree species composition and to visualise patterns across forest classes. We also calculated importance values (Relative frequency + Relative Density + Relative Dominance) for each species in each forest class to identify important species in both logged and unlogged forests (Skeen, 1973; Zhao-hua et al., 2001).

3. Results

Overall, 2450 individual trees were sampled in the 48 0.1 ha plots. These were sorted into 50 families and 176 morphospecies of which 118 were identified to species level, 55 to genus level and three unidentified (Supporting Information Table A.1). Fifty-seven species were found only in unlogged forest as compared to 54 in logged forests, while 65 occurred in both forest categories (Supporting Information Fig. A.1).

3.1. Recovery dynamics of tree richness

There was no major colinearity among the selected predictor variables (variance inflation factors all <2.06, with correlation coefficients ranging from –0.42 to 0.43). For species richness, the averaged LMM fit the data well (Pearson's R between observed and model-fitted values = 0.92) and comprised five models. The averaged model included time, soil N, distance to road, and distance to unlogged forest (Table 1).

Distance to road had a strong positive effect on species richness at 10 years post-logging (slope = 9.8, 95% CI = 4.69, 15.0) (Fig. 2a) and negative effects at 30 years post-logging (slope = –14.71; 95% CI = –22.66, –6.75) (Fig. 2b). The effect for 50 years post-logging was weakly negative (slope = –11.2; 95% CI = –19.41, –2.95) (Fig. 2c). Distance to unlogged forest had no effect on species richness at 10 years post logging (slope = –11.27; 95% CI = –1.64, 25.0) (Fig. 2d). At 30 and 50 years post-logging, distance to unlogged forest had strong negative effects on species richness (slope = –16.57; 95% CI = –22.44, –10.71 and slope = –17.12; 95% CI = –23.13, –11.10, respectively) (Fig. 2e and f). Although soil N was part of the averaged model, it did not have any important effect on species richness across recovery time (Table 1).

3.2. Recovery dynamics of species diversity

The averaged model for H' diversity fitted the data well (Pearson's R between observed and model-fitted values = 0.95). The average model consisted of nine models. The averaged model included time, harvest intensity, distance to road, and distance to

Table 1

The species richness candidate model set (only with AICc < 7) used in the LMM analyses, with associated effect degrees of freedom, AICc and Δ AICc values. Columns 2–12 represent the predictors used in the model (with columns 8–12 indicating interactions between each predictor and time. Slope coefficient for each predictor was shown if the predictors were included in the corresponding model. A '*' sign indicates that predictor–time interaction was included in the corresponding model. A '-' sign indicate that predictors or their interactions with time were not included in the corresponding model. An average model was generated from models with Δ AICc < 7 which only constituted distance to road and distance to unlogged forest and there interactions with time.

Model	BAH	Distuf	Distrd	Elev	Snitro	Time	BAH: Time	Distuf: Time	Distrd: Time	Elev: Time	Snitro: Time	df	AICc	Δ AICc
423	–	14.43	9.69	–	–	–22.54	–	*	*	–	–	11	126.1	0.00
295	–	–2.68	10.60	–	–	12.14	–	–	*	–	–	9	129.7	3.59
439	–	14.25	9.11	–	–0.73	–18.96	–	*	*	–	–	12	131.9	5.77
311	–	–2.64	10.19	–	–0.49	14.21	–	–	*	–	–	10	132.9	6.80
293	–	–	10.34	–	–	6.82	–	–	*	–	–	8	133.0	6.93

BAH = Basal area harvested, Distuf = Distance to nearest unlogged forest, Distrd = Distance to road, Elev = Elevation, Snitro = Soil nitrogen.

unlogged forest. However, harvest intensity and soil N had no important effect on H' diversity across recovery time (Table 2).

Distance to road had a weak positive effect on H' diversity at 10 years post-logging (slope = 0.62, CI = 0.11, 1.12) (Fig. 3a). The effect of distance to road was weakly negative for 30 years post-logging (slope = –0.96, CI = –1.25, –0.67) (Fig. 3b). In 50 years post-logging, the effect of distance to road was weakly positive (slope = 0.79, CI = 1.11, 0.47) (Fig. 3c). Distance to unlogged forest had a moderately positive effect on diversity at 10 years post-logging (slope = 2.07, CI = 2.17, 8.99) and moderate negative effects at 30 years (slope = –2.27, CI = –2.81, –1.73) and 50 years (slope = –2.24, CI = –2.74, –1.73) post-logging (Fig. 3d–f).

3.3. Recovery of tree species richness and diversity

Means of tree species richness of the three logged forests and unlogged forest categories were not significantly different

($F_{3,44} = 2.59$, $p = 0.0644$) with richness ranging from 16 to 22 species per plot. In contrast Shannon diversity means significantly differed between these forests ($F_{3,44} = 5.65$, $p = 0.0023$). Tukey's post hoc tests however revealed only two homogenous groups whereby H' diversity mean in 10 yrs. post-logged forests was significantly lower than those of older logged and unlogged forests (Supporting Information Fig. A.2).

3.4. Recovery of tree species composition

ANOSIM and pairwise comparisons revealed that tree species composition significantly differed across all four forest classes (Global $R = 0.47$, $p < 0.001$) (Fig. 4a). Across logged forest classes, tree compositional similarity was lowest between forests 10 and 50 years post-logging bearing a species similarity index of 20.8% ($R = 0.715$, $p < 0.001$), followed by the 10 and 30 year classes (26.8%; $R = 0.56$, $p < 0.001$). Tree compositional similarity was

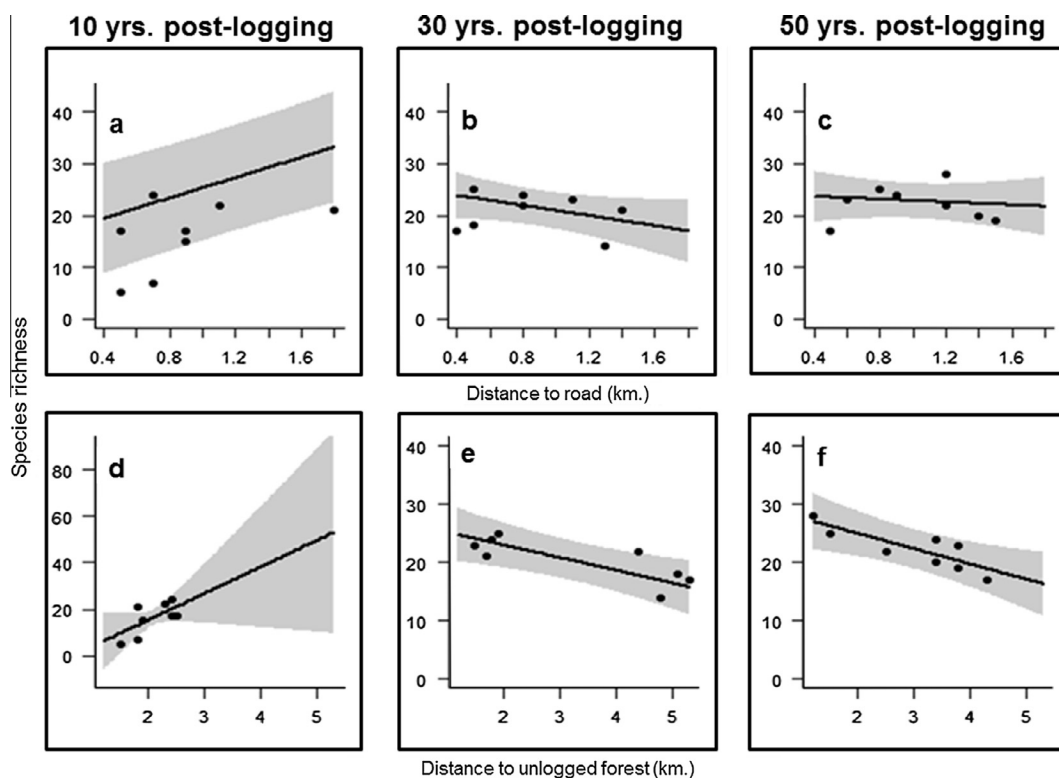


Fig. 2. The relationship between tree species richness and distance to road and distance to unlogged forest across recovery time. Solid lines represent fit (predicted) values from the LMM, and the grey polygons, the 95% CI associated with the modelled predictions. Both distance to road and distance to unlogged forest appear to have a varied influence on tree species richness across recovery time. Both had positive effects on recently logged forests i.e. 10 yrs. (a and d), and negatively influenced forests undergoing regeneration at 30 and 50 yrs. post-logging (b, c, e and f). Distance to propagule however had no pronounced effect on species richness in recently logged forests although the prediction line seems strongly positive due to the relative proximity of recently logged forests to propagule sources (d).

Table 2

The Shannon diversity candidate model set (only with AICc < 7) used in the LMM analyses, with associated effect degrees of freedom, AICc and Δ AICc values. Columns 2–12 represent the predictors used in the model (with columns 8–12 indicating interactions between each predictor and time. Slope coefficient for each predictor was shown if the predictors were included in the corresponding model. A ‘-’ sign indicates that predictor-time interaction was included in the corresponding model. A ‘+’ sign indicate that predictors or their interactions with time were not included in the corresponding model. An average model was generated from models with Δ AICc < 7 which only constituted distance to road and distance to unlogged forest and there interactions with time, basal area harvest and soil nitrogen. Nonetheless, the interactions between basal area harvested and soil nitrogen with time was not included in either of the best models, and therefore its influence on species richness cannot be predicted across post-logging recovery.

Model	BAH	Distuf	Distrd	Elev	Snitro	Time	BAH: Time	Distuf: Time	Distrd: Time	Elev: Time	Snitro: Time	df	AICc	Δ AICc
423	-	2.16	0.78	-	-	-4.58	-	*	*	-	-	11	28.5	0.00
1	-	-	-	-	-	-	-	-	-	-	-	3	28.8	0.36
5	-	-	0.33	-	-	-	-	-	-	-	-	4	30.0	1.53
17	-	-	-	-	-0.21	-	-	-	-	-	-	4	31.2	2.72
21	-	-	0.31	-	-0.20	-	-	-	-	-	-	5	32.8	4.32
2	-0.09	-	-	-	-	-	-	-	-	-	-	4	33.0	4.51
33	-	-	-	-	-	0.58	-	-	-	-	-	5	33.8	5.36
3	-	0.02	-	-	-	-	-	-	-	-	-	4	34.8	6.39
293	-	-	0.89	-	-	-0.20	-	-	*	-	-	8	35.0	6.51

BAH = Basal area harvested, Distuf = Distance to nearest unlogged forest, Distrd = Distance to road, Elev = Elevation, Snitro = Soil nitrogen.

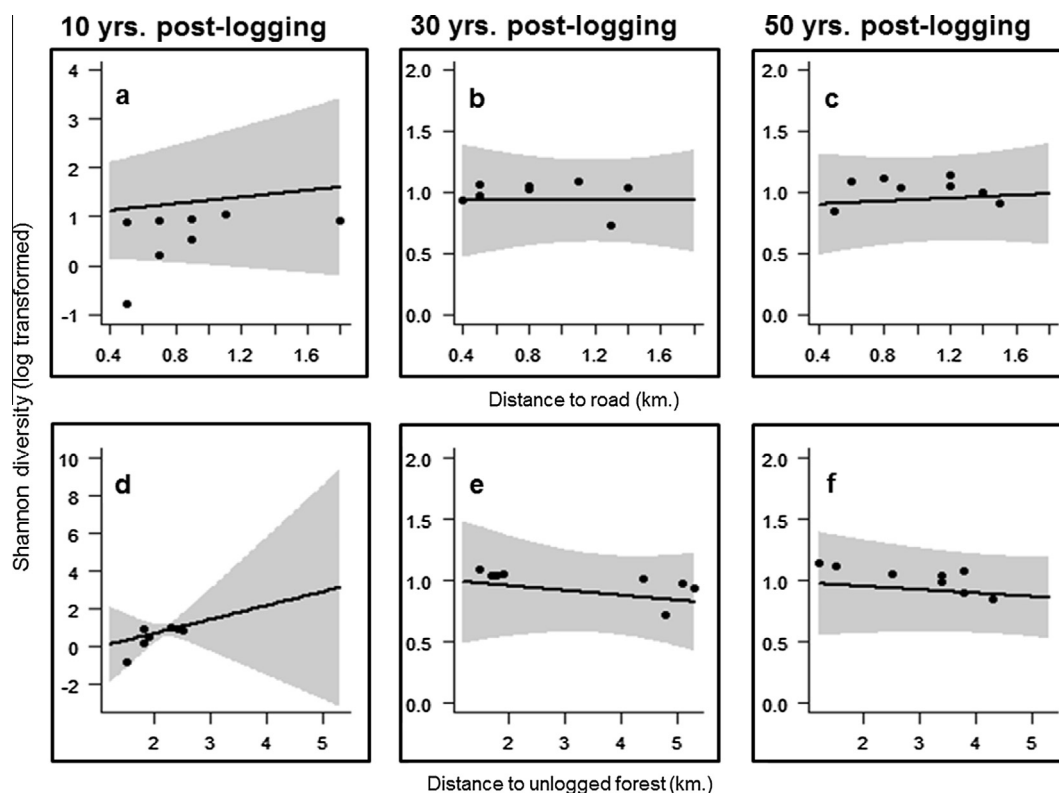


Fig. 3. The relationship between Shannon–Weiner diversity index (H') and distance to road and distance to unlogged forest across recovery time. Solid lines represent fitted (predicted) values from the LMM, and the grey polygons, the 95% confidence intervals associated with the modelled predictions. Both distance to road and distance to unlogged forest appear to have a varied influence on H' diversity across regeneration time. They both predicted a positive effect for recently logged forests i.e. 10 yrs. (a and d). Effects of distance to road on H' diversity was relatively weak for logged forests at 30 and 50 yrs. of recovery (b and c). Distance to unlogged forest, however, had a pronounced negative effect on H' diversity in these forests (e and f).

highest between the 30 and 50 year post-logging forests (39.7%; $R = 0.154$, $p < 0.05$). Tree species compositions of all post-logging-time categories were significantly different from those in unlogged forests: 10 years post-logging forests (20.9%; $R = 0.383$, $p < 0.001$), 30 years post-logging forests (22.9%; $R = 0.345$, $p < 0.001$) and 50 years post-logging forests (16.6%; $R = 0.587$, $p < 0.001$). Intra- and inter-coupe similarities across all forest classes were $\sim 50\%$ and $\sim 20\%$, respectively. Mean similarities across logged and unlogged forest forests were 32.8% and 29.9% respectively.

A two-dimensional MDS ordination showed strong associations with several ecological gradients (Fig. 4b). Axis 1 was strongly linked to elevation and harvest intensity ($R = -0.83$, $p < 0.0001$,

$R = 0.50$, $p = 0.013$, respectively). Axis 2 was strongly associated with liana abundance ($R = 0.51$, $p = 0.011$) and also revealed tree-species compositional change due to turnover between pioneer and shade-tolerant species across forest succession. The presence and abundance of ‘important species’ identified by MDS and ANOSIM varied greatly among forest classes (Fig. 5). Only *Camposperma brevipetiolata* and *Teijsmanniodendron ahernianum* were relatively important across all logged forest classes, of which *C. brevipetiolata* was the most important species (Fig. 5). The relative importance of *T. ahernianum* decreased from 10 to 30 years post-logging and then increased between 30 and 50 years post-logging. *T. ahernianum* was the most important species in unlogged forests.

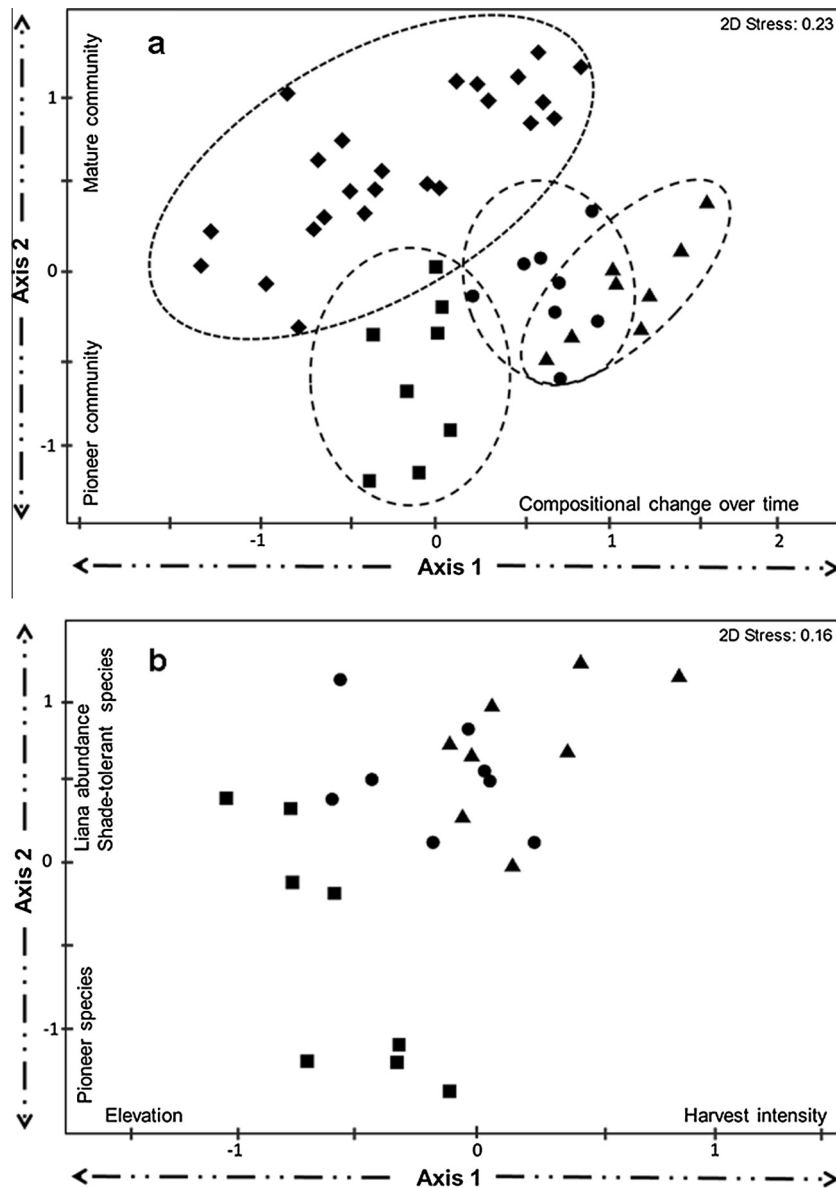


Fig. 4. Non-metric multi-dimensional scaling (MDS) for similarity of tree species composition between logged forests at 10 years of regeneration (■), 30 years of regeneration (●), 50 years of regeneration (▲) and unlogged forests (◆). MDS is based on Bray–Curtis similarity indices. Species compositions were significantly dissimilar between forest classes (a). Successional change in species composition across post-logging regeneration is highly associated with elevation and harvest intensity [Axis 1] and liana abundance [Axis 2] (b).

4. Discussion

4.1. Recovery dynamics of tree diversity

Of the potential predictors investigated, distance to logging road and distance to unlogged forest best explained changes in tree species diversity during post-logging recovery on Kolombangara. In contrast, a related study conducted in Borneo reported that the distance matrices between logged and unlogged forests have had trivial influence on post-logging retention of biodiversity (Fisher et al., 2011). Unlike forests in Borneo where harvesting was managed (i.e. cut size limit of 60 cm and 40 cm DBH at first and second harvest respectively), logging on Kolombangara was more intense (cut size limit of 30 cm DBH) and unregulated (Katovai et al., 2015a). Such highly excessive logging can impose serious damage on residual forests as well as arrest forest recovery (Leverkus et al., 2015). We suggest that excessive logging may

increase the reliance on unlogged forests as propagule sources for post-logging forest recovery.

Although being part of the average models, soil nitrogen (Tables 1 and 2), and basal-area harvest (Table 2) did not influence tree species richness and diversity in logged forests. Our results confirm the importance of maintaining propagule sources in close proximity to logged forests (Brown and Gurevitch, 2004; Duncan, 2006; Alvarez-Aquino et al., 2014; Harrison and Swinfield, 2015). Additionally, our findings suggest that the recovery of tree diversity were not influenced by small shifts in microclimate and soil attributes associated with local topographical variation.

4.1.1. Distance to road

We found varying effects of road distance on tree diversity across logged forests. In the 10-year post-logging plots, tree species richness and diversity both increased further from logging roads (Figs. 3a and 4a). This might result both from topographic effects

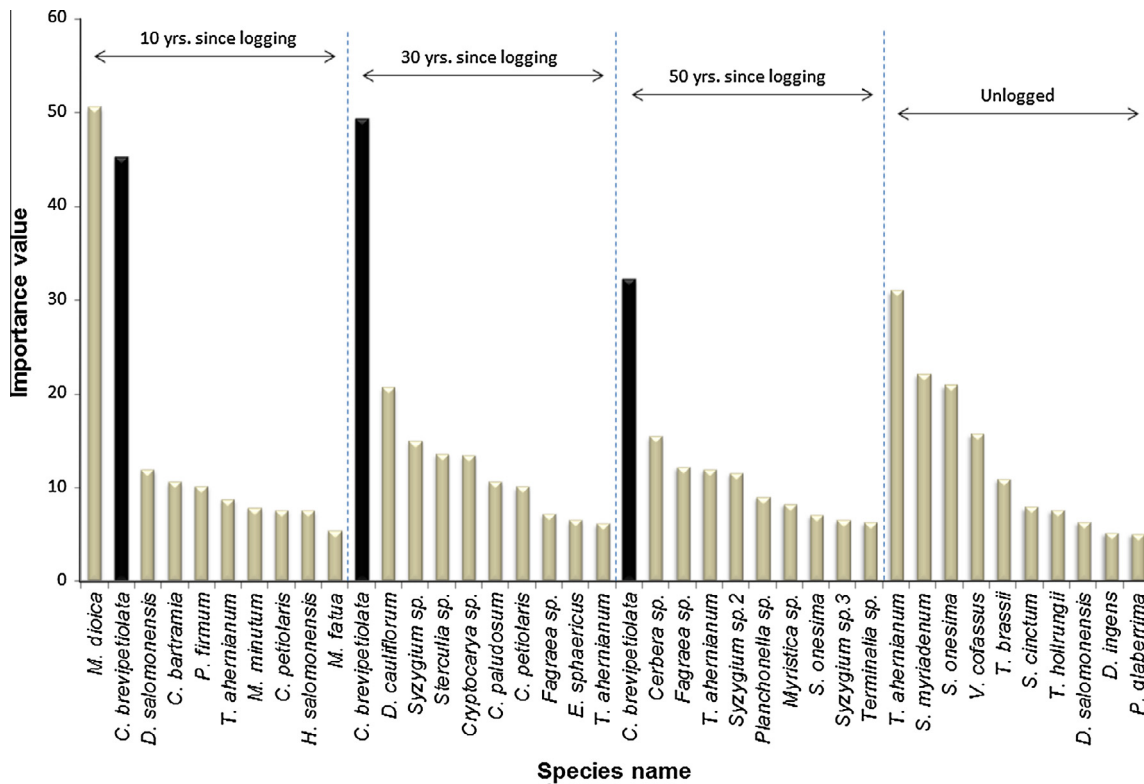


Fig. 5. Importance values of the top 10 dominant tree species in logged forest time classes and unlogged forests. *C. brevipetiolata* (in black) was highly dominant in logged forests.

and the greater intensity of damage associated with logging roads (Whitmore, 1989; Katovai et al., 2012). Abandoned logging roads in our study area were mostly located along plateaus on ridge tops that converge at the base of the central cone of the extinct volcano. Damage associated with log extraction and skidding trails were intense near roads on ridge plateaus, where trees were highly accessible. However, damage intensity decreased laterally away from roads as logging extended into highly challenging topography along steepening ridge slopes. An increase in species evenness in our plots likely arose from the strong recruitment of pioneer species in logged forests (e.g. Zimmerman and Kormos, 2012).

The increase in tree species richness and diversity near roads at 30 years post-logging may indicate a progressive mixing of long-lived pioneers and mid-successional species, increasing richness levels compared to areas of low disturbance (Asase et al., 2014). Recent studies have shown similar trends elsewhere in tropical forests where long-lived pioneer trees are prevalent (Asase et al., 2014; Wang et al., 2014). On Kolombangara Island, for instance, pioneer species such as *C. brevipetiolata* sp., *Macaranga* spp., *Calophyllum* spp. and *Dilenia* spp. remained an integral part of the forest stand along with several recently established mid-succession species such as *Dosyxyllum*, *Syzygium*, *Sterculia*, *Cryptocarya* and *Calophyllum* spp. (Bayliss-Smith et al., 2003).

4.1.2. Distance to unlogged forest

The influence of propagule sources on logged forests was weak in recently logged forests but became increasingly pronounced in mid to late succession stages (Figs. 3d–f and 4d–f). This suggests that pioneer recruitment mostly depends on soil seed banks that probably existed prior to disturbance (e.g. Schnitzer and Carson, 2001; Dalling and Brown, 2009; Tiansawat et al., 2014). This pattern is usually driven by survival strategies (i.e. prolific seed production in pre-disturbed forests, high seed dispersal and longevity) coupled

with favourable environments for disturbance-triggered germination in post-disturbed forests (Swaine and Whitmore, 1988; Dalling and Brown, 2009; Tiansawat et al., 2014). Seeds of pioneer tree species can also be rapidly dispersed into forest gaps by wind after logging due to their relatively small size, (Laurance et al., 2002; Correa et al., 2015).

The strong negative effect of distance to unlogged forest on tree diversity in 30 and 50 years post-logging forests highlights the importance of recruiting seeds of shade tolerant species into post-logged forests. The seeds of numerous shade tolerant species in wet tropical forests are desiccation-intolerant, resulting in short viability, and often do not contribute to soil seed banks (Berjak and Pammenter, 2013; O'Brien et al., 2013). Studies of the mainland tropics have suggested that ~50% of tree species in wet tropical forests are similarly recalcitrant in nature (Daws et al., 2006; Lan et al., 2014).

4.2. Recovery of tree species richness and diversity

Tree species richness and diversity in logged forests on Kolombangara can recover to pre-cut levels if allowed to regenerate without human disturbances such as re-entry logging or other land use activities. The high variation in species richness and diversity among plots at 10 yrs. post-logging may be the result of patchy logging damage (e.g., Berry et al., 2010; Bicknell et al., 2014; Burivalova et al., 2014). These irregularities usually result from varying topography and the distribution of timber trees within concession areas (Katovai et al., 2015a). Although species richness levels were similar across recovery times, tree diversity differed; diversity in 10 years post-logging forests was markedly lower than that found in 30 and 50 years post-logging forests. This may indicate low species evenness of trees (≥ 10 cm DBH) across recently logged forests, (e.g. Almazán-Núñez et al., 2012; Sandor and

Chazdon, 2014). Stem abundance of newly established trees at 10 yrs post-logging was relatively high because of many *Macaranga dioca* stems, but most trees of this species were <10 cm DBH and hence not included in the analysis. The recovery of tree diversity to pre-cut levels by 30–50 yrs post-logging suggests that tree species evenness had largely recovered, even in intensely logged areas. Several studies in tropical Asia and Africa have reported similar results (e.g. Berry et al., 2010; Wilcove et al., 2013; Asase et al., 2014).

4.3. Effects of logging on tree community assemblage

Unlike species richness and diversity, tree-community composition on logged forests of Kolombangara did not appear to recover to pre-cut levels (Fig. 5a). It has often been suggested that divergent recovery paths can occur where forests have been extremely damaged via mass tree removal (Magnusson et al., 1999; Chazdon et al., 2007; Bonnell et al., 2011; Cazzolla Gatti et al., 2015), although other studies have argued that log-felling does not permanently alter tree community composition (Bonnell et al., 2011; Bicknell et al., 2014). It appears that logging damage can be minimised through well-planned and managed harvest techniques. Intense or careless harvesting can create extreme levels of damage that alter regeneration dynamics by hampering the recovery potentials of the forest (Yamamoto, 2000; Bonnell et al., 2011; Cazzolla Gatti et al., 2015).

Post-logging regeneration across wet tropical forests generally relies on seed germination and establishment (e.g. Chazdon, 2003; Esaete et al., 2014; Valverde-Barrantes and Rocha, 2014). Seed-based recovery often varies across a spatial mosaic comprising gaps of various sizes (Chazdon, 2003; Katovai and Katovai, 2012; Arihafa and Mack, 2013). Large gaps (<90 m²), such as those evident across logged forests in this study, favour light demanding (pioneer) species. Initial light levels are usually very high in gaps of this size and shade-tolerant species are unable to exist under these conditions at the onset of gap-phase regeneration. The latter may gradually replace the former during the course of succession (Yamamoto, 2000; Cazzolla Gatti et al., 2015). Such transition is usually determined by the longevity and adaptability of the occurring species in response to the changing light-gap environment (Chazdon et al., 2007). For instance, on Kolombangara, recently logged forests are dominated by pioneer species including the highly prevalent *M. dioca* and *C. brevipedunculata* among others (Fig. 5). *Macaranga* dominance subsided within two decades of regeneration, whereas *C. brevipedunculata* is long-lived, retaining dominance even at 50 years post-logging. The latter is highly associated with forest disturbance in many parts of the Solomon Islands and other tropical oceanic islands where it is present (Sheely and Meagher, 1996; Bayliss-Smith et al., 2003).

The dominance of *C. brevipedunculata* may have stalled succession in logged forests by delaying growth and development of late-successional species. The frequent occurrence of important late succession species such as *Dellinia* spp., *Callophylum* spp. and *Terminalia* spp. in the understory and subcanopy layer of *C. brevipedunculata*-dominated forests on Kolombangara supports this view (e.g. Whitmore, 1989; Katovai et al., 2012). Although the importance of *C. brevipedunculata* declined between 30 and 50 yrs post-logging, the turnover between *C. brevipedunculata* and late succession species appeared protracted and may take several decades to fully play out (Chazdon et al., 2007). Such protracted succession may have implications on the recovery of forest functions and ecosystem provisioning on logged forests across Solomon Islands (Edwards et al., 2014).

Silviculture experiments involving post-logging thinning of *C. brevipedunculata* could potentially shed more light on its impact on floristic recovery. Since *C. brevipedunculata* is a commercially

exported hardwood (Bennett, 2000), extracted trees can provide economic benefits to local communities, as well as offset silvicultural costs. Studies in the tropical forests of Central Africa showed that post-logging thinning of pioneer trees facilitated species compositional recovery to pre-cut levels (Ouedraogo et al., 2011; Gourlet-Fleury et al., 2013). However, the success of such efforts relies on well-regulated forest management policies (Katovai et al., 2015a, 2015b). Failure of previous post-logging silviculture efforts has resulted from weak policies in regulating re-entry of logging and secondary forest management in the region (Zimmerman and Kormos, 2012). For example, the thinning long-lived pioneer species in Papua New Guinea enhanced growth of old growth species but prompted subsequent re-entry harvests that permanently damaged the forests (P. Shearman, pers. comm.).

5. Conclusion

In this study, we show that proximity to logging roads and to nearby unlogged forests strongly influenced patterns of tree regeneration in logged forests. While tree diversity was comparable between logged and unlogged forests, tree community composition in logged forests differed significantly to that of unlogged forests, even after 50 years of regeneration. We suggest that long-lived pioneer tree species in intensively degraded tropical forests can stall the succession process, which may inhibit the trajectory of species compositional recovery to pre-cut levels. We conclude that 50 years of post-logging regeneration is inadequate to return tree floristic composition to pre-cut levels, when initial logging damage is severe, as was the case on Kolombangara Island.

Since most of Kolombangara's lowland forests have been modified via logging and commercial tree plantations, it is vital that remnant patches of unlogged forests are protected to aid regeneration of logged forests. This is challenging, however, because most remaining uncut forests in the Solomon Islands are highly vulnerable to logging (Katovai et al., 2015a). Harvesting the dominant pioneer *C. brevipedunculata* in logged forests might provide economic returns to local communities while potentially removing a species that is limiting forest recovery. Across the Solomon Islands, policies that protect remaining unlogged forests and limit re-entry logging before stands have recovered are a key priority.

Results from this study also suggest that post-logging floristic recovery trends on tropical oceanic islands are generally similar to those across mainland tropics and associated landbridge islands. However, unlike in the mainland tropics where large expanses of unlogged forests still remain, most tropical oceanic islands, particularly those in East Melanesia, have been extensively logged. It is therefore vital that logging operations on islands abide by a set of management guidelines that limit the impacts of harvesting to ensure the potential for post-logging forest recovery is maximised.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.03.052>.

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